THÈSE

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Présentée et soutenue par :

M. LAURENT LARRIEU
le vendredi 5 d®cembre 2014

Titre :

LES DENDRO-MICROHABITATS: FACTEURS CLES DE LEUR OCCURENCE DANS LES PEUPLEMENTS FORESTIERS, IMPACT DE LA GESTION ET RELATIONS AVEC LA BIODIVERSITE TAXONOMIQUE

Ecole doctorale :
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Dynamiques et ®cologie des paysages agriforestiers - DYNAFOR UMR 1201

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Laurent LARRIEU

le : 5 décembre 2014

à : l'EIP

Titre

Les dendro-microhabitats : facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique

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EXORDE

La forêt couvre près de 30 % du territoire français. Pourvoyeuse de ressources pour l'Homme depuis des millénaires, sa gestion est organisée depuis le XVII^{e} pour fournir une large gamme de produits et de services correspondant aux demandes de la société. La gestion forestière repose sur des concepts techniques très orientés sur l'augmentation du volume de bois produit et le renouvellement des peuplements, et qui ont fait leurs preuves. Dans le contexte futur d'une perturbation du climat liée en grande partie au déstockage des énergies fossiles, le bois est considéré comme le matériau renouvelable par excellence. Il est amené à accroître encore sa place dans l'économie, mais dans un contexte socioculturel évolutif qui a intégré d'autres valeurs aux forêts, comme l'esthétique, un espace de loisirs et de détente, et un rôle essentiel dans la conservation de la biodiversité. Cette dernière est devenue un des axes fondamentaux de la gestion forestière dite « durable », définie lors du « Sommet de la Terre» de Rio de Janeiro (1992) et de la conférence ministérielle d'Helsinki (1993). Or, la tradition forestière freine parfois l'intégration de nouvelles orientations et l'émergence et la diffusion de concepts novateurs. Ce constat n'est pas surprenant si l'on considère la longueur des cycles de production pour la majorité des essences, et il faut reconnaître que, malgré les multiples atteintes qu'elles ont subies au cours de l'histoire, les forêts font partie des milieux terrestres qui comportent le plus de biodiversité. Pourtant, la résilience remarquable des écosystèmes forestiers ne doit pas nous dédouaner d'une réflexion sur la durabilité de nos systèmes de production.

Pour que le forestier intègre plus aisément et efficacement la biodiversité dans ses actes de gestion, en compléments des aspects forestiers classiques (stationnels, sylvicoles), économiques et sociaux, il est nécessaire d'accroitre nos connaissances et de développer des outils performants et pratiques. En effet, s'il a bien en sa possession de multiples références vis-à-vis de la production de bois, le gestionnaire forestier en manque sur la composition biologique des types de forêts qu'il gère, le rôle que les espèces jouent et les dysfonctionnements liés à l'absence de certaines d'entre-elles, présentes seulement dans les forêts non anthropisées. Comme il est impossible de réaliser des inventaires exhaustifs de la richesse en espèces d'un écosystème aussi diversifié qu'une forêt (plus de 10 000 espèces dans une grande forêt naturelle), une approche prometteuse est développée en analysant seulement certains taxons appelés bio-indicateurs et considérés comme intégrateurs de la diversité de l'ensemble des espèces et des processus fonctionnels la soutenant. Mais pour un gestionnaire non naturaliste, une approche indirecte est souvent plus intuitive et pratique à utiliser dans le travail quotidien, notamment en utilisant pour le diagnostic des caractéristiques clés pour les espèces, comme la diversité des essences, la présence de bois mort ou de certaines singularités des arbres (cavités, fentes, etc.). Néanmoins, les recherches sur certaines de ces caractéristiques sont encore balbutiantes et les connaissances sur leurs liens fonctionnels avec les espèces sont encore fragmentaires.

Ce travail de thèse résulte de l'opportunité d'un poste d'interface INRA/CNPF que j'ai eu la chance d'obtenir fin 2009 pour une durée de trois ans afin de concrétiser le développement d'un indicateur indirect de la diversité des espèces forestières au sein du laboratoire Dynafor de l'Inra Toulouse. Le contexte scientifique du laboratoire et l'appui sans réserve de la tribu des *Dynaforiens* m'a donné l'idée en 2011 de compléter ma formation d'Ingénieur Recherche et Développement par un travail plus académique, dans le but de valoriser une démarche exploratoire pluridisciplinaire et pluritaxonomique de la biodiversité des forêts amorcée dès 2003 sur un massif d'étude montagnard (Larrieu, 2007) puis, en 2008, sur un massif de plaine. Ce travail se réalisait sur la base d'un réseau de collaborations ponctuelles, tout en assurant mon rôle de conseiller forestier au sein du CRPF de Midi-Pyrénées. Ces conditions ne permettaient pas une rigoureuse exploitation des nombreuses données de terrain recueillies. Les « choses sérieuses » d'un point de vue scientifique ont donc réellement commencé en 2010, mais en bénéficiant largement de données et de l'expérience de terrain acquises les sept années précédentes. J'ai également bénéficié de l'appui d'un grand nombre de scientifiques, non seulement au sein de l'INRA, mais aussi de l'IRSTEA, ainsi que de naturalistes. Tous ont répondu très volontiers à toutes mes sollicitations, que ce soit pour des appuis scientifiques ou pour partager leurs bases de données taxonomiques.

Cette histoire explique pourquoi la recherche que nous avons menée sur les microhabitats est typiquement finalisée, dans un esprit de Recherche et Développement. Elle a ainsi pour objectif principal de fournir des éléments de réponse pratiques aux gestionnaires d'espaces forestiers, la plupart des questions posées émanant d'ailleurs de personnels de terrain. Les méthodes employées, comme par exemple la recherche quasi-systématique de seuils numériques significatifs pour la biodiversité, ou bien les échelles de travail - l'arbre, le peuplement - sont aussi en partie sélectionnées pour tenter de fournir des résultats facilement utilisables en routine par les gestionnaires forestiers soucieux de pratiquer une gestion intégrant la biodiversité. Cependant, la réflexion préalable aux mesures s'est toujours efforcée de placer cette recherche dans des cadres écologiques théoriques afin de participer modestement à l'amélioration des connaissances sur le fonctionnement et les dynamiques des écosystèmes forestiers.

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INTRODUCTION

INTRODUCTION

Les arbres sont les organismes fondateurs des écosystèmes forestiers. Même morts, ils constituent le milieu de vie de milliers d'espèces (Stokland *et al.* 2004) et le bois mort est ainsi l'objet de toutes les attentions des écologues et naturalistes forestiers depuis maintenant plusieurs décennies. La littérature est abondante et a déjà généré plusieurs synthèses successives (Maser & Trappe 1984 ; Harmon *et al.* 1986 : Maser *et al.* 1988 ; Speight 1989 ; Bobiec *et al.* 2005 ; Stokland *et al.* 2012). Un néologisme, le terme « saproxyliques », a même été créé par Dajoz dès 1966 pour désigner les insectes qui vivent dans le bois mort puis redéfini par Speight (1989) en élargissant le concept aux « organismes qui dépendent, pendant tout ou partie de leur cycle de vie, du bois mort ou mourant ou bien des organismes qui utilisent le même milieu». Néanmoins, Speight (1989) ne se contente pas de décrire la diversité des invertébrés qui vivent dans les arbres entièrement mourants ou morts, mais met en exergue l'intérêt pour ce groupe des cavités comportant du bois mort mais parfois portées par des arbres vivants, ainsi que des sporophores de champignons lignivores. Il ne regroupe cependant pas sous un nom générique ces structures de petite taille qui ne sont pas strictement du bois mort et il faut attendre la synthèse de Stokland *et al.* (2012) pour voir rassemblées sous le vocable « microhabitats » ces « portions discrètes de l'arbre qui hébergent des communautés d'espèces ». Peu de temps auparavant, Winter et Möller (2008) puis Vuidot *et al.* (2011) avaient, pour la première fois, étudié les « tree-microhabitats » indépendamment du bois mort.

Les microhabitats listés par Stokland *et al.* (2012) sont des objets couramment observés par les gestionnaires forestiers. Mais ils en ont bien souvent une perception très orientée par l'économie du bois et leur présence est alors seulement perçue comme une dévaluation de la valeur commerciale des arbres. Avec cette perception, les microhabitats sont des objets sylvicoles simples et bien catégorisés. Mais la réalité écologique est bien plus complexe.

Avant de rentrer dans le détail des travaux réalisés dans le cadre de cette thèse, je vais m'efforcer de définir précisément nos objets d'étude, les « dendro-microhabitats », en m'appuyant sur la littérature qui traite des milieux de vie en général. J'aborderai ensuite leur rôle écologique en m'inspirant de quelques cadres théoriques.

1 QU'EST CE QU'UN MICROHABITAT ?

1.1 HABITAT NATUREL, HABITAT D'ESPECE, MICROHABITAT

L'« habitat » est le plus fréquemment défini comme un synonyme de catégorie de végétation ou de biotope (Dennis *et al.* 2003) et sa description manque souvent de précision (Rosenzweig 1995). Les définitions les plus anciennes se limitent à la localité, à l'espace, et aux facteurs physiques dans lesquels vit un organisme (synthèse dans Dennis *et al.* 2003). Plus tard, les auteurs ont ajouté la nécessité d'occurrence d'un ensemble de ressources ainsi que l'assurance de survie et de reproduction de l'espèce concernée, et donc de persistance de la population (Hall *et al.* 1997 ; Weddell 2002).

Dans le cadre de la mise en place du réseau de conservation Natura 2000, Rameau *et al*. (2000) et Bensettiti *et al.* (2001) définissent « l'habitat naturel » comme un ensemble indissociable comprenant un compartiment stationnel, une végétation et une faune associée. Bastien et Gauberville (2011) indiquent que l'habitat concerne soit l'espèce, soit une population ou même une communauté et le différencient de l'écosystème qui, lui, intègre également les interactions fonctionnelles entre le milieu et les espèces ou entre les espèces elles-mêmes.

Rameau *et al.* (2000) précisent que « l'habitat d'espèce » est un habitat naturel où vit une population de l'espèce à l'un des stades de son cycle biologique, et qui lui procure au moins l'une des composantes de ses exigences environnementales : abri, nutrition et reproduction (voir Encadré 1). Pour Whittaker *et al.* (1973), l'habitat est un concept spécifique d'un organisme, défini comme la gamme des environnements dans lesquels une espèce peut être rencontrée. C'est un hyperespace défini par un grand nombre de variables d'environnement physique et chimique qui forment des gradients spatiaux à un endroit donné d'un paysage. Dans cet hyperespace, une espèce donnée occupe un hyper-volume définissant de fait son habitat propre. L'habitat inclut également les environnements actuellement non optimaux, mais qui pourraient le devenir. Harris (1984) différentie également des habitats primaires qui répondent à toutes les exigences de l'espèce, et des habitats secondaires qui sont utilisés par l'espèce mais ne répondent pas à toutes les exigences. Dennis *et al.* (2003) remarquent que ces définitions sur des bases environnementales et visant à décrire l'habitat comme une entité spatiale homogène rendent souvent les limites de l'habitat floues et ainsi son étude problématique et préconisent une approche alternative basée sur les ressources fonctionnelles (« functional ressource-based concept »). L'habitat d'une espèce est alors l'enveloppe rassemblant chacun des sites pourvoyant en ressources nécessaires à l'ensemble du cycle de vie de l'espèce, quelle que soit leur distribution spatiale. Lindenmayer & Franklin (2002) ont une définition plus restrictive de l'habitat et le considère comme un environnement où la reproduction d'une espèce s'effectue à un taux suffisamment haut pour maintenir à long terme une croissance de la population.

Hanski (2005) définit l'habitat comme la gamme de conditions environnementales dans lesquelles une espèce peut survivre et se reproduire. En effet, les schématisations de l'habitat d'une population montrent une certaine variabilité de la distribution des individus qui la composent. L'utilisation de l'espace peut ainsi légèrement varier d'un individu à l'autre au sein de la même espèce, définissant plusieurs habitats à l'échelle de l'individu. Cette variabilité offre des possibilités d'évolution adaptative (Hanski 2005). Comme pour Rameau *et al.* (2000), l'habitat peut être considéré également à l'échelle de l'écophase (Hanski 2005). Cette configuration est classique chez les Batraciens pour qui l'habitat aquatique des larves est parfois bien différent de l'habitat des adultes (ACEMAV 2003).

Plus récemment, Kolasa *et al.* (2012) décrivent l'habitat comme un ensemble hiérarchique de volumes multidimensionnels comprenant une mosaïque hiérarchique de taches (« patchs »), chaque niveau hiérarchique ayant un ensemble d'attributs résultants de processus distincts. Les espèces généralistes utilisent les unités d'habitat les plus grandes, et plus les espèces sont spécialisées, plus elles utilisent les unités d'habitat les plus petites. Les unités les plus petites sont appelées microhabitats, mais ces auteurs ne les définissent que par la taille. Hanski (2005) donne plusieurs exemples : les tas de crottes, les cadavres d'animaux, les végétaux en cours de décomposition, un tronc au sol, un volume de phloème à un stade de décomposition donné, ou encore des plans d'eau de petite surface (*e.g.* des mares). La gamme parait très large, mais il précise les caractéristiques communes aux microhabitats : (i) ils sont des habitats de petite taille pour des espèces de petite taille, (ii) la plupart sont très dynamiques et donc à fort taux de renouvellement, (iii) leurs habitants participent dans la plupart des cas activement à leur disparition ; néanmoins, certains microhabitats, comme par exemple certaines sources, sont, à l'inverse, très stables et peuvent ainsi héberger des populations très stables, (iv) on observe une dépendance parfois totale des espèces de petite taille à leurs microhabitats. Il résulte de cette conception que la différence entre habitat et microhabitat ne se résume plus à une seule différence d'échelle spatiale. Contrairement à l'habitat qui est le cadre de vie pourvoyant à toutes les fonctions vitales de l'individu ou de l'espèce, le microhabitat n'assure parfois qu'une fonction temporaire ou partielle, mais indispensable. Bien que de petite taille, les microhabitats jouent un rôle considérable pour la richesse spécifique globale d'un grand nombre d'habitats (Hanski 2005).

Encadré 1. Habitat d'espèce vs niche écologique : entre complément d'information et équivalence (d'après Blondel 1995, Hanski 2005 et Peterson et al. *2011)*

La « niche écologique » est à son origine un concept géographique et suprapopulationnel qui désigne l'ensemble des conditions climatiques et environnementales dans lesquelles vit une espèce dans son aire de distribution (Grinnell 1917). C'est un outil pour comprendre les déterminants de la distribution géographique des espèces. Elton (1927) perçoit plutôt la niche à travers les relations de prédation, compétition et parasitisme entre les espèces et la définit comme la position de l'espèce dans sa communauté locale et dans l'environnement biotique. L'approche est alors fonctionnelle et populationnelle, l'échelle d'analyse est plus restreinte, et niche et habitat complètent l'information sur l'espèce. Hutchinson (1957) modélise la niche comme un hypervolume à n dimensions de variables environnementales qui permet de la caractériser numériquement et de comparer, par exemple, les niches de plusieurs espèces. La niche désigne ici à la fois la fonction de l'espèce et l'ensemble des conditions d'habitats dans lequel elle la réalise. Whittaker (1973) reprend la distinction d'Elton en désignant comme niche le rôle fonctionnel de l'espèce dans la communauté, comme habitat la gamme des environnements dans lesquels on observe l'espèce, et appelle « écotope » l'agrégation de l'habitat et de la niche, mais ce terme sera très peu employé. En définitive, dans la plupart des cas, les concepts d'habitat d'espèce et de niche sont maintenant utilisés indifféremment.

1.2 DENDRO-MICROHABITAT ET ARBRE-HABITAT

Dans la gamme très large des microhabitats évoqués par Hanski (2005), certains sont strictement liés aux arbres (« tree-microhabitat », Winter & Möller 2008). Dans la littérature spécialisée dans ce domaine (*e.g.* Winter & Möller 2008 ; Michel & Winter 2009 ; Vuidot *et al.* 2011) le microhabitat recouvre des sens multiples et écologiquement inégaux. Ainsi, les listes de microhabitats publiées mélangent des milieux de vie comme des trous de pics avec des singularités pour lesquelles les communautés associées ne sont pas définies (*e.g.* les chancres sains de tronc) ou même des milieux abiotiques comme les exsudations de résine.

Afin de centrer les recherches sur un objet bien défini et de stabiliser la liste des microhabitats liés aux arbres, nous proposons d'appeler dendro-microhabitats (dmh ; du Grec *dendron*=arbre), un habitat d'espèce, de petite dimension, porté par un arbre vivant ou mort. Cet habitat correspond à une singularité morphologique du tronc, d'une branche, ou du houppier de l'arbre. Cette singularité peut recouvrir toute une gamme de types morphologiques, comme par exemple des parties mortes de l'arbre, des cavités, des fentes, ou encore des éléments biologiques plus ou moins externes à l'arbre, comme des carpophores de champignons lignivores ou des lianes. Un dendro-microhabitat peut donc être constitué de bois en décomposition (dendro-microhabitat saproxylique) ou non (dendro-microhabitat épixylique). Étant de petite dimension, le dendro-microhabitat peut constituer soit l'habitat complet de l'espèce, soit l'habitat d'une écophase, soit seulement un abri temporaire (mais alors récurent pour l'espèce). Outre sa morphologie, un dendro-microhabitat est défini par une communauté caractéristique qui lui est préférentiellement inféodée et dont c'est au moins temporairement le milieu de vie, et qui le différencie des autres dendro-microhabitats. Ainsi, les dendrotelmes de forêt tempérée sont des cavités dans le bois remplies au moins temporairement d'une lame d'eau riche en matière organique et peu oxygénée, dans laquelle se développent des micro-organismes et des insectes. En Europe, la moitié des insectes vivant dans les dendrotelmes leur sont strictement inféodés (Dajoz 2007). Par contre, des coulées de résine sont parfois exsudées par les conifères en réaction à une blessure ou une agression. Elles constituent des barrières de protection qui neutralisent les éventuels agresseurs. À notre connaissance, aucune espèce ne vit dans ces coulées. Seule *Formica paralugubris* utilise parfois la résine exsudée comme protection antibactérienne et antifongique après en avoir transporté des fragments dans sa colonie (Chapuisat *et al.* 2007 ; Castella *et al.* 2008) mais elle ne vit pas dans les exsudats. Cette ressource étant temporaire et non obligatoire, et l'espèce n'y réalisant pas au moins une partie de son cycle de vie, la coulée de résine n'est pas un dendro-microhabitat.

Seule une fraction des arbres d'un peuplement forestier porte des dendro-microhabitats. Ils sont appelés « arbres à faune » ("wildlife trees") par Hodge & Peterken (1998) ou encore «arbres habitats» («habitat-trees") par Bäuerle & Nothdurft (2011) et Bütler *et al.* (2013). Hodge & Peterken (1998) incluent dans leur définition les chandelles ou des arbres isolés qui jouent un rôle pour la faune locale sans nécessairement porter un dendro-microhabitat et Bäuerle & Nothdurft (2011) leur fixent un diamètre à hauteur de poitrine (dhp) minimum de 40 cm. Dans ce travail, nous appellerons « arbres porteurs de microhabitats » (« microhabitat-bearing trees ») tous les arbres porteurs d'au moins un dendro-microhabitat, quels que soient leurs dhp.

1.3 DENDRO-MICROHABITAT « ELEMENTAIRE » : DE LA THEORIE A LA PRATIQUE

S'il est assez aisé de lister les singularités pouvant être observées, par exemple, sur un très gros Hêtre vivant dans une forêt sub-naturelle (Fig. 1), il est bien plus difficile de définir exactement ce que sont les dendro-microhabitats correspondants. Un ancien trou de nidification de Pic noir (*Dryocopus martius*) creusé cinq ans auparavant est aisément identifiable et constitue, vu du sol, une unité facilement caractérisable : une cavité dans le tronc d'environ 15 litres de contenance, en connexion avec l'extérieur *via* un orifice ellipsoïde d'une dizaine de centimètres suivant son plus grand axe. Mais l'examen attentif de l'intérieur de cette cavité montre un ensemble de milieux de vie juxtaposés, révélés par exemple par les différents assemblages de coléoptères saproxyliques associés (Fig. 2).

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Figure 1. Principales singularités du Hêtre
(Emberger *et al.* 2013)

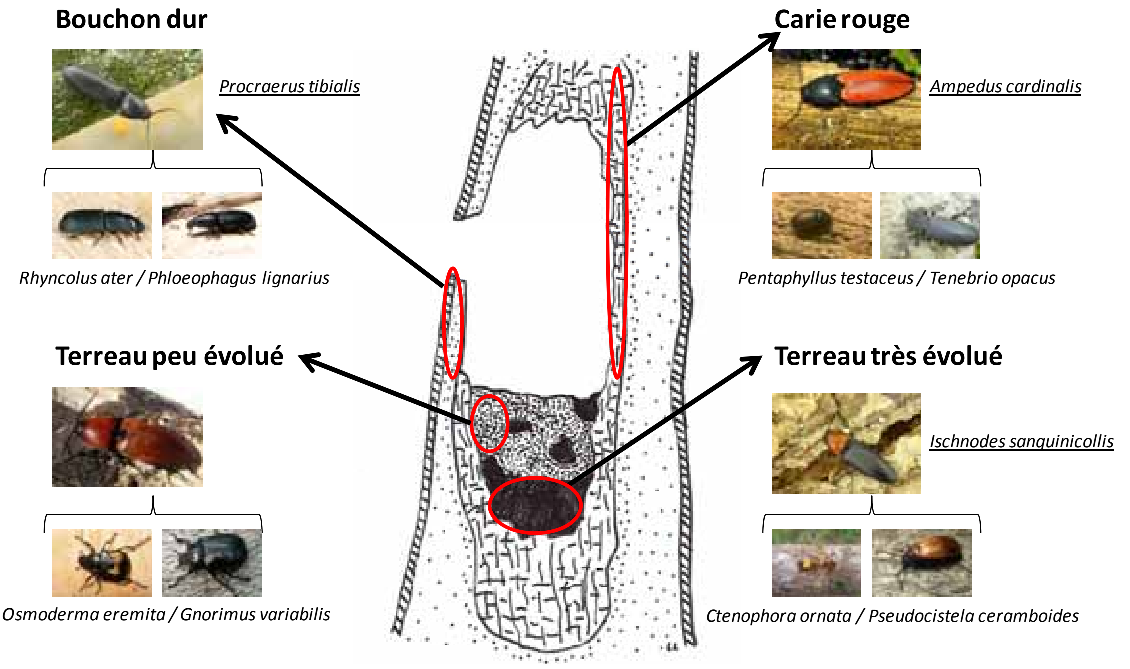

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Figure 2. Hétérogénéité interne d'une cavité de Pic noir (*Dryocopus martius*), illustrée par les Coléoptères Elateridae et leurs proies qui l'habitent
(d'après Stokland *et al.* 2012 et Brustel com. pers.)

De la même façon, un sporophore de *Fomitopsis pinicola* semble une entité bien définie mais rassemble pourtant en son sein trois assemblages de coléoptères qui utilisent exclusivement des parties bien précises du champignon (Fig. 3). Ainsi, l'Anobiidae *Dorcatoma punctulata* se nourrit de la trame (Nikistsky & Schigel 2004), le Staphylinidae *Gyrophaena boleti* des spores (Okland & Hagvar 1994) et le Trogossitidae *Peltis grossa* du mycélium situé à l'interface avec l'arbre porteur du sporophore (Nikistsky & Schigel 2004). Dans ce cas, cependant, les différentes parties ne peuvent exister séparément.

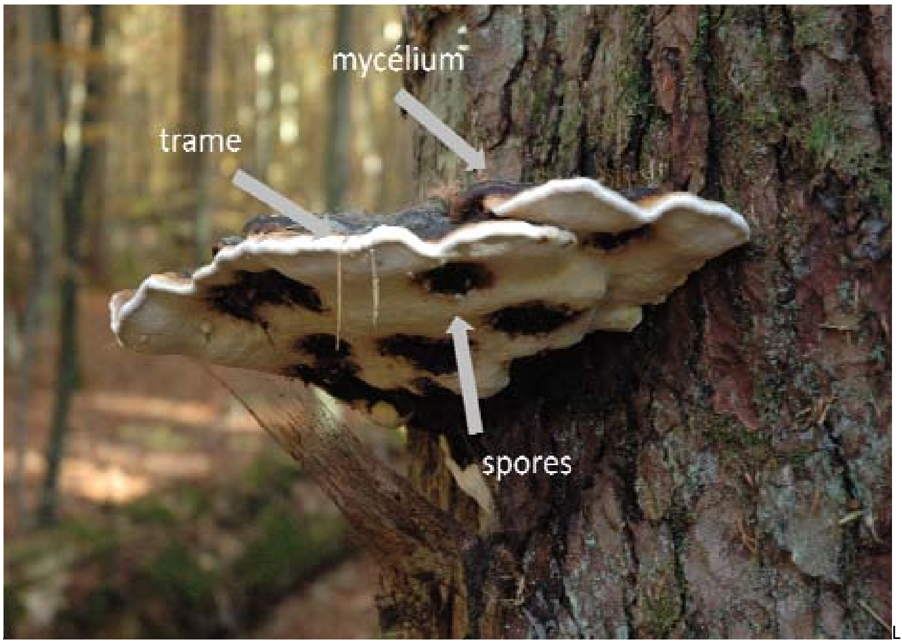

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Figure 3. Les sporophores de *Fomitopsis pinicola* rassemblent trois sources distinctes de nourriture pour les larves d'insectes : (i) le mycélium concentré sous l'écorce à la base du sporophore, (ii) la trame et (iii) les spores.

Le dendro-microhabitat ne déroge donc pas à la règle générale qui stipule que n'importe quel habitat est une mosaïque de plus petits habitats, eux-même sub-divisibles en encore plus petits microhabitats (Kolasa 2012). Pour des raisons essentiellement pratiques, l'échelle dimensionnelle que nous avons adoptée dans cette thèse pour le dendro-microhabitat élémentaire sera l'ensemble de la singularité. Dans le cas précis des deux exemples précédents, il sera donc, d'une part, la cavité de pic dans son ensemble et, d'autre part, le volume total du sporophore. Néanmoins, il est assez fréquent que certaines singularités soient composites de façon évidente. C'est le cas par exemple d'une plage de bois mort sans écorce à la surface de laquelle croît un sporophore. Considérant la différence nette de morphologie et de communautés associées à ces deux éléments, nous les identifierons séparément. Précisons ici que la singularité est bien une entité fondée sur la perception visuelle d'un observateur humain qui diverge fortement de la perception multi-sensorielle des organismes utilisateurs.

Comme la typologie des habitats qui utilise la phytosociologie et quelques plantes caractéristiques pour les discriminer (Bardat *et al.* 2004), nous utilisons des référents taxonomiques pour différentier les dendro-microhabitats ou, au contraire, pour les regrouper au sein d'unités supérieures (types de dendro-microhabitats, etc.). Ce choix est sous-tendu par l'idée d'utiliser les dendro-microhabitats comme indicateurs de diversité taxonomique, en accord avec Winter et Möller (2008). Néanmoins, la morphologie étant le seul critère qui permette d'identifier rapidement un dendro-microhabitat, on recherche parfois des éléments morphologiques ou qualitatifs plus précis discriminant des communautés différentes, comme par exemple le stade de décomposition d'une plage de bois sans écorce. Ce choix méthodologique occulte certaines voies de différenciation certainement encore plus discriminantes pour les espèces, comme par exemple les caractéristiques chimiques du bois (Dajoz 2007) ou du plan d'eau d'un dendrotelme (Schmidl *et al.* 2008) (Tableau 1). Néanmoins, celles-ci peuvent être parfois révélées grossièrement par la morphologie, comme dans le cas des types de pourritures du bois, brunes cubiques vs blanches fibreuses, qui révèlent les composantes principales du bois : la lignine dans le premier cas, la cellulose et les hémicelluloses dans le deuxième (Stokland *et al.* 2012).

Tableau 1 - Exemples de facteurs non morphologiques clés pour la composition des assemblages de quelques taxons liés à deux types de dendro-microhabitats

Types de dendro-microhabitat	Facteurs clés	Taxons	Niveau de connaissance	Références
Cavités à terreau	Composition du terreau :	Coléoptères	Faible	
	Degré de mélange avec de l'humus terrestre Degré d'humidité			Gouix 2011
	Proportion d'azote et de phosphore			Jönsson *et al.* 2004
Dendrotelmes	Température pH Taux d'oxygène dissous Taux d'Azote Taux de Phosphore	Diptères (*Metriocnemus cavicole, Myatropa florea Aedes. geniculatus)* *Coléoptère (Prionocyphon serricornis*)	Bon	Schmidl *et al*. 2008
		Autres espèces	Très faible	Vaillant 1978 ; Kitching 1971

Nous avons maintenant défini ce qu'est un dendro-microhabitat. Mais comment s'organisent les dendro-microhabitats à l'échelle du peuplement forestier ?

1.4 ORGANISATION HIERARCHIQUE DES DENDRO-MICROHABITATS AU SEIN DU PEUPLEMENT FORESTIER

Pour une population d'une espèce qui dépend du dendro-microhabitat « s », le peuplement forestier est composé : (i) de l'arbre porteur du dendro-microhabitat « s », (ii) d'arbres porteurs du même type de dendro-microhabitat que « s » (=population des arbres porteurs de dendro-microhabitat de type « s »), (iii) d'arbres porteurs d'autres types de dendro-microhabitats, (iv) d'arbres non porteurs de dendro-microhabitats, et enfin (v) des espaces interstitiels qui ne comportent pas d'arbres (milieux ouverts aquatiques, rocheux ou simples clairières) (Fig. 4). Pour les espèces ou écophases inféodées au dendro-microhabitat « s », les autres arbres, porteurs d'autres types de dendro-microhabitats ou non porteurs, constituent un ensemble d'habitats *a priori* inhospitaliers et pouvant même former une barrière au mouvement des individus : la matrice. La matrice peut néanmoins assurer un rôle indirect essentiel, comme la réduction de la variabilité des conditions climatiques. Ainsi, les larves des *Systenus* spp. (Diptères Dolichopodidae) sont strictement inféodées à un seul type de dendro-microhabitat, en l'occurrence les dendrotelmes (Vaillant 1988), et la persistance d'une lame d'eau pendant toute la durée de développement larvaire est facilitée par le couvert des arbres environnants. Par ailleurs, plusieurs types de dendro-microhabitats peuvent avoir des fonctions redondantes pour la même espèce. Ainsi, la chauve-souris Noctule de Leisler (*Nyctalus leisleri*) pourra utiliser comme gîte naturel tantôt une cavité de nidification récente de Pic épeiche (*Dendrocopos major*), tantôt une cavité de tronc issue de la pourriture du bois postérieure à la chute d'une charpentière et remplie en partie de terreau, et même des fentes dans le tronc (Meschede & Heller 2003). La matrice peut alors, directement, pourvoir en ressources complémentaires.

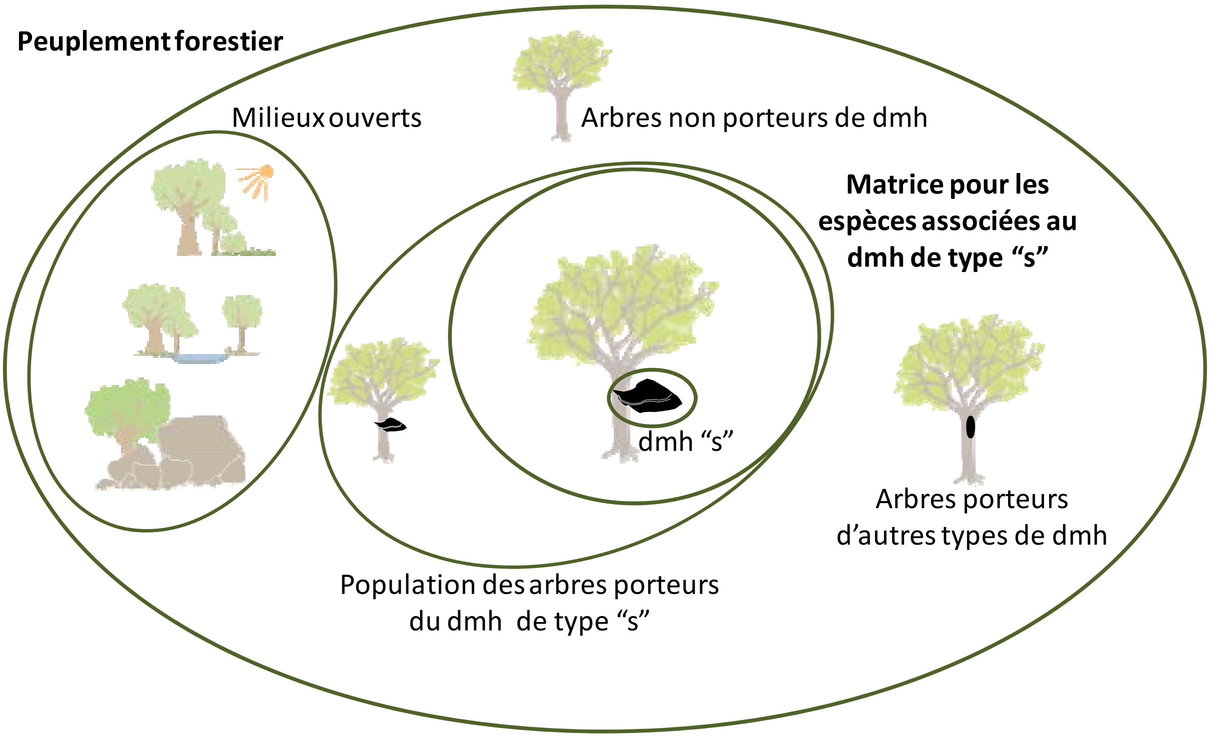

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Figure 4. Organisation hiérarchique des dendro-microhabitats (dmh) dans un peuplement forestier
Illustration avec un exemple de dendro-microhabitat : un sporophore de champignon saproxylique

En conclusion, le dendro-microhabitat est donc un niveau emboîté entre deux niveaux hiérarchisés : (i) ses subdivisions morphologiques élémentaires (ex. trame/spores/mycélium pour un polypore), et (ii) ses échelles spatiales d'agrégation (ex. arbre porteur, population des arbres porteurs, peuplement forestier).

2 ROLE ET DYNAMIQUE DES DENDRO-MICROHABITATS DANS LES ECOSYSTEMES FORESTIERS

Nous avons relaté dans le chapitre précédent que les dendro-microhabitats hébergent une grande diversité d'espèces. Mais comment s'intègre leur fonction d'habitat dans l'ensemble des fonctions réalisées par les autres structures composant le peuplement forestier ? Quel est leur rôle dans les réseaux trophiques et fonctionnels ? Leur dynamique suit-elle celle des arbres supports ?

2.1 LES DENDRO-MICROHABITATS VUS COMME DES « EPHEMERAL RESOURCE PATCHES » ; CONSEQUENCES POUR LES COMMUNAUTES ASSOCIEES

Les « ephemeral resource patches » (ERPs, Finn 2001) sont des ressources de grande qualité, discrètes et temporaires (car évolutives), et généralement colonisées seulement pendant une période limitée. Les communautés qui occupent les ERPs peuvent être taxonomiquement complexes, mais sont très dépendantes d'événements stochastiques, ce qui entraîne une large gamme de composition d'assemblages dans le même type d'ERP. Généralement, une seule génération se développe dans une ERP et participe activement à sa dégradation plus ou moins rapide, déterminant des stades d'évolution et des patrons de succession taxonomique. La compétition entre les différentes composantes taxonomiques de la communauté, mais aussi entre individus du même taxon, est parfois sévère (Finn 2001). Néanmoins, cette stratégie d'agrégation peut être une réponse adaptative au parasitisme (Rohlfs & Hoffmeister 2004). L'exploitation de ces ressources discrètes et temporaires est plus aisée pour les espèces ayant développé des traits de vie favorisant leur recherche active, comme par exemple des fortes charges alaires, des ailes manœuvrantes, et une grande taille qui permet de couvrir de grandes distances grâce à de plus grandes réserves métaboliques (Barton *et al.* 2013), ou encore des capacités de détection ou de communication chimique à longue distance (Stokland *et al*. 2012).

Les dendro-microhabitats correspondent au concept d'ERP : (i) ils sont indispensables à l'espèce, au moins à une période de son cycle vital, (ii) ils sont spatialement et temporellement limités (« discrete habitats », Kitching 1969 *in* Kitching 1971), (iii) la composition des communautés associées dépend fortement de facteurs stochastiques et on observe une certaine variabilité des assemblages au sein du même type de dendro-microhabitat. Dans le cas des dendro-microhabitats saproxyliques, le stade d'évolution influe sur les communautés (Gouix 2011 ; Fig. 5), comme on le constate également dans le bois mort où le degré d'altération du bois est un facteur clé pour la composition des assemblages (Dajoz 2007 ; Lassauce *et al.* 2012 ; Stokland *et al. 2012*). La durée utile du dendro-microhabitat est très variable en fonction du type : de quelques jours pour des dendrotelmes (Kitching 1971) ou des coulées de sève printanières liées aux fortes pressions lors du débourrement (Weber 2006) à plusieurs décennies pour les volumineuses cavités à terreau (Gouix 2011). Cette durée semble influencer le groupe taxonomique dominant. Ainsi, les communautés mycétophages des sporophores des champignons saproxyliques sont dominées par les Coléoptères dans le cas des sporophores pluriannuels de certains polypores (*e.g. Piptoporus betulinus, Polyporus squamosus, Laetiporus sulphureus*), mais par les Diptères dans le cas des sporophores fugaces des agaricales charnus (*e.g. Armillaria* spp. , *Pleurotus* spp., *Megacollybia* spp., *Pluteus* spp.) (Hanski 2005). De la même façon, les communautés des dendrotelmes sont dominées par des diptères dont les larves sont capables de résister à des variations extrêmes et rapides des conditions environnementales, de se multiplier rapidement pour profiter des courtes périodes favorables (présence d'une lame d'eau), et dont les adultes ont une forte capacité de dispersion pour rechercher un site de ponte favorable (Kitching 1971).

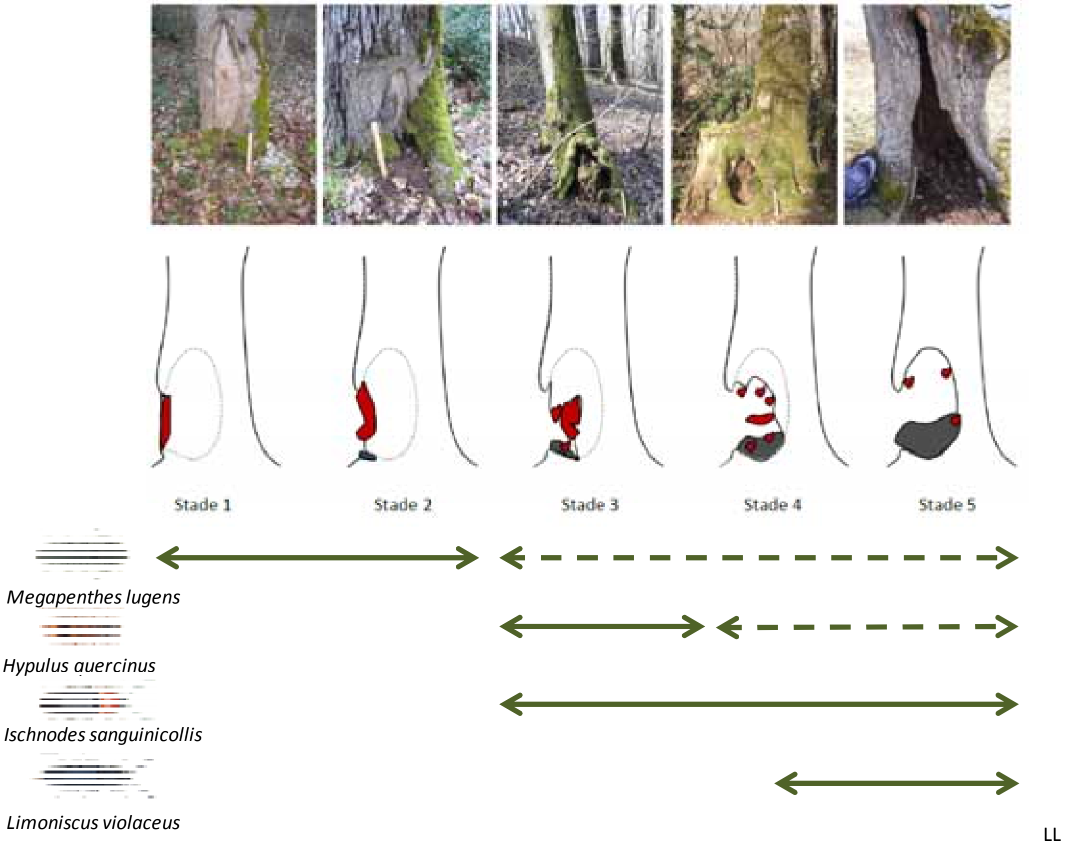

Figure 5. Exemples de Coléoptères saproxyliques Elateridae caractéristiques des cinq stades d'évolution d'une cavité basse de chêne
(d'après Gouix 2011)

Les populations d'espèces inféodées aux dendro-microhabitats sont prédisposées à fonctionner en métapopulations (Hanski 2005), c'est-à-dire des assemblages de populations distinctes (« population units ») qui peuvent potentiellement échanger des individus, comme il est suggéré pour bon nombre de Coléoptères saproxyliques (*e.g.* Ranius & Hedin 2001 ; Groove 2002 ; Schroeder *et al.* 2007). Néanmoins, à part pour les organismes qui bouclent leur cycle de vie entier dans le même dendro-microhabitat, comme les Coléoptères *Osmoderma eremita* et *Limoniscus violaceus* dans les vastes cavités à terreau (Ranius 2000 ; Gouix 2011), la matrice n'est pas toujours inhospitalière pour les habitants de dendro-microhabitats (ce point sera abordé plus en détail au paragraphe suivant). Il est alors plus difficile de délimiter les contours des différentes populations (Fig. 6) mais le concept de métapopulation reste applicable (Hanski 2005).

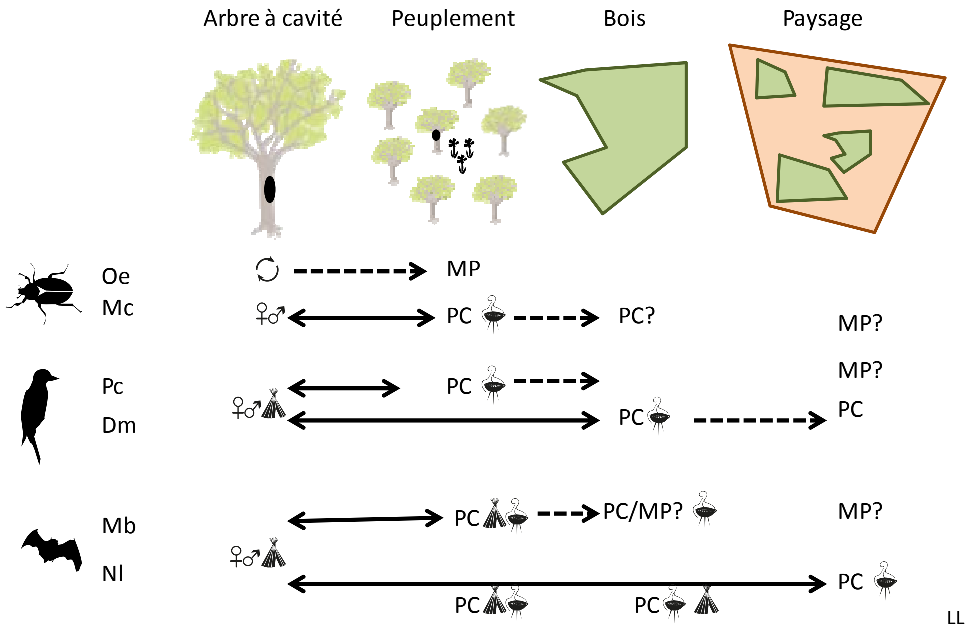

Figure 6. Échelle spatiale d'une population pour quelques exemples d'espèces liées aux dendro-microhabitats Métapopulation (MP) ou population continue (PC) ? Oe= *Osmoderma eremita* (Coléoptère Cetoniinae), Mc= *Milesia crabroniformis* (Diptère Syrphidae), Pc= *Parus caeruleus* (Mésange bleue), Dm= *Dryocopus martius* (Pic noir), Mb= *Myotis beichsteinii* (Vespertilionidae), Nl= *Nyctalus leisleri* (Vespertilionidae). Pictogrammes des rôles fonctionnels d'habitat: ↻ =cycle biologique complet ; ♀♂ =reproduction ; ▼ =nutrition ; ▲ =gîte

La connectivité des populations est indispensable au fonctionnement de la métapopulation et est assujettie à la distribution spatiale des habitats favorables, en fonction des capacités de dispersion des espèces associées (Hanski 2005). Ranius & Hedin (2001) puis Gouix (2011) ont montré respectivement pour *Osmoderma eremita* et *Limoniscus violaceus* que l'agrégation d'arbres porteurs de cavités basses à terreau favorise la conservation de ces espèces car elles ont de très faibles capacités de dispersion, de l'ordre d'à peine 200 m, ce qui limite les échanges entre les différentes populations trop éloignées ou la recolonisation d'un nouveau dendro-microhabitat lorsqu'il est trop distant. Les dendro-microhabitats étant éphémères, il convient d'assurer plus généralement la continuité de la ressource, c'est-à-dire sa connectivité spatiale durable (Hanski 2005).

2.2 LES RESSOURCES DE COMPLEMENTATION ET DE SUPPLEMENTATION

De nombreuses espèces ont besoin de plusieurs habitats ou ressources différents pour satisfaire l'ensemble de leurs besoins vitaux (Duelli 1997 ; « multi-habitat species » van Halder *et al.* 2008). Ainsi, tous les adultes de syrphes et de nombreuses espèces de Coléoptères sont anthophiles (Barbalat 1995 ; Speight *et al.* 2013), se nourrissant de nectar pour leurs besoins énergétiques ou de pollen comme source de protéines utiles à la maturation ovocytaire (Speight 1989; Schneider 1948 *in* Sommaggio 1999). La présence dans le paysage à la fois de l'habitat de la larve et de fleurs pour les adultes est obligatoire pour le maintien de l'espèce car ces deux ressources ne sont pas substituables. Ces « ressources de complémentation » (« complementation resource » Tilman 1982, ou « complementation landscape » Dunning *et al.* 1992 suivant l'échelle spatiale considérée), affectent à la fois la grandeur de la population et sa persistance (Dunning *et al.* 1992) ainsi que la distribution spatiale des individus à un stade de développement, conditionnée aux exigences des individus à un autre stade

(Ockinger 2008). Deux modalités de complémentation concernent les dendro-microhabitats (Fig. 7). **Premièrement**, le besoin de complémentation entre deux écophases de la même espèce. C'est le cas des fleurs décrit ci-dessus, avec comme exemple le Diptère Syrphidae *Myatropa florea* dont la larve vit dans les dendrotelmes. **Deuxièmement**, les ressources nécessaires à la même écophase : le pic *Dendrocopos leucotos* pond et élève ses jeunes dans des cavités d'arbres vivants et se nourrit de larves d'insectes chassées dans le bois mort (Cramp *et al.* 1985), la chauve-souris cavicole *Nyctalus leisleri* se repose le jour dans une cavité et fréquente régulièrement les plans d'eau à la tombée de la nuit pour s'abreuver avant la chasse (Arthur & Lemaire 2009). La fourmi des bois *Formica paralugubris* dont les dômes, souvent accolés à des arbres morts sur pieds, servent de microhabitat pour les larves des Diptères Microdontidae (Speight *et al.* 2013) et également des Coléoptères (Lapeva-Gjonova 2013), utilise parfois les coulées de résine des conifères blessés en transportant des fragments dans sa colonie pour en assurer sa protection antibactérienne et antifongique (Chapuisat *et al.* 2007). Les chauves-souris utilisent dans la saison de reproduction plusieurs cavités à caractéristiques microclimatiques différentes pour assurer une régulation thermique optimale (Meschede et Heller 2003). Cette forme de complémentation entre plusieurs types de dendro-microhabitats nous est peu décelable car les typologies employées ne prennent pas en compte ce type de critères de différenciation, mais le besoin pour les espèces est bien réel.

Les espèces utilisent souvent plusieurs dendro-microhabitats du même type disponibles dans son rayon d'action et parfois plusieurs dendro-microhabitats substituables (*i.e.* pouvant fournir la même fonction d'habitat) (Fig. 7). La chauve-souris *Barbastella barbastellus* utilise tout au long de l'année un grand nombre de gîtes arboricoles ayant une forme de fente qu'elle trouve dans le bois dur du tronc ou d'une branche, à l'intérieur de certaines cavités, ou sous forme d'une écorce décollée. De même, les larves du Diptère Syrphidae *Myatropa florea* sont observées dans presque tous les types de dendrotelmes (Schmidl *et al.* 2008). Ces « ressources de supplémentation » (« supplementation resource » Tilman 1982, ou « supplementation landscape » Dunning *et al.* 1992) permettent de compléter une offre trop restreinte à l'échelle du territoire de l'espèce, parfois en fournissant des habitats de moindre qualité qui n'hébergent alors que des populations « puits ». Ces dernières participent néanmoins au maintien, voire à l'augmentation numérique, de la population, car elles accueillent l'excédent d'émigrants provenant des populations sources (Dunning *et al.* 1992). Parfois, le seul changement de support suffit à altérer la qualité du dendro-microhabitat. Ainsi, les chauves-souris arboricoles utilisent plus fréquemment les cavités et fentes portées par les arbres vivants que par les arbres morts (Pénicaud 2000). Par contre, les passereaux cavicoles semblent indifférents à la santé du support (Géroudet 1984). La larve du Coléoptère saproxylique *Aesalus scarabeoides* se développe principalement dans des pourritures cubiques brunes de bois feuillus mais a été observé dans des cavités basses à terreau (Gouix com. pers.). Ces cavités constituent-elles un habitat naturel de substitution, c'est-à-dire un refuge pis-aller quand l'habitat est absent, ou bien un habitat de supplémentation de qualité en marge de l'enveloppe des habitats préférentiels et utilisé parfois par quelques individus d'une population florissante? C'est dans tous les cas un signe indiquant qu'une certaine redondance fonctionnelle d'habitat puisse exister entre les dendro-microhabitats saproxyliques, qui par définition sont composés au moins en partie de bois en décomposition, et le bois mort *sensu stricto*, c'est-à-dire les arbres morts encore sur pied, les chandelles, et les bois morts qui jonchent le sol.

La distribution spatiale des ressources de complémentation et de supplémentation est primordiale pour les espèces qui en dépendent. Pour jouer pleinement leur rôle, les ressources doivent absolument être connectées, c'est-à-dire dans le rayon de dispersion ou de prospection de l'individu et raccordées par un corridor ou séparées de la ressource primaire par une matrice perméable (« neighborhood effect », Dunning *et al. 1992*) (Fig. 7). Dans un système de paysage hétérogène (« heterogeneous landscape », Fahrig *et al.* 2011), on peut distinguer : (i) la matrice « dangereuse » qui n'offre pas de ressource et exige un coût actif pour la traverser en raison du haut risque de prédation ou de thermorégulation, (ii) la matrice « neutre » qui n'offre pas non plus de ressources mais le coût pour la traverser se résume à une simple perte de temps, et (iii) les taches « à bénéfice » qui offrent la ressource recherchée. Dunning *et al.* (1992) précise que la qualité d'un corridor dépend également de la taille et de la qualité des taches qu'il connecte.

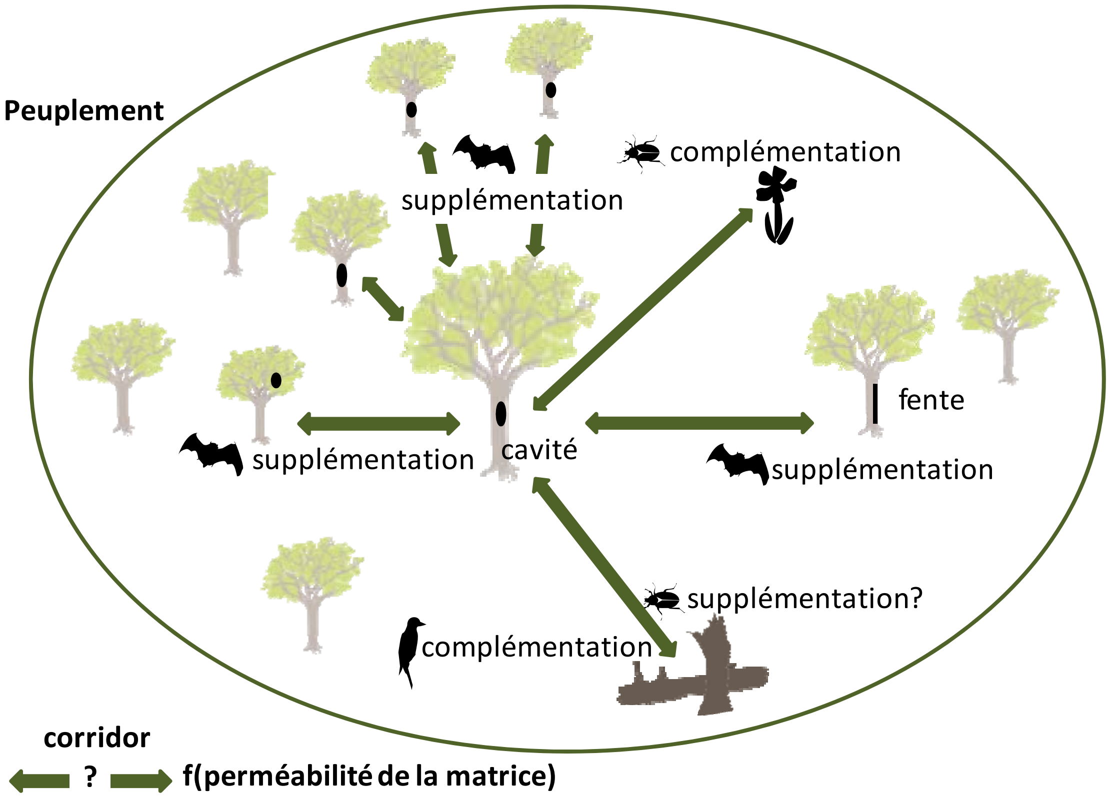

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Figure 7. Exemples de complémentation/supplémentation de ressources
Pics, coléoptères saproxyliques, et chauves-souris

On peut donc différentier trois grandes catégories de taxons associés aux dendro-microhabitats. **Premièrement**, les taxons qui semblent exclusivement liés au dendro-microhabitat, comme les champignons du bois dur sans écorce (*e.g. Stereum rugosum*) et du bois très dégradé des cavités évolutives (*e.g. Lentinellus ursinus*) ou les mousses du rebord de dendrotelme (*e.g. Zygodon forsteri*, *Anacamptodon splachnoides*) : ils ne sont pas mobiles et bouclent leurs cycles de vie dans le dendro-microhabitat. **Deuxièmement,** les taxons qui paraissent essentiellement dépendants du dendro-microhabitat car celui-ci localise la majeure partie du cycle de vie et les écophases qui ne lui sont pas dépendantes ne sont pas associées à des éléments particuliers de la matrice. C'est le cas par exemple des Coléoptères Scirtidae des dendrotelmes ou des Cetoninae des vastes cavités à terreau. Pour ces deux catégories, l'indépendance apparente à la matrice peut masquer des rôles cachés ou indirects comme le maintien d'une ambiance climatique tamponnée ou la mise à disposition de ressources non référencées dans les bases de traits de vie des espèces. De même, la perméabilité de la matrice vis-à-vis des individus les plus mobiles peut être déterminante pour la persistance de la métapopulation, comme par exemple la présence d'un épais sous-bois défavorable au vol lourd des Coléoptères (Nageleisen & Bouget 2009). **Enfin**, les taxons très dépendants de la matrice, pourvoyeuse de ressources indispensables de façon évidente, comme dans le cas des mammifères cavicoles.

2.3 LES DENDRO-MICROHABITATS AU SEIN DE RESEAUX FONCTIONNELS COMPLEXES

Nous avons vu dans les paragraphes précédents que les dendro-microhabitats assurent une large gamme de fonctions d'habitat, le plus souvent en association avec d'autres composantes de l'écosystème forestier. Mais les relations entre les dendro-microhabitats et les espèces associées ne sont pas toujours unilatérales et certaines d'entre elles contribuent activement à la dynamique spatiale des dendro-microhabitats. Les paragraphes suivants ont pour objectif d'illustrer ces relations bilatérales et d'expliquer pourquoi l'ensemble de ces relations dynamiques contribue à la complexité des écosystèmes forestiers.

2.3.1 LES DENDRO-MICROHABITATS SONT DES ELEMENTS CLES POUR L'HETEROGENEITE STRUCTURALE ET LA BIO-COMPLEXITE DES ECOSYSTEMES FORESTIERS

Classiquement, trois facteurs principaux structurent l'habitat : la variété des types de milieux, l'abondance dans chacun des types et leur agencement spatial (Blandin 1986). Pour les Araignées, les deux premiers facteurs influencent à la fois la richesse spécifique et l'abondance tandis que la distribution intervient dans le placement des individus (Blandin 1986). L'hétérogénéité spatiale des habitats est un facteur clé pour la biodiversité des systèmes écologiques car elle multiplie les possibilités d'exploiter les ressources environnementales (*e.g.* Bazzaz 1975), permet le maintien à petite échelle des espèces en dépit de disparitions localisées (Hanski 2005), et accroît le nombre de groupes fonctionnels (Huston 1994). Farhig *et al.* (2011) distinguent deux composantes de l'hétérogénéité : la gamme des types d'habitats présents et la configuration spatiale de ces habitats (appelées respectivement « compositional » et « configurational heterogeneity »). Ils proposent également de mesurer l'hétérogénéité fonctionnelle (« functional landscape heterogeneity »), c'est-à-dire la gamme des ressources présentes et nécessaires aux taxons ciblés, grâce à la diversité des types et leur équitabilité. Une partie des habitats et des ressources est non visible car indifférenciée par les critères de distinction communément employés, mais joue néanmoins un rôle essentiel dans l'hétérogénéité (concept d'« invisible mosaic », Vasseur *et al.* 2008).

Les dendro-microhabitats participent très fortement à accroitre la complexité écologique d'un habitat forestier (Fig. 8) : (i) ils sont très variés, (ii) ils sont impliqués dans les réseaux de complémentation et de supplémentation de ressources, (iii) ils évoluent constamment, chacun à sa propre vitesse, et certains types évoluent vers d'autres types voisins, et (iv) leur dynamique évolutive fait évoluer également leurs fonctions d'habitats et les communautés associées. Leur participation à la complexité écologique la plus évidente passe par leur contribution à l'hétérogénéité structurale des peuplements. Cette hétérogénéité est favorable à l'expression d'une grande richesse spécifique (Rosenzweig 1995), gage d'un effet tampon au regard des variations environnementales (« insurance hypothesis », Yachi & Loreau 1999) car les espèces peuvent répondre différemment à ces variations. Cette grande diversité d'espèces est probablement essentielle pour la stabilité des processus écosystémiques dans des environnements changeants (Loreau *et al.* 2001). L'hétérogénéité structurale confère de surcroît de la stabilité aux communautés car la disparition d'un milieu peut être instantanément compensée à une échelle spatiale fine (« stochastic equilibrium », Huston 1994) et favoriser un « effet de sauvetage » (« rescue effect », Brown & Kodric-Brown 1977), c'est-à-dire la future recolonisation par immigration. La variabilité des conditions environnant le dendro-microhabitat, en liaison bien souvent avec le couvert des arbres, peut induire de la variabilité dans les effets de la compétition et favoriser le maintien de communautés complexes car un compétiteur performant dans certaines conditions peut être dominé dans des conditions légèrement différentes (Horn & McArthur, in Huston 1994). Une grande hétérogénéité structurale des peuplements accroît également le nombre de groupes fonctionnels (Huston, 1994).

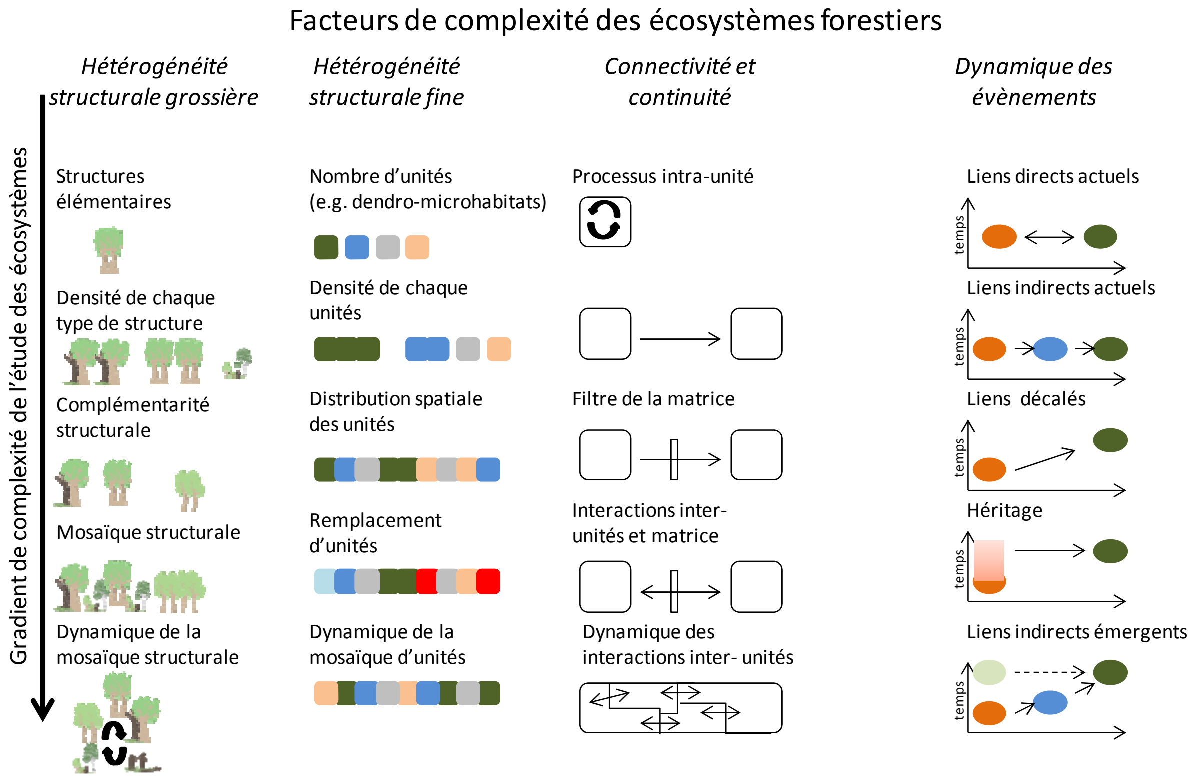

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Figure 8. Cadre théorique pour l'étude de la bio-complexité des écosystèmes forestiers (d'après Cadenasso *et al.* 2006, modifié)

2.3.2 ROLE DES ESPECES « INGENIEURS »

Certaines espèces jouent un rôle particulier dans les écosystèmes parce qu'elles causent des changements structuraux dans l'environnement qu'elles occupent, en créant, maintenant, ou modifiant les habitats, et en contrôlant ainsi la disponibilité d'une partie des ressources pour les autres espèces (Jones et al. 1997). Elles sont appelés espèces « ingénieurs » (« engineer species », Jones *et al.* 1994). Ces modifications de l'environnement physique sont cruciales pour les écosystèmes (Wright & Jones 2006). L'action peut être directe ou indirecte (les espèces sont appelées respectivement « autogenic» ou « allogenic engineers », Jones *et al.* 1994). Dans le premier cas, qui concerne le plus souvent des organismes incapables de se déplacer, c'est la propre structure physique de l'organisme qui modifie l'environnement (*e.g.* la présence d'arbres modifie les conditions climatiques locales). Ces espèces sont également appelées « fondatrices » (« foundation species », Dayton 1972 ; Ellison 2005) ou « structurantes » (« structural species », Huston 1994) car elles procurent une structure fondamentale au système, produisent de la variabilité dans les conditions physiques, les ressources et les habitats pour les espèces « interstitielles » (interstitial species », Huston 1994), et sont de ce fait irremplaçables (Dayton 1972). Dans le second cas, c'est la transformation de structures existantes qui provoque le changement : pour héberger la colonie, la fourmi rousse *Formica rufa* construit des dômes avec des matériaux récoltés aux alentours (brindilles, aiguilles de résineux, terre et gouttelettes de résine) (Torrossian & Gion 1983) et ces constructions servent de microhabitat pour les larves du Diptère Microdontidae *Microdon major* (Speight *et al.* 2013). Dans tous les cas, ces changements structuraux affectent les communautés (Jones et al. 2010), souvent en augmentant sensiblement leur richesse spécifique en liaison avec un accroissement de l'hétérogénéité structurale (Huston 1994), mais parfois en la réduisant à l'échelle locale (Jones *et al.* 1997 ; Byers *et al*. 2006), et peuvent avoir des répercussions sur la dynamique des populations de l'espèce ingénieur (Wright *et al.* 2004). La magnitude de ces effets dépend fortement de la proportion de l'écosystème impacté par les changements (Wright *et al.* 2004). Comme ces espèces ingénieurs impactent l'écosystème de façon disproportionnée par rapport à leur abondance, elles sont également des espèces « clé de voûte » (« keystone species », Power *et al.* 1996). Tous les écosystèmes hébergent et sont influencés par des espèces ingénieurs (Jones *et al.* 1994).

La grande majorité des espèces liées aux dendro-microhabitats les colonisent quand ils existent. Cependant, certaines espèces les créent, augmentant ainsi l'hétérogénéité structurale de l'arbre support. Leurs actions ont pour conséquence de modifier les communautés vivant en liaison avec cet arbre. Les modifications en cascade qu'elles provoquent peuvent leur bénéficier. Ces espèces ingénieurs allogènes appartiennent à une large gamme de taxons. Les pics creusent eux-mêmes chaque année les cavités qu'ils utilisent pour abriter leur ponte et couvée (Cramp *et al.* 1985), et sont appelés alors cavicoles primaires. Bien que ces cavités de nidification sont parfois utilisées par l'individu qui les a creusées pendant plusieurs années (Gorman 2011), elles sont surtout réutilisées par une grande diversité de cavicoles secondaires, jouant un rôle de structure clé de voute (« keystone structure », Tews *et al.* 2004) pour d'autres oiseaux (passereaux, rapaces, harles et canards, Cramp *et al.* 1985), des arthropodes (*e.g*. Bobiec *et al.* 2005), mais aussi des mammifères comme certains Gliridae (Le Louarn & Quéré 2003), Mustelidae (*e.g.* Labrid 1986) ou encore certaines chauves-souris (*e.g.* Arthur & Lemaire 2009). Il se constitue ainsi de véritables réseaux fonctionnels (« nest webs ») dont la complexité est comparable à celle des réseaux trophiques (Martin & Eadi 1999) (Fig. 9). Des Coléoptères sont également identifiés comme espèces ingénieurs. Certains créent de toutes pièces le dendro-microhabitat. Ainsi, les galeries larvaires du Grand capricorne (*Cerambyx cerdo*) affectent le tronc du chêne support, qui héberge alors des assemblages de Coléoptères saproxyliques plus diversifiés que les chênes voisins (Buse *et al.* 2008) et créent des abris parfois utilisés pour le repos diurne de la Pispistrelle commune (*Pipistrellus pipistrellus*) (Arthur & Lemaire 2009) et également par des Hyménoptères, des Diptères Syrphidae et d'autres Coléoptères (Ricarte *et al.* 2009, Speight *et al.* 2013). D'autres Coléoptères transforment significativement des dendro-microhabitats déjà existants. Le Coléoptère Pique prune (*Osmoderma eremita*) enrichit en azote et en phosphore le terreau de la cavité dans laquelle il est installé, ce qui semble être une des causes de l'accroissement de la diversité des assemblages de Coléoptères saproxyliques associés à ce dendro-microhabitat (Jönsson *et al.* 2004). Ces modifications structurales perdurent même après le départ ou la disparition de l'espèce ingénieur et la structure peut continuer à accueillir d'autres espèces tant qu'elle n'est pas totalement dégradée.

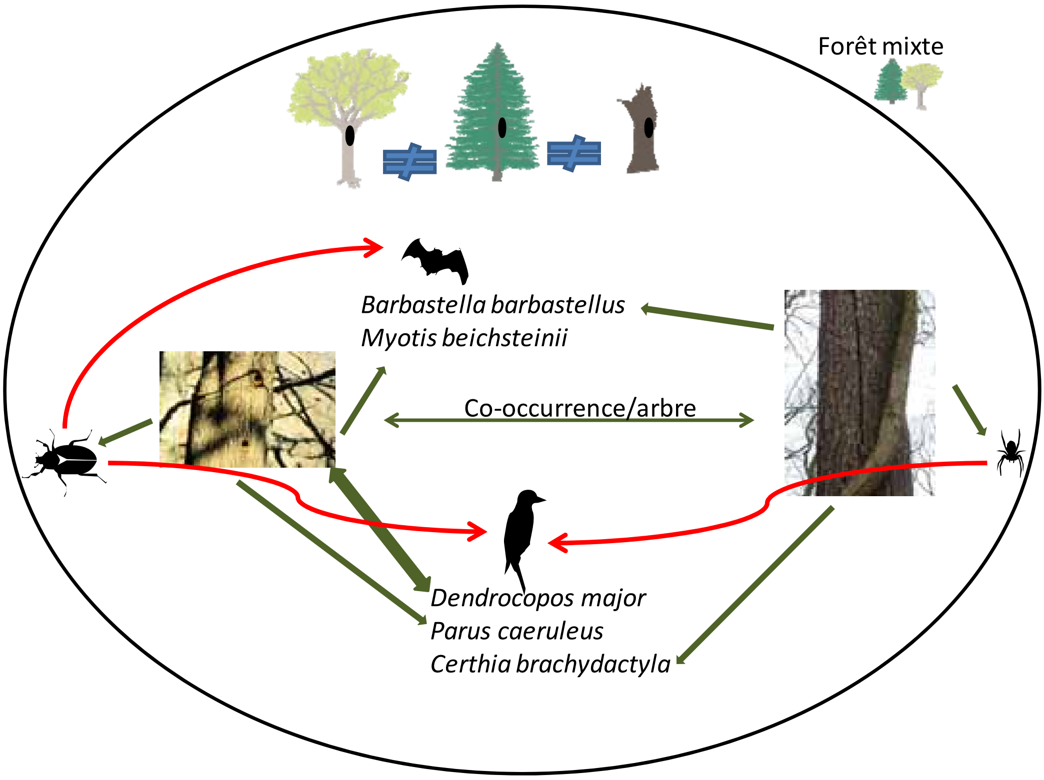

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Figure 9. Relations, dans une forêt mixte, entre deux types de dendro-microhabitats et quelques taxons associés
Les trois types de support des dendro-microhabitats (feuillus et résineux vivants, arbre mort) ne sont pas utilisés indifféremment par les espèces. Les flèches vertes illustrent des relations espèce/habitat et les rouges des relations prédateur/proie. La large flèche verte à double sens signale une espèce ingénieur.

2.3.3 LES DENDRO-MICROHABITATS SONT DES « STRUCTURES CLES DE VOUTE » POUR LES ECOSYSTEMES FORESTIERS

Les dendro-microhabitats assurent donc de multiples fonctions écologiques d'habitat pour un grand nombre d'espèces qui leur sont intimement liées: simple abri diurne ou nocturne, substrat de nutrition/hydratation pour une ou plusieurs écophases de l'espèce, de régulation de la température ou de l'humidité corporelle, de reproduction, d'hibernation, ou encore siège du cycle de vie complet de l'espèce. Ils jouent ainsi un rôle déterminant pour le maintien d'une forte diversité spécifique. Facilitant la redondance fonctionnelle (Huston 1994), c'est-à-dire le fait que plusieurs espèces de la même communauté puissent assurer la même fonction, cette diversité spécifique contribue à accroitre à la fois la productivité, la résistance et la résilience à long terme des écosystèmes forestiers (Thompson *et al.* 2009). Les dendro-microhabitats sont ainsi de véritables « structures clé de voûte » (« keystone structures », Tews *et al.* 2004). Néanmoins, Ives et Carpenter (2007) minimisent le rôle joué par la diversité des espèces dans la stabilité de l'écosystème. Elle ne semble être qu'un facteur secondaire pilotant la diversité (« driver ») parce qu'elle est elle-même sensible aux perturbations anthropiques qui affectent directement la stabilité, comme les modifications de régime hydrologique, ou, plus prés des dendro-microhabitats, les profondes modifications de l'habitat qui altèrent les dynamiques des populations, les interactions biotiques ou la production de biomasse et ainsi le fonctionnement global des écosystèmes forestiers.

2.4 LES COMMUNAUTES ASSOCIEES AUX DENDRO-MICROHABITATS SONT-ELLES SENSIBLES A LA FRAGMENTATION ?

La fragmentation est, avec la perte d'habitat, une des cinq principales causes de perte de biodiversité (Millenium Ecosystem Assessment 2005) et de nombreuses études quantifient ses effets sur les communautés. Mais la question est-elle pertinente pour les ERPs que sont les dendro-microhabitats ?

Autant une population du Coléoptère *Osmoderma eremita* se contente d'une seule cavité à terreau pour se perpétuer pendant plusieurs générations (Ranius 2000), autant certains taxons requièrent une densité minimale du même type de dendro-microhabitat pour satisfaire les exigences vitales d'une population. Une colonie de reproduction de Murin de Beichstein (*Myotis beichsteinii*) change environ tous les deux jours de gîte diurne pour réduire la probabilité de prédation, les effets délétères du parasitisme et également pour optimiser les conditions microclimatiques du gîte. Elle a ainsi besoin d'un minimum de 20 arbres à cavités par 100 ha de peuplement et par colonie (Meschede & Heller 2003).

On suppose que plus l'intensité de la relation dendro-microhabitat/taxon est forte, plus la présence du dendro-microhabitat peut être un facteur limitant pour la présence du taxon associé. On conçoit aisément qu'un simple abri peut être plus facilement remplacé qu'un milieu de reproduction, même si celui-ci ne concerne que quelques semaines du cycle biologique. L'étude de ces facteurs limitants est rendue difficile par l'existence des ressources de substitution, souvent mal appréhendées, et par les bases de données de traits de vie très incomplètes qui ne précisent souvent pas l'ensemble des rôles fonctionnels joués par le dendro-microhabitat vis-à-vis de ce taxon ainsi que la force de la relation (peu de bases de traits de vie utilisent un système de codage flou, c'est-à-dire codent sur un gradient de scores la probabilité d'y rencontrer l'espèce).

La fragmentation d'un habitat est souvent définie comme le processus durant lequel une surface importante de l'habitat se transforme en un certain nombre de petites unités de plus petite superficie totale, isolées les unes des autres par une matrice d'habitats différents de l'original. Elle est ainsi souvent confondue avec la perte d'habitat (Fahrig 2003) qui a un effet négatif sur la biodiversité (nombreuses références dans Fahrig 2003 et Hanski 2005). Pourtant, la fragmentation *per se*, c'est-à-dire l'augmentation du degré d'isolement des taches tout en gardant la même surface totale d'habitat, peut avoir des effets sur la biodiversité tantôt positifs (par la réduction de la prédation, du parasitisme ou de la compétition, ainsi que la réduction du risque d'extinction généralisé), mais le plus souvent négatifs (quand la surface unitaire des taches devient alors trop faible pour accueillir une population viable ou en liaison avec l'augmentation des effets de lisière néfastes) (synthèse dans Fahrig 2003).

Les dendro-microhabitats sont par essence des unités d'habitats de petite taille et discrets. La fragmentation *sensu stricto* d'un ensemble de dendro-microhabitats serait donc plutôt relative à un patron d'occurrence et de distribution spatiale dépendant des processus qui les produisent (ou les font disparaitre), réduisant ainsi la connectivité des populations d'espèces concernées en limitant les échanges entre dendro-microhabitats du même type ou entre le dendro-microhabitat et les ressources de complémentation associées. Cette réduction de connectivité peut être provoquée par l'éloignement des ressources ou par une moins bonne perméabilité de la matrice entre les ressources. Elle est plus fortement préjudiciable aux espèces qui exploitent principalement et durablement un seul dendro-microhabitat qu'aux espèces qui prospectent régulièrement à la recherche de ressources (Levins 1968, *in* Hanski 2005). Les patrons de distribution spatiale en forêt naturelle et de connectivité des dendro-microhabitats et des ressources n'ont à notre connaissance jamais été étudiés.

En ce qui concerne la réduction d'habitat au sens strict, elle prend dans notre cas la forme d'une plus faible densité de dendro-microhabitats. Précisons également que le type de relation entre la densité de dendro-microhabitats et la taille des populations de taxons associés n'est pas connu. Il est néanmoins probable que cette relation ne soit pas simplement proportionnelle, c'est-à-dire qu'une réduction du nombre de dendro-microhabitats réduit d'autant la taille de la population, mais qu'elle comporte un seuil d'extinction (« extinction threshold », Fahrig 2003), c'est-à-dire une densité en dessous de laquelle la population ne peut subsister à long terme.

3 ÉCHELLES SPATIALES DE L'ETUDE DES DENDRO-MICROHABITATS ET DES COMMUNAUTES ASSOCIEES

Nous avons vu précédemment (§ 1.4) que l'on distinguait pour les dendro-microhabitats (i) des subdivisions infra-unité correspondant à leurs subdivisions morphologiques élémentaires et (ii) plusieurs échelles spatiales d'agrégation : l'arbre porteur, la population d'arbres porteurs du même type de dendro-microhabitat et enfin le peuplement forestier. Voyons maintenant à quelles échelles ont-ils été principalement étudiés.

Certains dendro-microhabitats et leurs communautés associées sont étudiés depuis assez longtemps et ont suscité une abondante littérature. C'est le cas des dendrotelmes (Kitching 1971 et 1983 ; Vaillant 1978 ; Bradshaw & Holzapfel 1988 et 1992 ; Schmidl *et al.* 2008 ; Paradise 1999 ; Paradise *et al.* 2008), des cavités de picidés (*e.g.* Martin & Eadie 1999 ; Trudeau *et al.* 2011) et des sporophores de champignons saproxyliques (*e.g.* Jonsell *et al.* 1999). Mais ces études ont été réalisées le plus souvent hors contexte forestier et à l'échelle du dendro-microhabitat, en le déconnectant de son environnement proche. Cette échelle d'étude permet d'inventorier les communautés associées à chacun des dendro-microhabitats, de rechercher les caractéristiques internes discriminant les assemblages, d'appréhender la variabilité des communautés au sein du même type de dendro-microhabitat, et enfin d'alimenter les bases de données de traits de vie des espèces avec des variables fines de description des conditions environnementales.

Toutefois, même à l'échelle de l'arbre, les déterminants de la biodiversité associée à un dendro-microhabitat sont peu connus et encore à l'étude : par exemple, pour l'Amadouvier du Hêtre (*Fomes fomentarius*) et les Coléoptères (Rose & Bouget 2009) ou les cavités basses à terreau et les Coléoptères cavicoles (Gouix 2011). De plus, très peu d'études prennent en compte la dynamique du dendro-microhabitat, et toujours de façon synchronique (*e.g.* les cavités basses à terreau de feuillus dans Gouix 2011). L'échelle de l'arbre nécessite de replacer le dendro-microhabitat dans un contexte environnemental plus large et permet d'étudier si sa position sur l'arbre support influe sur les communautés. Elle permet également de regarder s'il existe des relations entre les attributs de l'arbre porteur (par ex. essence, diamètre ou âge) et le type de dendro-microhabitat porté ou s'il existe des relations de co-occurrence entre plusieurs types.

Les dendro-microhabitats ne sont étudiés que depuis 2008 dans un contexte forestier et à l'échelle du peuplement, en tant que « proxy » d'une partie de la biodiversité taxonomique (Winter & Möller 2008). Cette échelle spatiale correspond à l'unité de décision pour le gestionnaire forestier et généralement à « l'habitat naturel » du gestionnaire des espaces naturels. Elle intègre une grande partie des processus écologiques qui sous-tendent les compositions des communautés observées à des échelles plus fines. Elle est indissociable de l'échelle de l'arbre car les arbres sont des descripteurs incontournables du peuplement. Peu d'écosystèmes forestiers ont été étudiés dans cette optique avant nos travaux : les hêtraies médio-européennes de plaine (Winter & Moller 2008), la douglasaie Ouest-américaine (Michel & Winter 2009) et enfin un panel restreint de contextes Français (Vuidot *et al.* 2011). Cependant, l'approche était seulement quantitative (densité de dendro-microhabitats) et non qualitative (diversité des types). Des tendances de relations entre l'occurrence des dendro-microhabitats et l'essence ainsi que le diamètre de l'arbre porteur ont été mis en évidence, mais n'ont été ni chiffrées ni modélisées. Une relation positive entre le nombre total de dendro-microhabitats et la richesse spécifique en Coléoptères saproxyliques a été montrée par Winter & Moller (2008) dans les Hêtraies médio-Européennes. Les sections I et III de cette thèse apporteront des compléments substantiels à ces connaissances fragmentaires. Enfin, aucune étude à ce jour ne s'intéresse à la dynamique spatiale du réseau de dendro-microhabitats alors que cette connaissance paraît incontournable, à la fois pour mieux délimiter le rôle fonctionnel des dendro-microhabitats et pour mieux les prendre en compte dans la gestion forestière. Ce point sera débattu en section V.

L'échelle du peuplement soulève néanmoins quelques interrogations sur sa pertinence écologique pour l'étude des communautés associées aux dendro-microhabitats. En effet, dans le continuum d'un massif forestier, le peuplement forestier (au sens communément utilisé par les gestionnaires) n'est rien d'autre qu'un objet spatialement défini sur des critères de production ligneuse et ne prend ainsi en compte que la communauté d'arbres, sa composition dendrologique (les morts bois sont exclus), sa structure dendrométrique et le potentiel de production (Bastien et Gauberville 2011). D'autre part, l'échelle de résolution est bien plus large que celle du dendro-microhabitat et peut masquer de grandes différences de structure interne. Nous discuterons ces aspects dans la section IV.

4 TYPOLOGIE DES DENDRO-MICROHABITATS

L'étude des dendro-microhabitats nécessite de disposer d'une typologie claire. Aucune n'étant publiée en 2003 lorsque nous avons commencé les inventaires, j'en ai en donc bâti une. Les seuils de dimensions délimitant les dendro-microhabitats « élémentaires » étaient issus de connaissances naturalistes. Les définitions étaient avant tout morphologiques, permettant ainsi l'identification depuis le sol, mais s'appuyaient sur les relations avec les taxons présumés associés. La typologie permettait le regroupement des observations de dendro-microhabitats rares en groupes d'effectifs suffisants pour les exploiter statistiquement (e.g : « cavités vides » regroupant les trous de pics et les autres cavités peu évoluées, avec tous les seuils de dimension) tout en accumulant des données précises. Les publications ultérieures de Winter & Möller (2008), Michel & Winter (2009), Vuidot *et al.* (2011) ont permis de confronter cette typologie initiale avec d'autres approches et de l'amender. Mais les fondements de ces typologies s'écartent parfois assez fortement de notre idée initiale de toujours relier un dendro-microhabitat avec des taxons associés. Ainsi, Winter & Möller (2008) rassemblent les exsudations de résine dont nous avons précédemment relevé le caractère abiotique avec les coulées de sève qui hébergent un grand nombre d'arthropodes (Yoshimoto *et al.* 2005), et Vuidot *et al.* (2011) décrivent les excroissances chancreuses pour lesquelles la littérature et la connaissance naturaliste ne dit rien en termes de biodiversité associée. Bien que nous ayons abordé la difficulté de délimiter le dendro-microhabitat élémentaire, ces typologies donnent une gamme dimensionnelle et d'hétérogénéité morphologique parfois énorme, en considérant qu'une moitié de houppier morte constitue un dendro-microhabitat au même titre qu'un trou de pic. D'autre part, certains dendro-microhabitats pourtant bien identifiés comme hébergeant une faune spécifique, comme par exemple les dendrotelmes, sont absents de ces listes.

Tout au long de l'avancée des études dans les différents contextes, nous avons fait évoluer notre liste de référence des dendro-microhabitats. J'ai directement observé la grande majorité des dendro-microhabitats recensés sur nos sites d'étude. Forts de cette expérience, nous avons rassemblé ces dendro-microhabitats dans un cadre typologique qui se veut en même temps écologiquement pertinent et pratique. Après avoir consulté un éventail d'experts dans des groupes taxonomiques variés et réalisé une large recherche bibliographique sur les relations entre les dendro-microhabitats et les taxons associés, la nouvelle typologie proposée sera présentée en détail dans la section IV.

5 LES DENDRO-MICROHABITATS A LA CROISEE DE PLUSIEURS DOMAINES SCIENTIFIQUES

L'étude des dendro-microhabitats relève de plusieurs champs disciplinaires. En tout premier lieu, l'écologie forestière car nous avons vu que les dendro-microhabitats sont des éléments clés pour la complexité interne des écosystèmes forestiers, ont leurs propres dynamiques mais sont également dépendants de la dynamique des arbres supports. Ce sont des milieux de vie diversifiés hébergeant un très grand nombre de taxons qui remplissent des rôles fonctionnels variés et cruciaux pour les cycles fondamentaux, comme le recyclage de la matière organique ligneuse ou la pollinisation.

L'actuelle vague d'extinction et de dégradation de la diversité biologique (*e.g*. Peterson *et al.* 2011) concerne en premier chef les forêts car elles sont des réservoirs majeurs pour la biodiversité terrestre (FAO 2000). Eu égard au fort impact de la gestion forestière sur la biodiversité des forêts (Speight 1989 ; Stokland *et al.* 2012) notre approche des dendro-microhabitats relève également de la biologie (ou écologie) de la conservation. Cette science de la nature appliquée vise à générer les connaissances scientifiques nécessaires à conduire des politiques de conservation pertinentes (Soulé 1986, *in* Blondel 1995), et à fournir les outils pour aider la société à anticiper et réduire son impact écologique (Orians & Soulé 2001). Elle traite inévitablement d'un éventail de questions qui vont au-delà des disciplines biologiques et écologiques, en incluant les biens et services publics et les politiques institutionnelles (Burgman & Yemshanov 2013). Elle s'applique bien aux dendro-microhabitats car d'une part un grand nombre des taxons spécifiques aux dendro-microhabitats sont devenus rares ou ont disparu des peuplements exploités, et, d'autre part, la grande majorité des forêts tempérées et boréales est actuellement exploitée (Gilg 2005). De plus, les dendro-microhabitats peuvent constituer un outil pertinent pour aider les gestionnaires forestiers à mieux prendre en compte et suivre la diversité spécifique, comme Winter & Möller (2008) le préconisent. Mais, pour réussir, les scientifiques doivent absolument appréhender correctement le contexte dans lequel leur outil sera utilisé, et le construire en conséquence (Burgman et Yemshanov 2013). Nous développerons cet aspect dans la section IV consacrée à la mise en pratique des nouvelles connaissances, étant persuadés que les dendro-microhabitats fournissent un cadre de travail pertinent pour le transfert de connaissance, car ils sont pour la plupart bien connus des forestiers de terrain, certes encore le plus souvent comme « défauts » des arbres abaissant leur valeur économique, mais il est peut-être plus facile de juste changer le regard que d'apprendre à regarder. Par leur action directe ou indirecte sur la composition des peuplements forestiers, leur structure interne et les fonctions remplies, les dendro-microhabitats rentrent tout à fait dans le cadre plus général des outils d'évaluation indirecte de la biodiversité taxonomique (« Biodiversity Evaluation Tools ») mis en exergue par Larsson *et al.* (2001).

En permettant de mieux identifier les filtres environnementaux déterminants pour les communautés locales (*i.e.* à l'échelle du peuplement forestier), les dendro-microhabitats peuvent être des objets pertinents en écologie des communautés. Ainsi, Bouget (2013), dans un schéma conceptuel syncrétique présentant les principaux filtres de la composition des assemblages locaux de Coléoptères saproxyliques, propose le stock de dendro-microhabitats comme facteur déterminant à l'échelle de la tache d'habitat.

Enfin, nous avons vu précédemment que, pour un taxon associé à un dendro-microhabitat, le peuplement forestier peut être appréhendé comme un ensemble hiérarchisé d'objets qui ont une occurrence et une organisation spatiale fortement dépendantes des itinéraires sylvicoles mis en œuvre par le gestionnaire car la grande majorité des écosystèmes forestiers tempérés sont exploités. Cette organisation spatiale et les possibilités de connexions semblent primordiales pour les communautés associées aux dendro-microhabitats et les notions de matrice, de corridor, de tache, de mosaïque s'avèrent pratiques pour décrire les processus. En référence à Burel & Baudry (1999), tous ces éléments suggèrent que certaines approches et techniques employées en écologie du paysage pourraient être pertinentes, mais une expertise plus approfondie de cette discipline me serait nécessaire pour en préciser la liste.

6 SYLVICULTURE ET DENDRO-MICROHABITATS

Les premiers aménagements forestiers étaient rédigés dans la nécessité de limiter l'impact de l'Homme sur la forêt (Duchiron, 1994). Mais, malgré le fait que l'aménagement d'une forêt doit tenir compte de « toutes » les fonctions possibles, c'est-à-dire la production, la protection (en réalité plutôt jusqu'alors orientée sur les biens et les personnes), l'accueil du public et les activités cynégétiques (Anonyme, 1977), les différents schémas sylvicoles ont toujours été mis au point dans le but d'accroître avant tout la quantité de bois produite et d'assurer une proportion de bois d'œuvre maximale. Bien que les prix de la matière première sur les marchés du bois soient assez fluctuants et difficiles à prévoir plusieurs dizaines d'années à l'avance, on conçoit alors très bien que l'arbre idéal possède un tronc sans défaut important qui pourrait réduire l'éventail de l'utilisation de son bois. L'arbre fendu, troué, très branchu sur le tronc ou porteur de champignons lignivores est de ce fait vu par le forestier comme indésirable et, contrairement à des sujets plus productifs, les forestiers pensent généralement qu'il ne «paye pas sa place» (Hubert *et al.* 1980). Ainsi, traditionnellement, les coupes de bois exploitent les arbres : (i) dont le diamètre dépasse le diamètre d'exploitabilité (qui d'ailleurs tend à se réduire de plus en plus), (ii) qui portent des singularités sur le tronc qui réduisent la valeur commerciale de leur bois (*e.g.* de nombreux nœuds apparents, des cavités, des sporophores de champignons saproxyliques), (iii) dont la durée de survie est estimée inférieure à la durée moyenne des rotations des coupes et (iv) appartenant à des essences secondaires dont le bois est, à terme, moins rémunérateur.

Dans un grand massif appartenant à un même propriétaire, la création de « parcelles forestières» permet d'homogénéiser les peuplements sur d'assez vastes surfaces unitaires (15 à 30 ha). Ceci facilite la gestion par une meilleure prévision des récoltes et par une mise en marché plus aisée des bois récoltés. Une desserte routière suffisamment dense permet d'exploiter efficacement les volumes de chablis ou de bois dépérissants. Dans ces conditions, seules des conditions extrêmement défavorables à l'accessibilité, d'ordre topographiques (pente, gorges) ou stationnelles (lapiaz ou tourbière), un fort éloignement des grands axes routiers ou une absence de gestion liée au désintéressement du propriétaire permet, au moins momentanément, la présence en quantité naturelle de bois mort, d'arbres porteurs de dendro-microhabitats ou d'essences à faible valeur commerciale.

On constate néanmoins une profonde inflexion depuis quelques années. La sylviculture « proche de la Nature » de type Pro Sylva reconnaît l'aide amenée par les essences secondaires pour «accompagner» la croissance des arbres objectifs, exclut les coupes fortes sur des grandes surfaces, et vise le développement d'arbres de gros diamètre pour une production optimale de bois de qualité (Anonyme, 1993). En France, les forêts bénéficiant du régime forestier utilisent des normes empiriques pour conserver une petite population d'arbres porteurs de dendro-microhabitats, à la fois dans les peuplements exploités et en laissant, temporairement ou pas, des îlots en libre évolution (ONF 2009). De leur côté, les propriétaires privés adhérant au système de certification PEFC (« Programme for the Endorsement of Forest Certification ») s'engagent à conserver au moins un arbre à cavité ou un très gros arbre à l'hectare (PEFC 2011). Cependant, ces critères dans les standards de certification volontaire résultent de négociations et ne sont pas fondés sur des seuils ou objectifs écologiques basés sur des résultats scientifiques avérés (Angelstam *et al.* 2013). La section I de cette thèse apportera des éléments de réflexion chiffrés pour amender ces standards.

Malgré ces préconisations récentes en faveur du maintien sur pied d'arbres portant des dendro-microhabitats, la rigueur des éclaircies sélectives et la fréquence des passages en coupe leur laisse peu de place (de Turckheim 2005). Pourtant, il n'y a une réelle compétition directe entre production et conservation que pour un nombre limité d'arbres (environ 10 % dans Bruciamacchie 2005). Certains propriétaires considèrent que l'effort écologique consenti doit être rémunéré en surplus comme pourvoyeur d'aménités pour la société (de Turckheim 2005).

7 OBJECTIFS DE LA THESE

Bien que les dendro-microhabitats semblent être des structures clés de voûte pour la diversité biologique et le fonctionnement des écosystèmes forestiers, leur étude est récente et les connaissances logiquement fragmentaires. Pourtant, ces structures sont bien connues des forestiers, et nous pensons qu'elles pourraient être intégrées à un vocabulaire partagé avec les naturalistes et les biologistes de la conservation, et ainsi faciliter le débat et la prise en compte de la biodiversité dans la gestion forestière courante.

En conséquence, les objectifs poursuivis dans ce cadre de ce travail sont principalement de :

- Préciser le type et la magnitude de la relation signalée dans la littérature entre l'essence et le diamètre (ou l'âge) des arbres et les dendro-microhabitats. Ces deux variables sont en effet relevées en routine par les gestionnaires forestiers et pourraient constituer des proxys faciles à intégrer dans la gestion courante.
- Ébaucher l'étude des dynamiques naturelles des dendro-microhabitats.
- Quantifier l'influence de la gestion des peuplements forestiers sur les relations arbre/dendro-microhabitat et les dynamiques des dendro-microhabitats.
- Établir, en croisant l'approche indirecte par les dendro-microhabitats, et directe par des taxons bio-indicateurs, le cadre dans lequel les dendro-microhabitats pourraient être utilisés comme proxy dans le suivi courant de la diversité des espèces en forêt.
- Établir une typologie de référence des dendro-microhabitats bâtie et argumentée sur des bases scientifiques.
- Intégrer les dendro-microhabitats dans des outils d'aide à la gestion durable des forêts.

Le manuscrit s'articule autour de cinq sections thématiques. La section I expose les résultats concernant la densité et la diversité du bois mort et des dendro-microhabitats dans les forêts exploités et non exploités. Elle précise les relations entre les dendro-microhabitats, l'essence et le diamètre des arbres, à l'échelle de l'arbre mais aussi du peuplement forestier. La section II étudie d'une part les dynamiques naturelles des dendro-microhabitats et du bois mort au cours du cycle sylvigénétique des peuplements mixtes de montagne, et, d'autre part, la reconstitution des populations de dendro-microhabitats après l'exploitation forestière des peuplements feuillus de plaine. La section III expose les résultats sur les liens entre diversité taxonomique et dendro-microhabitats à l'échelle du peuplement forestier. La section IV propose une nouvelle typologie des dendro-microhabitats, bâtie sur la base d'un système hiérarchisé offrant toute une gamme d'avantages et de possibilités d'évolution et présente deux exemples concrets d'intégration des dendro-microhabitats dans des outils d'aide à la gestion forestière durable. Enfin, la section V propose un ensemble de recommandations pratiques pour la gestion des dendro-microhabitats et suggère des perspectives scientifiques autour de nouvelles questions de recherche. La démarche résumée est illustrée par la figure 10.

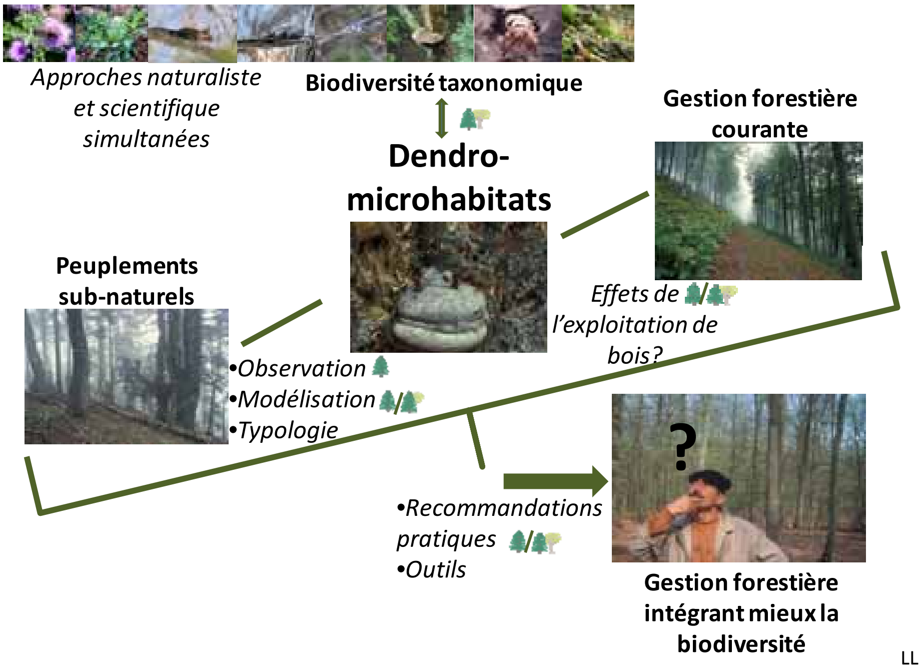

Figure 10. Schématisation de la démarche de recherche adoptée dans cette thèse
🌲=échelle de l'arbre ; 🌳🌲=échelle du peuplement forestier

Pour simplifier la lecture du manuscrit, et l'ouvrir au plus grand nombre, les sections I, II et III sont résumées succinctement par un aperçu de la problématique spécifique, des principaux résultats obtenus et de quelques considérations prospectives. Compte tenu de leur complémentarité pour les communautés saproxyliques (Stokland *et al.* 2012) et d'une certaine redondance fonctionnelle pressentie entre le bois mort et le groupe des dendro-microhabitats saproxyliques, bois mort et dendro-microhabitats ont été souvent étudiés simultanément et apparaissent donc dans les publications. En revanche, les résumés de ces sections focaliseront sur les dendro-microhabitats.

La section I regroupe des travaux publiés, sous presse ou soumis (Tableau 2). Les sections II, III et IV présentent également le contexte, les méthodes et les principaux résultats d'études complémentaires qui n'ont pas encore fait l'objet de publications mais qui nous semblent utiles au débat. Ces publications en préparation sont présentées en Français et sous une forme synthétique.

8 METHODOLOGIE GENERALE DES TRAVAUX CONDUITS DANS CETTE THESE

Les méthodes propres à chacune des études sont bien sûr détaillées dans la partie « Matériel et méthodes » des publications. Néanmoins, afin de mettre en exergue la cohérence méthodologique de l'ensemble, nous présentons ci dessous les grands traits communs à l'ensemble des études.

8.1 ÉCOSYSTEMES, TYPES DE PEUPLEMENTS ET CONTEXTES DE GESTION ETUDIES

Nous nous sommes principalement intéressés à deux écosystèmes forestiers tempérés : (i) les peuplements mixtes de montagne, notamment les hêtraies-sapinières montagnardes ; (ii) les hêtraies-chênaies collinéennes. Les hêtraies-sapinières montagnardes sont présentes dans la plupart des chaînes de montagnes européennes, couvrant environ 380 000 km², soit plus de 4 % de la surface totale des forêts européennes (MCPFE 2007 ; Euforgen 2012). Les peuplements comportant des chênes couvrent également de vastes étendues, surtout en basse altitude, et produisent localement du bois de très haute valeur économique.

Ces forêts ont non seulement une grande valeur économique mais sont également connues pour leur rôle clé dans la conservation de la biodiversité en Europe. Müller *et al.* (2012) ont montré que les forêts dominées par le Hêtre constituent un habitat « parapluie » pour les Coléoptères saproxyliques d'Europe centrale car 70 % de ces espèces peuvent être observées dans ce type de forêt. Quant aux chênes, ils sont identifiés comme support d'une grande biodiversité (Vodka *et al*. 2009).

Pour les forêts montagnardes, nous avons focalisé sur le type de gestion dominant : la futaie irrégulière. Dans les forêts collinéennes, nous avons couvert l'ensemble des patrons, c'est-à-dire la gestion par l'Office National des Forêts (ONF), la gestion privée sous Plan Simple de Gestion (PSG) agréé par l'autorité compétente (Centre Régional de la Propriété Forestière) et enfin la gestion privée sans document de gestion agréé. Nous nous sommes également intéressés à la gestion des lisières agricoles des bois morcelés.

8.2 INVENTAIRES DES DENDRO-MICROHABITATS

Les inventaires des dendro-microhabitats et du bois mort ont été réalisés suivant deux procédures fortement emboitées, différentiées par le niveau de détail des variables relevées. Elles sont généralement spatialement distinctes, mais ont été utilisées parfois simultanément pour permettre leur confrontation *a posteriori*. La première procédure consiste à inventorier tous les bois morts et les dendro-microhabitats de tous les arbres de la placette avec une grande précision, en utilisant des dimensions de pré-comptage très petites et un grand nombre de classes catégorielles au sein du même élément. Pour l'illustrer, on peut citer l'inventaire autant que faire se peut exhaustif des dendrotelmes qui, en se basant sur la littérature décrivant les communautés associées, différentie deux types (à fond dur ou carié), trois classes de diamètre de la cavité (3-5 cm, 6-20 et > 20 cm) et deux positions dans l'arbre (<2m du sol ou plus haut). La deuxième procédure utilise un référentiel simplifié issu de l'Indice de Biodiversité Potentielle (IBP, Larrieu & Gonin 2008) et n'inventorie par exemple que les dendrotelmes de plus de 10 cm de diamètre, sans distinction de type ou de forme, observés sur un échantillon d'arbres lors d'un parcours méthodique, mais non exhaustif, de la placette. J'ai mené la quasi-intégralité des observations, dans le but premier d'accumuler de l'expérience. Ceci a permis également de réduire au maximum un éventuel effet observateur, bien qu'aucune publication ne permette à ce jour d'évaluer sa magnitude.

La littérature récente mettait en évidence un éventuel effet de la diversité des attributs (*e.g.* le bois mort), en plus ou à la place de leur densité (Siitonen 2001 ; Brin *et al.* 2009). Nous nous sommes alors attachés à toujours considérer en parallèle ces deux aspects, bien qu'ils soient dans certains cas très corrélés (Müller & Bütler 2010). Pour permettre un transfert aisé des résultats aux gestionnaires, nous avons souvent exprimé la densité des dendro-microhabitats par la densité des arbres porteurs de dendro-microhabitats. Nous verrons plus loin que, dans le cadre d'une approche indirecte de la biodiversité associée à ces dendro-microhabitats, nous manquons cruellement d'arguments scientifiques pour privilégier la densité réelle.

8.3 MA CONTRIBUTION AUX PUBLICATIONS ACADEMIQUES ASSOCIEES A CES TRAVAUX

Il est évident qu'un travail comme cette thèse résulte de nombreuses collaborations, en particulier dans l'exercice ô combien difficile de valorisation des données. Le tableau 2 résume ma contribution à chacune des publications académiques, en précisant si j'étais « acteur majeur » (m), si ma participation était majeure seulement pour une partie de la tâche comme dans le cas de protocoles dendrométriques couplés avec des protocoles taxonomiques (pp) ou si ma contribution était secondaire (s). La mention « so » signifie que la tâche est sans objet (par exemple lorsque la tâche n'a pas nécessité de mesures de terrain).

Tableau 2 - Contribution de LL à chacune des publications académiques

« m » = acteur majeur, « pp » = participation majeure seulement pour une partie de la tâche, « s» = contribution secondaire. « so » = tâche sans objet

Papier	1er auteur	Statut à la date de soutenance	Année de publication ou (soumission)	Revue	Impulsion projet	Rédaction protocoles	Mesures terrain	Utilisation de bases de données extérieures	Plan d'analyse (objectifs)	Réalisation analyses	Interprétation analyses	Rédaction
11	Larrieu	publié	2012	Canadian Journal of Forest Research	m	m	m	non	m	s	m	m
12	Larrieu	publié	2014	European Journal of Forest Research	m	m	m	non	m	s	m	m
13	Larrieu	publié	2012	European Journal of Forest Research	m	m	m	non	m	s	m	m
14	Lassauce	publié	2013	Insect Conservation and Diversity	s	pp	pp	Oui (Irstea)	pp	s	pp	pp
15	Ouin	accepté	(oct. 2014)	Forest Ecology and Management	m	m	pp	non	m	s	pp	pp
21	Larrieu	publié	2014	Forest Ecology and Management	m	pp	pp	Oui (Irstea/WSL/Univ. Dresde)	m	s	m	m
22	Bouget	publié	2014	Animal Conservation	s	pp	pp	Oui (Irstea)	s	s	pp	pp
23	Larrieu	en préparation	-	European Journal of Forest Research?	m	m	m	Oui (Dynafor)	m	s	m	m
31	Bouget	publié	2013	Biodiversity and Conservation	s	pp	pp	Oui (Irstea)	s	s	pp	pp
32	Bouget	publié	2014	Ecological Indicators	s	pp	pp	Oui (Irstea)	s	s	pp	pp
33	Larrieu	en révision	(oct. 2014)	European Journal of Entomology	m	m	m	non	m	s	m	m
34	Herrault	soumis	(oct. 2014)	Landscape Ecology	pp	pp	pp	Oui (Dynafor)	m	s	pp	pp
35	Müller	publié	2014	Ecography	s	s	pp	Oui (multiples)	s	s	s	s
36	Larrieu	en préparation	-	Biological Conservation?	m	pp	pp	Oui (Irstea/ONF/GEVFP/Dynafor)	m	m	m	m
41	Larrieu	en préparation	-	Ecological Indicators ?	m	m	m	non	m	s	pp	m

Section I- Densité et diversité des dendro-microhabitats dans les forêts exploitées et non exploitées. Relations entre l’occurrence et la diversité des dendro-microhabitats et l’essence et le diamètre des arbres

SECTION I - DENSITE ET DIVERSITE DES DENDRO-MICROHABITATS DANS LES FORETS EXPLOITEES ET NON EXPLOITEES. RELATIONS ENTRE L'OCCURRENCE ET LA DIVERSITE DES DENDRO-MICROHABITATS ET L'ESSENCE ET LE DIAMETRE DES ARBRES

Les questions principales qui sous tendent cette section I sont les suivantes : dans les forêts sub-naturelles (i) quelles sont les relations entre les deux variables les plus couramment utilisées en gestion - l'essence et le diamètre à 1,3 m de l'arbre - et l'occurrence des dendro-microhabitats ? (ii) quels sont les patrons « naturels » d'occurrence relative des différents types de dendro-microhabitats ? Afin d'amener des éléments concrets de réflexion pour améliorer la prise en compte des dendro-microhabitats dans les forêts exploitées, nous avons étudié également comment les actes de gestion influençaient ces patrons.

Plusieurs contextes d'étude ont permis de couvrir à la fois deux types forestiers occupant une grande surface en France et un échantillon des principaux modes de gestion. En hêtraie-sapinière montagnarde, nous nous sommes placés dans le cas le plus général de grands massifs forestiers et de peuplements mixtes à structure irrégulière. Nous avons étudié un échantillon de peuplements inexploités depuis plusieurs décennies (Larrieu & Cabanettes 2012 ; Larrieu *et al.* 2014), supposés posséder des patrons structuraux relativement proches de ceux des forêts naturelles, et nous les avons comparés à des peuplements régulièrement exploités par une coopérative forestière (Larrieu *et al.* 2012 ; Larrieu *et al.* 2014). En chênaie collinéenne, nous avons sélectionné deux contextes extrêmes : (i) le grand massif forestier de Tronçais (Allier) dans lequel les peuplements sont gérés en structure régulière par l'Office National des Forêts (Lassauce *et al.* 2013) et (ii) les bois « ruraux » morcelés des coteaux de Gascogne (Haute-Garonne), gérés principalement par des agriculteurs sans documents de gestion, et dans lesquels nous nous sommes focalisés sur les dendro-microhabitats des lisières (Ouin *et al.* soumis).

1 PRINCIPAUX RESULTATS

- Les peuplements mixtes sub-naturels de montagne ont montré qu'il est plus fréquent d'observer des dendro-microhabitats sur les feuillus que sur les résineux. Ainsi, le Hêtre et les feuillus secondaires portent des dendro-microhabitats avec une fréquence d'environ 70 % alors que seuls 18 % des sapins pectinés sont porteurs.
- Les *cavités* sont le type de dendro-microhabitat le plus fréquent et les *fentes* le moins fréquent.
- Plus un arbre est gros, plus la probabilité qu'il porte un dendro-microhabitat est forte : les seuils de diamètre les plus significatifs sont 73 et 89 cm pour le Hêtre et 99 cm pour le Sapin pectiné. Alors que 73 cm correspond à la classe de diamètre « très gros bois » déjà usitée dans la gestion, les deux autres seuils nécessitent de créer une classe de gestion supplémentaire pour leur application.
- Seuls les plus gros arbres, c'est-à-dire les hêtres de diamètre supérieur à 50 cm et les sapins de plus de 65 cm, peuvent porter tous les types de dendro-microhabitats.
- L'essence et le diamètre expliquent ensemble environ 25 % de la variabilité de l'occurrence des dendro-microhabitats.
- Certains dendro-microhabitats semblent associés : *bois dur sans écorce* avec *cavités à terreau*, *cavités vides* avec *dendrothelmes* et *fentes*, sont des associations significatives à la fois pour le Hêtre et le Sapin.

- Les chandelles contribuent à l'abondance des dendro-microhabitats, principalement pour les *fentes* et les *sporophores de champignons lignivores*.
- Vingt ha sont nécessaires pour assurer toute la diversité des dendro-microhabitats en hêtraie-sapinière sub-naturelle.

Les patrons d'occurrence observés en forêt exploitée sont drastiquement différents de ceux observés en forêt inexploitée. Dans les peuplements exploités de Tronçais, on observe une réduction de la diversité des types présents et une modification des proportions en densité de chaque type. Dans les hêtraies-sapinières, le même type de résultat a été observé et nous avons mis en évidence que la réduction du nombre d'arbres porteurs de dendro-microhabitats résulte de l'exploitation des gros arbres pour le Sapin, mais, pour le Hêtre, plutôt de la sélection par le marteleur. De surcroît, les volumes et les patrons d'occurrence des différents types de bois morts observés en forêt exploitée sont profondément différents de ceux observés en forêt inexploitée.

Il y a plus d'arbres porteurs de dendro-microhabitats en lisière qu'à l'intérieur (+ 140 %) car (i) la densité des arbres est plus forte (+ 70 %), et (ii) la proportion d'arbres porteurs est plus forte (+ 40 %) car les arbres sont plus gros et la composition dendrologique est différente. Les *bois durs sans écorce*, les *fentes*, les *coulées de sève* et les *épiphytes* sont significativement plus nombreux en lisière qu'à l'intérieur du bois. La gestion des lisières n'a pas d'effet significatif sur l'abondance et la diversité des dendro-microhabitats mais la hauteur de la base du houppier est corrélée positivement à leur abondance, en raison d'un plus grand nombre de dendro-microhabitats portés par les arbres porteurs.

2 DISCUSSION ET PERSPECTIVES

Il est pratique de constater que l'association de l'essence et du diamètre explique 25 % de la variance de l'occurrence des dendro-microhabitats dans les hêtraies-sapinières. C'est un résultat encourageant pour la vulgarisation d'itinéraires sylvicoles efficaces pour la conservation de la biodiversité associée à ces dendro-microhabitats et simples à mettre en œuvre par les gestionnaires. Néanmoins, quels sont les déterminants environnementaux sous-jacents à la création et à la présence des dendro-microhabitats et qui expliqueraient, au moins en partie, les 75 % de variance non encore expliqués ? Nous n'apporterons pas d'éléments de réponse à cette question dans ce travail, mais nous proposerons en partie V un projet de plan d'échantillonnage pour tenter d'y parvenir.

La gestion réduit à la fois (i) la diversité des supports potentiels de dendro-microhabitats, par la réduction du nombre d'essences en favorisant les essences dont le bois a une valeur commerciale élevée et par la réduction de la densité de chandelles, et (ii) la quantité de ces supports, par réduction de la densité des arbres les plus gros et par le contrôle de la densité des arbres porteurs de dendro-microhabitats. Les techniques de sylviculture de masse, c'est-à-dire à l'échelle d'un peuplement de plusieurs hectares, sont en France les plus couramment employées, et concourent *de facto* à une homogénéisation du peuplement. Elles intègrent difficilement des propositions visant à hétérogénéiser la structure interne du peuplement (au sens le plus large, pas seulement la structure verticale de la végétation, comme dans les traitements irréguliers). Des techniques alternatives de sylviculture à l'échelle de l'arbre sont développées et largement vulgarisées depuis les années 1980, dans un but d'optimiser le rendement économique de la gestion en produisant une part maximale de bois d'œuvre de valeur commerciale élevée. Elles pourraient faciliter l'adoption de mesures conservatoires en faveur des supports de dendro-microhabitats et d'arbres pourvoyeurs de bois mort diversifié car elles focalisent sur une faible densité d'arbres « objectifs » pour produire le bois et pourraient de ce fait intégrer la présence en continu d'arbres strictement dévolus au maintien d'une hétérogénéité structurale. En forêt de montagne, cela semble d'autant plus aisé à mettre en œuvre que les contraintes topographiques et géographiques augmentent les coûts d'extraction des billes commerciales car les terrains sont accidentés et les forêts éloignées des centres de transformation. Une première approche de recommandations autour de la conservation des Coléoptères saproxyliques et des champignons avait d'ailleurs été économiquement validée en 2005 et 2008 par des exploitants forestiers, mais par simple enquête orale et sans suivi économique de chantiers réels (cf. en annexe les plaquettes Larrieu *et al.* 2005 et Larrieu & Corriol 2008). Quelle est réellement le coût du maintien d'une grande densité et diversité de dendro-microhabitats, par à la fois la mise en place d'îlots de conservation en libre évolution, la conservation perpétuelle dans la matrice exploitée d'arbres à rôle strictement écologique et l'adoption de pratiques en faveur de la moindre extraction d'éléments clés pour la biodiversité ? Cet aspect ne sera pas traité dans ce travail, mais mériterait d'être étudié avec l'aide d'économistes forestiers car les résultats faciliteraient la vulgarisation impartiale d'une gestion forestière intégrée. L'analyse devra être précise car si ce type de gestion semble *a priori* coûteux, il nous semble néanmoins qu'il peut être économique dans certaines circonstances, même à très court terme. Il restera difficile de chiffrer le bilan économico-écologique, en quantifiant également le service rendu au propriétaire par la conservation d'une plus grande biodiversité.

Les lisières de bois sont le plus souvent mal considérées par le gestionnaire forestier car elles produisent des arbres de faible qualité marchande et sont sources de conflit avec le voisinage. Elles sont pourtant clairement identifiées comme des interfaces utiles à la conservation de la biodiversité à la fois des écosystèmes agricoles adjacents (*e.g.* Roume *et al.* 2011a et 2011b) et des écosystèmes forestiers auxquels elles appartiennent (Salek *et al.* 2014). Des études complémentaires ciblées sur leur gestion et le rôle des essences secondaires dans l'offre de dendro-microhabitats permettraient de recommander des itinéraires de gestion pour mieux prendre en compte leur rôle écologique.

Les arbres sont des structures longévives et les cycles, même de production de bois, sont longs et dépassent dans la plupart des cas le temps d'observation d'une génération humaine. Néanmoins, les écosystèmes forestiers sont dynamiques. Pour l'instant, nous avons développé une étude synchronique conduisant à une vision plutôt statique de la disponibilité en dendro-microhabitats et bois mort, mais il serait intéressant de comprendre comment cette disponibilité évolue au cours de la vie du peuplement. Ainsi, la phase sylvigénétique influence-t-elle la disponibilité en bois mort et en dendro-microhabitats ? La section II apportera des éléments de réponse à cette question.

3 PUBLICATIONS

11. **Larrieu** L., Cabanettes A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree-microhabitats in subnatural montane beech–fir forests. *Canadian Journal of Forest Research* 42: 1433–1445

12. **Larrieu** L., Cabanettes A., Brin A., Bouget C., Deconchat M., 2014. Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry; *European journal of Forest Research* 133: 355–367. DOI 10.1007/s10342-013-0767-1

13. **Larrieu** L., Cabanettes A., Delarue A., 2012. Impact of sylviculture on dead wood and on the distribution and frequency of tree microhabitats in Montane Beech-Fir forests of the Pyrenees; *European journal of Forest Research* Vol. 131 (3):773-786

14. Lassauce A., **Larrieu** L., Paillet Y., Lieutier F., Bouget C., 2013. The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest. *Insect Conservation and Diversity*. 6, 3, 396–410

15. Ouin A., Cabanettes A., Deconchat M., Roume A., Vigan M., **Larrieu** L., (soumis). Comparisons of tree microhabitat abundance and diversity in edges and interior of small temperate woods. *Forest Ecology and Management*

Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests[1]

Laurent Larrieu and Alain Cabanettes

Abstract: Because quantitative data on the distribution of whole microhabitat sets are still lacking to indirectly assess taxonomic biodiversity in forests, we studied the distribution of seven key microhabitat types in 10 montane European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forests (Pyrénées, France) that had not been harvested for several decades. We examined 2105 live trees and 526 snags. Frequencies of cavities and dendrothelms were significantly higher on live beech than on fir. Sap runs were strictly found on live fir. Frequencies of cracks and saproxylic fungi were significantly higher on snags than on live trees. Seventy percent of live beeches but only 18% of firs carried one or more microhabitats. For both beech and fir and for each microhabitat type, we found, using the recursive partitioning method, one to three diameter thresholds that each corresponded to a significant change in the probability of microhabitat presence. When considering the whole microhabitat set, the most significant diameter thresholds were 42, 60, 73, and 89 cm for beech and 99 cm for fir. We suggest that forest managers conserve (*i*) mixed stands and (*ii*) beech with a diameter at breast height >90 cm and fir >100 cm. These rules should be adapted for each forest ecosystem.

Résumé : Étant donné qu'il n'y a pas encore de données quantitatives sur la distribution d'ensembles complets de microhabitats qui permettraient d'obtenir une évaluation indirecte de la biodiversité dans les forêts, nous avons étudié la distribution de sept types clés de microhabitats dans 10 forêts montagnardes (Pyrénées, France) de hêtre (*Fagus sylvatica* L.) et de sapin (*Abies alba* Mill.) qui n'ont pas été récoltées depuis plusieurs décennies. Nous avons examiné 2 105 arbres vivants et 526 chicots. La fréquence des cavités et des dendrotelmes était significativement plus élevée sur les tiges vivantes de hêtre que sur le sapin. Des écoulements de sève ont été observés uniquement sur les tiges vivantes de sapin. La fréquence des fentes et des champignons saproxyliques était significativement plus élevée sur les chicots que sur les arbres vivants. Il y avait au moins un microhabitat sur 70% des hêtres mais sur seulement 18% des sapins. Tant sur le hêtre que sur le sapin et pour chaque type de microhabitat, nous avons trouvé, à l'aide d'une méthode de partitionnement récursif, entre un et trois diamètres seuils. Chaque diamètre seuil correspondait à un changement significatif dans la probabilité de la présence d'un microhabitat. Lorsqu'on tient compte de l'ensemble complet des microhabitats, les diamètres seuils les plus importants sont 42, 60, 73 et 89 cm chez le hêtre et 99 cm chez le sapin. Nous suggérons que les gestionnaires forestiers conservent (*i*) des peuplements mixtes ainsi que (*ii*) les hêtres et les sapins dont le diamètre à hauteur de poitrine est respectivement plus grand que 90 et 100 cm. Ces règles devraient être adaptées pour chaque écosystème forestier.

[Traduit par la Rédaction]

Introduction

Using only a few species to assess taxonomic biodiversity in forest ecosystems is not satisfactory and it is rather preferable to use whole taxonomic groups (Lindenmayer and Franklin 2002). Further, direct bioindicator records are very expensive and require taxonomic specialists (Puumalainen et al. 2003). Most importantly, the relationships between indicator taxa and total biodiversity are not yet well established (Lindenmayer et al. 2000; McElhinny et al. 2005). Therefore, forest managers need alternative approaches to assess biodiversity in forests. Lindenmayer et al. (2000) suggested using structure-based variables as indirect biodiversity indicators. Indicators based on key structural factors have been shown to be a practical and efficient way to ensure that taxonomic biodiversity is taken into account in current forest management (Larsson 2001). Similarly, Tews et al. (2004) proposed using "crucial keystone structures", such as dead wood, for biodiversity management. Lindenmayer et al. (2006) pub-

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lished a checklist of strategies to guide forest biodiversity conservation that encompasses the maintenance of key elements of stand structural complexity.

Tree microhabitats (such as cavities or cracks) are key components of forest stands (Michel and Winter 2009) because they host a wide taxonomic biodiversity (Speight 1989). So, they are relevant and practical proxies to assess taxonomic biodiversity at the stand scale (Winter and Möller 2008). Several authors have demonstrated the important role of very large trees (Ranius and Jansson 2000; Grove 2002; Branquart et al. 2005; Bauhus et al. 2009), tree species (Gosselin and Larroussinie 2004), and snags (Jonsell and Weslien 2003) on taxonomic biodiversity. However, in most types of forest, few data are available regarding the distribution of tree microhabitats in natural stands and the links between tree species, diameter, status (live tree or snag), and microhabitat occurrence.

To improve our knowledge of the distribution of tree microhabitats in natural forests, and particularly to better understand the role of tree species and tree diameter on microhabitat occurrence, we observed tree microhabitats in montane European beech (*Fagus sylvatica* L.) – silver fir (*Abies alba* Mill.) forests that had not been logged for at least 60 years. Beech–fir forest is a common forest community, present in most of the European mountain ranges, and has a great economic and ecological importance. It is also a mixed forest where biocenoses partially differ between broadleaved trees and conifers (Nascimbene et al. 2009).

We chose a set of seven microhabitat types that seem to be very important for taxonomic diversity in forests because the associated taxonomic groups are numerous and varied or very specific: empty cavities, cavities with mould, sporophores of saproxylic fungi, dendrothelms (water-filled holes in the wood), sap runs, missing bark, and cracks. Empty cavities are used for protection against bad weather conditions or predators by more than 25% of vertebrate species in northeastern North American forests (DeGraaf and Shigo 1985). Moreover, in France, 41% of forest birds are cavity-dwelling species (Blondel 2005). Cavities with mould are inhabited by arthropods (Ranius 2002) and create favorable conditions for epiphyte species of conservation concern (Fritz and Heilmann-Clausen 2010). Sporophores of saproxylic fungi support a varied insect fauna (Dajoz 2007), especially when they are tough (polypores s.l.) or pulpy (e.g., oyster fungi). Some parasitic fungi also use saproxylic fungi as a resource (Lisiewska 1992). Dendrothelm-dwelling species are not numerous (Dajoz 2007) but very specialized (Kitching 1971). Sap runs host syrphid larvae (Speight et al. 2010) and are used by the adults of several Coleoptera species (Alexander 2002). Cracks are important microhabitats for spiders (Stanska et al. 2010), birds (Cramp 1980), flat bugs (Heiss and Pericart 2007), and bats (Pénicaud 2000). Cavities, cracks, and missing bark are indicators of natural forests (Michel and Winter 2009; Remm and Lõhmus 2011).

This paper aims at (*i*) evaluating the role in terms of supply of microhabitats of the tree species that compose beech–fir forests independently of their relative abundance and (*ii*) identifying critical diameter thresholds for both microhabitat abundance and diversity. Then, in the context of sustainable management practices, we suggest some practical recommendations and a management strategy to conserve microhabitats.

Materials and methods

Studied forests and sampling design

The 10 studied forests (Table 1) are situated in the central Pyrénées mountain range (Fig. 1) and have not been logged for more than 60–100 years. They are natural habitats of beech–fir forest (Bardat et al. 2004). However, stands host a very variable proportion of fir, which is directly linked to historic human intervention that favored beech at the expense of fir (Métailié 2001). For the analysis, we pooled all of the studied forests because local conditions of fertility were not markedly different and we did not sample forests growing in extreme conditions of infertility (e.g., site with PODZOSOL). Observations were carried out in 2008 and 2009 on a sample of 62 plots, 2105 live trees, and 526 snags (Table 1). Although the leaf canopy may hinder observations, all of the plots were set up in summer because these sites are covered by snow for a large part of the year. Because of the presence of leaves, we expected an underestimation of the number of microhabitats on beech and on the other broadleaved species. For the evergreen species such as fir or common yew (*Taxus baccata* L.), data taken in the vegetation period or in winter are more easily comparable.

Measurements and observation of microhabitats

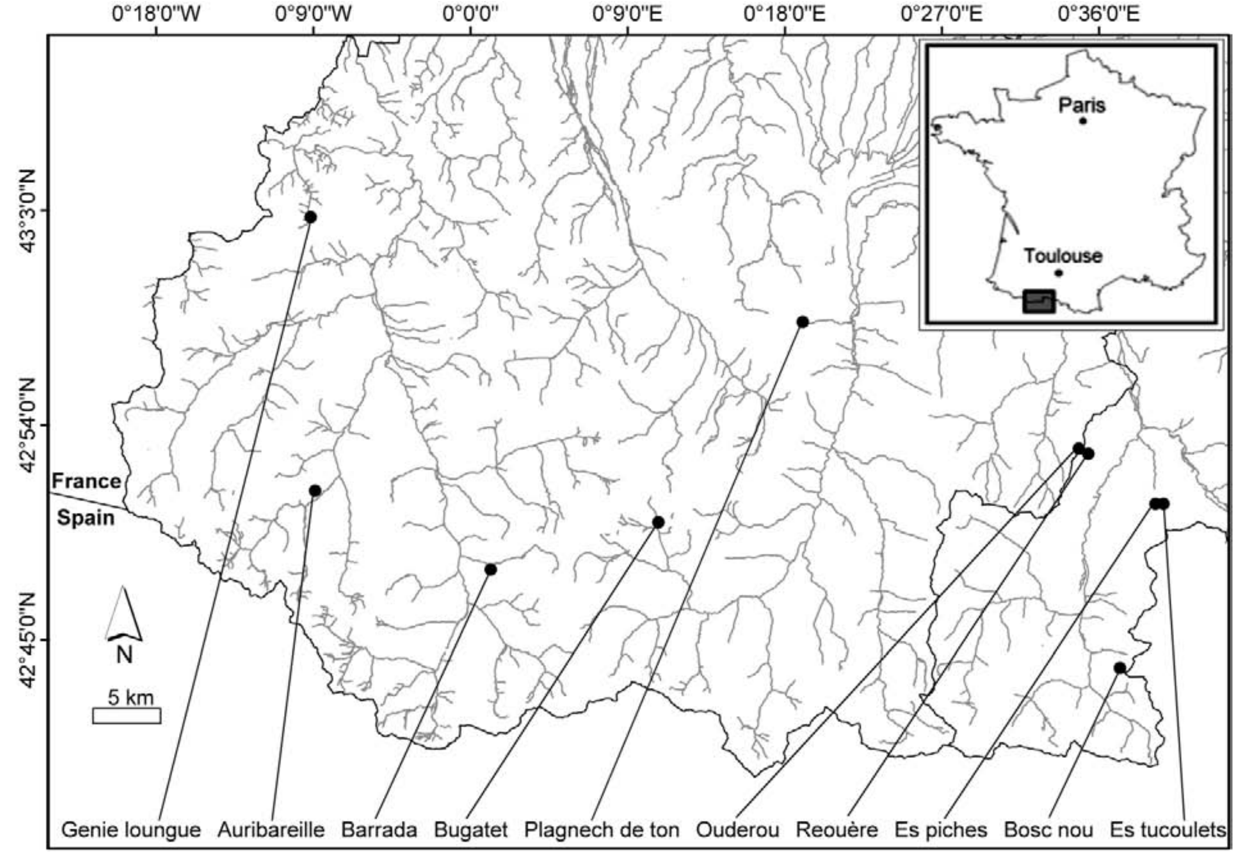
Plots were circular and of variable sizes set up using the No. 1 strip (return angle of 1/50) of a Bitterlich relascope (Pardé and Bouchon 1988). This device uses a constant angle. The measurement errors due to terrain slope are automatically corrected by the relascope, which is very practical in the mountains. The use of a relascope allows a high sampling rate of large trees that are richer in microhabitats (Winter and Möller 2008; Larrieu et al. 2011). Plot locations were positioned approximately on a map before the field phase in relation to accessibility. Then, the precise locations of plots were established in relation to topographical constraints (such as cliffs) and plot centres were always a minimum of 100 m apart. Trees were observed individually. We noted the status (live tree or snag), identified the tree to species level, and measured the diameter on the outside of the bark at breast height (dbh) to the nearest centimetre when the diameter exceeded 5 cm. We carefully examined the trunk from the ground to the top of the tree to note microhabitats hosted on the visible part of the trunk both beneath and within the tree crown. We recorded a set of seven microhabitats types as follows. (*i*) "Empty" cavities with an entrance above 3 cm in width. We did not use a device such as a camera mounted on a telescopic pole to ensure the cavity volume. Therefore, we pooled in this category all woodpecker breeding holes, holes made by woodpeckers when feeding and deep enough to host a vertebrate, deep cavities formed between roots, and also natural cavities low enough on the tree to enable verification that they were empty and that they were not at a stage where mould could develop. (*ii*) Cavities with mould. We pooled in this category the other natural cavities and cavities with mould with an entrance above 3 cm in width and also missing bark patches with an area above 100 cm^2 with wood in a decay stage of more than 3 (in reference to a scale with

Table 1. Main characteristics of the studied European beech (*Fagus sylvatica*) – silver fir (*Abies alba*) forests and sampling design.

								Diameter at breast height (cm)			
Forest	Vegetation level	Dominant tree species	History	Studied area per forest (ha)	No. of plots	No. of observed trees	No. of observed snags	Live beeches	Beech snags	Live firs	Fir snags
Plagnech de ton	Lower montane	Beech and fir	Not logged since 1900	23	10	332	93	15.9 62.9 127.3	11.1 53.4 95.5	8.0 44.4 124.1	22.3 70.4 109.8
Reouère	Lower montane	Beech	Old pasture woodland not logged for more than 110 years	43	8	295	40	11.1 67.0 152.8	8.0 53.1 162.3		
Auribareille	Lower montane	Fir	Never logged	12	2	61	14	15.9 50.9 78.0	63.7 63.7 63.7	22.3 70.6 130.5	19.1 64.0 89.1
Genie loungue	Lower montane	Beech	Not logged since 1900	16	5	122	14	21.6 54.4 114.6	11.8 25.6 33.1	47.4 47.4 47.4	
Bugatet	Upper montane/ subalpine	Fir	Not logged since 1908	18	5	185	36			7.0 49.2 111.4	22.9 68.0 140.1
Barrada	Upper montane	Fir	Only logged once (1953) by selective logging	13	5	221	63	11.1 20.3 25.5		11.1 58.6 171.9	19.1 61.2 125.7
Bosc nou	Upper montane/ subalpine	Beech and fir	Never logged	13	5	178	55	29.0 36.1 42.7		9.5 57.5 114.6	21.6 59.7 101.9
Es tucoulets	Upper montane	Beech and fir	Not logged since 1900	34	9	265	82	24.8 31.8 38.8	19.1 19.1 19.1	9.5 53.7 130.5	15.9 60.9 154.4
Es piches	Upper montane	Beech and fir	Not logged since 1900	17	5	153	20	15.9 56.2 95.5	31.8 35.0 38.2	11.1 56.8 135.3	12.7 62.5 124.1
Ouderou	Upper montane	Fir	Old pasture woodland not logged for more than 100 years	25	8	293	109	14.3 36.0 78.0	12.7 28.2 60.5	10.2 65.9 135.9	13.0 65.4 133.7

Note: For diameters at breast height, the three values are successively the minimum, mean, and maximum.

Fig. 1. The 10 studied forests are situated on the northern slopes of the Pyrénées mountain range (the southwest of France).



five steps: see Table S1[2] (describes in detail wood decay stages)). (*iii*) Sporophores of saproxylic fungi without taxonomic identification. We noted only tough fungi (polypores s.l.) or pulpy fungi (e.g., *Pleurotus ostreatus* (Jacq.) P. Kumm. 1871). (*iv*) Dendrothelms, when the entrance was more than 3 cm in width. In the dry period, observation of traces of water flow on the trunk allowed the diagnostic of inaccessible dendrothelms. (*v*) Sap runs with a minimal length of 10 cm. (*vi*) Missing bark (i.e., wood patches with bark loss) of at least 100 cm^2, with wood in a decay stage of less than 2. (*vii*) Cracks in the tree trunk with a width of 1–5 cm and situated over 1 m above the ground or bark in the process of peeling and that formed a shelter. Their importance for several species of bats (Meschede and Heller 2003) was the justification for pooling these two microhabitats and using these thresholds.

On each tree, we counted every microhabitat type as often as it appeared, except in the case of fungi, which were only noted as presence–absence.

Beech (658 live trees observed) and fir (1310 live trees observed) were the main tree species but we also observed 137 live trees of more than 10 secondary species (European mountain-ash (*Sorbus aucuparia* L.), European white birch (*Betula pendula* Roth), downy birch (*Betula pubescens* Ehrh.), European ash (*Fraxinus excelsior* L.), sweet cherry (*Prunus avium* (L.) L.), field maple (*Acer campestre* L.), Norway ample (*Acer platanoides* L.), common yew, largeleaf linden (*Tilia platyphyllos* Scop.), and *Salix* spp.). Secondary species were pooled in the analysis because of their low number. Stand maturity allowed us to explore a large diameter gradient: 6–172 cm for fir, 11–153 cm for beech, and 5–95 cm for other species.

Calculations and statistical procedures

The theoretical tree frequency per hectare was calculated by allocating the coefficient N, related to its diameter (D), to every tree observed in the relascope sampling (Pardé and Bouchon 1988):

$$ND = \pi 10^8[\arctan(1/50)/\pi D]^2$$

where “arctan” is the trigonometrical “arctangent” function.

All statistical calculations were done using R software (R development Core Team 2007).

Basic data were measured and analyzed at the level of the individual tree: tree species, tree diameter, type, and number of microhabitats. However, the effect of tree species was tested using the average data per plot and per species. The role of the tree species in the supply of microhabitats was evaluated independently of their relative abundance.

Comparisons of frequencies, per species, of the trees that bear microhabitats and of frequencies of microhabitat co-occurrences per species were carried out using the χ^2 test (Snedecor and Cochran 1971).

The hypothesis of independence between the three species categories (i.e., beech, fir, and the third that pooled all secon-

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[2] Supplementary data are available with this article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-077.

Table 2. Tree species (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others) effect on microhabitat frequency: results for the comparison tests on live trees and snags (significant results in bold).

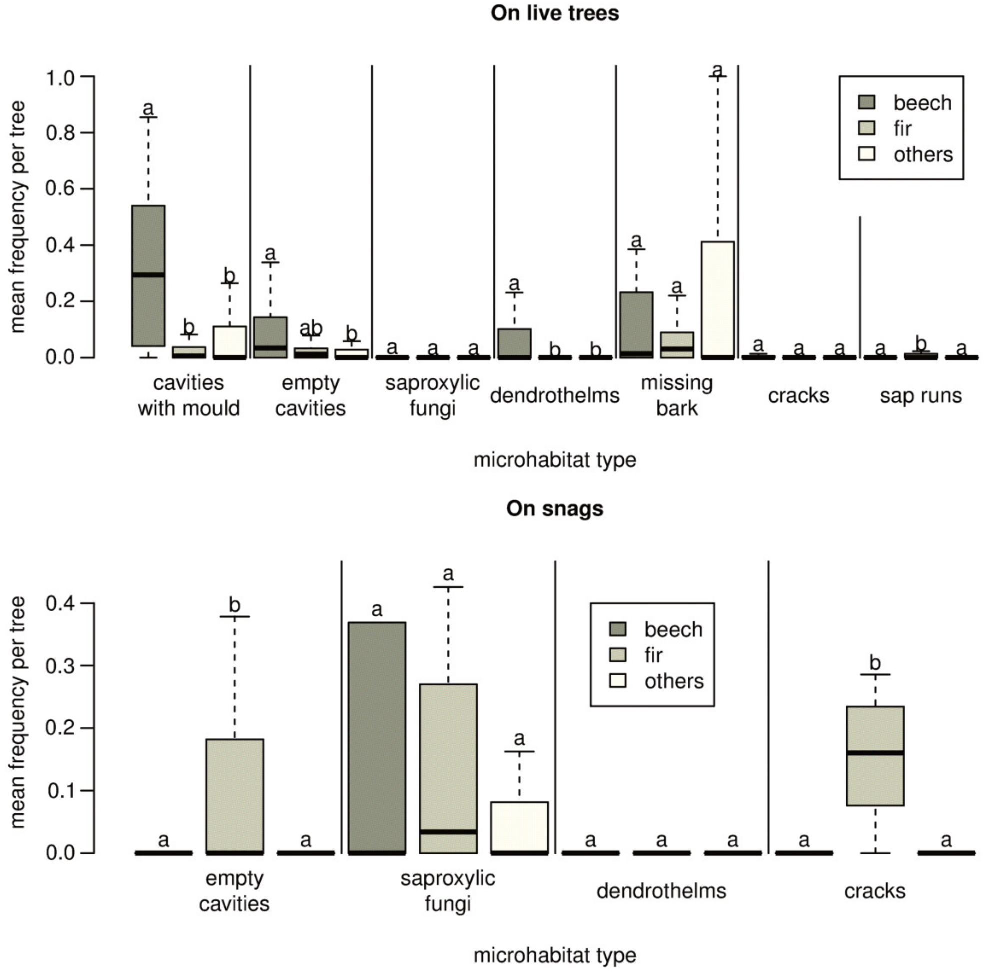
Microhabitat	Tree status	All-categories comparison (*p*)	Pairwise comparison	*p*
Cavities with mould	Live trees	**<0.001**	**Beech/others**	**<0.001**
			fir/others	0.841
			Fir/beech	**<0.001**
Empty cavities	Live trees	**0.005**	**Beech/others**	**0.005**
			Fir/others	0.503
			Fir/beech	0.161
Saproxylic fungi	Live trees	0.424	Beech/others	0.424
			Fir/others	0.779
			Fir/beech	0.871
Dendrothelms	Live trees	**<0.001**	**Beech/others**	**<0.001**
			Fir/others	0.978
			Fir/beech	**<0.001**
Missing bark	Live trees	0.988	Beech/others	0.976
			Fir/others	0.999
			Fir/beech	0.999
Cracks	Live trees	0.212	Beech/others	0.211
			Fir/others	0.688
			Fir/beech	0.733
Sap runs	Live trees	<0.001	Beech/others	0.711
			Fir/others	**0.002**
			Fir/beech	**<0.001**
Total	Live trees	**<0.001**	Beech/others	0.366
			Fir/others	**0.011**
			Fir/beech	**<0.001**
Empty cavities	Snags	**0.005**	Beech/others	0.512
			Fir/others	**0.001**
			Fir/beech	**0.005**
Saproxylic fungi	Snags	0.48	Beech/others	0.569
			Fir/others	0.483
			Fir/beech	0.902
Dendrothelms	Snags	0.21	Beech/others	0.153
			Fir/others	0.633
			Fir/beech	1.000
Cracks	Snags	**0.007**	Beech/others	0.42
			Fir/others	**0.007**
			Fir/beech	**0.04**
Total	Snags	**0.022**	Beech/others	0.593
			Fir/others	0.064
			Fir/beech	**0.022**

Note: We distinguished three categories of tree species: beech alone, fir alone, and other tree species pooled. Values are *p* values from a χ^2 test.

dary species) and the response variable (frequency of one or all microhabitats or frequency of microhabitat type) was assessed using multiple testing of resampled data (Hothorn et al. 2006). The response variable was analyzed as a rank variable. The *p* value obtained by this procedure was adjusted for multiple comparisons using a step-down max-T approach. In addition, for each response variable, a post hoc test (Tukey all-pair comparisons) was applied to assess the differences between each pair of categories. The corresponding *p* values were adjusted for all comparisons performed here. This analysis procedure is based on implementation of the above procedures in the add-on package "coin" (Hothorn and Hornik 2005).

The relation between microhabitat frequency and tree diameter was analyzed using tree-based regression and classification models. We tested the hypothesis that there is a threshold-based relation between the number of microhabitats and dbh because we found this kind of relation in a previous analysis of comparable data (Larrieu et al. 2011). These threshold values were calculated by recursive partitioning (Hothorn and Zeileis 2008). This approach allows simultaneous identification of a threshold and assessment of its significance by means of a statistical test procedure. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics. Their validity is judged by multiple test procedures. Once the data set is divided into

Fig. 2. Microhabitat frequency distributions split by species for live trees (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others) (2.1) and snags (2.2) represented as boxplots. Each bar corresponds to the two interquartiles Q1 and Q3 of the distribution. The horizontal central line is the median. The length of the whiskers (broken lines) is 1.5 × (Q3 – Q1). Outlying points are not represented. Different letters indicate significant differences between species. The deviations in the boxplots are based on average plot data.



two subsets by the threshold with the highest explanatory power, each subset is evaluated for additional thresholds. This method provides a decision tree with *p* values for one or more critical thresholds. Based on 10 000 bootstrap samples, a confidence interval (at 80%) was calculated for all thresholds. The calculations were performed on "presence–absence" data using the add-on package "party" (Hothorn and Hornik 2006).

Furthermore, to make an explicit link with forest management practices, we also discuss our results by using "management diameter thresholds" that separate diameter categories used by all managers in French forestry to describe and manage stands. These management diameter thresholds are 20 cm ≤ small tree ≤ 25 cm, medium tree ≤50 cm, large tree ≤70 cm, and very large tree >70 cm (Bastien and Gauberville 2011).

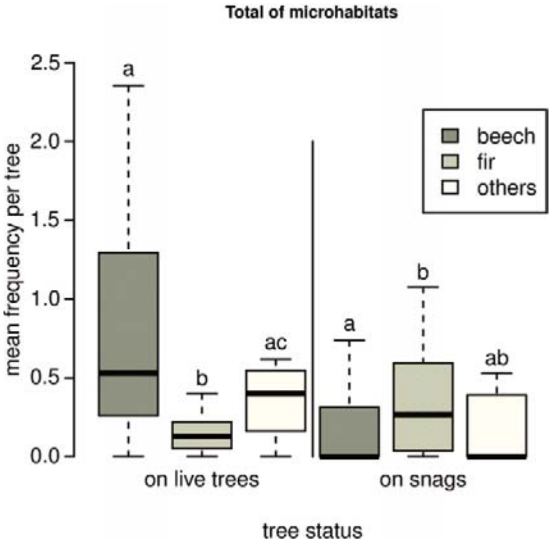
Results

Tree species effect (live trees and snags)

Tree species affects the occurrence of different microhabitat types and the total number of microhabitats per tree, independently of the relative densities of the different tree species

The species of the live trees significantly affected the frequency of empty cavities, cavities with mould, dendrothelms, and sap runs (Table 2; Fig. 2). The first three microhabitats were mostly associated with beech, whereas sap runs were exclusively associated with fir. Secondary species played an intermediary role. The frequencies of saproxylic fungi, missing bark, and cracks were not related to tree species. On snags, in contrast, fir carried a higher quantity of empty cav-

Fig. 3. Total microhabitat distributions split by tree status and species (European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and others). Each bar corresponds to the two interquartiles Q1 and Q3 of the distribution. The horizontal central line is the median. The length of the whiskers (broken lines) is 1.5 × (Q3 – Q1). Outlying points are not represented. Letters indicate if differences between species are statistically significant or not.



ities and cracks than beech. The frequencies of dendrothelms and saproxylic fungi were not influenced by snag tree species. Fir carried all microhabitat types (seven) whereas beech carried only a maximum of six.

In total, beech carried significantly more microhabitats than fir on live trees (Table 2; Fig. 2). Secondary species did not differ from beech and also carried significantly more microhabitats than fir. For snags, only fir differed from beech.

Beech and secondary species carried more than five times more microhabitats on live trees than on snags whereas fir carried twice as many microhabitats on snags than on live trees (Fig. 3).

Tree species affects the density of microhabitat-bearing live trees

Seventy percent of the beech trees carried one or more microhabitats whereas we observed microhabitats on only 18% of firs. Others species carried as many microhabitats as beech (75%).

Live tree species affects the conditional probability of occurrence of microhabitat types

The following microhabitat associations on a given tree were significantly more probable than random for both beech and fir (Table 3): (*i*) cavities with mould and missing bark and (*ii*) empty cavities, dendrothelms, and cracks. Concerning beech only, the following associations were found: (*i*) cavities with mould, empty cavities. and saproxylic fungi and (*ii*) saproxylic fungi and dendrothelms. On fir only, the following associations were significant: (*i*) empty cavities and saproxylic fungi, (*ii*) dendrothelms and missing bark, (*iii*) missing bark and cracks, and (*iv*) sap runs on the one hand and dendrothelms, missing bark, and cracks on the other hand.

Tree diameter effects on microhabitat richness

Tree diameter affects the presence of each microhabitat type

We found one to three significant diameter thresholds for each microhabitat type where the probability of its presence varied significantly (Table 4). Thresholds were less numerous in the fir data than in the beech data. Multiple thresholds correspond to microhabitats likely to occur more than once per tree (this was only the case for cavities, dendrothelms. and missing bark).

Tree diameter affects the total number of microhabitats and the number of microhabitat types

For beech (Fig. 4 and Fig. 5), the four first diameter thresholds, which correspond to a gradual increase in the median of total numbers of microhabitats from zero to four, were significant and spaced at regular intervals (of roughly 15 cm). There was no significant threshold beyond four microhabitats per tree (between four and 16). For fir (Fig. 4 and Fig. 5), only the higher diameter threshold (99 cm) corresponded to a significant increase of the median number of microhabitats from zero to one. Beyond one microhabitat (between one and seven), we did not detect any significant threshold. For beech and fir, the first microhabitat occurred, respectively, at 41 and 60 cm dbh (median values).

Concerning the total number of microhabitat types per tree (Table 4): (*i*) for beech, only the two first thresholds (42 and 60 cm, similar to the thresholds for the total number of microhabitats per tree) significantly increased the median of the number of microhabitat types per tree from zero to one and then from one to two and (*ii*) for fir, the same threshold as for the total number of microhabitats per tree (99 cm) significantly increased the median from zero to one.

The proportion of microhabitat-bearing trees increased markedly with increasing diameter as specified for the management categories (Table 5). However, the shape of this relationship differed between tree species.

As dbh increased, the first microhabitat types that occurred on beech were cavities with mould and missing bark on small trees, then empty cavities, dendrothelms, and saproxylic fungi on medium trees, and finally cracks on large trees and very large trees. For fir, cavities and missing bark occurred on small trees, sap runs and cracks appeared on medium trees, and finally dendrothelms and saproxylic fungi on large trees and very large trees.

On average, when all the diameter categories were represented, a beech–fir stand carried 71 microhabitats/ha and a total of the seven microhabitat types. Large and very large trees carried 48% of the microhabitats.

Discussion

Only a few papers describe the role of tree species and tree diameter for distribution patterns of a set of microhabitats. Indeed, in most cases, authors focused on only one microhabitat type. The most documented microhabitats are cavities (e.g., McClelland and Frissel 1975; Cline et al. 1980; Mannan et al. 1980; Fan et al. 2003*b*, 2005; Drapeau et al. 2005; Remm and Lõhmus 2011) and dendrothelms (Kitching 1971; Vaillant 1978; Schmidl et al. 2008). Due to this lack of available results, our work provides new insights on microhabitat key factors.

Table 3. Independence tests between microhabitat frequencies (microhabitat type co-occurrences).

	Cavities with mould	Empty cavities	Saproxylic fungi	Dendrothelms	Missing bark	Cracks	Sap runs
Cavities with mould	—	**<0.000**	**0.010**	0.09	**0.007**	0.56	
Empty cavities	0.44	—	0.75	**0.01**	0.2	**0.011**	
Saproxylic fungi	0.156	**0.0015**	—	**0.017**	0.58	0.96	
Dendrothelms	1	**0.007**	0.05	—	0.98	0.35	
Missing bark	**<0.000**	0.71	0.61	**0.034**	—	0.75	
Cracks	0.147	**0.0005**	1	1	**<0.000**	—	
Sap runs	0.23	0.71	1	**0.011**	**0.0001**	**0.002**	—

Note: Values are p values from a χ^2 test for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Values above the diagonal concern beech and those below the diagonal concern fir. Results in bold indicate significant “positive” dependence between the two microhabitat types.

Table 4. Diameter thresholds and confidence intervals per tree species (European beech (*Fagus sylvatica*) and silver fir (*Abies alba*)), on live trees, for the presence of each microhabitat and their total or type frequencies.

	Beech		Fir	
Microhabitat	Threshold	Confidence interval	Threshold	Confidence interval
Cavities with mould	41	33–51	65	47–81
	63	**53–78**	**87**	**81–113**
	79	75–88		
Empty cavities	41	40–49	57	54–76
	65	**48–88**	**94**	**64–99**
	126	86–126		
Saproxylic fungi	**100**	**100–121**	**61**	**61–94**
Dendrothelms	43	42–73	**99**	**81–103**
	86	**60–93**		
Missing bark	**110**	**72–110**	47	31–75
			98	**60–99**
Cracks	**72**	**72–81**	**100**	**86–102**
Sap runs			**76**	**74–102**
Total microhabitat frequency	42	41–60	*47*	*47–57*
	60	*44–60*	81	67–81
	73	**60–79**	**99**	**81–99**
	89	*80–107*		
Microhabitat type frequency	42	40–43	50	47–57
	60	**59–67**	**81**	**80–99**
	86	64–116	99	94–103

Note: The division level of the dichotomous branching is indicated as follows: bold, first level division in the set; regular, second level division of the two subsets; italic, third level division. All thresholds were statistically significant at $p < 0.05$.

Role of the tree species on microhabitat distribution

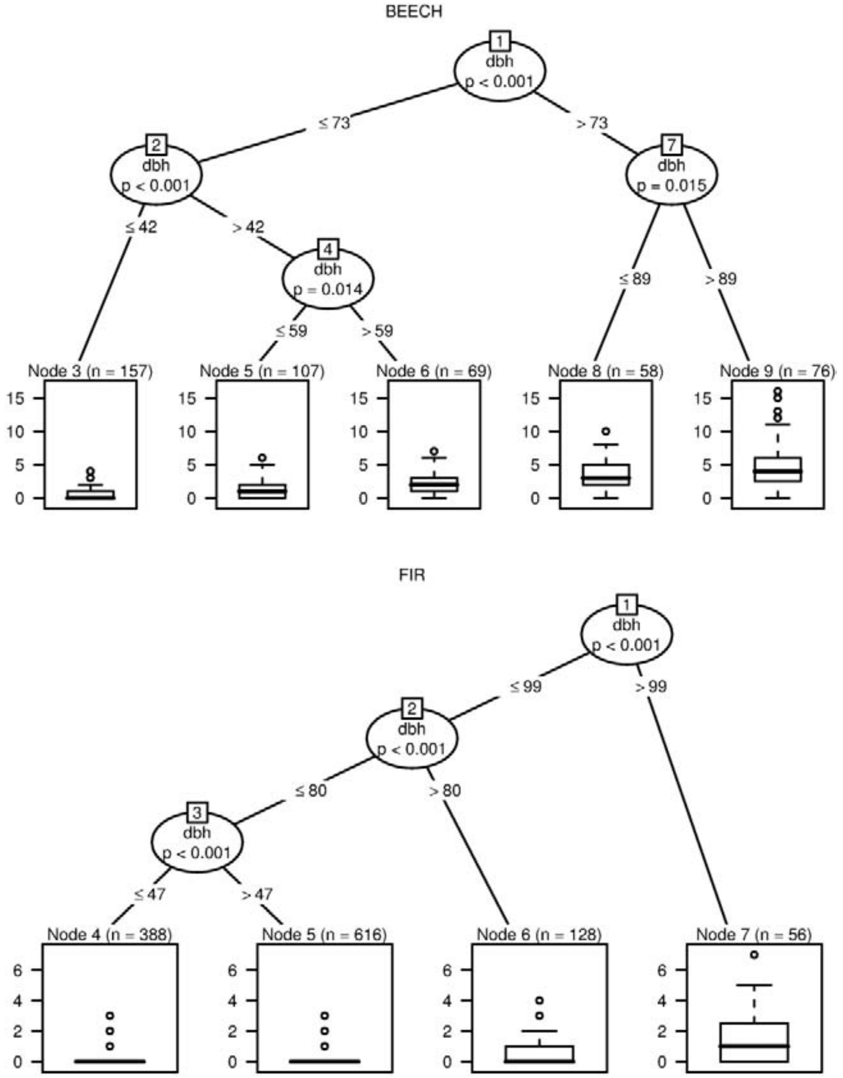
Live beech and secondary species trees carried microhabitats more often than live fir and certain microhabitat types were associated with beech or fir, sometimes exclusively

Tree species influences the number of different microhabitat types per tree as well as the occurrence of each microhabitat, and beech carries microhabitats more often than fir (Vuidot et al. 2011). In keeping with this, we showed that, at a given diameter, the proportion of microhabitat-bearing trees was mostly higher in beech and the other broadleaves species than in fir. However, we found that fir carried more microhabitat types than beech.

Beyond these general trends, each microhabitat shows particular variations.

The probability that a tree carries a cavity varies with tree species (Fan et al. 2003*b*). Remm and Lõhmus (2011) showed that cavity density is higher in deciduous forests than in mixed forests. McClelland and Frissel (1975), Cline et al. (1980), Mannan et al. (1980), as well as Drapeau et al. (2005) pointed out that cavities are rare in live conifers. However, Bull et al. (1997) revealed the important role of grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), western redcedar (*Thuja plicata* Donn ex D. Don), and western larch (*Larix occidentalis* Nutt.) in the supply of cavities for wildlife in forests dominated by conifers of the Columbia River basin (United States). On live trees, we found that cavities were mostly linked to beech. Trunk cavities result from woodpecker excavations or fungi colonization. Empty cavities are sometimes shaped by tree roots, more frequently when the slope is steep. Woodpeckers prefer broadleaved species

Fig. 4. Recursive partitioning tree for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) diameter at breast height (dbh) (cm) from total microhabitat frequency data. The *p* values indicate the level of statistical significance of each node and *n* indicates the numbers of trees per group. Only live trees. The difference between the two first box plots is linked to the number of outlying points that are merged.



to construct their nest cavities because of resin runs in conifers (Cramp 1980). In deciduous riverine forests of Estonia, cavity occurrence is determined by tree species, with a strong preference for European aspen (*Populus tremula* L.) for woodpecker-excavated cavities and black alder (*Alnus glutinosa* (L.) Gaertn.) for cavities created by fungi (Remm et al. 2006).

We found that dendrothelms were mainly linked to beech and that fir rarely carries dendrothelms, in agreement with Vaillant (1978). Silver fir very exceptionally provides favorable conditions to create dendrothelms, probably because of a centripetal deterioration (the external layers rot quite quickly and fall off, while the heart resists much longer). Vaillant (1978) indicated in addition that beech and linden (*Tilia* spp.) carry dendrothelms more often than European white birch. Kitching (1971) indicated that dendrothelms occur most abundantly in European beech, but also occur in European ash, sycamore, birch, linden, and silver fir in the British Isles. Dendrothelms have been observed in other tree species: yellow poplar (*Liriodendron tulipifera* L.), horse chestnut (*Aesculus hippocastanum* L.), European chestnut (*Castanea sativa* Mill.), European hornbeam (*Carpinus betulus* L.), durmast oak (*Quercus petraea* (Matt.) Liebl.), elms (*Ulmus* spp.), London plane (*Platanus* ×*hybrida* Brot.), northern red oak (*Quercus rubra* L.), and black alder (Vaillant 1978; Schmidl et al. 2008).

Although they are indicated on many genera present in montane beech–fir forests such as *Acer*, *Betula*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Tilia*, *Ulmus*, and *Salix* (Speight et al. 2010), sap runs were strictly linked to fir trees in our studied forests. We personally observed sap runs on beech in the Vosges Mountains (the northeast of France), but very rarely.

In spite of its thin bark, beech did not bear more missing bark than the other tree species, contrary to what we observed in managed beech–fir stands (Larrieu et al. 2011). In subnatural stands, missing bark forms mainly as fall scars of dying trees or stones on steep slopes. Missing bark that we observed on common yew mainly resulted from elk (*Cervus elaphus* Linnaeus, 1758) bark peeling occurring in winters

Fig. 5. Distribution for European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) of the diameter at breast height (dbh) per number of microhabitats. The vertical lines correspond to the dbh thresholds that are statistically significant and correspond to an increase of a minimum of one unit in the median value for microhabitat number.

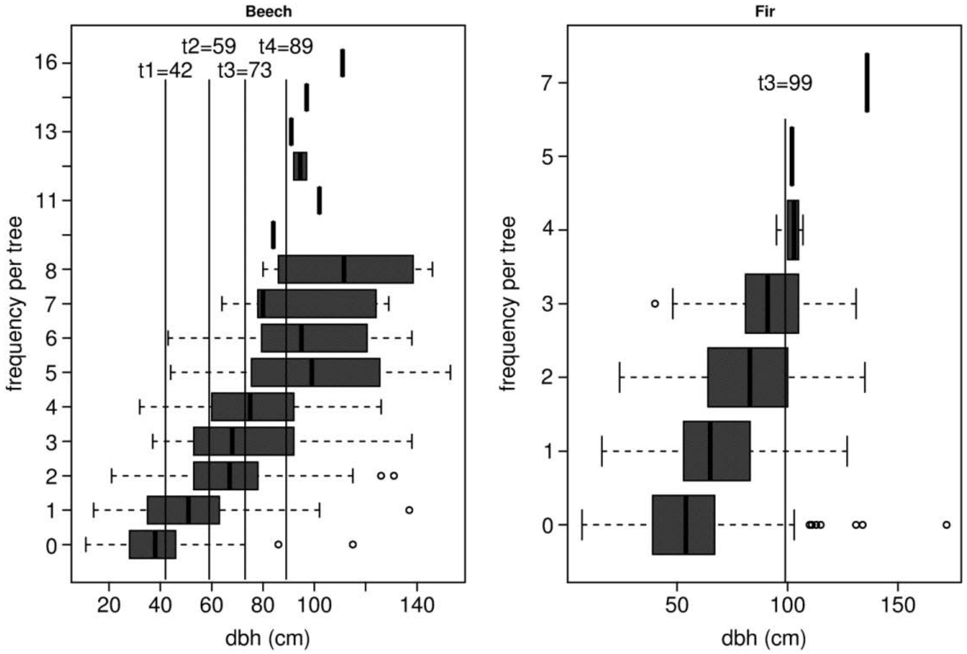


Table 5. Proportion of microhabitat-bearing trees (European beech (*Fagus sylvatica*) and silver fir (*Abies alba*)) per management diameter category.

	% of microhabitat-bearing trees	
Management diameter category	Beech	Fir
Small trees (20 ≤ dbh < 25 cm)	35	6
Medium trees (25 ≤ dbh < 50 cm)	43	9
Large trees (50 ≤ dbh < 70 cm)	78	21
Very large trees		
dbh ≥ 70 cm	92	32
dbh ≥ 89 cm	99	
dbh ≥ 99 cm		70

Note: dbh, diameter at breast height.

with exceptionally great snowfalls (personal observation), in spite of the strong toxicity of the yew bark for animals (Cornevin 1887). We did not observe any significant association between missing bark and saproxylic fungi, although these bark injuries facilitate parasitic fungi colonization (Girompaire and Ballon 1992). This is all the more surprising for beech because its wood has a low resistance to fungi attacks (Keller 1986).

The association between empty cavities and saproxylic fungi was not significant in our beech data, probably because the main woodpecker species living in the study forests, black woodpecker (*Dryocopus martius* Linnaeus, 1758), dig holes in trees colonized by fungi but that are apparently healthy (Zahner et al. 2012), contrary to the other woodpecker species that dig their cavity nest in wood showing clear signs of decay (Cramp 1980).

The secondary species were rich in microhabitats but they did not play an important role because of their low abundance in the stands, except for certain taxa that are strictly associated with a given tree species.

Beech and fir are complementary in their supply of microhabitats: beech provides quantity and fir may provide more diversity. Furthermore, the communities associated with a given microhabitat differ depending on whether the tree is a conifer or a broadleaved tree (Cramp 1980; Meschede and Heller 2003; Dajoz 2007; Speight et al. 2010).

Snags and live trees were complementary in the supply of microhabitats (Fig. 2)

Vuidot et al. (2011) showed the important role that snags play in the supply of tree microhabitats by finding that snags carry almost twice as many microhabitats as live trees. However, Fan et al. (2003*b*) showed, on the contrary, that cavity abundance in the old-growth hardwood forests of the east-central United States is about twice the percentage for live trees than for snags. In fact, even though snags concentrate certain microhabitats, particularly for fir in our data, their relatively low density could explain their low contribution in most stands.

In our data, cracks were linked to snags rather than to live trees. The cracks that we observed on fir snags were mostly in the form of bark in the process of peeling. One or 2 years after the death of a fir, bark fragments and peels off slightly. Before falling on the ground, this space under the bark lasts several years, offering shelter for medium-sized animals such as bats. Beech bark is very adhesive and peels off several years after the death of the tree, only in small fragments offering very little shelters to crack-dwelling mammals. However, this shelter can be used by other taxa, such as arboreal spiders (Chai and Liu 1998), flat bugs (Heiss and Pericart 2007), or beetles (Alexander 2002).

We also observed that snags carried sporophores of saproxylic fungi much more often than live trees. That said, a high hygrometry in dead wood is necessary for saprophyte fungi to develop carpophores, while lignicolous saprophyte fungi parasitizing weak trees are less dependent on atmospheric conditions.

Role of tree diameter in microhabitat distribution

Winter and Möller (2008) found a strong link between the number of microhabitats and the diameter of the host tree. Vuidot et al. (2011) revealed that diameter is the main factor influencing the number and probability of occurrence of cavities, cracks, and missing bark. In Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) stands, the abundance of many bark microhabitats increased with tree diameter and several bark microhabitats were not observed in the smaller diameter classes (Michel et al. 2011). In a review, Fan et al. (2003*a*) concluded that cavity occurrence is strongly related to tree diameter. So, large trees are more favorable than smaller trees to cavity creation (DeGraaf and Shigo 1985). Dufour (2003) also showed a positive correlation between tree diameter and cavity occurrence. From Kitching (1971), dendrothelm density increases in beech trees with diameter above 50 cm.

Our results showed that the number of microhabitats per tree, and also the number of microhabitat types per tree, markedly increased with tree diameter. We found statistically significant diameter thresholds that could be used by forest managers. Most of these thresholds are situated above dbh = 50 cm (73% for beech and 90% for fir), which is used by forest managers, in most of the managed stands in the Pyrénées Mountains, as the diameter at which it is economically optimal to cut trees (ONF 2006). The harvest of the trees with dbh $\geq$ 50 cm significantly reduces the number of microhabitats per hectare by 48% and leads to the total elimination of one microhabitat out of six for beech and two microhabitats out of seven for fir.

Practical recommendations to improve sustainable forestry

Beech and fir play complementary roles in the supply of microhabitat diversity. Secondary species (*Tilia* spp., *Acer* spp., *Betula* spp., etc.) are often scarce but often bear microhabitats. Furthermore, the broadleaved–conifer mixture (*i*) is the natural stand composition in most montane forests, (*ii*) facilitates management of a complex vertical structure that is favorable to several taxa (e.g., birds, Orthoptera), and (*iii*) is a means to stabilize income for the small forest estates because the markets fluctuate and are sometimes favorable to broadleaved trees and sometimes favorable to conifers. In theory, we could also manage monospecific stands within a single landscape to achieve a high level of taxonomic biodiversity at the landscape scale. However, this approach is likely to provoke problems for species that are strictly associated with either broadleaved trees or conifers and that have a low dispersal capacity, as they may be unable to disperse across such a fragmented landscape. Thus, we suggest conserving mixed stands.

Very large trees play a significant role because they host all microhabitat types and the proportion of microhabitat-bearing trees is very high. We consider that current management diameter thresholds at 50 cm (lower limit of the large tree category) and 70 cm (lower limit of the very large tree category) are relevant with respect to microhabitats. Indeed, by taking into account the confidence intervals (CI) at 80%, we consider them equivalent to the significant thresholds that we found: respectively, 42 cm (CI 41–60 cm), 60 cm (CI 44–60 cm), and 73 cm (CI 60–79 cm) for beech and 47 cm (CI 47–57 cm) and 81 cm (CI 67–81 cm) for fir. We observed other diameter thresholds at 89 cm for beech (CI 80–107 cm) and 99 cm for fir (CI 81–99 cm) that are significant with respect to the number of microhabitats per tree and also to the number of microhabitat types per tree. Therefore, for forest management, we suggest creating a supplementary diameter category ("largest trees") with a lower limit at dbh = 90 cm for beech and at dbh = 100 cm for fir to better take into account the ecological role of these trees.

To promote the idea of "largest trees" category and thus to conserve microhabitat-bearing trees, we recommend developing silvicultural practices that allow, at the stand scale, a proportion of the trees to finish their complete natural cycle. The modeling of the microhabitat distribution at the stand level and the analysis of the abundant bibliography focusing on green retention trees will help us to work towards a consensual management strategy for mixed montane forests by fixing a proportion of trees to be conserved according to the stand characteristics.

The largest living trees seem to play a key role in all forest ecosystems. For example, they are key features from tropical (Grove 2002) to boreal (Martikainen et al. 2000) domains for the invertebrate assemblages. According to our results, conserving large trees and the diversity of tree species should help to manage taxonomic biodiversity in all forest ecosystems at the condition of defining the diameter thresholds and the role of each tree species in each ecosystem type.

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References

Alexander, K. 2002. The invertebrates of living and decaying timber in Britain and Ireland — a provisional annotated checklist. English Nature Research Reports No. 467. Department for Environment, Food and Rural Affairs and English Nature, Cranfield University at Silsoe, Bedfordshire, U.K.

Bardat, J., Bioret, F., Botineau, M., Boullet, V., Delpech, R., Géhu, J. M., Haury, J., Lacoste, A., Rameau, J.C., Royer, J.M., Roux, G., and Touffet, J. 2004. Prodrome des végétations de France. MNHN, Paris, France.

Bastien, Y., and Gauberville, C. (*Coordinators*). 2011. Vocabulaire forestier. Ecologie, gestion et conservation des espaces boisés. IDF, Paris, France.

Bauhus, J., Puettmann, K., and Messier, C. 2009. Silviculture for old-growth attributes. For. Ecol. Manage. **258**(4): 525–537. doi:10.1016/j.foreco.2009.01.053.

Blondel, J. 2005. Bois mort et à cavités: leur rôle pour l'avifaune cavicole. *In* Bois morts et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 137–142.

Branquart, E., Vandekerkhove, K., Bourland, N., and Lecomte, H. 2005. Les arbres sur-âgés et le bois mort dans les forêts de Flandre, de Wallonie et du Grand-Duché de Luxembourg. *In* Bois mort et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 19–29.

Bull, E.L., Parks, C.G., and Torgesen, T.R. 1997. Trees and logs important to wildlife in the interior Columbia River basin. U.S. For. Serv. Gen. Tech. Rep. PNW-391.

Chai, L.Y., and Liu, C.Y. 1998. Preliminary investigation report on the overwintering arthropod species in the cracks on stems of apple trees in the north of Henan. Acta Agric. Univ. Henanensis, **32**(1): 52–54.

Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. **44**(4): 773–786. doi:10.2307/3808305.

Cornevin, C. 1887. Des plantes vénéneuses et des empoisonnements qu'elles déterminent. Institut National Agronomique, Paris, France.

Cramp, S. (*Coordinator*). 1980. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Oxford University Press, New York.

Dajoz, R. 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier. 2nd ed. Tec et Doc Lavoisier, Paris, France.

DeGraaf, R.M., and Shigo, A.L. 1985. Managing cavity trees for wildlife in the Northeast. U.S. Gen. Tech. Rep. NE-101.

Drapeau, P., Nappi, A., St Germain, M., and Angers, V.A. 2005. Les régimes naturels de perturbations, l'aménagement forestier et le bois mort dans la forêt boréale québécoise. *In* Bois mort et à cavités: une clé pour des forêts vivantes. *Edited by* Vallauri et al. Tec et Doc Lavoisier, Paris, France. pp. 46–54.

Dufour, D. 2003. Étude de l'influence du bois mort sur l'avifaune cavernicole en forêt feuillue. Mémoire de fin d'études. FUSAGx, Gembloux.

Fan, Z.F., Larsen, D.R., Shifley, S.R., and Thompson, F.R. 2003*a*. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. For. Ecol. Manage. **179**(1–3): 231–242. doi:10.1016/S0378-1127(02)00522-4.

Fan, Z.F., Shifley, S.R., Spetich, M.A., Thompson, F.R., III, and Larsen, D.R. 2003*b*. Distribution of cavity trees in midwestern old-growth and second-growth forests. Can. J. For. Res. **33**(8): 1481–1494. doi:10.1139/x03-068.

Fan, Z.F., Shifley, S.R., Spetich, M.A., Thompson, F.R., and Larsen, D.R. 2005. Abundance and size distribution of cavity trees in second-growth and old-growth central hardwood forests. North. J. Appl. For. **22**(3): 162–169.

Fritz, O., and Heilmann-Clausen, J. 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Biol. Conserv. **143**(4): 1008–1016. doi:10.1016/j.biocon.2010.01.016.

Girompaire, L., and Ballon, P. 1992. Conséquences de l'écorçage du Cerf élaphe dans le massif des Vosges alsaciennes [Results of barking by red deer in the Alsacian Vosges]. Rev. For. Fr. **44**(6): 501–511. doi:10.4267/2042/26354.

Gosselin, M., and Larroussinie, O. 2004. Biodiversité et gestion forestière: connaître pour préserver. Synthèse bibliographique. Cemagref, Nogent sur Vernisson, France.

Grove, S.J. 2002. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol. Indic. **1**(3): 171–188. doi:10.1016/S1470-160X(01)00016-4.

Heiss, E., and Pericart, J. 2007. Hemiptères Aradidae Piesmatidae et Dipsocoromorphes euro-méditerranéens. Fédération Française des Sociétés de Sciences Naturelles, Paris, France.

Hothorn, T., and Hornik, K. 2005. The coin package, conditional inference procedure in a permutation tes-framework, 0.4-1. Available from http://CRAN.R-project.org.

Hothorn, T., and Hornik, K.Z.A. 2006. Party: a laboratory for recursive part(*y*)itioning. Available from http://CRAN.R-project.org.

Hothorn, T., and Zeileis, A. 2008. Generalizes maximally selected statistics. Biometrics, **64**(4): 1263–1269. doi:10.1111/j.1541-0420.2008.00995.x. PMID:18325074.

Hothorn, T., Hornik, K., Van de Wiel, M.A., and Zeileis, A. 2006. A Legosystem for conditional inference. Am. Stat. **60**(3): 257–263. doi:10.1198/000313006X118430.

Jonsell, M., and Weslien, J. 2003. Felled or standing retained wood — it makes a difference for saproxylic beetles. For. Ecol. Manage. **175**(1–3): 425–435. doi:10.1016/S0378-1127(02)00143-3.

Keller, R. 1986. Identification et classement des bois français. ENGREF, Nancy, France.

Kitching, R.L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. J. Anim. Ecol. **40**(2): 281–302. doi:10.2307/3247.

Larrieu, L., Cabanettes, A., and Delarue, A. 2011. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech–fir forests of the Pyrenees. Eur. J. For. Res. **131**(3): 773–786. doi:10.1007/s10342-011-0551-z.

Larsson, T.B. (*Compiler*). 2001. Biodiversity evaluation tools for European forests. Ecol. Bull. **50**: 75–81.

Lindenmayer, B., and Franklin, J.F. 2002. Conserving forest biodiversity; a comprehensive multiscaled approach. Island Press, Washington, D.C.

Lindenmayer, D.B., Margules, C.R., and Botkin, D.B. 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. **14**(4): 941–950. doi:10.1046/j.1523-1739.2000.98533.x.

Lindenmayer, D.B., Franklin, J.F., and Fischer, J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. **131**(3): 433–445. doi:10.1016/j.biocon.2006.02.019.

Lisiewska, M. 1992. Macrofungi on special substrates. *In* Fungi in vegetation science. *Edited by* W. Winterhoff. Kluwer, the Netherlands. pp. 151–182.

Mannan, R.W., Meslow, E.C., and Wight, H.M. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. **44**(4): 787–797. doi:10.2307/3808306.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., and Rauh, J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. **94**(2): 199–209. doi:10.1016/S0006-3207(99)00175-5.

McClelland, B.R., and Frissell, S.S. 1975. Identifying forest snags useful for hole-nesting birds. J. For. **73**(7): 414–417.

McElhinny, C., Gibbons, P., Brack, C., and Bauhus, J. 2005. Forest and woodland stand structural complexity: its definition and measurement. For. Ecol. Manage. **218**(1–3): 1–24. doi:10.1016/j.foreco.2005.08.034.

Meschede, A., and Heller, K.G. 2003. Écologie et protection des chauves-souris en milieu forestier. Le Rhinolophe, **16**.

Métailié, J.-P. 2001. Un patrimoine historico-environnemental: les forêts pastorales dans les Pyrénées. *In* Proceedings of "126 ème congrès des sociétés historiques et scientifiques", Toulouse, France. pp. 33–47.

Michel, A.K., and Winter, S. 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. For. Ecol. Manage. **257**(6): 1453–1464. doi:10.1016/j.foreco.2008.11.027.

Michel, A.K., Winter, S., and Linde, A. 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can. J. For. Res. **41**(2): 300–308. doi:10.1139/X10-207.

Nascimbene, J., Marini, L., and Nimis, P.L. 2009. Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. Can. J. For. Res. **39**(4): 785–791. doi:10.1139/X09-013.

ONF. 2006. Schéma régional d'aménagement des forêts pyrénéennes. ONF, Direction territoriale Sud-Ouest. Toulouse, France.

Pardé, J., and Bouchon, J. 1988. Dendrométrie. 2nd ed. ENGREF, Nancy, France.

Pénicaud, P. 2000. Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe, **14**: 37–68.

Puumalainen, J., Kennedy, P., and Folving, S. 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. J. Environ. Manage. **67**(1): 5–14. doi:10.1016/S0301-4797(02)00183-4. PMID:12659799.

R Development Core Team. 2007. R: a language and environment for statistical computing. Available from http://www.R-project.org.

Ranius, T. 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodivers. Conserv. **11**(5): 931–941. doi:10.1023/A:1015364020043.

Ranius, T., and Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. **95**(1): 85–94. doi:10.1016/S0006-3207(00)00007-0.

Remm, J., and Lõhmus, A. 2011. Tree cavities in forests — the broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manage. **262**(4): 579–585. doi:10.1016/j.foreco.2011.04.028.

Remm, J., Lõhmus, A., and Remm, K. 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? For. Ecol. Manage. **221**(1–3): 267–277. doi:10.1016/j.foreco.2005.10.015.

Schmidl, J., Sulzer, P., and Kitching, R.L. 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia, **598**(1): 285–303. doi:10.1007/s10750-007-9163-5.

Snedecor, G.W., and Cochran, W. 1971. Méthodes statistiques. [Translated from English by H. Boelle and E. Camhaji.] ACTA, Paris, France.

Speight, M.C.D. 1989. Saproxylic invertrebrates and their conservation. Rep. 42. Council of Europe, Strasbourg, France.

Speight, M.C.D., Castella, E., Sarthou, J.-P., and Monteil, C. 2010. Species accounts of European Syrphidae (Diptera). Syrph the Net, the database of European Syrphidae. Syrph the Net Publications, Dublin, Ireland.

Stanska, M., Rozwaka, R., and Kowalczyk, K. 2010. *Dipoena torva* (Thorell, 1875), spider living on tree stems. Lesne Prace Badawcze, **71**(2): 201–205.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. **31**(1): 79–92. doi:10.1046/j.0305-0270.2003.00994.x.

Vaillant, F. 1978. Les *Systenus* et leur habitat dendrotelme (Dipt. Dolichopodidae). Bull. Soc. Entomol. Fr. **83**: 73–85.

Vuidot, A., Paillet, Y., Archaux, F., and Gosselin, F. 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. **144**(1): 441–450. doi:10.1016/j.biocon.2010.09.030.

Winter, S., and Möller, G.C. 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manage. **255**(3–4): 1251–1261. doi:10.1016/j.foreco.2007.10.029.

Zahner, V., Sikora, L., and Pasinelli, G. 2012. Heart rot as a key factor for cavity tree selection in the black woodpecker. For. Ecol. Manage. **271**: 98–103. doi:10.1016/j.foreco.2012.01.041.

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ORIGINAL PAPER

Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry

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Abstract Recent studies have highlighted the key role of tree microhabitats in forest habitat complexity and have suggested using them as surrogates for local taxonomic biodiversity. However, few practical guidelines have been published to help foresters in managing microhabitats at the stand scale. This paper provides scientific background information to help to develop such guidelines. We surveyed trees in nine long-unmanaged beech–fir forests to model tree microhabitat occurrence and diversity at the tree level. Data were upscaled to a size range of tree cluster, i.e., at the tree population scale, by aggregating observed values of microhabitat occurrence. Accumulation curves were used to estimate the minimum number of trees required to make all the microhabitat types available. Two managed forests were then studied to quantify management effects on microhabitats. Diameter at breast height (dbh) and tree species, respectively, explained 16 and 10 % of the variations in the number of microhabitat-bearing trees, and 21 and 10 % for the number of microhabitat types. Beech trees and firs with a dbh of less than dbh 50 and 65 cm, respectively, did not ensure the provision of all microhabitat types. At least 20 ha of unmanaged forest were necessary to conserve all the microhabitat types. Current management practices have reduced the number of microhabitat-bearing beeches both by reducing the number of very large trees (dbh > 67.5 cm) and by tree selection within mid-size diameters. For fir, only the logging of very large trees (dbh > 62.5 cm) negatively affected microhabitats. These figures may inspire guidelines for conservation-friendly forestry.

Keywords *Fagus sylvatica* · *Abies alba* · Mixed forest · Sustainable forest management · Upscaling

Introduction

Beech–fir forests are present in most European mountain ranges and cover 380,000 km^2 (4 % of the European forest area) (MCPFE 2007; Euforgen 2012). They are of great economic value, but they are also known for their key role in the conservation of forest biodiversity in Europe. Müller et al. (2012) showed that beech-dominated forests are an umbrella habitat for central European saproxylic beetles; indeed, 70 % of these species can be found in such forests.

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Deadwood is one of the most species-rich components in forest ecosystems (Grove 2002) and has often been used as a structural indicator for naturalness and biodiversity (Larsson 2001). Tree microhabitats (such as cavities or cracks) are also key features of natural stands (Michel and Winter 2009) since they host a wide taxonomic diversity (Stokland et al. 2012). More than 25 % of the taxonomic diversity in forest ecosystems is actually made up of saproxylic species (Stokland et al. 2012), i.e., species that depend on deadwood and tree microhabitats. Consequently, there are strong concerns about the impact of managing for wood production in beech–fir forests, where silvicultural practices tend to reduce the availability of deadwood (Gossner et al. 2013) and tree microhabitats (Winter and Möller 2008; Larrieu et al. 2012). While many previous studies have already established links between deadwood and biodiversity, ecological knowledge and practical recommendations are still lacking for microhabitats, despite the important role they play in forest ecosystems. However, more recently, the focus has switched from highlighting their key role in forest habitat complexity (Michel and Winter 2009) to conserving tree microhabitats, and currently, their use as surrogates of taxonomic diversity is being studied (Winter and Möller 2008). Like stand age (Moning and Müller 2009) and deadwood amounts (Müller and Bütler 2010), tree microhabitats can be both pedagogical and practical indicators for forest managers who want to take taxonomic diversity into account.

The key features needed for tree microhabitat occurrence in montane-mixed forests have already been identified. The number of microhabitats per tree and the number of microhabitat types depend on tree species and increase with diameter at breast height (dbh) (Winter and Möller 2008; Vuidot et al. 2011; Larrieu and Cabanettes 2012). Larrieu and Cabanettes (2012) identified two dbh classes crucial for microhabitats: very large trees and the largest trees (see below for numerical thresholds). Indeed, these two size classes host all microhabitat types and contain the highest proportion of microhabitat-bearing trees. However, the studies did not attempt to scale up the results from the probability of microhabitat occurrence according to species and tree size to microhabitat density in a given forest stand, with its specific dendrometric characteristics, and this is the information needed by forest managers to adapt their practices. Since logging and management operate at the stand scale, recommendations are needed at this scale. Authors also refer to the stand scale when recommending guidelines for microhabitat conservation: For example, for forest-bat conservation, Meschede and Heller (2003) recommend developing a roost-site network to permanently maintain 20–30 tree cavities per hectare in mature stands. Though several previous studies have modeled cavity-tree abundance at the stand scale (Fan et al. 2003, 2004; Eskelson et al. 2009; Lee and Fan 2012), they did not take into account other microhabitat types. To meet biodiversity conservation commitments, French State Forest managers use empirical standards to conserve microhabitat-bearing trees, typically preserving at least two cavity-bearing trees or very large trees per hectare for management units of roughly 20 ha, and maintaining 1 % of the total forest area permanently unmanaged (ONF 2009). Private owners who have joined the Programme for the Endorsement of Forest Certification have undertaken to conserve at least one cavity-bearing or overmature or very large tree per hectare (PEFC 2011). In addition, a few timber purchasers in France comply with the Forest Stewardship Council standards, which are even more binding. However, since forest certification mainly reflects the result of a process of social negotiation (Angelstam et al. 2013), none of these standards are based on accurate scientific evidence.

The minimum size enabling strict forest reserves to host comprehensive communities is another key issue in forest biodiversity conservation (Lindenmayer and Franklin 2002). However, by combining microhabitat frequency data with minimum requirements for density and diversity of associated species, it is possible to infer the minimum size needed for forest reserves.

To give forest managers practical information to help them to improve tree microhabitat conservation, this paper (1) fits statistical relationships at the tree level to estimate the occurrence and diversity of tree microhabitats in montane beech–fir forests, regardless of stand characteristics, (2) upscales to sets of trees defined by the number of trees, tree diameter category, and range of occupied area, and (3) illustrates, at the stand level, the effects of two management practices on microhabitats.

Materials and methods

Forests studied and sampling design

The forests studied (Table 1) are situated in the Pyrenees mountain range (France). These forests are within the natural distribution range of beech and fir (Bardat et al. 2004). However, as a direct result of historic human intervention, the stands selected host a variable proportion of the two species (Métailié 2001). All the stands are located within an altitude range of 800–1,800 m (Table 1), which corresponds to the montane bioclimatic zone in the Pyrenees.

Data from nine long-unmanaged stands were used to estimate the occurrence and diversity of microhabitats without the influence of forest management, which, as we mentioned above, is known to reduce microhabitat density and diversity (Vuidot et al. 2011; Larrieu et al. 2012). Dbh in these stands varied from 11 to 127 cm for beech and from 7 to 172 cm for fir.

Table 1 Main characteristics of the study forests and sampling design (CI = 95 % confidence interval)

Forest	Vegetation level	Dominant tree species	History	Basal area G (m^2/ha)	Studied area per forest (ha)	Number of plots	Number of observed live trees	Diameter at breast height (cm) Mean (min–max)	
				Deadwood + live trees Mean [CI]				Beech	Fir
Unmanaged									
Plagnech de ton	Lower montane	Beech and fir	Not logged since 1900	40 [33–48]	23	10	332	62.9 (15.9–127.3)	44.4 (8.0–124.1)
Auribareille	Lower montane	Fir	Never logged	55 [48–62]	12	2	61	50.9 (15.9–78.0)	70.6 (22.3–130.5)
Genie loungue	Lower montane	Beech	Not logged since 1900	33 [28–39]	16	5	122	54.4 (21.6–114.6)	47.4 (47.4–47.4)
Bugatet	Upper montane	Sub-pure fir forest	Not logged since 1908	50 [36–64]	18	5	185	–	49.2 (7.0–111.4)
Barrada	Upper montane	Fir	Only logged once (1953) by selective logging	67 [51–82]	13	5	221	20.3 (11.1–25.5)	58.6 (11.1–171.9)
Bosc nou	Upper montane	Beech and fir	Never logged	52 [44–59]	13	5	178	36.1 (29.0–42.7)	57.5 (9.5–114.6)
Es tucoulets	Upper montane	Beech and fir	Not logged since 1900	49 [45–53]	34	9	265	31.8 (24.8–38.8)	53.7 (9.5–130.5)
Es piches	Upper montane	Beech and fir	Not logged since 1900	46 [36–55]	17	5	153	56.2 (15.9–95.5)	56.8 (11.1–135.3)
Ouderou	Upper montane	Fir	Old pasture woodland not logged since 1900	63 [53–75]	25	8	293	36.0 (14.3–78.0)	65.9 (10.2–135.9)
Managed									
Mouné	Lower montane	Fir	Logged 3 times by selective logging in the last 20 years (total logged volume = 75 m^3 ha^{-1})	38 [31–46]	18	11	267	34.4 (11.1–60.5)	25.4 (6.4–65.3)
Seti–Touzet	Lower montane	Beech	Logged twice by selective logging in the last 20 years (total logged volume = 50 m^3 ha^{-1})	35 [31–39]	22	10	280	45.6 (4.8–73.2)	11.1 (11.1–11.1)

In addition, samples from two forests managed by the same commercial operator were used to comparatively quantify the effect of management on microhabitats. Currently, the typical management of French beech–fir forests entails selective cuts every 10–20 years on average to improve the overall commercial quality of the wood produced. Thinning removes the following: (1) trees, which exceed the commercial girth limit (i.e., the dbh at which trees provide a maximum economic yield), (2) those which have trunk characteristics that reduce the quality of their wood ("defects" such as numerous large knots, woodpecker cavities, saproxylic fungi), (3) those whose remaining life expectancy is estimated to be inferior to the next cutting interval, and (4) disseminated tree species other than beech and silver fir whose wood has lower commercial value. Generally, thinning removes a limited number of stems (on average only 10–30 % of the total number of trees overall) and mostly concerns large trees. Management intensity was estimated by adapting Schall and Ammer's (2013) Silvicultural Management Intensity index ("SMId"). The SMId is based on the ratio between the mean basal area observed in each forest (Gobs) and the maximal basal area observed in long-unmanaged forests (Gmax). The management index was calculated at the forest scale as follows: Index = 1 − (Gobs/Gmax), in which G encompasses both dead and live wood.

Measurements and observation of microhabitats

Seventy-five plots were set up with the n°1 strip (with a return angle of 1/50) of a Bitterlich relascope (Bitterlich 1984), and the trees were surveyed by the same observer from 2003 to 2010. Plot areas were depended on the spatial distribution of the largest trees. The theoretical number of trees per hectare was calculated by allocating the coefficient N_{dbh} to every tree observed in the relascope sampling, in relation to its dbh:

- $N_{\mathrm{dbh}} = \pi\ 10^8\ [\mathrm{ArcTan}(1/50)/(\pi\ \mathrm{dbh})]^2$ (Pardé and Bouchon 1988).

Overall, 750 live beech trees, 1,471 live firs, and 136 live trees belonging to other species were surveyed in the unmanaged and managed forests combined, but only beech and fir data were used for analysis. On each plot, for all trees with a dbh greater than 5 cm, diameter was measured to the nearest centimeter outside the bark at breast height (dbh). The trunk was carefully examined from the ground to the top of the canopy, and microhabitats observed on the visible part of the trunk both beneath and within the tree crown were recorded. We defined a set of nine microhabitat types: (1) empty cavities at the base of the tree, (2) empty cavities on the trunk, (3) cavities at the base of the tree containing mold, (4) cavities on the trunk containing mold, (5) sporocarps of saproxylic fungi, (6) dendrothelms, (7) sap runs, (8) missing bark, and, finally, (9) cracks in the tree trunk and bark in the process of peeling which formed a shelter (for more details, see Larrieu and Cabanettes 2012). The two variables used in the analyses were the presence/absence of microhabitats and the number of microhabitat types at the tree level.

Calculations and statistical procedures

All the analyses were carried out with R software v.2.14.2 (R Development Core Team 2011).

Microhabitat modeling at the tree scale

With tree species and diameter as fixed variables, generalized linear mixed models of microhabitat occurrence and number of microhabitat types at the tree level were carried out with binomial (GLMocc) and Poisson (GLMnb) error distributions, respectively; *p* values were obtained from a chi-square test based on the difference between the null deviance and the model deviance (Hosmer and Lemeshow 2000). We used Nagelkerke's R squared (R package fmsb; Nakazawa 2012) to assess goodness of fit as an indication of the explanatory power of the models (Agresti 2002; Thompson 2009). For the binomial models (GLMocc), sensitivity (i.e., the proportion of true positives detected among observed positive values), specificity (i.e., the proportion of true negatives detected among observed negative values), precision (i.e., the proportion of true positives among all positive predictions), and error (i.e., the proportion of wrong predictions) were assessed with a confusion matrix (Menard 2002).

Scaling up to clusters of trees

In order to upscale from the individual tree to the population scale (i.e., to groups of trees large enough to simulate forest management units), we aggregated the observed values of microhabitat occurrence and the number of microhabitat types either from randomly selected individual trees or from the whole sample. Cluster sizes were set to correspond to typical management scales in France. These nonspatially explicit clusters of trees were built with bootstrap methods for the number of microhabitat types.

To estimate the influence of the tree set size on the confidence interval of the estimated occurrence of microhabitat-bearing trees, we compared observed values with the fitted model values obtained from a range of sample sizes (number of trees). This comparison provided an estimate of the relative error induced by scaling up from a smaller sample size. Confidence intervals per number of tree classes were calculated after resampling the total population with replacement, as in standard nonparametric bootstrapping (Canty and Ripley 2012).

To estimate the minimum number of trees required to ensure a given supply of microhabitat types in managed stands, we used accumulation curves (Gotelli and Colwell 2001) implemented with the "exact" method (R package "vegan"; Oksanen et al. 2011). For each tree species, we computed the mean number of microhabitat types according to the number of trees sampled. We first considered all diameter classes and then computed separate accumulation curves for each diameter class. We used management diameter thresholds that are currently being applied: 17.5 cm $\leq$ small tree (ST) $\leq$ 27.5 cm; medium tree (MT) $\leq$ 47.5 cm; large tree (LT) $\leq$ 67.5 cm; very large tree (VLT) > 67.5 cm for broadleaved species, and 17.5 cm $\leq$ ST $\leq$ 27.5 cm; MT $\leq$ 42.5 cm; LT $\leq$ 62.5 cm; VLT > 62.5 cm for conifers (Bastien and Gauberville 2011). Following Larrieu and Cabanettes (2012), we added another category—"largest trees" (LST) (dbh $\geq$ 87.5 cm for beech and dbh $\geq$ 97.5 cm for fir)—to take into account the special ecological role of these trees. Since sap runs were not surveyed in the "Plagnet de ton" forest, only eight microhabitat types were included in the accumulation curves.

Application: estimated effects of management on microhabitats

We assessed the potential management effect on microhabitats in beech and fir stands by simulating the effects on the density of microhabitat-bearing trees of two major forest practices typical of near-to-nature management strategies in European beech-dominated forests (Gossner et al. 2013). We estimated (1) the "diameter effect," directly linked to the manager's choice to cut all trees with a diameter above a certain economically defined threshold, and (2) the "selection effect," in reference to the manager's choice of trees to remove during thinning according to trunk shape or the presence of the so-called trunk defects. The diameter effect was calculated by removing the microhabitats recorded on trees larger than the logging diameter limit (i.e., trees which would systematically be removed). The selection effect was calculated by comparing the estimated potential and the observed numbers of microhabitat-bearing trees in managed stands. In accordance with Larrieu et al. (2012), we divided the microhabitats into two categories: (1) microhabitats a priori favored by management (i.e., observed in larger densities in managed stands than in unmanaged stands), namely dendrothelms and missing bark; and (2) microhabitats a priori impaired by management, namely cavities, cracks, and saproxylic fungi. For the diameter effect alone, we considered only long-unmanaged stands "with" or "without large trees" [i.e., with dbh >67.5 cm (beech) or >62.5 cm (fir)]; all microhabitat types were taken into account. Confidence intervals for the number of microhabitats or microhabitat-bearing trees were calculated with a standard bootstrap method ("boot" function in "boot" R-package; Canty and Ripley 2012).

Table 2 Independent and combined relationships between dbh, tree species, and the occurrence of microhabitat-bearing trees

Variables	B0	B1	*p* value	R2-NK (%)
Dbh	−3.087	0.034	***	15.53
Species	−0.032	−1.332	***	9.51
Dbh + species	−2.188	0.038 −1.595	***	25.78

B0 is the origin *y* value, and B1 is the slope of the linearized form of the logistic equation. The significance level is expressed as follows: *** $p < 0.001$, ** $0.01 < p < 0.001$, * $0.05 < p < 0.01$. The R2-NK is Nagelkerke's R squared

Results

The "long-unmanaged" and "managed" forest clusters have significantly different management indices, respectively, 0.25 [0.19–0.31] and 0.45 [0.39–0.52]. For beech and fir, respectively, we observed 16.7 ± 3.5 and 18.7 ± 3 microhabitat-bearing trees per hectare on average (Table A8 in supplementary material). For the two species combined, the least frequent microhabitat type ($0.22\ \text{ha}^{-1} \pm 0.1$) was dendrothelms on fir, whereas the most frequent was missing bark on fir ($11.8\ \text{ha}^{-1} \pm 2.3$).

Microhabitat modeling at the tree scale

Occurrence of microhabitat-bearing trees as a function of tree species and tree dbh

For fir and beech data combined, dbh and tree species, respectively, explained around 16 and 10 % of the variations in occurrence of microhabitat-bearing trees. A combination of dbh and tree species variables gave an explanatory value of 26 % (Table 2). For all fir microhabitat types and most beech microhabitat types, dbh was significantly and positively correlated with microhabitat occurrence (Table A7, in supplementary material). The dbh variable explained from 5 to 23 % of the variations in microhabitat occurrence in fir and from 4 to 14 % in beech.

Properties of the microhabitat occurrence models The fir models were less efficient than the beech models in

Table 3 Confusion matrix for the GLM_{occ} for each tree species (see "Materials and methods" section for the definitions of sensitivity, specificity, precision, and error)

Tree species	Sensitivity	Specificity	Precision	Error
Beech	0.61	0.68	0.65	0.35
Fir	0.17	0.98	0.65	0.19

predicting which trees would bear microhabitats compared to the "true" bearing trees (lower sensitivity for fir models) (Table 3). However, because the fir models were better predictors of the "true" nonbearing trees which were more numerous (high specificity), their precision was equivalent to that of the beech models and their total ranking error was lower.

Microhabitat diversity as a function of tree species and tree dbh

Tree dbh was significantly correlated with the number of microhabitat types per tree for both fir and beech (Table 4). The explanatory value of dbh was slightly higher for fir (25 %) than for beech (19 %). When fir and beech data were combined, dbh and tree species, respectively, explained 10 and 21 % of the variations in the number of microhabitat types; both variables together explained 31 % of the variation (Table 5).

Table 4 Results from GLM analyses on the relationship between dbh and number of microhabitat types for each tree species

Tree species	B0	B1	*p* value	R2-NK
Beech	−1.630	0.019	***	18.65
Fir	−3.327	0.029	***	25.44

B0 is the origin *y* value, and B1 is the slope of the linearized form of the exponential equation. The significance level is expressed as follows: *** $p < 0.001$, ** $0.01 < p < 0.001$, * $0.05 < p < 0.01$. The R2-NK is Nagelkerke's R squared

Table 5 Independent and combined relationships between dbh, tree species, and the number of microhabitat types

Variables	B0	B1	*p* value	R2-NK
Dbh	−2.681	0.024	***	20.83
Species	−0.459	−0.936	***	10.47
Dbh + species	−2.080	0.025 −0.997	***	31.06

B0 is the origin *y* value, and B1 is the slope of the linearized form of the exponential equation. The significance level is expressed as follows: *** $p < 0.001$, ** $0.01 < p < 0.001$, * $0.05 < p < 0.01$. The R2-NK is the Nagelkerke's R squared

Microhabitats at the stand scale

Distribution of the observed microhabitats

The relative error for the estimated number of microhabitat-bearing trees decreased as the number of trees increased, with a more rapid decrease for fir than for beech (Fig. 1). To maintain an acceptable 10 % error, minimum clusters of 50–60 beeches and 170 firs are necessary in unmanaged forests.

We modeled the occurrence of microhabitat-bearing trees according to stand size and the distribution of the trees among the diameter classes (cf. observed frequencies of each microhabitat in unmanaged plots in Table A8, supplementary material).

The very large and the largest diameter classes were the least numerous in the study stands. However, since they bore the most microhabitats, their contribution to total microhabitat supply was higher than for smaller diameter classes, especially for fir (Fig. 2).

Microhabitat diversity according to stand size and the distribution of trees among the diameter classes

As shown by the accumulation curves, an average of about 500 firs or 100 beeches, irrespective of diameter, are necessary to observe the eight microhabitat types (Fig. 3).

The recruitment rate for the eight microhabitat types increased with increasing diameter (Fig. 4). For beech, it took five times as many large or medium trees than it did for very large or largest trees to obtain all the microhabitat types. The same pattern was observed for fir when comparing large or very large trees with largest trees. The two smallest diameter classes (small and medium) never provided all microhabitat types for either fir or beech.

At least 10 ha of unmanaged forest were required to observe all the microhabitat types if the stands included firs larger than dbh 97.5 cm and beech trees larger than 47.5 cm (Fig. 5). However, in this case, only one diameter class was able to supply the full range of microhabitat types. A minimum of 20 ha is required to obtain at least two diameter classes that supply full microhabitat diversity (Fig. 5).

Estimated management effects on microhabitats

Selection effect was not significant for fir. For beech, the selection effect significantly increased the number of microhabitat-bearing trees for the set of microhabitats favored by logging (from 22 to 56 ha^{-1}), whereas it significantly reduced their number for the set of microhabitats impaired by harvesting (from 38 to 23 ha^{-1}, cumulating at a 39 % decrease (Table 6)). By comparison, the diameter

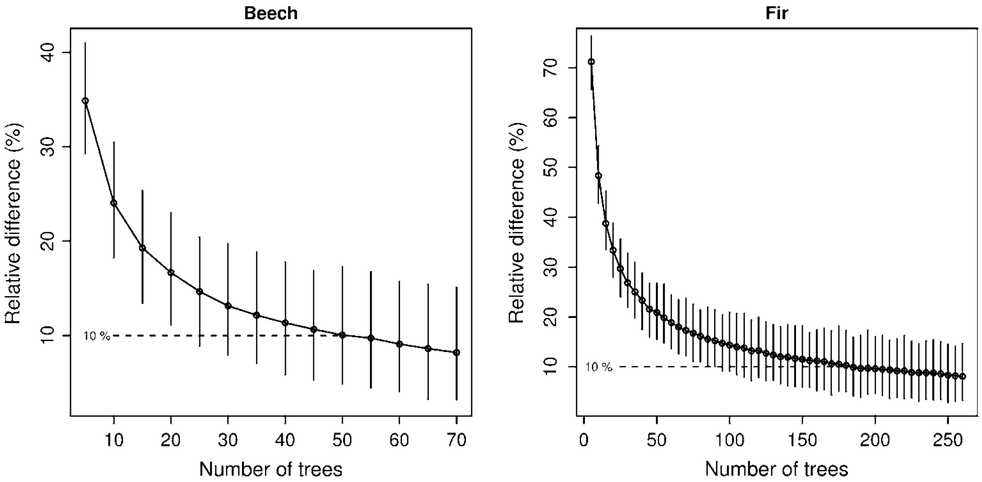

Fig. 1 Mean difference between the observed and predicted number of microhabitat-bearing trees in a given cluster of trees according to the size of the cluster (i.e., number of trees). *Vertical bars* indicate the 95 % confidence intervals

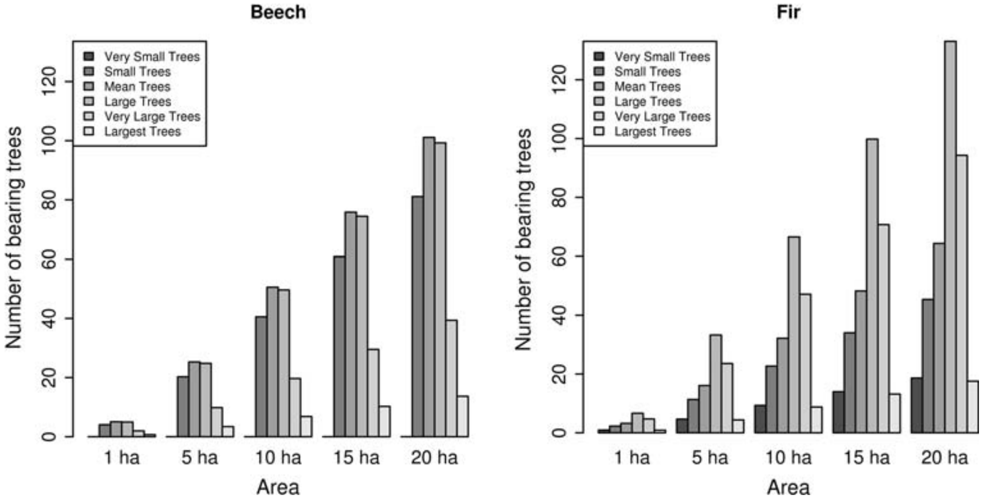

Fig. 2 Number of microhabitat-bearing trees per commercial diameter category, as a function of the cluster area, for beech and fir (see the "Materials and methods" section for further details on the diameter classes)

effect, the economic limit directly linked to maximum dbh for logging, revealed a nonsignificant decrease of 30 and 16 % for fir and beech, respectively.

Discussion

Are dbh and tree species practical management factors for microhabitats?

The correlation between diameter class or tree species and the probability of microhabitat occurrence had already been pointed out by several authors, but was never fully quantified (Fan et al. 2004; Winter and Möller 2008; Ranius et al. 2009; Michel et al. 2011; Larrieu and Cabanettes 2012; Larrieu et al. 2012). Only one study found more nuanced results (Vuidot et al. 2011). By modeling the occurrence of ten microhabitat types (presence of ivy, non-woodpecker cavities, conks, woodpecker cavities, cankers, dead crown, cracks, bark pockets, bark losses, and bryophytes), the authors found that dbh alone was significantly related to the occurrence of non-woodpecker cavities. They also found that tree species alone only influenced the occurrence of cankers. However, when dbh and tree species together were associated with the variables *management type*, *vitality*, and *site*, they were significantly related to bark loss (analogous to our microhabitat type "missing bark").

Our study confirms how important it is for managers to take into account these two factors when their goal is to improve microhabitat availability in forests. Indeed, we provided detailed information about the strength of the significant correlation between diameter class or tree species and the probability of microhabitat occurrence. Though part of the variability remains unexplained (e.g., 69 % of variations in the number of microhabitat types), biotic and abiotic factors (woodpecker population density, very steep slopes, cliffs, very windy, or cold areas, etc.) are likely to be at play; these factors can facilitate the formation of microhabitats, but are not, or only very slightly dependent on management. Management history before set-aside may also partially explain this variability.

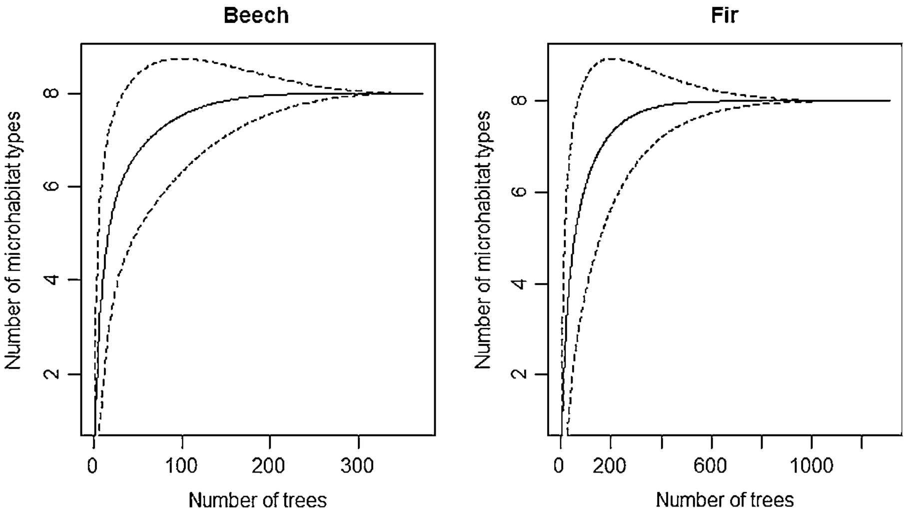

Fig. 3 Cumulative number of eight microhabitat types as a function of the number of trees for beech stands and fir stands. 95 % confidence intervals are symbolized with *dashed lines*

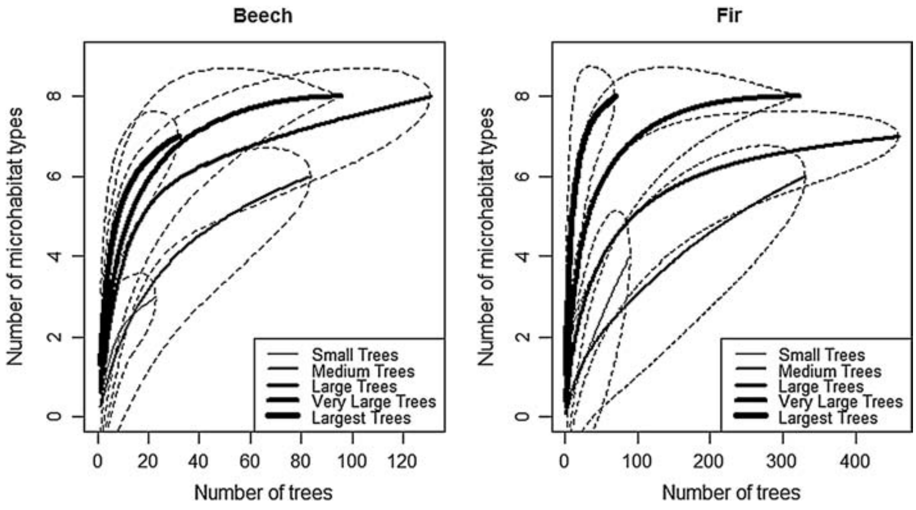

Fig. 4 Cumulative number of eight microhabitat types as a function of the number of trees according to their diameter class for beech and fir stands (see the "Materials and methods" section for further details on the diameter classes). 95 % confidence intervals are symbolized with *dashed lines*

Density, diversity, and spatial distribution of microhabitat-bearing trees in managed stands

Our tree-level models can be applied to all beech–fir stands. However, since the upscaled results were strongly impacted by the structure of the study stands (relative % of beech and fir and diameter distribution), managers must take care to apply the models to data from a representative sample of the stand being managed. Moreover, estimation accuracy strongly depends on sample size (Fig. 1). For our data, the risk of microhabitat removal associated with logging related to dbh and harvested tree species may be inferred from Figs. 2 and 5. For a given logging rate, it is clear that management practices that focus on the removal of the very large and largest trees strongly reduce both microhabitat density and diversity.

Of course, microhabitat management should not only include conservation measures; it is also essential to plan for the recruitment of new microhabitats. Gibbons et al. (2010) recommended recruiting twice the target number of hollow-bearing trees in Australian eucalypt forests in order to compensate for the mortality of some of the microhabitat-bearing trees between harvesting events. Furthermore, not all microhabitats have a similar natural lifespan. For example, in European boreal forests, woodpecker-excavated cavities do not persist as long as cavities created by decay (Cooke and Hannon 2012). Therefore, forest managers should take the mean lifespan of the microhabitat types into account in recruitment plans.

We have shown that at least 10 ha of long-unmanaged forest—much more than current management standards require—must be maintained to supply all the nine microhabitat types. This is consistent with Jakoby et al. (2010) who modeled deadwood availability in unmanaged islands and found that 2 ha is the minimum area required to sustain a diversity of deadwood types over several decades.

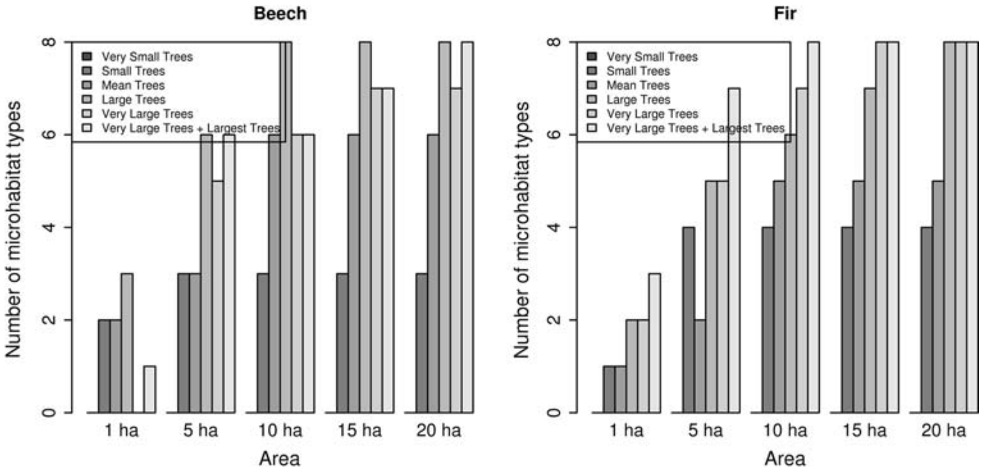

Fig. 5 Number of microhabitat types per commercial diameter category, as a function of cluster area, for beech and fir (see the "Materials and methods" section for further details on the diameter classes)

Table 6 Mean number and 95 % confidence intervals for microhabitat-bearing trees per hectare for two tree species (beech and fir) and two microhabitat sets: "favored" (microhabitats favored by management) and "impaired" (microhabitats impaired by management)

Management effect	Microhabitat set	Beech		Fir	
		Mean	CI	Mean	CI
Selection	"Favored" set, observed data	55.8	48.2–64.2	4.9	0–14.7
	"Favored" set, calculated data	21.6	17.7–27.3	11.6	10.3–13.5
	"Impaired" set, observed data	22.7	16.4–30.5	2.8	0–7.9
	"Impaired" set, calculated data	37.6	32.4–44.9	2.6	2.3–2.9
Diameter	With very large trees	16.7	13.7–20.3	18.7	15.4–22.4
	Without very large trees	14.1	10.9–17.5	13.1	10.9–18.2

CI 95 % confidence interval. The "very large trees" category corresponds to trees with dbh >67.5 cm (beech) or >62.5 cm (fir)

Obviously, however, 10 ha set-asides do not guarantee the presence of numerous microhabitats in each type nor the preservation of all microhabitat-dwelling species.

Neither do our results allow us to determine how microhabitat-bearing trees should be spatially distributed, though this factor should not be ignored by forest managers. Indeed, the effect of aggregation on saproxylic diversity, or inversely, the regular distribution of cavity trees throughout the stand, seems to vary from one taxon to another (Bouget and Gosselin 2005). Ranius (2000) showed that the cavity-dwelling beetle *Osmoderma eremita* requires a minimum number of aggregated, suitable trees to sustain local populations. For the fungivorous beetle *Bolitotherus cornutus*, spatial isolation had the strongest negative effect on beetle frequency in wooded patches within an agricultural matrix and was most significant for clusters of trees bearing *Fomes fomentarius* sporocarps which host the beetle (Kehler and Bondrup-Nielsen 1999). However, there was also a negative effect of sporocarp spatial isolation at the individual log scale (Kehler and Bondrup-Nielsen 1999). Despite these caveats, dispersing microhabitat-bearing trees throughout the stand is more likely to limit the impact of the accidental disappearance of bearing trees, which could result in a massive reduction in microhabitats if the trees were grouped together. Furthermore, dispersing of bearing trees throughout the stand would probably ensure greater diversification of contexts (e.g., shade, humidity, or temperature gradients) shown, in a companion study (Bouget et al. 2014), to influence the microhabitat effect on biodiversity.

Correlating microhabitat abundance with the number of microhabitat-bearing trees is of practical interest for the forest manager. Indeed, it is much easier and faster for managers to count microhabitat-bearing trees than to count the microhabitats themselves. Moreover, by conserving the valuable largest trees which bear the most microhabitats, forest managers could optimize both economic and ecological goals.

At the landscape level, several authors suggest conserving 20–30 % of favorable habitats for biodiversity preservation. Nilsson et al. (2001) recommended conserving 20 % of the original density of ancient/hollow trees and large dead trees. A similar threshold is also recommended by Wiktander et al. (2001) for the lesser spotted woodpecker (*Dendrocopos minor*), while Wegge and Rolstad (1986) identify a minimum landscape threshold of 30 %

old-growth forests for the conservation of the Capercaillie (*Tetrao urogallus*), a threatened bird in the montane forests of western Europe. For the three-toed woodpecker (*Picoides tridactylus*), Bütler et al. (2004) suggested conserving at least 5 % of standing dead trees over forest areas larger than 100 ha. These thresholds correspond to the amount of habitat below which fragmentation may affect population persistence (Andren 1994; Fahrig 1998). The extinction threshold is defined as the minimum amount of habitat below which a population goes extinct; this can occur at any amount of remaining habitat depending on the species concerned and the quality of the matrix (Fahrig 2001; Ranius and Fahrig 2006). For example, *O. eremita* is not systematically present in stands under 10 ha, even when several trees contain suitable cavities (Ranius 2000).

Not all microhabitat types have the same sensitivity to management. Some types are renewed more or less annually, for example, woodpecker breeding holes (Cramp 1980), at least at the spatial scale of the woodpecker's territory. However, rare microhabitat types such as cracks on live trees (Larrieu et al. 2012) resulting from stochastic events (e.g., windstorms, lightning strikes), or large cavities with mold (Ranius et al. 2009) associated with overmature trees, require special conservation efforts because their removal can lead to temporal as well as spatial gaps in their supply.

It would be difficult to define a management trade-off between deadwood and tree microhabitats given their relative conservation interest. Saproxylic databases do indeed illustrate that assemblages associated with deadwood and tree microhabitats are not redundant or nested, but rather dissimilar (e.g., Möller 2009). For example, the Coleoptera *O. eremita* and *Limoniscus violaceus* live only in cavities with mold and never in snags or logs (Ranius 2000; Gouix et al. 2012). Many arthropods such as the Coleoptera *B. cornutus* live exclusively in the sporocarps of lignivorous fungi (Kehler and Bondrup-Nielsen 1999).

The selection effect of management depends on tree species

The near-to-nature management strategies that have been used in European beech-dominated forests since the 1980s (Brunet et al. 2010) promote autochthonous tree species, natural regeneration, and the use of selective cutting to mimic natural process. However, cutting pressure on microhabitat-bearing trees is quite different from a natural process. Since microhabitats can last several decades on live trees (Stokland et al. 2012) where they initiate the decaying process, forest managers typically log microhabitat trees every 10 years on average because they are focusing on the commercial quality of the wood. The dissimilar selection effect we observed between beech and fir may be partly explained by the fact that even small-diameter beech trees often bear microhabitats, whereas only large firs do so. Furthermore, beech trunks are easier to observe, while the dense foliage on fir trees hides the higher part of the trunk. In the case of microhabitat types impaired by management, thinning affects the number of microhabitat-bearing trees both by reducing the number of very large trees and by culling less desirable trees within smaller diameter classes. For fir—which infrequently bears microhabitats, and then essentially when dbh is high—implementing a low commercial girth limit negatively impacts microhabitat richness much more than does selection within smaller diameter classes. To improve the general applicability of our results, data from a wider sampling of managed forests and a wider range of management practices would be useful.

Relevance of the standards used by forest managers

Since the standards used by many forest managers (e.g., in France) to conserve deadwood and microhabitats focus only on cavities and maintaining a few very large trees and small unmanaged areas, they are insufficient to preserve microhabitat diversity at the stand scale.

The microhabitat density recommended by Blondel (2005) for the conservation of cavity-dwelling birds is a minimum of 40 cavities per hectare. For bat conservation, Meschede and Heller (2003) suggest retaining a network of seven to ten live cavity- or crack-bearing trees per hectare. These thresholds are higher than current management standards (e.g., 2 cavity-bearing trees per hectare in French state forests). We observed cavity densities far below these recommendations. However, this difference may be linked with the procedure we used: Microhabitats were surveyed only on trunks and on live trees, and we only modeled microhabitat presence–absence. Cavities and cracks borne by large low branches were not surveyed, resulting in an underestimated real density of cavities for beech. Moreover, the leaf canopy may have hindered the observations conducted during leaved periods and could have contributed to an underestimation of microhabitat number on the trunk inside the tree crown. Finally, most cracks borne by fir are found on snags (Larrieu and Cabanettes 2012), not on live trees, and they were therefore not included in our dataset. However, most of the references in the literature also give fairly low mean densities. For example, the mean density of suitable cavities for cavity-dwelling birds in riverine aspen and birch stands in central Estonia was only about 4 ha^{-1} (Remm et al. 2006), and Remm and Lohmus (2011) quoted a mean of 5.6 cavities ha^{-1} in the Paleartic region. On average in old oak forests, Robles et al. found 15 cavities ha^{-1} in 2011 and only 11 cavities ha^{-1} in 2012. Certain forest types seem to naturally supply more cavities:

For example, in Missouri, 52 cavity trees ha^{-1} were found on average in riparian forests (Gwaze and Elliott 2011) and 25–55 cavity trees ha^{-1} in old-growth hardwood stands (Fan et al. 2005). All these references highlight the fact that the norms used for certification standards are more related to economic than to ecological arguments (Angelstam et al. 2013).

Properly investigating the relationships between microhabitat density or richness on the one hand and management intensity and taxonomic biodiversity on the other seems to be the next step toward appropriate forest management recommendations. In a companion study (Bouget et al. 2014), we demonstrated that the density of cavity trees positively affected the abundance of rare saproxylic beetles in lowland beech and spruce–fir forests as well as the total number of saproxylic beetle species in highland beech forests. To our knowledge, very few studies have provided data for other taxa. However, Müller (2005) found that a minimum of seven small cavity-bearing trees is critical for the colonization of beech stands by *Ficedula* species. Using a regression tree, Kanold et al. (2009) showed that the presence of only five cavities per hectare approximately doubled the number of cavity-breeding species compared with stands without any cavity in montane beech–fir–spruce forests.

Transposition of the results to other forest contexts

A new fitting should be calculated for other forest types (e.g., oak forests). Our results for beech and fir indicate that at the tree scale, a minimum of about 60 trees from each species is needed to obtain significant models (Fig. A6 in supplementary material).

Only beech and fir were considered in our study because of the scarcity of other tree species in the study forests. However, it is worth stressing that these secondary species play an important role in the supply of microhabitats (Larrieu and Cabanettes 2012) and must be taken into account when they are present in significant numbers.

Conclusion

Sustainable forest management must preserve microhabitats in terms of both relevant density and total diversity. Based on previous results and our own computations, we recommend the following sustainable management practices in managed forests: (1) set-aside areas without management, which are larger than 20 ha to ensure microhabitat diversity, (2) before each logging operation, simulate the effect of the removal of marked trees on microhabitats and plan the recruitment of new microhabitat-bearing trees, (3) make special efforts to conserve the rarest microhabitats (saproxylic fungi on live trees, cracks, sap runs, and dendrothelms on fir) and the microhabitats that require a long time to develop (e.g., large cavities with mold).

Applying our approach will help forest managers to easily assess both the diversity and density of microhabitats in managed forests and to verify the suitability of their current practices for the conservation of microhabitat-bearing trees. It can also help them to optimize the number of retention trees by allowing them to analyze several scenarios for different stand structures. We assume that this approach can be applied across a wide range of forest types to improve the conservation of taxonomic biodiversity by indirect assessment.

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References

Agresti A (2002) Categorical data analysis. Wiley, London

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Angelstam P, Roberge JM, Axelsson R, Elbakidze M, Bergman KO, Dahlberg A, Degerman E, Eggers S, Esseen PA, Hjalten J, Johansson T, Müller J, Paltto H, Snall T, Soloviy I, Tornblom J (2013) Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: the Swedish Forest Stewardship Council Standard as a case study. Ambio 42:229–240

Bardat J, Bioret F, Botineau M, Boullet V, Delpech R, Géhu JM, Haury J, Lacoste A, Rameau JC, Royer JM, Roux G, Touffet J (2004) Prodrome des végétations de France. MNHN, Paris

Bastien Y, Gauberville C (coord.) (2011) Vocabulaire forestier. Écologie, gestion et conservation des espaces boisés. IDF/CNPF, AgroParisTech, ONF

Bitterlich W (1984) The relascope idea: relative measurements in forestry. Commonwealth Agricultural Bureaux, Farnham Royal

Blondel J (2005) Bois mort et à cavités: leur rôle pour l'avifaune cavicole. In: Vallauri D et al (eds) Bois morts et à cavités: une clé pour des forêts vivantes. Tec et Doc Lavoisier, Paris, pp 137–142

Bouget C, Gosselin F (2005) Distribution spatiale du bois mort: enjeux pour la conservation des espèces cavicoles et saproxyliques. In: Vallauri D et al (eds) Bois morts et à cavités: une clé pour des forêts vivantes. Tec et Doc Lavoisier, Paris, pp 107–113

Bouget C, Larrieu L, Brin A (2014) Key features for saproxylic biodiversity from rapid habitat assessment in temperate forests. Ecol Indic 36:656–664

Brunet J, Fritz Ö, Richnau G (2010) Biodiversity in European beech forests: a review with recommendations for sustainable forest management. Ecol Bull 53:77–94

Bütler R, Angelstam P, Ekelund P, Schlaeffer R (2004) Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biol Conserv 119:305–318

Canty A, Ripley B (2012) Boot: bootstrap R (S-plus) functions. R package version 1.3–7

Cooke HA, Hannon SJ (2012) Nest-site selection by old boreal forest cavity excavators as a basis for structural retention guidelines in spatially-aggregated harvests. For Ecol Manage 269:37–51

Cramp S (ed) (1980) Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Paleartic. Oxford University Press, New York

Eskelson BNI, Temesgen H, Barrett TM (2009) Estimating cavity tree and snag abundance using negative binomial regression models and nearest neighbor imputation methods. Can J For Res 39:1749–1765

EUFORGEN (2012) Distribution map of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). http://www.euforgen.org

Fahrig L (1998) When does fragmentation of breeding habitat affect population survival? Ecol Model 105:273–292

Fahrig L (2001) How much habitat is enough? Biol Conserv 100:65–74

Fan ZF, Larsen DR, Shifley SR, Thompson FR (2003) Estimating cavity tree abundance by stand age and basal area, Missouri, USA. For Ecol Manag 179:231–242

Fan ZF, Shifley SR, Thompson FR, Larsen DR (2004) Simulated cavity tree dynamics under alternative timber harvest regimes. For Ecol Manag 193:399–412

Fan ZF, Shifley SR, Spetich MA, Thompson FR, Larsen DR (2005) Abundance and size distribution of cavity trees in second-growth and old-growth central hardwood forests. North J Appl For 22:162–169

Gibbons P, McElhinny C, Lindenmayer DB (2010) What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. For Ecol Manag 260:975–982

Gossner M, Lachat T, Brunet J, Isacsson G, Bouget C, Brustel H, Brandl R, Weisser W, Müller J (2013) Current "near-to-nature" forest management effects on functional trait composition of saproxylic beetles in beech forests. Conserv Biol 27:605–614

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gouix N, Mertlik J, Jarzabek-Mueller A, Nemeth T, Brustel H (2012) Known status of the endangered western Palaearctic violet click beetle (*Limoniscus violaceus*) (Coleoptera). J Nat Hist 46:769–802

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Gwaze D, Elliott A (2011) Cavity trees, snags, and overstory density in a riparian forest in North-eastern Missouri. North J Appl For 28:105–109

Hosmer DW, Lemeshow S (2000) Applied Logistic Regression, 2nd edn. Wiley, London

Jakoby O, Rademacher C, Grimm V (2010) Modelling dead wood islands in European beech forests: how much and how reliably would they provide dead wood? Eur J For Res 129:659–668

Kanold A, Rohrmann N, Müller J (2009) Einflussfaktoren auf das Baumhöhlenangebot und dessen Auswirkungen auf die Arten und Dichten von Höhlenbrütern in Bergwäldern. Ornithologischer Anzeiger 47:116–129

Kehler D, Bondrup-Nielsen S (1999) Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus*, at different spatial scales in fragmented and continuous forests. Oikos 84:35–43

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can J For Res 42:1433–1445

Larrieu L, Cabanettes A, Delarue A (2012) Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech–fir forests of the Pyrenees. Eur J For Res 131:773–786

Larsson TB (ed) (2001) Biodiversity evaluation tools for European forests. Ecol Bull 50:1–240

Lee S, Fan Z (2012) Effect of spatial scale on modeling and predicting mean cavity tree density: a comparison of modeling methods. Open J For 2(4):219–224. doi:10.4236/ojf.2012.24027

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multi-scaled approach. Island Press, Washington

MCPFE (2007) State of Europe's forests. In: The MCPFE report on sustainable forest management in Europe. Ministerial conference on the protection of forests in Europe. Warsaw, Poland

Menard S (2002) Applied logistic regression analysis, 2nd ed. Series: Quantitative applications in the social sciences, no. 106. Sage Publications, Beverley Hills

Meschede A, Heller KG (2003) Ecologie et protection des chauves-souris en milieu forestier. Le Rhinolophe 16:1–248

Métailié JP (2001) Un patrimoine historico-environnemental: les forêts pastorales dans les Pyrénées. Actes du 126 ème congrès national des sociétés historiques et scientifiques. Paysages, territoires et aménagement dans le sud de la France. Toulouse, 33–47

Michel AK, Winter S (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. For Ecol Manag 257:1453–1464

Michel AK, Winter S, Linde A (2011) The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can J For Res 41:300–308

Möller G (2009) Habitats and Substrates of Saproxylic Invertebrates, mainly beetles. Dissertation Freien Universität, Berlin

Moning C, Müller J (2009) Critical forest age thresholds for diversity of lichens, molluscs and birds in temperate beech (*Fagus sylvatica* L.) plant communities. Ecol Indic 9:922–932

Müller J (2005) Waldstrukturen als Steuergröße für Artengemeinschaften in kollinen bis submontanen Buchenwäldern. In: Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt. Technische Universität, München, http://mediatum.ub.tum.de, p 197

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations. Eur J For Res 129:981–992

Müller J, Brunet J, Brin A, Bouget C, Brustel H, Bussler H, Förster B, Isacsson G, Köhler F, Lachat T, Gossner M (2012) Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conserv Diver. doi:10.1111/j.1752-4598.2012.00200.x

Nakazawa M (2012) Package 'fmsb'. http://cran.r-project.org/web/packages/fmsb/fmsb.pdf

Nilsson SG, Hedin J, Niklasson M (2001) Biodiversity and its assessment in boreal and nemoral forests. Scand J For Res 10–26

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2011) 'Vegan' package: community ecology package. http://cran.r-project.org/web/packages/vegan/vegan.pdf

ONF (2009) Conservation de la biodiversité dans la gestion courante des forêts publiques. INS-09-T-71, Paris

Pardé J, Bouchon J (1988) Dendrométrie. ENGREF, Nancy

PEFC France (2011) Cahier des charges relatif à la gestion durable de la forêt. http://www.pefc-france.org

R Development Core Team (2011) R: a language and environment for statistical computing. Vienna Austria, R Foundation for Statistical Computing

Ranius T (2000) Minimum viable metapopulation size of a beetle, *Osmoderma eremita*, living in tree hollows. Anim Conserv 3:37–43

Ranius T, Fahrig L (2006) Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scand J For Res 21:201–208

Ranius T, Niklasson M, Berg N (2009) Development of tree hollows in pedunculate oak (*Quercus robur*). For Ecol Manag 257:303–310

Remm J, Lohmus A (2011) Tree cavities in forests: the broad distribution pattern of a keystone structure for biodiversity. For Ecol Manag 262:579–585

Remm J, Lohmus A, Remm K (2006) Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? For Ecol Manag 221:267–277

Robles H, Ciudad C, Matthysen E (2011) Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. For Ecol Manag 261:1428–1435

Robles H, Ciudad C, Matthysen E (2012) Responses to experimental reduction and increase of cavities by a secondary cavity-nesting bird community in cavity-rich Pyrenean oak forests. For Ecol Manag 277:46–53

Schall P, Ammer C (2013) How to quantify forest management intensity in Central European forests. Eur J For Res 132:379–396

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in deadwood. Cambridge University Press, Cambridge

Thompson LA (2009) R (and S-PLUS) Manual to Accompany Agresti's Categorical Data Analysis (2002). 2nd edition, 276 p. http://www.math.tau.ac.il/~yekutiel/CDA/Thompson_manual.pdf

Vuidot A, Paillet Y, Archaux F, Gosselin F (2011) Influence of tree characteristics and forest management on tree microhabitats. Biol Conserv 144:441–450

Wegge P, Rolstad J (1986) The spacing of capercaillie leaks in relation to habitat and social organization. Behav Ecol Sociobiol 19:401–408

Wiktander U, Olsson O, Nilsson S (2001) Seasonal variation in home range size, and habitat area requirement of the lesser spotted wood pecker *Dendrocopos minor*. Biol Conserv 100:387–395

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. For Ecol Manag 255:1251–1261

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ORIGINAL PAPER

Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees

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Abstract In forest ecosystems, the level of biodiversity is strongly linked to dead wood and tree microhabitats. To evaluate the influence of current forest management on the availability of dead wood and on the abundance and distribution of microhabitats, we studied the volume and diversity of dead wood objects and the distribution and frequency of cavities, dendrothelms, cracks, bark losses and sporophores of saproxylic fungi in montane beech-fir stands. We compared stands unmanaged for 50 or 100 years with continuously managed stands. A total of 1,204 live trees and 460 dead wood objects were observed. Total dead wood volume, snag volume and microhabitat diversity were lower in the managed stands, but the total number of microhabitats per ha was not significantly different between managed and unmanaged stands. Cavities were always the most frequent microhabitat and cracks the least frequent. Dendrothelm and bark loss were favored by management. Beech (*Fagus sylvatica*) carried many more microhabitats than silver fir *(Abies alba*), especially cavities, dendrothelms and bark losses. Fir very scarcely formed dendrothelms. Secondary tree species played an important role by providing cracks and bark losses. The proportion of microhabitat-bearing trees increased dramatically above circumference thresholds of 225 cm for beech and 215 cm for fir. Firs with a circumference of less than 135 cm did not carry microhabitats. In order to conserve microhabitat-providing trees and to increase the volume of dead wood in managed stands, we recommend conserving trees that finish their natural cycle over 10–20% of the surface area.

Keywords Dead wood · Cavity · Crack · Dendrothelm · Bark loss · Girth threshold

Introduction

Forests are complex terrestrial ecosystems (Rameau et al. 2000; Gosselin and Laroussinie 2004; Dajoz 2007), and a large part of this complexity is linked to woody plants, living or dead (Maser et al. 1984; McMinn and Crossley 1996; Vallauri et al. 2002; Dajoz 2007), and in particular to the heterogeneity provided by tree microhabitats (Winter and Möller 2008; Michel and Winter 2009). Because more than 25% of forest species are saproxylic organisms (Stokland et al. 2004; Bobiec et al. 2005) in boreal and temperate forests, the level of biodiversity is strongly linked to dead wood and tree microhabitats which are key structural attributes of old-growth forests (Bauhus et al. 2009).

As is the case for all temperate forests in Europe, the montane forests of the Pyrenees have been impacted by a high level of anthropization due to thousands of years of livestock-herding (Métailié 1984) and through the high demand in terms of energy for industry during the XVIIIth

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and XIXth centuries (Wonoroff 1984; Davasse 1992; Métailié 2001). Today, the main goal of the owners of Pyrenean forests is the production of saw timber. The current management of montane beech-fir forests in the Pyrenees consists of carrying out selective cuts, every 10–20 years on average, to improve the overall commercial quality of the wood produced. Thinning removes the trees: (1) which exceed the economic girth limit, (2) which have characteristics that reduce the quality of their wood (e.g., a lot of big knots, woodpecker cavities, saproxylic fungi), (3) whose remaining life expectancy is estimated as inferior to the cutting interval, and (4) disseminated tree species or those whose wood has little commercial value, in favor of beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.). Generally, thinning removes a fairly low number of stems (on average only 10–30% of the total number of trees), but mostly focuses on large trees.

The impact of these forestry methods on the biodiversity of montane forest ecosystems is little documented, as the references currently available mostly concern the boreal context (Fridman and Walheim 2000; Darveau and Desrochers 2001; Siitonen 2001), the forests of the North-West coast of the USA (e.g., Maser et al. 1984), or the tropical forests of Australia (Grove 2002a, b). However, the make-up of these forests, their dynamics and the forestry methods used in these zones are very different from those that occur in the montane forests of Europe. Almost all of the studies currently available have described the impact of forestry on biodiversity using bio-indicators such as Carabidae Coleoptera (Du Bus de Warnaffe and Lebrun 2004), saproxylic Coleoptera (Martikainen et al. 2000), mammals (Carey et al. 1999; Loeb 1999), saprophytic fungi (Sippola and Renvall 1999; Norsted et al. 2001), birds (Martikainen et al. 1998; Moning and Müller 2008, 2009), molluscs (Moning and Müller 2009) or lichens (Moning et al. 2009; Moning and Müller 2009). However, biodiversity assessment in forests using bio-indicator tools is very expensive and requires taxonomic specialists. Therefore, this approach cannot be used as a routine method for forest managers, and the focus on tree microhabitats as a proxy of taxonomic biodiversity is recommended (Winter and Möller 2008). However, relatively few studies that link forest structure and biodiversity are currently available. The majority of studies have focused on dead wood and its marked contribution to the level of biodiversity observed in forests (Harmon et al. 1986; Samuelsson et al. 1994; Darveau and Desrochers 2001; Norden et al. 2004; Odor et al. 2006). The most studied tree microhabitats are cavities (Healy et al. 1989; Fan et al. 2003; Branquart and Liégeois 2005). Deconchat (1994) pointed out the important role of mature trees as a source of biodiversity, and Nilsson et al. (2002) showed the positive effect of the presence of mature trees on the presence of endangered taxa. Gilg (2004) affirmed that "forestry methods, by taking away dead wood, destroy more than half of the microhabitats present in a natural forest." Winter and Möller (2008) observed microhabitats in lowland pure beech forests and Michel and Winter (2009) studied microhabitats in Douglas-fir forests.

However, to our knowledge, microhabitats in mixed beech-fir forests of Europe have not yet been studied despite the fact that this is a forest type with great economic and ecological importance, existing in most of the European mountain ranges.

Furthermore, the respective contribution of the different tree species in terms of the supply of microhabitats has not generally been looked at. Finally, the types of microhabitats carried by mature trees have not generally been specified.

In this study, besides dead wood, we focused on a set of five microhabitats: cavities, cracks, dendrothelms (water filled holes in the wood), bark loss and sporophores of saproxylic fungi; we studied these elements in stands that have been unmanaged for more than 50 years or more than 100 years, as well as in continuous managed stands, within montane beech-fir forests of the central Pyrenees. These five microhabitats seem to be very important for taxonomic diversity in forests because the associated taxonomic groups are numerous and varied (Table 5 in supplementary material), or very specific. Cavities are used for protection against bad weather conditions or predators for more than 25% of vertebrate species in the north-eastern North American forests (DeGraaf and Shigo 1985; Healy et al. 1989) and in France, 41% of forest birds are cavity-dwelling species (Blondel 2005). Furthermore, cavities, cracks and bark loss are the indicators of natural forests (Michel and Winter 2009). Dendrothelm-dwelling species are not numerous, but very specialized: there are only 14 species in Europe, but six of them are specifically associated with dendrothelms (Kitching 1971). Sporophores of saproxylic fungi support a varied entomofauna (Dajoz 2007), especially when they are tough (polypores s.l.) or pulpy (e.g., Oyster fungi). Some parasitic fungi also use saproxylic fungi as a resource (Lisiewska 1992; Ellis and Ellis 1998). Even though sporophores of fungi are not representative of the strict spatial distribution of the species (Schmit and Lodge 2005), nor of the quantity of mycelium and the number of individuals (Richard et al. 2005), a high abundance of sporophores of saproxylic species has significance because it can be correlated with the presence of rare species (Bässler and Müller 2010) and a lot of insects live in the sporophores (Dajoz 2007).

This paper aims to: (1) evaluate the influence of silvicultural practices and time since logging on dead wood and on the abundance and distribution of these five tree microhabitats; (2) evaluate the role of the different tree species in terms of the supply of microhabitats, independently of their abundance; (3) identify critical girth tree thresholds for microhabitat presence.

We discuss the results in the context of sustainable management practices and then we propose a management strategy that could help to conserve a variety of tree microhabitats and dead wood objects in commercial stands.

Materials and methods

Study area

The stands studied are situated in the foothills of the central Pyrenees (WGS 84, Lat/Lon: 43°N/0.34°E). The dominant substrata are alkaline rocks of the Mesozoic, but older acid rocks may be observed very locally (Barrère et al. 1982, 1984; Ternet et al. 1995, 1996). The mesoclimate is of an Atlantic montane type, which is fairly harsh. Dominant winds are westerly and the position of the first mountain slopes provokes high rainfall (more than 1,500 mm/year on average). This precipitation falls partly in the form of snow, but also as mist. The topoclimates linked to exposition, slope and confinement are strongly contrasted. The conditions of the sites are overall very favorable to the growth of native tree species, at least up to the altitude of 1,500 m.

Characteristics of stands observed and samples used

All the stands studied are natural habitats of beech-fir forest (Bardat et al. 2004). However, the sylvofacies hosts a very variable proportion of fir, which is directly due to past management, with a high level of anthropization generally favoring beech at the expense of fir (Métaillé 2001). These stands are all located at an altitude of between 950 and 1,100 m, which corresponds to the Lower Montane bioclimatic zone in the Pyrenees.

We studied four zones for three levels of time since logging (Fig. 1). "BF-reference" contains the more mature beech-fir stands with no logging since 1900. "B-cable" contains stands dominated by beech, in a zone logged by a gravity cable technique in 1960 and unmanaged since. We distinguished two modalities in the group of stands logged up until the present day: "B-managed" and "F-managed" contain stands respectively dominated by beech and fir and logged 2 or 3 times in the last 20 years (see Fig. 5 and Fig. 6 in supplementary material). All the managed stands were under the control of the same manager.

Observations were carried out between 2003 and 2005 on a sample of 40 plots (Table 1). All plots were set up based on an approach of relascope sampling using the no 1 strip (with a return angle of 1/50) of a Bitterlich relascope (Bitterlich 1984; Pardé and Bouchon 1988; Rondeux 1993). This device enables the production of a stand inventory using a constant angle. The error due to terrain slope is automatically corrected for by the device, which is very practical in the mountains. The use of a relascope leads to a high sampling rate of mature trees a priori richer in microhabitats (Winter and Möller 2008), but a high level of imprecision in the density of smaller trees, which seem to play a less important role in estimates of microhabitat richness. As the relascope sampling of fallen coarse woody debris is very sensitive to surveyor judgement (Ringvall and Stahl 1999), all the observations were carried out by the same operator.

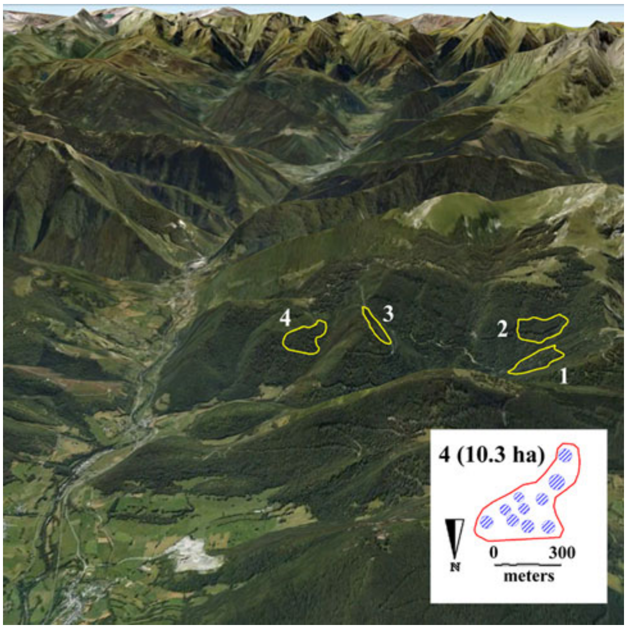

Fig. 1 Localization of the stands. *1*: BF-reference stands; *2*: B-cable stands; *3*: F-managed stands; *4*: B-managed stands. The zoom shows the spatial repartition of plots (*black-hatched* areas) within the B-managed zone

To incorporate correctly the variability of each management category, each one of them was sampled with 9–11 plots. The plot surface was 0.3 ha on average and the distance between two plots was, at least, 100 m (Fig. 1; Table 1).

Measurements and observation of microhabitats

One thousand two hundred and four live trees and 460 dead wood objects were observed individually. All the live trees included in the relascope sampling were identified to species level and measured for the circumference on the outside of the bark, at breast height, to the nearest centimetre, without the notion of minimum girth being taken into account. Then, by going around the whole tree, we carefully examined the trunk from the ground to the crown to note the microhabitats hosted on the visible part of the

Table 1 Study design. The surface of the sampled area per modality is the sum of the plot surfaces, estimated with the distance between the plot center and the most distant tree observed

Modality	Number of plots	Total area sampled (ha)	Number of live trees observed	Numbers of dead wood items observed
BF-reference	10	4,684	371	84
B-cable	9	2,130	286	124
B-managed	10	2,386	280	73
F-managed	11	3,292	267	179
Total	40	12,492	1,204	460

trunk. Logs were grouped with snags and were not included in the stand basal area. In the case of standing dead wood, we distinguished "high stumps," when the dead part of the tree had a height of between 0.5 and 1.5 m, from "snags," whose height exceeded 1.5 m. In the unmanaged stands, high stumps corresponded to snags in a state of ultimate decay. All dead wood items were identified and measured in length and in girth beyond a circumference of 60 cm at the smallest extremity. The circumference was measured in the middle for logs and snags of under 4 m, at the cut for high stumps, and at breast height for snags of over 4 m, with the circumference being measured along the outside of the bark when this was present. Dying or dead trees were classed on a saproxylation scale of 6 levels (see Table 6 in supplementary material). For the large dead wood objects that showed a certain heterogeneity in the level of decay, the decay stage noted corresponded to the stage most present (in terms of volume) on the observed item. We used the French management girth classes: circumference at breast height (CBH) 65 cm $\leq$ Small Tree $\leq$ 85 cm; Medium Tree $\leq$ 150 cm; Large Tree $\leq$ 210 cm; Very Large Tree $>$ 210 cm.

In addition to the dead wood, we observed the following microhabitats, both on alive and dead trees. We defined the microhabitats partly with thresholds.

1. Cavities, with a distinction between "empty" cavities and cavities with wood mould (in a decay stage of more than 3). Cavities were not observed on logs. We distinguished the cavities situated at less than 0.5 m from the ground because logging does not remove them.
2. Cracks in the tree trunk, of a width of between 1 and 5 cm and situated over 1 m from the ground, in the wood or in the form of bark in the process of peeling. Bats were the benchmark for these thresholds (Meschede and Heller 2003).
3. Dendrothelms, when the orifice diameter was more than 3 cm.
4. Sporophores of saproxylic fungi (without taxonomic identification). Each tree or item of wood inventoried was classed in relation to the presence or not of sporophores, without estimating their numbers. In connection with the dates of observations, the great majority of fungi noted were species that produce perennial sporophores (Polypores *sl.*).
5. Patches with bark loss of at least 10 cm × 10 cm, only on live or dying trees. Wood was in a decay stage of less than 2.

We focused on microhabitats borne by the living trees because they are directly concerned by forest management. For the role of the tree species to the supply of microhabitats, we focused on BF-reference stands to avoid interaction between the effects of tree species and management.

Calculations and statistical procedures

The theoretical number of trees per hectare was calculated by allocating to every tree observed in the relascope sampling the coefficient N_C, in relation to its circumference (C): $N_C = \pi\ 10^8\ [\mathrm{ArcTan}(1/50)/C]^2$ (Pardé and Bouchon 1988).

The volumes of the stumps, snags smaller than 4 m and dead wood items on the ground were calculated by considering them as cylinders. The volume of standing wood was estimated using Schaeffer's cubage rates (Schaeffer 1949). Dead wood was expressed in $m^3\ ha^{-1}$ and also in % of total wood volume (dead + alive) to take into account the level of productivity of the habitat (Sippola et al. 1998). The proportion of snags was calculated because is a pertinent indicator of stand maturity (Gonin 1988).

For the variables expressed per surface unit, we analyzed the sum per plot. On the other hand, to analyze the relations with the girth (thresholds), we used individual variables of each observed tree.

All statistical calculations were done using "R" software (R Development Core Team 2007).

Comparisons of frequencies of tree-bearing microhabitats per species were carried out with the chi-square test (Snedecor and Cochran 1971). The test of Kruskal–Wallis (Sprent 1992) was used to compare the number of stump cavities and the number of trunk cavities. The data on dead wood volume were analyzed with analysis of variance.

For the relation between numbers of microhabitats and tree girth, we used tree-based regression and classification models. Threshold values were calculated by recursive partitioning (Lausen and Schumacher 1992; Hothorn and Lausen 2003; Hothorn and Zeileis 2008). This approach allows simultaneous identification of a threshold and assessment of its significance by means of a statistical test procedure. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics. Their validity is judged by multiple test procedures. Once the data set is divided into two subsets by the threshold with the highest explanatory power, each subset is evaluated for additional thresholds. This method provides a decision tree with *P* values for one or more critical thresholds. Based on 10,000 bootstrap samples, a confidence interval (80%) was calculated for all thresholds. The calculations were performed on "presence–absence" data, using the add-on package "party" (Hothorn et al. 2006b). The girth thresholds were calculated only for BF-reference stands (1) to only use data that were independent of management, (2) to observe a wide gradient in terms of tree girth, given that very large trees are rare in managed stands.

The global hypothesis of independence between the four stand categories and the response variable (number of one or all microhabitats) was assessed using multiple testing of re-sampled data (Westfall and Young 1993; Hothorn et al. 2006a). The *P* value obtained by this procedure was adjusted for multiple comparisons utilizing a step-down max-T approach. In addition, for each response variable, a post hoc test (Tukey all-pair comparisons) was applied to assess the differences between each pair of categories. The corresponding *P* values were also adjusted for all comparisons performed here. This analysis procedure is based on implementation of the above procedures in the add-on package "coin" (Hothorn and Hornik 2005).

Results

Dead wood and microhabitats

All stands had less than 58 m^3/ha of dead wood per ha (Fig. 2). The average total volume of dead wood reached between 1.8 and 11% of the total volume of wood (live + dead). The total volume of dead wood was lower in the managed stands (B-managed stands and F-managed stands together) than in the unmanaged stands (BF-reference stands and B-cable stands together) ($F = 18$, $P < 0.001$), and the significant difference between the means of the two

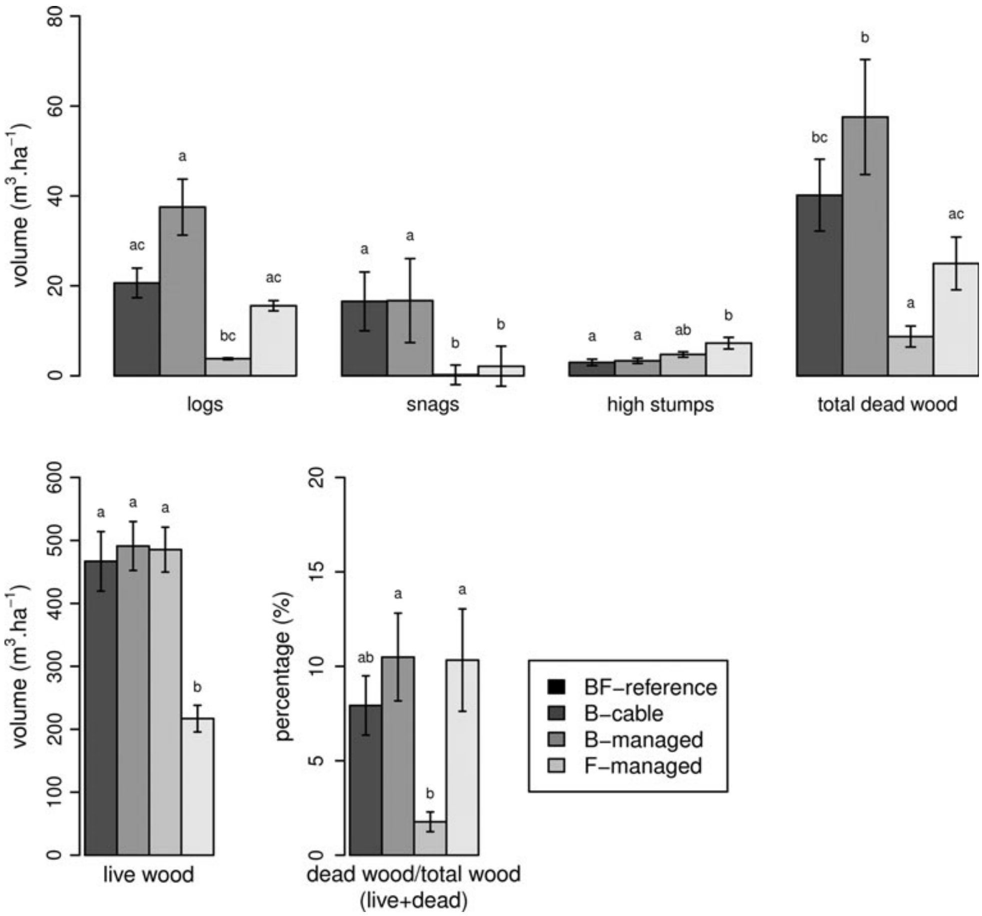

Fig. 2 Distribution of dead wood per type of support and quantification in relation to live wood (Montane beech-fir forests in central Pyrenees). *Vertical lines* indicate the standard error and *letters* indicate significant differences

modalities was evaluated to 5.2 $m^3\ ha^{-1}$ (Tukey-test $t = 4.3, P < 0.001$). Nevertheless, we observed 25 $m^3\ ha^{-1}$ in F-managed stands. Logs generally dominated the dead wood volume, but the volumes of logs and snags did not differ significantly in the BF-reference stands. In managed stands, the standing dead wood was mainly represented by high stumps: 54 and 29%, respectively, for B-managed stands and F-managed stands. We observed an almost complete absence of snags in B-managed stands.

Patterns of the distribution of decay stages of dead wood were very different between unmanaged and managed stands (Fig. 3 and see also Table 7 in supplementary material). BF-reference stands showed quite a high presence of dying trees (stage 0.5) and the main decay stage was the 4th. B-cable curve culminated in decay stage 2. Managed stands did not include the dying tree stage and showed a curve culminating in stage 2 or 3. In B-managed stands, only the stages of decay 3 and 4 occurred in the field.

Beech and fir showed almost the same profiles of decay.

Considering live trees only, beech carried more microhabitats than fir, especially in terms of cavities ($P < 0.001$), dendrothelms ($P < 0.001$) and bark losses ($P < 0.001$). Fir formed dendrothelms very scarcely (Table 2). In B-reference stands, the secondary tree species (*Acer* spp., *Prunus avium*, *Taxus baccata* and *Tilia platyphyllos*), in spite of their low densities, had an important role in providing microhabitats, particularly for cracks and bark loss.

Cavities were always by far the most frequent microhabitat and cracks the least frequent (6% of microhabitat-bearing trees in the BF-reference stands).

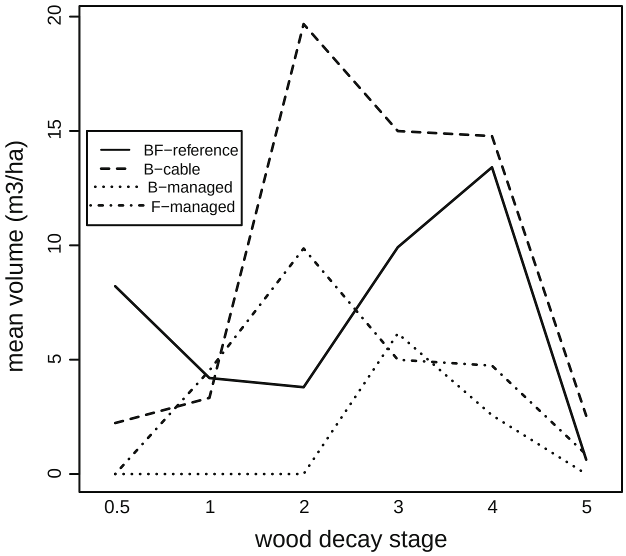

Fig. 3 Distribution of dead wood volume per decay stage. (Montane beech-fir forests in central Pyrenees)

In the BF-reference stands, 29% of the trees bearing microhabitats and almost 90% of the trees bearing saproxylic fungi were standing dead wood.

The comparison of the stand types showed significant differences for microhabitat density of dendrothelms, cracks, saproxylic fungi and bark losses (Tables 2, 3). Cracks were not observed in the F-managed stands and were mainly linked to the deciduous tree species. Cracks observed on standing dead trees were mostly in the form of bark in the process of peeling. The number of live trees that carried saproxylic fungi was very low (0.3 per ha) in the B-managed stands. We noted also a reduction in the trunk cavity number in managed stands, but the difference was not significant. Management led to a reduction in abundance of these three microhabitats. Dendrothelms and bark losses were more numerous in stands dominated by beech. B-managed stands offered more microhabitats than F-managed ones.

In B-reference stands, the cavities were as numerous on the trunk as at the foot of the tree ($P = 0.5$, NS). Cavities with decaying wood represented more than 70% of the cavities observed. There was less than four empty trunk cavities per ha. More than 80% of the cavities were borne by live trees.

Tree circumference thresholds

There were significant thresholds for the CBH at 225 cm for beech (80% confidence interval: 205–239 cm) and at 135 and 215 cm for fir (80% confidence intervals, respectively: 135–170 and 135–230 cm) (Fig. 4 and see also Fig. 7 and Fig. 8 in supplementary material). Fir did not bear microhabitats if the CBH was below 135 cm. Beech carried on average twice as many microhabitats when CBH $\geq$225 cm; in this case, beech carried on average almost one microhabitat per tree. When CBH $\geq$225 cm, beech carried on average twice as many microhabitats as fir.

Considering the usual circumference classes used in French forestry, beech provided microhabitats in all circumference classes, whereas fir did not provide microhabitats in the Small tree class (CBH $\leq$85 cm; Table 4).

Discussion

Dead wood

Gonin showed in 1988 that montane beech-fir forests have a natural cycle of 300–400 years. This cycle is made up of five phases: "rejuvenation," "initial," "optimal," "terminal" and "decline." This latter phase is characterized by high volumes of dead and live wood and an aggregated distribution of very large dead trees. The results of dead

Table 2 Distribution of tree bearing microhabitats per species and per microhabitat in the stands (montane beech-fir stands, central Pyrenees)

Microhabitat	Beech	Fir	Other tree species	Live trees	Standing dead trees	All trees
BF-reference						
Cavities	37.41 (85.8%)	4.12 (9.4%)	2.08 (4.8%)	35.11 (80.5%)	8.50 (19.5%)	43.61
Dendrothelms	8.39 (99.9%)	0 (0%)	0.05 (0.1%)	7.70 (91.2%)	0.74 (8.8%)	8.44
Cracks	1.39 (29%)	0.78 (16%)	2.66 (55%)	3.96 (82.0%)	0.87 (18.0%)	4.83
Fungi	12.03 (84.0%)	2.2 (16.0%)	0 (0%)	1.47 (10.3%)	12.85 (89.7%)	14.32
Bark losses	1.32 (12.5%)	0.74 (7.0%)	8.50 (80.5%)	9.69 (91.8%)	0.87 (8.2%)	10.56
Sub-total/ha[a]	60.54 (74.0%)	7.93 (9.7%)	13.29 (16.3%)	57.93 (70.9%)	23.83 (29.1%)	81.76
Dead wood (m^3/ha)	11.79 (29.4%)	25.67 (63.9%)	2.70 (6.7%)	–	–	40.16
B-cable						
Cavities	46.7 (96.1%)	1.92 (3.9%)	0 (0%)	48.6 (100%)	0 (0%)	48.64
Dendrothelms	17.83 (100%)	0 (0%)	0 (0%)	17.8 (100%)	0 (0%)	17.83
Cracks	6.37 (100%)	0 (0%)	0 (0%)	4.32 (67.8%)	2.05 (32.2%)	6.37
Fungi	36.52 (97.6%)	0.88 (2.4%)	0 (0%)	8.86 (23.7%)	28.54 (76.3%)	37.40
Bark losses	71.01 (45.3%)	3.30 (2.1%)	82.51 (52.6%)	156.8 (100%)	0 (0%)	156.82
Sub-total/ha[a]	178.4 (66.8%)	6.1 (2.3%)	82.51 (30.9%)	236.38 (88.5%)	30.59 (11.5%)	267.06
Dead wood (m^3/ha)	52.38 (91.0%)	5.18 (9.0%)	0 (0%)	–	–	57.56
B-managed						
Cavities	43.14 (100%)	0 (0%)	0 (0%)	42.86 (99.4%)	0.28 (0.6%)	43.14
Dendrothelms	54.8 (100%)	0 (0%)	0 (0%)	54.8 (100%)	0 (0%)	54.8
Cracks	2.34 (100%)	0 (0%)	0 (0%)	2.34 (100%)	0 (0%)	2.34
Fungi	8.24 (89.6%)	0.96 (10.4%)	0 (0%)	0.35 (3.8%)	8.85 (96.2%)	9.20
Bark losses	73.83	0 (0%)	0 (0%)	73.8 (100%)	0 (0%)	73.83
Sub-total/ha[a]	182.3 (99.5%)	0.96 (0.5%)	0 (0%)	174.15 (95.0%)	9.13 (5.0%)	183.28
Dead wood (m^3/ha)	8.36 (95.9%)	0.36 (4.1%)	0	–	–	8.72
F-managed						
Cavities	25.53 (81.6%)	5.75 (18.4%)	0 (0%)	30.18 (96.5%)	1.09 (3.5%)	31.28
Dendrothelms	11.49 (99.6%)	0.05 (0.4%)	0 (0%)	9.4 (81.5%)	2.14 (18.5%)	11.54
Cracks	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Fungi	10.87 (68.2%)	2.52 (15.8%)	2.5 (16.0%)	3.45 (21.7%)	12.48 (78.3%)	15.93
Bark losses	0 (0%)	9.33 (100%)	0 (0%)	9.3 (100%)	0 (0%)	9.33
Sub-total/ha[a]	47.89 (70.3%)	17.65 (25.9%)	2.54 (3.8%)	52.33 (76.9%)	15.67 (23.1%)	68.08
Dead wood (m^3/ha)	3.45	19.13	2.40	–	–	24.98

The first numbers are averages per hectare of the number of trees that carry the microhabitat and those in brackets represent the rate of participation of each species for the microhabitat

[a] This total includes the possibility that certain trees might host several types of microhabitat, which would have the effect of diminishing the number of host trees

Table 3 Impact of silviculture and dominant tree species on microhabitat abundance

	Trunk cavities	Cracks	Saproxylic fungi	Dendrothelms	Bark losses	Total
1-BF-reference	236^{a}	48^{ab}	1.5^{b}	84^{bc}	97^{a}	467^{ab}
2-B-cable	146^{a}	57^{a}	8.9^{ad}	194^{b}	684^{b}	$1{,}090^{a}$
3-B-managed	100^{a}	23^{ab}	0.3^{cd}	608^{a}	827^{b}	$1{,}559^{c}$
4-F-managed	142^{a}	0^{b}	3.5^{abcd}	127^{bc}	103^{a}	375^{b}

Stand comparisons were performed with a step-down max-T approach. Scores are linear statistic *T* values. Live trees only. (Montane beech-fir stands; central Pyrenees). Letters indicate significant differences

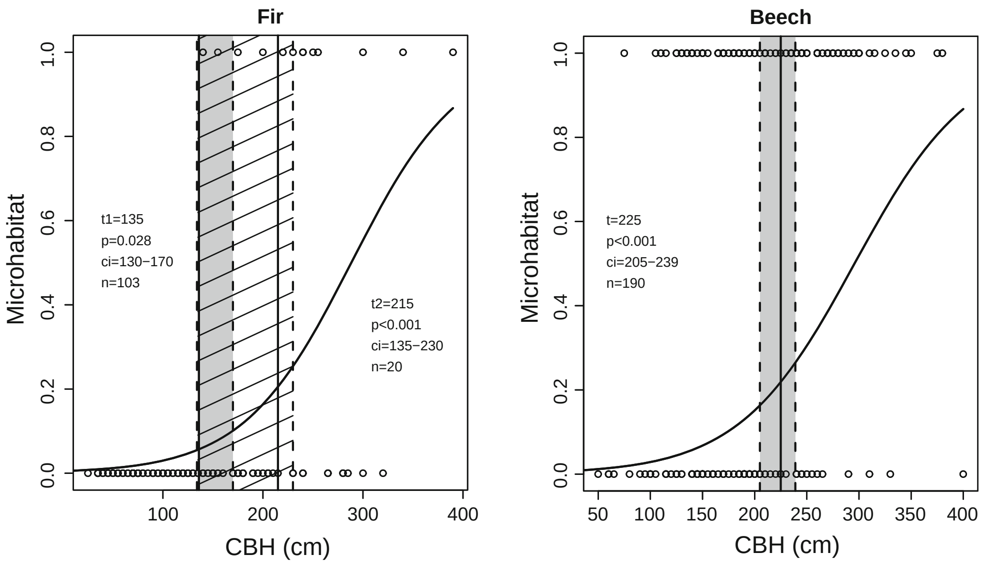

Fig. 4 Data distribution for CBH cm (*X*-axis) and presence/absence of microhabitats (*Y*-axis) for beech (*Fagus silvatica)* and fir (*Abies alba)* with logistic regression curves. BF-reference stands. The *black vertical lines* indicate the threshold values and the two *dotted vertical lines* the range of its 80% confidence intervals (two thresholds for the fir: *gray box* indicates the CI for $t = 135$ cm and the *hatched box* indicates the CI for 215 cm). *t* threshold value, *CI* confidence interval of the threshold value and *n* number of observed trees. Microhabitats on live trees only: cavities, sporophores of saproxylic fungi, dendrothelms, bark losses and cracks. (Montane beech-fir stands in central Pyrenees)

Table 4 Distribution of tree microhabitats (dead wood excluded) and host trees of microhabitats per category of girth

Category of girth	Beech			Silver Fir		
	N total/ha	% of host trees per girth category	% of host trees per stand	*N* total/ha	% of host trees per girth category	% of host trees per stand
Small trees	2.2	53.2	6.42	0	0	0
Medium trees	16.1	33.5	35.76	1.3	1.4	30.62
Large trees	12.6	43.9	30.38	1.2	1.3	29.67
Very large trees	12.4	70	27.45	1.9	2.1	39

Circumference at breast height (CBH): 65 cm $\leq$ Small Tree $\leq$ 85; Medium Tree $\leq$ 150; Large Tree $\leq$ 210; Very Large Tree $>$ 210). Poles (CBH $<$ 65 cm) are not taken into account. Results are expressed as: (1) total number of microhabitats per hectare, (2) relative abundance of the host trees in the girth category, (3) contribution of the girth category to the total number of host trees of the stand. (Montane beech-fir stands in central Pyrenees)

wood volumes (Fig. 2) and field observations showed an absence of the phase of "decline," even in BF-reference stands. It is probable that the long history of anthropization ended too recently to allow the tree communities to finish a complete natural cycle. The modal phase observed in B-cable stands is "terminal," whereas B-managed and F-managed are in an "optimal" phases: management is in the process of rejuvenating stands.

In all the stands that we studied, the volumes of dead wood were inferior to the data given in the literature for sub-natural forests (Christensen et al. 2005). If we express the results on dead wood in % of the total volume of wood (live + dead), Siitonen (2001) gives values much superior to the values that we found: 18–40% (on average 28%) for the forests of common spruce [*Picea abies* (L.) H. Karst.] and Scots pine (*Pinus sylvestris* L.), in keeping with Sippola (2001) who indicates 20–30% for Scandinavian forests. Bobiec et al. (2005) indicate a norm superior to 25% for unmanaged Central European forests. Continuing on from varied bibliographical sources, Gilg (2004) indicates average volumes of 20–40% (from 10 to 50% in extremes). The absence in the BF-reference stands of intense disturbance (storm damage, fire) throughout the last century may also have contributed to this low percentage of dead wood. Dead wood represented 11% of the total volume in the F-managed stands, while it represented only 1.8% in the B-managed stands. The predominance of fir in the F-managed stands explains this difference because, at the time of the last logging, only the stems of fir had a commercial value and industrial softwood was not removed. The volume of dead wood in the B-cable stands is partly linked with several windfall gaps. Nevertheless, only B-managed stands had a lower volume than the threshold range of 20–50 m^3 ha^{-1} revealed by Müller and Bütler (2010) for biodiversity conservation.

All authors point out the relative rarity of dead wood in the form of snags when compared with ground dead wood in very mature stands. Compiling a large amount of data on the forests of Fennoscandia and the North of Russia, Siitonen (2001) gives an average proportion of volume snags/total vol. dead wood as 30%. Muller and Liu (1991) state that, in the mixed forests of North America, snags represent 18% of total volume of dead wood. For Sippola (2001), in European boreal forests, 60–80% of total volume of dead wood is on the ground and only 18–35% is in the form of snags. Nilsson et al. (2002) give an average of 20–40% of volume of standing dead wood for the Polish forest of Bialowieza. Christensen et al. (2005) report that the ratio vol. snags/total vol. dead wood of an unmanaged European beech forest is 41% (22–60%). Dead wood in the form of snags measured in the BF-reference stands (41%) and in the B-cable stands (29%) are in agreement with these proportions (Table 2). On the other hand, the low amounts observed in B-managed (2.4%) and F-managed (8.5%) illustrates a strong effect of silviculture on dead wood proportions.

Christensen et al. (2005) point out that in a beech forest that was unmanaged for a long time, dead wood is to be found in all stages of decay, but we did not find any references giving the distribution of dead wood items per decay stage for the forests of Western Europe. The results obtained for the BF-reference stands are in keeping with the logic of the recycling of dead wood: the volume increased from stage 2 to stage 4 through simple increase in the duration of the stage itself (Maser et al. 1984) and numerous dying trees supplied the dead wood cycle. The volume at stage 5 was relatively low because this stage combines great difficulty in terms of observation with a reduction in volume due to loss in the contours of the piece of wood, as well as the dispersion of the heavily altered woody material. This final result is not in accordance with the observations of McMillan et al. (1977) who showed a volume at stage 5 much superior to the volume of each of the other stages in old stands of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco]. This is certainly linked to the different behavior of the naturally durable wood of Douglas fir compared with the easily altered wood of beech and silver fir. The dead wood cycle was broken in the B-managed stands, and the main decay stage was linked to the last logging. The renewal in dead wood can be compromised by silviculture. The volume of the available dead wood may sometimes remains high when market conditions for wood are unfavorable to the extraction of certain low value products (e. g., industrial softwood), but the structure and the dynamics of the dead wood are dramatically disturbed.

Tree microhabitats

In the Pyrenees, a lot of mixed beech-fir forests were in the past transformed into pure beech forests. As beech is a much richer microhabitat provider than fir, this transformation increased the total supply of microhabitats per hectare. So, B-managed stands offered more microhabitats than F-managed ones, dominated by fir. But the comparison of beech and fir as regards organisms that are exclusively associated with one or the other tree species shows the importance of the biodiversity which is strictly associated with fir (Larrieu et al. 2010). Furthermore, a mixture of tree species is a guarantee of economic resilience because it is difficult to predict developments in the wood market.

With a total of 47 host trees ha^{-1} (Table 2), cavities were found on 61% of all microhabitat-bearing trees. Garrigue and Magdalou (2000) document 60 trees/ha with cavities in a protected nature reserve. Vallauri et al. (2002) think that at least one cavity per hectare is indispensable and that the optimum is about 10–20 cavity-bearing trees per hectare. Blondel (2005) thinks that the minimum for cavity-dwelling fauna is about 40 cavities/ha usable for birds, which is in keeping with the recommendations of Meschede and Heller (2003) for forest bats. The difference observed between beech and fir (fir only hosts 10% of the total number of cavities in BF-reference stands) is in keeping with the observations of Cline et al. (1980), Mannan et al. (1980) and McClelland and Frissell (1975) as well as Drapeau et al. (2005), who point out generally that cavities are rare in live conifers. Cavities are difficult to observe from the ground, and in deciduous trees, many small cavities are borne by big branches (Tillon 2006). This certainly leads to an underestimate of their number. In spite of trees bearing cavities being removed by thinning, reduction in the trunk cavity number in managed stands was not significant, maybe because this microhabitat is quickly renewed by woodpeckers and the fall of branches.

Dendrothelms were present in the BF-reference stands in only 10% of microhabitat-bearing trees. This result suggests that this microhabitat is quite rare in natural mixed forests, while it is a very frequent microhabitat in artificial beech forests in agricultural landscapes (Kitching 1971). Contrary to beech and maybe in connection with its mode of centripetal deterioration (the external layers rot quite quickly and fall off, while the heart resists much longer), the wood of silver fir only very exceptionally provides conditions favorable to the creation of dendrothelms. By creating surfaces which are subjected to decay, thinning favors the creation of the dendrothelms. Dendrothelms were more numerous in B-managed stands which combine high logging intensity with a predominance of beech. We could not find any references on the effect of dendrothelm densities on taxonomic biodiversity. We think that an increase in the dendrothelm frequency should not have a significant effect on taxonomic biodiversity because there are only a few dendrothelm-dwelling species and dendrothelms make up essentially one taxonomic group only.

In managed stands, logging creates bark losses at the foot of the trees, especially when the slope is steep. The thin bark of the beech facilitates bark loss. In B-cable stands, several windfall gaps and the construction of a forest road created numerous bark losses.

By trying to eliminate trees with characteristics that reduce the quality of their wood, current silvicultural practices reduce the number of microhabitats on live trees. Nevertheless, if a microhabitat is frequent initially (e.g., cavities), it does not disappear during the first thinning, as the forestry norms for harvesting levels are between 20 and 30% of live stems. However, certain microhabitats which are naturally infrequent, such as cracks, may be almost eradicated in one or two logging operations only. The only microhabitats favored by logging are dendrothelms and bark losses. Even if these fertile ecosystems provide a high yield in wood, the fairly short period of rotation between logging operations is certainly a limitation for the enrichment in microhabitats in managed stands.

The impact of management was not directly a reduction in the number of live trees hosting microhabitats. However, there was a trend to a reduction in the abundance of the trunk cavities, cracks and saproxylic fungi. On the contrary, dendrothelms and bark losses are encouraged by recent logging.

Tree circumference thresholds

Our data show clear threshold effects with a threshold of 225 cm circumference for beech and two thresholds, at 135 and 215 cm, for fir. Fan et al. (2003) indicate that there is a minimal girth tree threshold for bearing a cavity but they did not give any details about it, and they indicate that the probability of bearing cavities increases dramatically as tree circumference increases, without any indication of a significant threshold value. In the same way, Winter and Möller (2008) show that in beech forests which were unmanaged for more than 100 years, the number of microhabitats per tree is positively correlated with the girth of the tree, without any threshold effect. Dufour (2003) remarks too that there is an increase in the supply of cavities with circumference but identifies a threshold of 300 cm circumference, above which 1/3 of trees bear cavities. In stands dominated by sessile oak (*Quercus petraea* Liebl.), Tillon (2006) did not observe cavities in trees below a CBH of 38 cm and noted that the girth of cavity-bearing trees was significantly greater than that of trees without cavities. This very low threshold confirms that threshold values differ among tree species.

Considering the usual circumference classes used in French forestry, the increase in % of host trees that we observed concerns mainly the categories Large Tree and Very Large Tree (beech: +59% and fir: +62%). Because of differences of tree density per girth category, the total number of microhabitats per girth category is balanced in the categories Medium trees, Large trees and Very Large trees (Table 4).

Dufrêne et al. (2005) rather indicate an age threshold, pointing out that the availability of microhabitats becomes very high beyond 2/3 of the natural longevity of the tree species, which is approximately 200–250 years for beech and fir. In the context of average montane conditions of the central Pyrenees, a CBH = 220 cm corresponds roughly to an age of 200/250 years. Trees of this age support a great diversity of cavity-dwelling birds (Moning and Müller 2008), epiphytic lichens and molluscs (Moning and Müller 2009) in Bavarian montane forests.

Reconstitution of maturity in montane beech-fir forests

Although surveys of "sub-natural" forests have already been carried out in the Pyrenees using the discriminating criteria of a 50-year management-free period (Ponthus 1996), the characteristics of B-cable stands illustrate that 50 years is too short a period to allow the complete structural maturity of a stand. Indeed, natural stands have a more complex vertical structure, higher dendrological diversity in the bushy and arborescent strata, a higher proportion of Very Large trees and a bigger volume of dead wood, particularly in the form of snags (Greenberg et al. 1997; Nilsson et al. 2002; Christensen et al. 2005).

The characteristics of the BF-reference stands show that in the montane zone of the Pyrenees, more than 100 years without management is necessary to allow the return of a maturity close to that of natural stands.

These considerations are in keeping with the observations of Winter and Möller (2008).

Conclusion and suggestions to improve the current silviculture

Management of montane beech-fir stands reduces the total volume of dead wood and the snag volume, modifies the pattern of decay stages and also reduces the tree species diversity and the diversity of tree microhabitats.

We suggest managing montane mixed stands with an uneven-aged silvicultural system because it facilitates conservation of old-growth forests attributes which are necessary to conserve a wide range of species (Bauhus et al. 2009).

In Pyrenees forests, we are currently seeing the spread of a strategy of reduction in the girth of the largest logged trees, with the aim of increasing the supply to the wood industry and avoiding the depreciation of a high volume of wood. We have shown that in the montane beech-fir stands, the supply of microhabitats is strongly linked to the presence of large trees. It is indispensable to conserve permanently some trees with a CBH of more than 210 cm.

Silver fir hosts a specifically associated biodiversity (Nascimbene et al. 2009; Larrieu et al. 2010). As fir is a much poorer host for microhabitats than beech, it is necessary to favor a higher proportion of fir in the beech/fir mix to favor equal contributions of the tree species in terms of the supply in microhabitats. We suggest also conserving secondary tree species because they carry an associated taxonomic biodiversity.

We suggest that a beech-fir forest which is managed over the long term for the production of wood must consist of a unit made up of two sub-populations of trees. The first sub-population can be intensively managed with a short economic cycle (between 80 and 150 years) for wood production of quality, e.g., to avoid formation of red heartwood in beech wood. For the second sub-population, the natural sylvigenetic cycle should be respected to supply the microhabitats essential to a great part of forest biodiversity and also to increase the volume and the diversity of dead wood. Because it is important to assure the renewal of these attributes, a minimum of 10–20% of the surface area could be given over to the conservation or recruitment of trees with microhabitats (not including the area occupied by dead wood on the ground). This surface can be situated in a more or less aggregated manner, taking advantage of particular conditions such as rocks or steep slopes. To take into account the sometimes very low ability of certain taxa to spread (see for ex. Speight 1989; Ranius and Henin 2001; Dajoz 2007), care must also be taken to conserve biologically valuable trees which are isolated, to satisfy the necessity of a certain spatial continuity of microhabitats. This combination is recommended by Franklin et al. (1997). The microhabitat-bearing trees have generally little commercial value: a high proportion is waste wood and a high percentage is wood of pulp quality. In the context of montane forests, the cost of removing them is therefore often higher than their commercial value. Their preservation within the stand therefore improves the economic output of forestry stands. The surface area which is occupied and “non productive” may be counterbalanced by their high functional interest.

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References

Bardat J, Bioret F, Botineau M, Boullet V, Delpech R, Géhu JM, Haury J, Lacoste A, Rameau JC, Royer JM, Roux G, Touffet J (2004) Prodrome des végétations de France. (Patrimoines naturels, 61). MNHN, Paris

Barrère P, Bouquet C, Debroas EJ, Pélissonnier H, Peybernès B, Soulé JC, Souquet P, Ternet Y (1982) Carte géologique de la France (1/50000), feuille Arreau (1072). BRGM, Orléans

Barrère P, Bouquet C, Debroas EJ, Pélissonnier H, Peybernès B, Soulé JC, Souquet P, Ternet Y (1984) Notice explicative de la Carte géologique de la France (1/50000), feuille Arreau (1072). BRGM, Orléans

Bässler C, Müller J (2010) Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. Fungal Biol 114:129–133

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. For Ecol Manage 258:525–537

Bitterlich W (1984) The relascope idea: relative measurements in forestry. Commonwealth Agricultural Bureaux, Farnham Royal

Blondel J (2005) Bois mort et cavités: leur rôle pour l’avifaune cavicole. In: Vallauri D et al (eds) Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, pp 137–142

Bobiec A, Gutowski JM, Zub K, Pawlaczyk P, Laudenlayer WF (eds) (2005) The afterlife of a tree. WWF Poland, Warszawa-Hajnowka

Branquart E, Liégeois S (2005) Normes de gestion pour favoriser la biodiversité dans les bois soumis au régime forestier (complément à la circulaire no 2619). Ministère de la Région wallonne, Direction Générale des Ressources Naturelles et de l’Environnement

Carey AB, Kershner J, Biswell B, Dominguez de Toledo LS (1999) Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildl Monogr 142:1–71

Christensen M, Hahn K, Mountford E, Odor P, Standovar T, Rozenbergar D, Diaci J, Wijdeven S, Meyer P, Winter S, Vrska T (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. For Ecol Manage 210:267–282

Cline SP, Berg AB, Wight HM (1980) Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J Wildl Manage 44:773–786

Cramp S (Chief ed) (1980) Handbook of the birds of Europe, the middle east and north Africa, vol 2 et 4. Oxford, Oxford University Press

Dajoz R (2007) Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier, 2ème édn. Tec et Doc Lavoisier, Paris

Darveau M, Desrochers A (2001) Le bois mort et la faune vertébrée; état des connaissances au Québec. Université de Laval, Centre de recherche en biologie forestière, Ministère des ressources naturelles

Davasse B (1992) Anthracology and carbonized forested areas. Some examples from east Pyrenees. Bulletin de la société Botanique de

France; Actualités botaniques. Colloque sur le charbon, les écosystèmes anciens et le rôle de l'Homme. Montpellier 139(2–4):597–608

Deconchat M (1994) Les boisements des terres agricoles comme outils d'aménagement écologique du paysage. Tome 1: Synthèse et catalogue bibliographique des effets des bois sur la biodiversité. INRA-URSAD/SOLAGRO

DeGraaf RM, Shigo AL (1985) Managing cavity trees for wildlife in the northeast. USDA Forest Service, General technical report NE-101

Drapeau P, Nappi A, St Germain M, Angers VA (2005) Les régimes naturels de perturbations, l'aménagement forestier et le bois mort dans la forêt boréale québécoise. In: Vallauri D et al (eds) Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, pp 46–54

Du Bus de Warnaffe G, Lebrun P (2004) Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. Biol Conserv 118:219–234

Dufour D (2003) Étude de l'influence du bois mort sur l'avifaune cavernicole en forêt feuillue. Mémoire de fin d'études. FUSAGx, Gembloux

Dufrêne M, Branquart E, Henin J-M, Fayt P (2005) Vieux arbres et bois mort: des composantes essentielles de la biodiversité forestière. In: Résumé des interventions de la journée d'étude «Gestion forestière et biodiversité». Gembloux, Ministère de la Région wallonne, Direction Générale des Ressources Naturelles et de l'Environnement, pp 22–24

Ellis MB, and Ellis JP (1998) Microfungi on miscellaneous substrates. An identification handbook. Richmond Publishing, Slough, England

Fan Z, Shifley S, Spetich MA, Thompson FR, Larsen D (2003) Distribution of cavity trees in Midwestern old-growth and second-growth forests. Can J For Res 33:1481–1494

Franklin JF, Berg DR, Thornburgh DA, Tappeiner JC (1997) Alternative silvicultural approaches to timber haversting: variable retention harvest systems. In: Kohm KA, Franklin JF (eds) Creating a forestry for the 21 st century. The science of ecosystem management. Island Press, Washington, pp 111–139

Fridman J, Walheim M (2000) Amount, structure and dynamics of dead wood on managed forestland in Sweden. For Ecol Manage 131:23–26

Fritz O, Heilmann-Clausen J (2010) Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Biol Conserv 143:1008–1016

Garrigue J, Magdalou JA (2000) Réserve naturelle de la Massane: suivi forestier et cartographie assisté par SIG. Laboratoire Arago, Observatoire océanologique de Banyuls/Mer. Travaux scientifiques 55:44

Gilg O (2004) Old-Growth forests; characteristics, conservation and monitoring. GIP ATEN, habitat and species management. Technical report no 74

Girompaire L, Ballon P (1992) Conséquences de l'écorçage du cerf élaphe dans le massif des Vosges alsaciennes. Revue Forestière Française XLIV(6):501–511

Gonin P (1988) Contribution à l'étude de l'évolution des forêts non exploitées dans les Pyrénées. Association Forêts Pyrénéennes, St. Gaudens, p 45

Gosselin M, Laroussinie O (coord.) (2004) Biodiversité et Gestion forestière: connaître pour préserver. Synthèse bibliographique. Cemagref, Nogent sur Vernisson France

Greenberg CH, McLeod DE, Loftis DL (1997) An old-growth definition for Western and mixed mesophytic forest. USDA, Southern research station, Gen tech rep SRS-16. USDA Forest Service, Southern Research Station, Asheville, p 14

Grove SJ (2002a) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Grove SJ (2002b) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rain forest. Biol Conserv 104:149–171

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Advances in ecological research, vol 15. Academic Press, London, pp 133–302

Healy WM, Brooks RT, DeGraaf RM (1989) Cavity trees in sawtimbersize oak stands in central Massachusetts. Nor J Appl For 6:61–65

Heiss E, Pericart J (2007) Hemiptères Aradidae Piesmatidae et Dipsocoromorphes euro-méditerranéens. Faune de France (France et régions limitrophes) 91. Fédération Française des sociétés de sciences naturelles

Hothorn T, Hornik K (2005) The coin package—conditional inference procedure in a permutation tes-framework, 0.4-1. http://CRAN.R-project.org

Hothorn T, Lausen B (2003) On the exact distribution of maximally selected rank statistics. Comput Stat Data Anal 43(2):121–137

Hothorn T, Zeileis A (2008) Generalized maximally selected statistics. Biometrics 64:1263–1269

Hothorn T, Hornik K, Van de Wiel MA, Zeilis A (2006a) A Lego-system for conditional inference. Am Stat 60:257–263

Hothorn T, Hornik K, Zeileis A (2006b) Party: a laboratory for recursive part(y)itioning. http://CRAN.R-project.org/

Kitching RL (1971) An ecological study of water-filled tree-holes and their position in the woodland ecosystem. J Animal Ecol 40(2): 281–302

Larrieu L, Brustel H, Cabanettes A, Corriol G, Delarue A, Harel M, Loireau JN, Sarthou JP (2010) Impact de l'anthropisation ancienne sur la biodiversité d'un habitat de hêtraie-sapinière montagnarde. Revue Forestière Française 4–2009:351–368

Lausen B, Schumacher M (1992) Maximally selected rank statistics. Biometrics 1(48):73–85

Lisiewska M (1992) Macrofungi on special substrates. In: Winterhoff W (ed) Fungi in vegetation science. Kluwer, Netherlands, pp 151–182

Loeb S (1999) Response of small mammals to coarse woody debris in a south-eastern pine forest. J Mammal 80(2):460–471

Lucan RK, Hanak V, Horacek I (2009) Long-term re-use of tree roosts by European forest bats. For Ecol Manage 258:1301–1306

Mannan RW, Meslow EC, Wright HM (1980) Use of snags by birds in Douglas-fir forests, western Oregon. J Wildl Manage 44:787–797

Martikainen P, Kaila L, Haila Y (1998) Threatened beetles in white-backed woodpecker habitats. Cons Biol 12(2):293–301

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of coleoptera in mature managed and old-growth boreal forest in southern Finland. Biol Conserv 94:199–209

Maser C, Trappe JM, Cline SP, Cromack K, Blaschke H, Sedell JR, Swanson FJ (1984) The seen and unseen world of the fallen tree. Gen Tech Rep PNW 164. USDA Forest service, Pacific Northwest Forest and Range Experiment Station, Portland, OR

McClelland BR, Frissell SS (1975) Identifying forest snags useful for hole-nesting birds. J For 73(7):414–417

McMillan PC, Means J, Hawk GM, Crmack KJ, Fogel R (1977) Log decomposition in an old growth Douglas-fir forest. In: Northwest scientific association abstract of papers presented at the 50th annual meeting, Washington State University Press, Pullman, WA

McMinn JW, Crossley DA (eds) (1996) Biodiversity and coarse woody debris in southern forests. Proceedings of the workshop on coarse woody debris in the southern forest: effect on biodiversity. USDA Forest Service, southern Research Station, Asheville, NC, p 146

Meschede A, Heller KG (2003) Ecologie et protection des chauves-souris en milieu forestier. MHN de Genève. Le Rhinolophe 16:1–248

Métailié JP (1984) La forêt paysanne dans les Pyrénées centrales. Revue Géographique des Pyrénées et du Sud-Ouest 55(2): 231–238

Métailié JP (2001) Un patrimoine historico-environnemental: les forêts pastorales dans les Pyrénées. In: Actes du 126ème congrès national des sociétés historiques et scientifiques, Toulouse. Paysages, territoires et aménagement dans le sud de la France, pp 33–47

Michel AK, Winter S (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. For Ecol Manage 257:1453–1464

Moning C, Müller J (2008) Environmental key factors and their thresholds for the avifauna of temperate montane forests. For Ecol Manage 256:1198–1208

Moning C, Müller J (2009) Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. Ecol Indic 9:922–932

Moning C, Werth S, Dziock F, Bässler C, Bradtka J, Hothorn T, Müller J (2009) Lichen diversity in temperate montane forests is influenced by forest structure more than climate. For Ecol Manage 258:745–751

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur J Forest Res 129:981–992

Muller RN, Liu Y (1991) Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can J For Res 21:1567–1572

Nascimbene J, Marini L, Nimis PL (2009) Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. Can J For Res 39(4):785–791

Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P, Ljungberg H, Mikusinnski G, Ranius T (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. For Ecol Manage 161:189–204

Norden B, Ryberga M, Gotmark F, Olaussona B (2004) Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biol Conserv 117:1–10

Norsted G, Bader P, Ericson L (2001) Polypores as indicators of conservation value in Corsican pine forests. Biol Conserv 99:347–354

Odor P, Heilmann-Clausen J, Christensen M, Aude E, van Dort KW, Piltaver A, Siller I, Veerkamp MT, Walleyng R, Standovar T, van Hees AFM, Kosec J, Matocec N, Kraigher H, Grebenc T (2006) Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biol Conserv 131:58–71

Pardé J, Bouchon J (1988) Dendrométrie, 2ème édn. ENGREF Nancy, France

Pénicaud P (2000) Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe 14:37–68

Ponthus C (1996) Inventaire des forêts subnaturelles des Pyrénées françaises. Mémoire de fin d'études. ENSA Toulouse (ONF)

Radek K, Lucan R, Hanak V, Horacek I (2009) Long-term re-use of tree roosts by European forest bats. For Ecol Manage 258:1301–1306

Rameau JC, Gauberville C, Drapier N (2000) Gestion forestière et diversité biologique; identification et gestion intégrée des habitats et espèces d'intérêt communautaire. IDF, Paris

Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91

Ranius T, Henin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126:363–370

R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. http://www.R-project.org

Richard F, Millot S, Gardes M, Selosse MA (2005) Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by *Quercus ilex* L. New Phytol 166:1011–1023

Ringvall A, Stahl G (1999) On the field performance of transect relascope sampling for assessing downed coarse woody debris. Scand J For Res 14:552–557

Rondeux J (1993) La mesure des arbres et des peuplements forestiers. Les presses agronomiques de Gembloux

Samuelsson J, Gustafsson L, Ingelög T (1994) Dying and dead trees: a review of their importance for biodiversity, Swedish threatened species unit, Uppsala

Schaeffer L (1949) Tarifs rapides et tarifs lents. Revue Forestière Française 1:7–13

Schmidl J, Sulzer P, Kitching RL (2008) The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physico-chemical factors. Hydrobiologia 598:285–303

Schmit JP, Lodge DJ (2005) Classical methods and modern analysis for studying fungal diversity. In: Dighton J, White J, Oudemans P (eds) The fungal community; Its organization and role in the ecosystem, 3rd edn (Mycology Volume 3). CRC Taylor & Francis, Boca Raton, pp 193–214

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49:11–41

Sippola AL (2001) Forest structure and biodiversity in northern boreal forests; effects of regeneration cutting on flying beetles and wood-decomposing fungi. Artic Centre Reports 35. Helsinki: Hakapaino Oy

Sippola AL, Renvall P (1999) Wood-decomposing fungi and seed-tree cutting: a 40 years perspective. For Ecol Manage 115: 183–201

Sippola AL, Siitonen J, Kallio R (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scand J For Res 13:204–214

Snedecor GW, Cochran WG (1971) Méthodes statistiques. Traduction française Boelle H, Camhaji E. ACTA, Paris

Speight MCD (1989) Saproxylic invertrebrates and their conservation. Council Eur Nat Environ Ser 42:1–79

Sprent P (1992) Pratique des statistiques non paramétriques. Traduction française Ley JP. INRA, Paris

Stanska M, Rozwaka R, Kowalczyk K (2010) *Dipoena torva* (Thorell, 1875) spider living on tree stems. Lesne Prace Badawcze 71(2): 201–205

Stokland JN, Tomter SM, Söderberg U (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti M (ed) Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality, EFI workshop, November 12th–15th 2003, Firenze, Italy, vol 51

Ternet Y, Barrère P, Debroas EJ (1995) Notice explicative de la Carte géologique de la France (1/50000), feuille Campan (1071). BRGM Orléans

Ternet Y, Barrère P, Dallas S, Debon F, Debroas EJ, François JM, Pouget P (1996) Carte géologique de la France (1/50000), feuille Campan (1071). BRGM, Orléans

Tillon L (2005) Biodiversité, dynamique et conservation des petits mammifères cavicoles en France. In: Vallauri D et al (eds) Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, pp 145–155

Tillon L (2006) Etude des gîtes sylvestres en forêt domaniale de Rambouillet. Symbioses 15:11–14

Vaillant F (1978) Les *Systenus* et leur habitat dendrotelme. Bull Société Ent Fr 83:73–85

Vallauri D, André J, Blondel J (2002) Le bois mort, un attribut vital de la biodiversité de la forêt naturelle, une lacune de la forêt gérée. WWF-France, Paris

Vane CH, DrageTC SnapeCE (2006) Bark decay by the white-rot fungus *Lentinula edodes*: Polysaccharide loss, lignin resistance and the unmasking of suberin. Inter Biodeter Biodegr 57:14–23

Westfall PH, Young SS (1993) On adjusting P-values for multplicity. Biometrics 49:941–945

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. For Ecol Manage 255:1251–1261

Wonoroff D (1984) Forges prédatrices, forges protectrices. Revue Géographique des Pyrénées et du Sud-Ouest, tome 55(2): 213–218

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The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest

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Abstract. 1. In French oak high forests, current silvicultural trends include two seemingly opposed practices: shortening the forestry cycle, which contributes to forestry intensification, and lengthening rotations in temporary set-aside stands, called 'ageing islands', to favour biodiversity and high-quality large-diameter tree production.

2. To derive the potential effects of these two trends, we studied habitat structure and saproxylic beetles biodiversity along an age gradient in a French oak high forest. Four age classes were surveyed: premature (i) 160/180 years and (ii) 180/200 years, (iii) mature 200/220 years, and (iv) overmature 300-year-old stands. Structural features were noted: deadwood volumes, density of large trees with or without microhabitats, number of cavities, presence of dead large canopy branches, sap droppings and sporophores of saproxylic fungi.

3. Results showed that beetle species richness was positively related to stand age. Globally, overmature stands differed significantly from younger premature and mature forests in species composition and structure. Younger stands tended to show both fewer structural features and lower levels of saproxylic biodiversity. As the forest aged, the overall structural complexity and saproxylic biodiversity increased. However, no individual stand characteristic influenced preferentially biodiversity, and stand age was the best explaining factor.

4. In conclusion, we discuss how (i) shorter rotations in the high forest production cycle and (ii) temporary set-aside forest islands affect forest structure and deadwood-associated assemblages. Shortening rotation length in oak high forests may negatively impact saproxylic biodiversity, whereas temporary set-asides may play a key role for biodiversity conservation in a managed forest matrix.

Key words. Ageing islands, biodiversity, rotation length, saproxylic beetles, set-aside, stand features.

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Introduction

In France, oak [*Quercus petrae* (M.) Liebl and *Q. robur* L.], high forests currently represent 12.4% of the total forest surface area, and account for 25.3% of the total high forest surface area [Inventaire Forestier National (IFN) (2010)]. Due to the production of high-quality oak timber, these stands are of crucial economic importance for French wood market. In addition, oak species are known to provide a support for rich biodiversity as it matures (Vodka *et al.*, 2009). Currently, the final harvesting in oak high forest normally occurs between 180 and 220 years depending on forest site productivity and targeted wood products.

In French oak high forests, current silvicultural trends include two seemingly opposed practices around the rotation age. Firstly, observable increase in forest productivity and tree growth (Bergès *et al.*, 2000), as well as increasing demand for timber, may lead to shortened rotation length in oak high forests in a close future. The decrease in rotation length but also the selective thinning of defects-bearing trees in intensive managed forests leads to the removal of old, large, and/or microhabitat-bearing trees due to their low economic value, and results in stands that are mostly uniform in tree species, size, and spacing (Hansen *et al.*, 1991). The amount of dead wood and the mean age of forest sites may be reduced at the landscape scale. Conversely, overmature old forests are generally characterised by higher proportions of large, old trees, multiple age classes, and high volumes of fallen and standing dead wood (Larsson, 2001; Humphrey, 2005). Moreover, features such as rough bark, trunk hollows, exposed dead wood, cavities, dead branches, and dead tops are often present in old, large trees, and these provide habitats for numerous species (Winter & Möller, 2008; Vuidot *et al.*, 2011). The disappearance of such structures at the landscape scale and the subsequent homogenisation and habitat loss may result in local extinctions of sensitive species (Heliovaara & Vaisanen, 1984; Niemela, 1997; Ulyshen, 2011). Generally, younger managed stands host fewer individuals or saproxylic species than older forests and species assemblages differ as well (Grove, 2002). Indeed, in both living and dead trees, several saproxylic species are restricted to large trees (Ranius & Jansson, 2000; Siitonen & Saaristo, 2000). Johansson *et al.* (2007) for lichens and Penttilä *et al.*(2004) for polypores have demonstrated that tree age and size have an important role in explaining tree-level species richness and composition in Fennoscandia.

Secondly, to preserve saproxylic biodiversity and produce high-quality large-diameter trees, temporary set-aside stands ('ageing forest islands') are being promoted by extending the final harvesting by at least 20 years to twice as much as the traditional rotation age [Office National des Forêts (ONF) (2009)]. Nowadays, only a small proportion of the productive forestland in Europe has escaped intensive harvesting. Overmature temperate deciduous forests with old, dying, and dead trees, have declined to a very small fraction of their original extent (Hannah *et al.*, 1995). In France, high forests with overmature stands are very rare. Only 2.4% of all high forests have a higher-than-normal rotation age, and the proportion is much lower for highly productive species such as oaks (Ministère De L'Agriculture Et De La Pêche, 2006). As these measures have been applied quite recently, little is known about their effects on biodiversity.

In our study, we aimed to assess stand characteristics and identify saproxylic beetle assemblages in premature, mature, and overmature stands, relative to traditional rotation length. To our knowledge, this study is the first to analyse saproxylic beetle biodiversity along a temperate oak high forest age gradient. In other words, we endeavoured to answer the following questions: Does structural heterogeneity systematically increase with stand age? Do older forest stages host different species assemblages and do they have richer assemblages than younger managed high forests? Is there a relationship between saproxylic beetle biodiversity and changing structural features? We thus hoped to reveal the potential impact of both shortened and lengthened rotations on forest features and microhabitats available for saproxylic beetle assemblages as well as on the beetle assemblages themselves.

Material and methods

Study area, sample plots, and stand characteristics

The study was conducted in the Tronçais forest in central France (02°44′42.9″E; 46°39′52.6″N; Fig. 1). This temperate forest covers an area of 10 583 hectares. *Q. petraea* dominates (73%), mixed with *Fagus sylvatica* L. (9%), *Q. robur* (8%), and some *Carpinus betulus* L. and *Pinus sylvestris* L. The study area has a long history of forest management dating back to the middle of the 16th century so that management operations were documented since (in particular stand ages). This forest was one of the first French forests to be gradually converted to high forest around 1835. Current management consists of thinning operations every 10 years during the forestry cycle and a final harvest in these highly productive stands not occurring until 220 years (instead of 180/200 years in other French oak high forests). In particular, high-quality oak wood from Tronçais is used to produce barrel staves. Diameter at breast height (DBH) of harvestable oaks varies from 60 to 80 cm according to the quality of the wood required. In addition, some stands are managed with close-to-nature harvesting methods and contain trees over 300 years of age. These could mimic overmature 'ageing islands' used for biodiversity conservation (nevertheless, we should keep in mind that the natural longevity of oak trees is usually between 350 and 500 years). Consequently, the range of stand ages in the Tronçais forest is exceptionally broad.

Using a synchronic approach, we benefited from this gradient to set up 31 stands in the following 4 age classes, according to a normal rotation length of 220 years for the Tronçais forest: pre-mature 160/180 years (9 stands) and 180/200 years (7 stands), mature 200/220 years (12 stands), and overmature >300 years old (3 stands). These latter stands were very rare in the forest (covering only

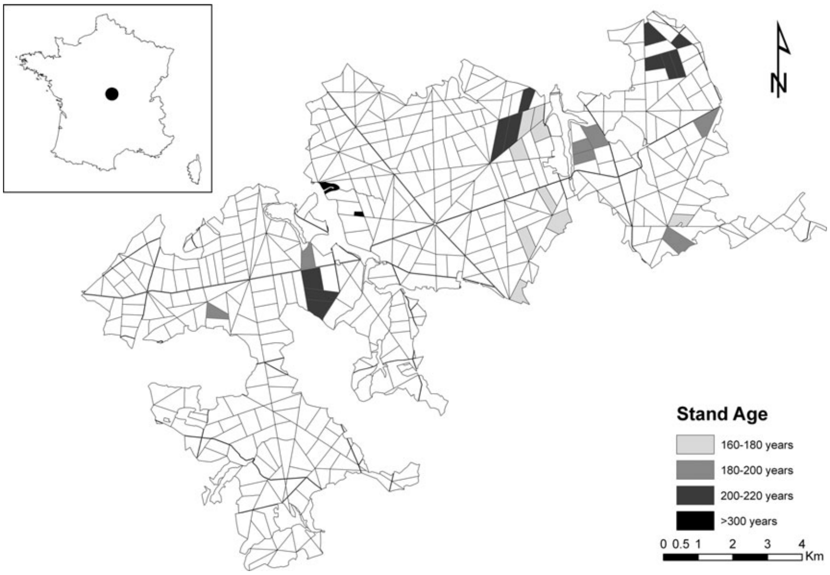

Fig. 1. Location of the Tronçais forest in central France and the different stands selected: pre-mature stands: 160/180 years (9 stands) and 180/200 years (7 stands); mature stands: 200/220 years (12 stands); and overmature stands: >300 years old (3 stands).

15 ha in total) so the sample was unbalanced for this age class. The age classes we chose are consistent with the classification used for management planning documents (Office National des Forêts, unpublished data). These different stands were randomly distributed within the forest, without any spatial autocorrelation in our dataset. Indeed we checked for spatial autocorrelation between plots using the Moran I test (R-package: spdep, $P = 0.3$) (Fig. 1).

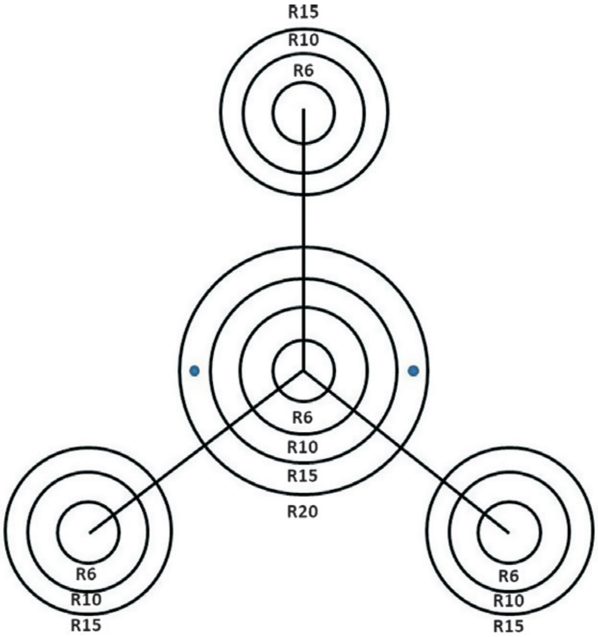

Fig. 2. Plot design for dendrometric measurements. Four subplots of different radii were set up: one 20-m radius central subplot (R20) and three circular 15-m radius satellite subplots. In each subplot, living trees, snags, and stumps were measured. In addition, the amount of downed woody debris larger than 2.5 cm in diameter was surveyed along three 50-m long transects.

Living trees and deadwood measurements

In each stand, in the centre, we selected a plot with a total surface area of 0.34 ha. Plots comprised four subplots of different radii: one central subplot with a radius of 20 m and three circular satellite subplots each with a radius of 15 m (Fig. 2). On each subplot, we measured living trees and snags as follows: all living trees with a DBH > 10 cm (all snags with DBH > 5 cm) were measured within a radius of 5 m, DBH > 20 cm (all snags with DBH > 10 cm) within a radius of 10 m, DBH > 30 cm within a radius of 15 m (all snags with DBH > 15 cm), and DBH > 40 cm (all snags DBH > 20 cm) within a radius of 20 m (central subplot only, see Fig. 2). Stumps larger than 20 cm in diameter were measured in the entire subplots. The density of large trees (DBH > 40 cm) was measured in a 50 m radius centred on the previous 0.34 ha plots. In the same radius, whenever present, the following microhabitats were recorded: cavity, missing bark (surface 10 × 10 cm), bark pocket, broken stem, broken fork, crack (width 1–5 cm), sap drop, ivy, >20% of dead crown and sporophores of saproxylic fungi – and their density was estimated. In addition, we measured the amount of downed woody debris larger than 2.5 cm in diameter on three 50 m-long transects, following the Line Intersect Sampling method (Woodall & Williams, 2005). All types (snags and logs) of deadwood were classified into one of two decay stages based on a 'knife test' and remaining bark cover: (i) 'Fresh': bark is present, or at least partially present, and usually firmly attached; the knife tip penetrates <1/3 of the diameter, the wood is hard; (ii) 'Decayed': moderately to strongly decayed wood, form is still apparent but soft or partly destroyed wood appears, the knife tip penetrates >1/3 the diameter. These measurements were conducted in autumn 2009, just after beetle sampling.

Beetle sampling and identification

We sampled beetles using the multidirectional Polytrap^{TM} (EIP, Toulouse, France; Brustel, 2004), a cross-vane window flight trap with a cumulative panel area of 1 m^2 (Bouget *et al*., 2009). The traps were placed at a height of about 1 m. Each window trap consisted of two perpendicular intercepting transparent plastic panes (40–60 cm), with a funnel leading into a 1L container below the panes. In the containers, a mixture of salt water and detergent was used for insect preservation. Two traps were located approximately 30 m apart in each sample stand, for a total number of 62. The traps were emptied four times during the sampling period (9 April to 30 July, 2009). All saproxylic beetles were identified to the highest possible taxonomic level (Appendix A). Species were defined as rare taxa according to a patrimoniality index assigned in Bouget *et al*. (2008).

Data analysis

We first analysed the influence of stand age on stand characteristics using Wilcoxon tests for continuous variables and quasi-Poisson generalised linear models (GLM) for count data stand variables (R software v. 2.10.1; R Development Core Team, 2007). We considered the following continuous response variables among stand features: basal area of living trees (basal Area) (m^2 ha^{-1}), total deadwood volume (DWT) (m^3 ha^{-1}), total log volume (DWL) (m^3 ha^{-1}), total snag volume (DWS) (m^3 ha^{-1}), total volume of fresh deadwood ('Fresh') (m^3 ha^{-1}), and total volume of decayed deadwood ('Decayed') (m^3 ha^{-1}). Count variables were density of large living trees per hectare (DBH > 70 cm) (TGB), density of large microhabitat-bearing trees (DBH > 70 cm) (TGBmicro) per hectare, and the ratio deadwood volume/(deadwood volume + living tree volume) (RATIO). More specifically, concerning the density of microhabitats per hectare, we tested the density of cavities (with or without mould), sporophores of saproxylic fungi (sporophores), dead large canopy branches (deadwood in the canopy above 20% and branches/broken tops with a diameter larger than 20 cm), and sap droppings. Tukey tests were used for pair-wise comparison of these factors.

Second, we used a generalised linear model with a Poisson error distribution to analyse the influence of stand age on species richness and a negative binomial error distribution (glm.nb function in the MASS library) to analyse the influence of stand age on species abundance. We considered the total abundance and the total species richness of saproxylic beetles or rare species as response variables. Finally, we tested the effect of each environmental variable, after the covariate 'age', on the abundance and richness of saproxylic beetles. As none of these additional variables significantly improved the 'age' model AICc, results were not included in this article.

We used rarefaction methods (software 'EstimateS v.7' Colwell, 2005) to analyse the accumulation rate of species. Appropriate standardisation to compare species richness between stand age classes may consider the number of sampling units or individuals (Heilmann-Clausen & Christensen, 2004). As the mean volume and surface area of living tree varied significantly among age classes in our study, we chose the number of traps as units to have a sufficient number of points. This means that, because there were two polytraps per plot (stand), the sampling design is marginally pseudo-replicated.

We performed a Canonical Analysis of Principal Coordinates (CAP) to examine variation in assemblage structure related to the explanatory variables. In addition to a traditional unconstrained ordination (principal coordinates analysis), this technique allowed us to perform a constrained ordination with reference to a specific *a priori* hypothesis – in our case, that there was no difference among traps. We carried out an inertia partitioning with the '*capscale*' function from the vegan R-library, which provided us with the total inertia as well as the inertia explained by each variable (Anderson & Willis, 2003). We tested the hypothesis of diverging composition of saproxylic beetle assemblages between stand age classes by running PERMANOVA (Anderson & Willis, 2003) with the Bray-Curtis similarity index on 4999 permutations. Species assemblage data were square-rooted to reduce the importance of extremely abundant species in the analysis. Pair-wise tests were performed to determine whether there were differences in the composition of beetle assemblages between stand ages. We applied this non-parametric permutation procedure to rank similarity matrices underlying sample ordinations. The test compares between- and within-group distances. Singletons were excluded from the analysis. In addition, we used the Sørensen dissimilarity index (β_{sor}) to compare the dissimilarity between age classes. This measure incorporates both true spatial turnover ((β_{sim}) and nestedness processes (β_{nes}) (i.e. the species from samples with lower species richness are subsets of the species found in richer samples, reflecting a non-random process of species loss). Distance matrices were computed with the 'beta-pairwise.R' functions (Baselga, 2010).

To identify species positively associated with a stand age or a combination of stand age, we used the point-biserial group-equalised phi coefficient (Pearson correlation) as described by De Caceres and Legendre (2009). The MULTIPATT procedure was used in the Indicspecies package (De Caceres *et al*., 2010) of R version 2.12.1. Correlation coefficients produced by this analysis take into account the absences outside the target group and these absences contribute to increasing the power of the associations as well as presences in stands of that group. This makes the analysis more context-dependent than indicator value indices [IndVal index, Dufrêne and Legendre (1997)] for the determination of species–habitat associations (De Caceres & Legendre, 2009). We excluded singleton and doubleton species.

Results

A total of 9308 specimens corresponding to 236 species were recorded. This included 450 rare individuals belonging to 29 rare species. The most abundant species were: *Xyleborus dispar* (Scolytidae) (12% of the catches), *Xylosandrus germanus* (Scolytidae) (12%) and *Isoriphis melasoides* (Eucnemidae) (5%).

Age effects on stand characteristics

First, we observed that there were no significant differences between 180/200-year-old stands and 200/220-year-old stands in terms of forest characteristics (Table 1). Secondly, only a few significant differences appeared between 160/180-year-old stands and 180/200 or 200/220-year-old stands. Actually, there were no differences among these age classes regarding mean basal area, deadwood volume and deadwood/living tree volume ratio. However, 160/180-year-old stands had a statistically fewer large trees and microhabitat-bearing large trees than the 180/200 and 200/220-year-old stands (Table 1). More specifically, the density of dead large canopy branches per hectare increased in 180/200-year-old stands compared with 160/180-year-old stands, although the density of cavities, sporophores, and sap droppings did not differ between age classes (Table 1). Finally, the 300-year-old stands were totally different for some forest characteristics. Indeed, mean basal area tended to be significantly higher in 300-year-old stands than in younger stands (Table 1).

Mean log and total deadwood volumes were significantly higher in the 300-year-old stands than in all the other age classes, whereas mean snag volume and the ratio deadwood volume/(deadwood volume + living tree volume) did not significantly differ. The proportion of fresh deadwood differed significantly only between 180/220-year-old stands and 300-year-old stands. The same pattern was found for variable RATIO. Globally, the number of large trees (DBH > 45 cm) both with and without microhabitats (respectively 16.4 and 40.4 trees per ha) was significantly higher in the old forest than in the younger stands. In addition, the density of sporophores and sap droppings, the density of dead large canopy branches and the number of cavities (empty or mould-filled) increased in the 300-year-old stands (Table 1).

Stand age effect on biodiversity

The stand age has a significant effect on the mean richness of all saproxylic beetle species. The 300-year-old stands had a significantly higher mean species richness (79 species) than the three younger age classes (respectively 60, 55, and 63 species). Species richness was lower in the 180/200-year-old stands than in the 200/220-year-old stands (Fig. 3), with the lowest richness measured in the 180/200-year-old stands (55 species on average; Fig. 3). No significant difference was observed between age classes in terms of total abundance and abundance of rare species.

Rarefaction curves suggest significant contrasts in cumulative species richness among the four age classes (Fig. 4). The highest and lowest saproxylic species

Table 1. Stand features (mean ± SD). Letters in rows indicate differences at $P < 0.05$ level in Wilcoxon tests for continuous stand characteristics and using quasi-Poisson generalised linear models for count data stand variables.

	Mean (±SD)			
Variables	160/180-Year-old stands	180/200-Year-old stands	200/220-Year-old stands	300-Year-old stands
Basal area	36.02 (±5.15) a	33.52 (±3.29) a	35.64 (±4.88) a	47.77 (±8.12) b
DWT	16.2 (±8.66) a	14.48 (±5.86) a	16.20 (±.73) a	32.88 (±9) b
DWL	8.59 (±8.64) a	7.26 (±4.81) a	9.33 (±6.29) a	24.67 (±6.91) b
DWS	2.18 (±3.74) a	0.69 (±1.66) a	1.12 (±3.21) a	0.48 (±0.83) a
Fresh	7.31 (±4.62) ab	6.52 (±2.13) a	5.70 (±2.84) a	17.68 (±11.12) b
Decayed	8.89 (±5.60) a	7.96 (±4.68) a	10.49 (±6.80) a	15.20 (±2.34) a
Ratio	0.30 (±0.09) a	0.3 (±0.09) a	0.30 (±0.10) a	0.41 (±0.05) a
TGBmicro	1.11 (±1.96) a	4.43 (±2.37) b	4.75 (±3.91) b	16.67 (±4.51) c
TGB	8.56 (±8.23) a	19.71 (±15.55) b	22.33 (±9.29) b	44.33 (±9.71) c
Cavity	2.89 (±2.67) a	4.57 (±1.4) a	4.50 (±2.65) a	17 (±2.65) b
Sporophores	0.67 (±1.41) a	0.43 (±0.53) a	0.25 (±0.62) a	1.33 (±0.58) a
Dead large canopy branches	1.56 (±2.40) a	4.57 (±2.3) b	2.17 (±1.99) ab	12 (±8.544) c
Sap droppings	0.22 (±0.44) a	0.43 (±0.79) a	0.42 (±0.67) a	0.33 (±0.58) a

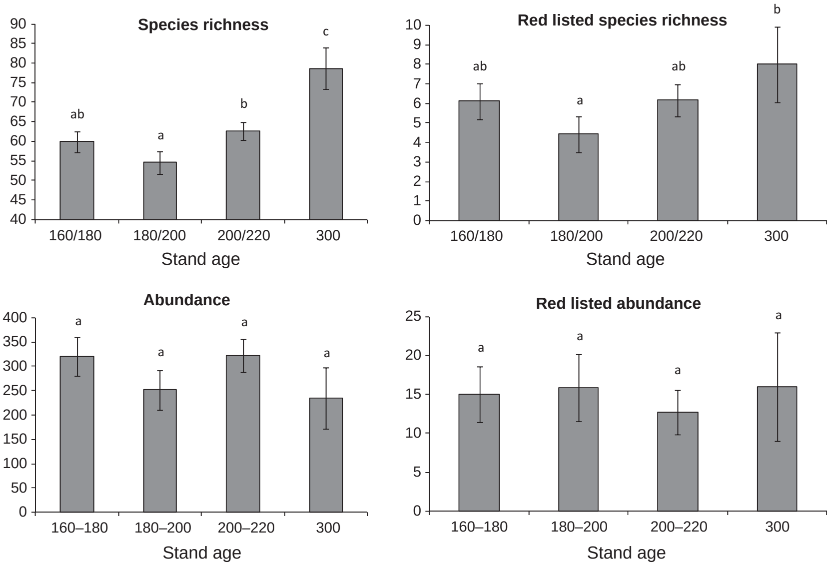

Fig. 3. Estimated species number or abundance of saproxylic beetles or rare saproxylic species per stand per age class derived from generalised linear models. Error bars are standard errors. Different letters indicate significantly different levels among age classes.

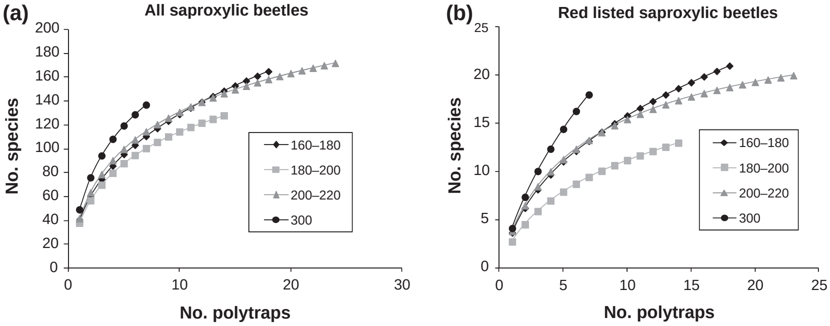

Fig. 4. Rarefied cumulative beetle species richness in the four age classes. (a) all species, (b) rare species only.

richness were respectively found in the 300-year-old and the 180/200-year-old stands, whereas the 160/180 and 200/220-year-old stands were intermediate. Only the 300-year-old age class was significantly different from the others in respect to the confidence limits intervals at the point of comparison.

The mean number of rare species was significantly lower in the 180/200-year-old stands (4.4 species) than in 300-year-old stands (8 species) (Fig. 3). We found similar results for cumulative richness using rarefaction curves (Fig. 4).

From the CAP, the studied factors (i.e. stand characteristics such as age, basal area, deadwood volumes, number of large trees with or without microhabitats, and the deadwood/living tree ratio) explained 60% of the total inertia in beetle data. The 'stand age' factor provided the highest contribution to the variance in saproxylic beetle assemblages (25%, Table 2). The density of cavities and the number of large microhabitat-bearing trees explained 13% and 12% of the constrained inertia respectively (Table 2).

PERMANOVA showed a significant age effect on species composition. Post-hoc tests showed that assemblages in 160/180-year-old stands were statistically different from 180/200-year-old stands. Moreover, assemblage composition significantly differed between old (300 years) and younger stands (Table 3). The assemblage composition of rare species was also significantly affected by age, the 160/180 and 300-year-old stands being significantly contrasted (Table 3). The Sørensen dissimilarity between age classes was around 45% for all species combined, and 60% for rare species only. The nestedness component of dissimilarity was quite low – much lower than spatial turnover, which was the dominant underlying pattern in the community divergence between the different age classes (Table 4).

Table 2. Effect of stand features on saproxylic beetle assemblages (Canonical Analysis of Principal Coordinates).

	Total inertia	*P*	% Constraint inertia
Stand age	1.06	0.005	24.94
Cavity	0.54	0.005	12.66
TGBmicro	0.51	0.01	12.10
Dead large canopy branches	0.40	0.02	9.43
TGB	0.33	0.083	7.87
Sap droppings	0.31	0.2	7.30
Ratio	0.30	0.14	7.14
Basal area	0.29	0.14	6.91
DWT	0.27	0.34	6.35
Decayed	0.26	0.31	6.17
DWL	0.25	0.48	5.83
Sporophores	0.24	0.49	5.71
Fresh	0.23	0.55	5.39
DWS	0.13	1	3.10
Residuals	3.20		

The species–habitat associations analysis revealed that 1 specie was associated with 180/200-year-old stands and that eight species were associated with 300-year-old stands. Moreover, the analysis showed that two species (Salpingus ruficollis and Pediacus depressus) were associated with the combination 160/180 + 180/200 + 200/220 year-old stands. In the same way, one species was associated with the two oldest stands (200/220 + 300 year-old stands) (Table 5).

Discussion

To our knowledge, this study is the first to deal with an age gradient in temperate oak forests. To date, most studies on the ecological effects of forest ageing have been conducted in Scandinavia by comparing different successional stages of coniferous forests, e.g. young, clearcut, mature, overmature, and old growth forests (Martikainen *et al.*, 2000; Similä *et al.*, 2002; Gibb *et al.*, 2006; Stenbacka *et al.*, 2010). Forest age per se seems to be a key parameter for several taxa including birds, lichens, and molluscs (Moning & Müller, 2009); this is true in particular for saproxylic insect species and some red-listed or declining species associated with oldest stages (Martikainen *et al.*, 2000; Stenbacka *et al.*, 2010). In our study, the total saproxylic beetle richness was highest in 300-year-old stands and rare species richness was higher in 300-year-old than in 180/200-year-old stands. Moreover, although these are not rare species, almost all the indicator species were found in 300-year-old stands. These old forests significantly differ from young forests in species composition and stand structure. The structural complexity resulting from ageing plays an important role in sustaining biodiversity and forest ecosystem functions (Lindenmayer & Franklin, 2002). However, no correlation between beetle biodiversity and forest characteristics was clearly demonstrated in our study. Forest age effect may consequently be interpreted as the combination of different joint effects influencing biodiversity, including structural features such as tree size, microhabitat density, deadwood volumes, and management history. We showed that both the basal area and the density of large-diameter trees increased with stand age which is consistent with Fan *et al.* (2003) and Nascimbene *et al.* (2009). Although tree growth obviously relates to site productivity, large diameters are usually associated with older trees. In many studies, large-diameter trees are an important forest component. Often absent in managed forests, they are a source of large snags and logs, and microhabitats used by many animals (Franklin *et al.*, 2002). Ranius and Jansson (2000) found higher saproxylic beetle species richness in stands with large, free-standing trees. In Sweden, Palm (1959) showed that large oaks sustain the most diverse beetle fauna associated with old trees.

In addition, the density of large microhabitat-bearing trees was significantly higher in overmature stands than in younger ones in our study. More specifically, the density of dead large canopy branches and cavities increased in 300-year-old stands, and also in 180/200-year-old stands for dead large canopy branches. Our results were consistent with Larsson (2001) and Humphrey (2005), who stated that old forests are characterised by higher proportions of large, old trees, multiple age classes and high volumes of fallen and standing dead wood. The available literature supports a strong correlation between microhabitat density and tree diameter only in old stands (Michel & Winter, 2009; Vuidot *et al.*, 2011), but not in managed or recently unmanaged stands (Winter & Möller, 2008). These factors are especially important for saproxy-

Table 3. Age effect on species composition of saproxylic beetle assemblages. Only significant differences are displayed (PERMANOVA).

		d.f.	M^2	*F* Model	R^2	Pr(>*F*)	Comparisons	*P*
Saproxylic beetles	Stand age	3	0.176	1.68	0.152	<0.001***	160/180 ≠ 180/200	<0.001***
	Residuals	27	0.105		0.848		160/180 ≠ 300	<0.001***
							180/200 ≠ 300	0.041*
Rare species	Stand age	3	0.355	1.60	0.146	0.0488*	160/180 ≠ 300	0.014*
	Residuals	27	0.222		0.854			

*$P < 0.05$; ***$P < 0.001$.

Table 4. Sorensen dissimilarities between age classes, in grey for rare species only and in white for all saproxylic beetle species. The relative contribution of nestedness is displayed in parentheses. Reminder: Sorensen dissimilarity = spatial turnover + nestedness.

Stand age	160/180 (%)	180/200 (%)	200/220 (%)	300 (%)
160/180		0.63 (14)	0.61 (15)	0.64 (12)
180/200	0.43 (6)		0.60 (17)	0.63 (13)
200/220	0.44 (5)	0.43 (6)		0.62 (7)
300	0.46 (9)	0.44 (11)	0.43 (7)	

lic organisms (see Winter and Möller (2008) for microhabitats in general and Bouget *et al*. (2011a) for canopy deadwood). Microhabitats, such as broken crowns and stem cavities, are mainly associated with decreasing tree vitality (Jonsell *et al*., 1999; Franklin *et al*., 2002). In Sweden, many threatened forest species have very specific substrate requirements and depend largely on the diversity of microhabitats provided by old trees, logs, and snags (Berg *et al*., 1994; Jonsson *et al*., 2005).

Finally, we recorded higher volumes of logs and total deadwood in the older stands (300 years). We assumed the reduced saproxylic beetle abundance and richness and the distinct assemblage composition in younger forests compared with the 300-year-old stands to be partly due to the limited amount of dead wood and to different habitat/microclimatic conditions. Indeed, the number of saproxylic beetle species depends partly on the amount and diversity of deadwood (Müller *et al*., 2008; Lassauce *et al*., 2011). Saproxylic beetle species are known to be adapted to particular deadwood substrates, to deadwood spatial organisation (Schiegg, 2000) and to the continuity of dead wood availability over time (Siitonen & Saaristo, 2000; Sverdrup-Thygeson & Lindenmayer, 2003; Ranius *et al*., 2008). The low dispersal ability of some saproxylic species is assumed to be one reason for their endangered status (Schiegg, 2000; Ranius & Hedin, 2001).

Research perspectives and implications for conservation and forest management

Our study reveals fewer structural features and lower levels of saproxylic biodiversity in younger stands. The 160/180-year-old stands had a lower density of large trees (with or without microhabitats) and 180/200-year-old stands had the lowest levels of saproxylic beetle diversity. Nevertheless, the youngest premature stands (160/180 years old) were not the least species-rich. Conversely, the 300-year-old stands had greater species richness than the younger stands for all species combined as well as for rare species only. Moreover, they had higher levels of structural attributes that are potentially favourable to saproxylic biodiversity. However, due to the absence of 220-300-year-old stands, our sampling design suffers from a large age gap that remains to be investigated to specify both the dynamics of oak forests and the response of biodiversity to habitat change during this time lapse.

In high forest, age is one of the parameters which can be most easily controlled by forest management. Our study deals only with the premature to overmature phases of the forest cycle, but we can extrapolate from our results the potential consequences of a decrease in rotation length (i.e. a harvesting in the premature stands) and an increase in rotation length aiming at preserving biodiversity (i.e. preserving overmature stands). Indeed,

Table 5. Beetle species significantly associated ($P < 0.05$) with a particular stand age or with a combination of stand age. The Phi coefficient is the point-biserial group-equalised phi coefficient (Pearson correlation; see De Caceres & Legendre, 2009 for details), which is an estimate of the strength of an association.

Stand age	Family	Taxa	Phi coefficient	*P*-value
180/200	Cantharidae	*Malthinus flaveolus*	0.665	0.023*
300	Scraptiidae	*Anaspis thoracica*	0.822	0.003**
	Eucnemidae	*Hylis olexai*	0.808	0.004**
	Silvanidae	*Uleiota planatus*	0.750	0.005**
	Trogossitidae	*Nemozoma elongatum*	0.709	0.019*
	Eucnemidae	*Microrhagus pygmaeus*	0.690	0.009**
	Scarabaeidae	*Valgus hemipterus*	0.667	0.029*
	Laemophloeidae	*Laemophloeus kraussi*	0.665	0.016*
	Cerambycidae	*Anoplodera sexguttata*	0.640	0.040*
200/220 + 300	Melyridae	*Dasytes aeratus*	0.707	0.012*
160/180 + 180/200 + 200/220	Salpingidae	*Salpingus ruficollis*	0.881	0.02*
	Cucujidae	*Pediacus depressus*	0.841	0.05*
160/180 + 180/200 + 300	Elateridae	*Stenagostus rhombeus*	0.844	0.033*
	Curculionidae	*Scolytus intricatus*	0.767	0.048*
180/200 + 200/220 + 300	Anobiidae	*Hemicoelus nitidus*	0.774	0.028*
	Melandryidae	*Orchesia undulata*	0.764	0.020*

*$P < 0.05$; **$P < 0.01$.

our results suggest that a decrease in rotation length may reduce the density of large-diameter trees and microhabitats as well as species diversity.

The current trend to intensify forest production partly relies on shortening rotation lengths and subsequently, mean stand age, the density of large microhabitat-bearing trees and the quantity/diversity of deadwood will probably be reduced. To compensate for the negative effects of shortened rotation lengths, forest management solutions may be found in a combination of integrated and conservation-oriented forest management practices. Integrated forest management aims at preserving biodiversity and includes practices that retain microhabitat-rich tree types (Winter & Möller, 2008; Michel & Winter, 2009; Vuidot *et al.*, 2011) such as large-diameter snags (see Bouget *et al.*, 2011b), large logs, old decadent trees, and tree species such as oak and beech, and increase rotation lengths (Curtis, 1997; Franklin *et al.*, 2002; Vuidot *et al.*, 2011). Ranius and Jansson (2000) indicated that managing areas to maintain old oaks may help preserve red-listed saproxylic beetle fauna.

In addition, extended rotations have also been proposed as a method of preserving species associated with late successional stages (Curtis, 1997). But very few papers really associate the level of biodiversity with an age gradient (Holien, 1998). This study is one of the first to indirectly assess the effects of such measures on saproxylic biodiversity in the temperate biome. Temporarily setting aside overmature stands (i.e. creation of ageing islands) in French high forests may be used as a management tool for biodiversity conservation and restoration (Ericsson *et al.*, 2005). In addition, ageing islands are partly analogous to other international concepts, which preserve small forest areas, with the exception that ageing islands are only set aside temporarily rather than permanently. For example, Woodland Key Habitats (WKHs) or Green Tree Retention (GTR) patches practised in Fennoscandia (Timonen *et al.*, 2011) have been shown to significantly favour biodiversity and habitats. Indeed, Jonsson *et al.* (2005) showed that GTR patches generally have higher deadwood volumes than managed forest stands and, overall, contain many old-growth features (e.g. large old trees, microhabitats) which help maintain biodiversity (Jönsson & Jonsson, 2007). Djupström *et al.* (2008) showed that the WKHs provide high-quality habitats and high saproxylic beetle species richness. Even individual retention trees are important for saproxylic biodiversity (Kaila *et al.*, 1997).

Finally, conservation-oriented forest management recommends establishing a denser network of strict forest reserves, which can act as a refuge and source areas for logging-sensitive taxonomic groups (Moning & Müller, 2009). At the landscape scale, small permanent or temporary set-asides may be able to supplement the existing network of larger forest reserves and increase the availability and connectivity of potential habitats for several taxa, including saproxylic beetles.

In conclusion, the 300-year-old overmature stands clearly have a higher conservation value than the ordinary mature and premature stands. However, a better understanding of the explanatory factors for saproxylic biodiversity is therefore required to improve conservation targets in high forests, which are being primarily managed for wood production. Silvicultural practices preserving natural-like structural features for biodiversity conservation should be promoted in production-oriented forest management.

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References

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511–525.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M. & Weslien, J. (1994) Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology*, **8**, 718–731.

Bergès, L., Dupouey, J.-L. & Franc, A. (2000) Long-term changes in wood density and radial growth of Quercus petraeain northern France since the middle of the nineteenth century. *Trees - Structure and Function*, **14**, 398–408.

Bouget, C., Brin, A. & Brustel, H. (2011a) Exploring the "last biotic frontier": are temperate forest canopies special for saproxylic beetles? *Forest Ecology and Management*, **261**, 211–220.

Bouget, C., Brustel, H., Brin, A. & Valladares, L. (2009) Evaluation of window flight traps for effectiveness at monitoring dead wood-associated beetles: the effect of ethanol lure under contrasting environmental conditions. *Agricultural and Forest Entomology*, **11**, 143–152.

Bouget, C., Brustel, H. & Zagatti, P. (2008) *The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status.* <http://frisbee. nogent.cemagref.fr/index.php/en/> 30th July 2011.

Bouget, C., Nusillard, B., Pineau, X. & Ricou, C. (2011b) Effect of deadwood position on saproxylic beetles in temperate forests and conservation interests of oak snags. *Insect Conservation and Diversity*, **5**, 264–278.

Brustel, H. (2004) 'Polytrap^{TM}' a window flight trap for saproxylic beetles. *Proceedings of the 3rd Symposium and Workshop on the Conservation of Saproxylic Beetles, Latvijas entomologs*, (Suppl VI), pp. 128–129. Petrovskis & Ko, Riga, Latvia.

Colwell, R.K. (2005) *EstimateS 7.5: statistical estimation of species richness and shared species from samples.* <http://viceroy.eeb.uconn.edu/estimates>.

Curtis, R.O. (1997). The Role of Extended Rotations. *Creating a Forest for the 21st Century, Island* (ed. by K.A. Kohm and J.F. Franklin), pp. 165–170. Island Press, Washington, District of Columbia.

De Caceres, M. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, **90**, 3566–3574.

De Caceres, M., Legendre, P. & Moretti, M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos*, **119**, 1674–1684.

Djupström, L.B., Weslien, J. & Schroeder, L.M. (2008) Dead wood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *Forest Ecology and Management*, **255**, 3340–3350.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Ericsson, T.S., Berglund, H. & Östlund, L. (2005) History and forest biodiversity of woodland key habitats in south boreal Sweden. *Biological Conservation*, **122**, 289–303.

Fan, Z.F., Shifley, S.R., Spetich, M.A., Thompson, F.R. & Larsen, D.R. (2003) Distribution of cavity trees in midwestern old-growth and second-growth forests. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **33**, 1481–1494.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J.Q. (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, **155**, 399–423.

Gibb, H., Hjältén, J., Ball, J.P., Atlegrim, O., Pettersson, R.B., Hilszczanski, J., Johansson, T. & Danell, K. (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography*, **29**, 191–204.

Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of Forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Hannah, L., Carr, J.L. & Landerani, A. (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation*, **4**, 128–155.

Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. (1991) Conserving biodiversity in managed forests: lessons from natural forests. *BioScience*, **41**, 382–392.

Heilmann-Clausen, J. & Christensen, M. (2004) Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *Forest Ecology and Management*, **201**, 105–117.

Heliovaara, K. & Vaisanen, R. (1984) Effect of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennica*, **189**, 1–32.

Holien, H. (1998) Lichens in spruce forest stands of different successional stages in central Norway with emphasis on diversity and old growth species. *Nova Hedwigia*, **66**, 283–324.

Humphrey, J.W. (2005) Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. *Forestry*, **78**, 33–53.

Inventaire Forestier National (IFN) (2010) *La forêt française.* <http://www.ifn.fr>.

Johansson, P., Rydin, H. & Thor, G. (2007) Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience*, **14**, 81–91.

Jonsell, M., Nordlander, G. & Jonsson, M. (1999) Colonization patterns of insects breeding in wood-decaying fungi. *Journal of Insect Conservation*, **3**, 145–161.

Jönsson, M.T. & Jonsson, B.G. (2007) Assessing coarse woody debris in Swedish woodland key habitats: implications for conservation and management. *Forest Ecology and Management*, **242**, 363–373.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood - Lessons for dead wood management. *Silva Fennica*, **39**, 289–309.

Kaila, L., Martikainen, P. & Punttila, P. (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation*, **6**, 1–18.

Larsson, T.B. (2001) Biodiversity evaluation tools for European forests. *Ecological Bulletins*, **50**, 1–237.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **5**, 1027–1039.

Lindenmayer, D.B. & Franklin, J.F. (2002) *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*. pp. 351. Island Press, Washington, District of Columbia.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, **94**, 199–209.

Michel, A.K. & Winter, S. (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *Forest Ecology and Management*, **257**, 1453–1464.

Ministère De L'agriculture Et De La Pêche (2006). *Les indicateurs de gestion durable des forêts françaises (Indicators for the sustainable management of French forests), MAP, Paris.* <http://www.ifn.fr/spip/IMG/pdf/IDG2005_en-2.pdf>.

Moning, C. & Müller, J. (2009) Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. *Ecological Indicators*, **9**, 922–932.

Müller, J., Bussler, H. & Kneib, T. (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation*, **12**, 107–124.

Nascimbene, J., Marini, L., Motta, R. & Nimis, P. (2009) Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodiversity and Conservation*, **18**, 1509–1522.

Niemela, J. (1997) Invertebrates and boreal forest management. *Conservation Biology*, **11**, 601–610.

Office National des Forêts (ONF) (2009) Conservation de la biodiversité dans la gestion courante des forêts publiques. *Instruction nationale INS-09-T-71*, 11 pp.

Palm, T. (1959) Die Holz- und Rindenkäfer der süd- und mittelschwedischen Laubbäume. *Opuscula Entomologica*, **Supplement 16**, 1–374.

Penttilä, R., Siitonen, J. & Kuusinen, M. (2004) Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation*, **117**, 271–283.

R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ranius, T., Eliasson, P. & Johansson, P. (2008) Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. *Biodiversity and Conservation*, **17**, 2371–2381.

Ranius, T. & Hedin, J. (2001) The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows. *Oecologia*, **126**, 363–370.

Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, **95**, 85–94.

Schiegg, K. (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience*, **7**, 290–298.

Siitonen, J. & Saaristo, L. (2000) Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. *Biological Conservation*, **94**, 211–220.

Similä, M., Kouki, J., Mönkkönen, M. & Sippola, A.-L. (2002) Beetle species richness along the forest productivity gradient in northern Finland. *Ecography*, **25**, 42–52.

Stenbacka, F., Hjältén, J., Hilszczanski, J. & Dynesius, M. (2010) Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications*, **20**, 2310–2321.

Sverdrup-Thygeson, A. & Lindenmayer, D.B. (2003) Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. *Forest Ecology and Management*, **174**, 353–363.

Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. (2011) Hotspots in cold climate: conservation value of woodland key habitats in boreal forests. *Biological Conservation*, **144**, 2061–2067.

Ulyshen, M.D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, **261**, 1479–1489.

Vodka, S., Konvicka, M. & Cizek, L. (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation*, **13**, 553–562.

Vuidot, A., Paillet, Y., Archaux, F. & Gosselin, F. (2011) Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, **144**, 441–450.

Winter, S. & Möller, G.C. (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management*, **255**, 1251–1261.

Woodall, C. & Williams, M.S. (2005) Sampling protocol, estimation, and analysis procedures for the down woody materials indicator of the FIA program. General Technical Report – North Central Research Station, USDA Forest Service, 1:47.

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Appendix A

Species list. Trophic group: Sapro: saproxylophagous. Myc: mycetophagous. Pred: predator. Xy2: secondary wood decayer. Sap: saprophagous. Patrimoniality value: common. quite common. quite rare and rare (red listed species)

Family	Species	Trophic group	Patrimoniality value	Abundance
Aderidae	*Aderus populneus*	Sapro	Quite common	1
	Euglenes pygmaeus	Sapro	Quite rare	1
Anobiidae	*Dorcatoma chrysomelina*	Myc	Quite common	2
	Gastrallus immarginatus	Xy2	Quite common	3
	Gastrallus laevigatus	Xy2	Quite common	5
	Grynobius planus	Xy2	Quite common	1
	Hadrobregmus denticollis	Xy2	Quite rare	5
	Hemicoelus costatus	Xy2	Common	213
	Hemicoelus fulvicornis	Xy2	Common	34
	Hemicoelus nitidus	Xy2	Common	32
	Ochina ptinoides	Xy2	Quite common	2
	Oligomerus brunneus	Xy2	Common	14
	Ptilinus fuscus	Xy2	Quite rare	31
	Ptilinus pectinicornis	Xy2	Quite common	2
	Ptinomorphus imperialis	Xy2	Quite common	5
	Ptinus bidens	Sap	Common	1
	Ptinus lichenum	Sap	Quite common	3
	Ptinus sp.	Sap	NA	108
	Ptinus subpilosus	Sap	Quite common	7
	Xestobium plumbeum	Xy2	Quite common	50

Appendix A (Continued)

Family	Species	Trophic group	Patrimoniality value	Abundance
Anthribidae	*Choragus sheppardi*	Myc	Quite common	2
	Dissoleucas niveirostris	Sapro	Quite common	3
	Platyrhinus resinosus	Sapro	Quite common	3
	Platystomos albinus	Sapro	Quite common	17
	Tropideres albirostris	Sapro	Quite common	4
Biphyllidae	*Biphyllus lunatus*	Myc	Quite rare	1
	Diplocoelus fagi	Myc	Common	88
Bothrideridae	*Oxylaemus cylindricus*	Pred	Quite common	11
	Teredus cylindricus	Pred	Quite rare	4
Cantharidae	*Malthinus balteatus*	Pred	Quite common	1
	Malthinus fasciatus	Pred	Quite common	1
	Malthinus flaveolus	Pred	Common	6
	Malthinus seriepunctatus	Pred	Common	2
	Malthinus sp.	Pred	NA	3
Cerambycidae	*Alosterna tabacicolor*	Xy2	Common	9
	Anaglyptus mysticus	Xy2	Quite common	13
	Anoplodera sexguttata	Xy2	Quite common	3
	Cerambyx scopolii	Xy2	Common	5
	Clytus arietis	Xy2	Common	3
	Cortodera humeralis	Xy2	Quite common	12
	Leiopus nebulosus	Xy2	Common	11
	Leptura aurulenta	Xy2	Quite common	3
	Mesosa nebulosa	Xy2	Common	11
	Phymatodes testaceus	Xy2	Common	1
	Poecilium pusillum	Xy2	Quite common	1
	Pogonocherus hispidulus	Xy2	Quite common	5
	Prionus coriarius	Xy2	Quite common	4
	Pyrrhidium sanguineum	Xy2	Common	5
	Rhagium bifasciatum	Xy2	Quite common	16
	Rhagium mordax	Xy2	Quite common	78
	Rhagium sycophanta	Xy2	Quite common	53
	Rhamnusium bicolor	Xy2	Quite rare	2
	Rutpela maculata	Xy2	Common	19
	Stenurella melanura	Xy2	Common	16
	Stictoleptura scutellata	Xy2	Quite common	3
	Xylotrechus arvicola	Xy2	Quite common	4
Cerylonidae	*Cerylon deplanatum*	Pred	Quite rare	4
	Cerylon fagi	Pred	Quite common	1
	Cerylon ferrugineum	Pred	Common	30
	Cerylon histeroides	Pred	Common	2
	Cerylon impressum	Pred	Quite rare	1
Ciidae	*Cis boleti*	Myc	Common	1
	Cis fissicollis	Myc	Rare	1
	Cis micans	Myc	Common	39
	Cis rugulosus	Myc	Common	1
	Ennearthron cornutum	Myc	Common	1
	Octotemnus glabriculus	Myc	Common	1
	Orthocis alni	Myc	Common	1
	Orthocis festivus	Myc	Common	3
	Orthocis vestitus	Myc	Common	13
	Xylographus bostrichoides	Myc	Quite common	1
Cleridae	*Clerus mutillarius*	Pred	Common	5
	Opilo domesticus	Pred	Quite common	1
	Opilo mollis	Pred	Quite common	3
Corylophidae	*Arthrolips* sp.	Sap	NA	12
	Sericoderus lateralis	Sap	Common	6
Cucujidae	*Pediacus depressus*	Pred	Quite rare	68
	Pediacus dermestoides	Pred	Quite common	15

Appendix A (Continued)

Family	Species	Trophic group	Patrimoniality value	Abundance
Curculionidae	*Camptorhinus statua*	Sapro	Quite rare	2
	Cyclorhipidion bodoanus	Xy2	Quite common	61
	Dryophthorus corticalis	Xy2	Common	2
	Platypus cylindrus	Xy2	Common	1
Scolytidae	*Dryocoetes villosus*	Xy2	Common	1
	Ernoporicus fagi	Xy2	Common	14
	Hylastes opacus	Xy2	Quite common	3
	Scolytus intricatus	Xy2	Common	50
	Scolytus rugulosus	Xy2	Common	7
	Taphrorychus bicolor	Xy2	Common	89
	Taphrorychus villifrons	Xy2	Common	142
	Trypodendron domesticum	Myc	Common	21
	Trypodendron signatum	Myc	Common	108
	Xyleborinus saxesenii	Xy2	Common	217
	Xyleborus cryptographus	Myc	Quite common	2
	Xyleborus dispar	Xy2	Common	1091
	Xyleborus dryographus	Myc	Common	4
	Xyleborus monographus	Myc	Common	30
	Xylosandrus germanus	Myc	Common	1079
Dermestidae	*Ctesias serra*	Sap	Common	2
	Dermestes murinus	Sap	Common	1
	Megatoma undata	Sap	Common	12
	Trinodes hirtus	Sap	Quite common	1
Elateridae	*Ampedus cinnaberinus*	Pred	Quite common	8
	Ampedus erythrogonus	Pred	Quite common	6
	Ampedus glycerus	Pred	Quite common	32
	Ampedus nigerrimus	Pred	Quite common	17
	Ampedus pomorum	Pred	Quite common	19
	Ampedus quercicola	Pred	Common	268
	Ampedus rufipennis	Pred	Quite common	1
	Ampedus sanguineus	Pred	Common	1
	Brachygonus megerlei	Pred	Quite common	4
	Calambus bipustulatus	Pred	Quite rare	13
	Denticollis linearis	Pred	Common	9
	Hypoganus inunctus	Pred	Quite rare	5
	Lacon querceus	Pred	Quite rare	1
	Melanotus castanipes	Pred	Common	5
	Melanotus villosus	Pred	Common	152
	Stenagostus rhombeus	Pred	Quite common	32
Endomychidae	*Symbiotes latus*	Myc	Quite rare	5
Erotylidae	*Dacne bipustulata*	Myc	Common	26
	Triplax lepida	Myc	Quite common	3
	Triplax russica	Myc	Common	2
	Tritoma bipustulata	Myc	Common	1
Eucnemidae	*Hylis olexai*	Xy2	Quite common	6
	Hylis simonae	Xy2	Quite rare	7
	Isoriphis marmottani	Xy2	Quite rare	139
	Isoriphis melasoides	Xy2	Quite common	1036
	Melasis buprestoides	Xy2	Common	72
	Microrhagus lepidus	Xy2	Quite common	2
	Microrhagus pygmaeus	Xy2	Quite common	17
	Nematodes filum	Xy2	Quite rare	10
Histeridae	*Abraeus perpusillus*	Pred	Quite common	5
	Gnathoncus buyssoni	Pred	Quite rare	7
	Paromalus flavicornis	Pred	Common	2
	Paromalus parallelepipedus	Pred	Common	1
	Plegaderus dissectus	Pred	Quite common	5

Appendix A (Continued)

Family	Species	Trophic group	Patrimoniality value	Abundance
Laemophloeidae	*Cryptolestes duplicatus*	Sap	Common	4
	Cryptolestes ferrugineus	Sap	Common	1
	Laemophloeus kraussi	Sap	Quite rare	4
	Placonotus testaceus	Sap	Common	1
Latridiidae	*Cartodere constricta*	Myc	Quite common	2
	Cartodere nodifer	Myc	Common	25
	Corticaria sp.	Myc	NA	316
	Enicmus brevicornis	Myc	Common	1
	Enicmus rugosus	Myc	Common	100
	Enicmus testaceus	Myc	Common	149
	Enicmus transversus	Myc	Common	4
	Latridius hirtus	Myc	Quite common	1
	Latridius minutus	Myc	Common	1
	Stephostethus angusticollis	Myc	Common	37
Leiodidae	*Agathidium nigripenne*	Myc	Quite common	6
Lucanidae	*Dorcus parallelipipedus*	Sapro	Common	1
	Lucanus cervus	Xy2	Common	1
	Platycerus caprea	Sapro	Quite common	2
	Platycerus caraboides	Sapro	Quite common	33
Lymexylidae	*Hylecoetus dermestoides*	Xy2	Common	1
Melandryidae	*Abdera bifasciata*	Myc	Common	3
	Melandrya barbata	Sapro	Quite rare	15
	Melandrya caraboides	Sapro	Quite common	11
	Orchesia fasciata	Sapro	Quite rare	1
	Orchesia undulata	Myc	Quite common	21
Melyridae	*Aplocnemus impressus*	Pred	Quite common	3
	Dasytes aeratus	Pred	Common	8
	Dasytes caeruleus	Pred	Common	59
	Dasytes nigrocyaneus	Pred	Quite rare	4
	Dasytes pauperculus	Pred	Quite rare	81
	Dasytes plumbeus	Pred	Common	2
	Dasytes virens	Pred	Common	3
	Trichoceble floralis	Pred	Quite rare	10
Monotomidae	*Monotoma picipes*	Sap	Quite common	2
	Rhizophagus bipustulatus	Pred	Common	940
	Rhizophagus dispar	Pred	Common	1
	Rhizophagus ferrugineus	Pred	Common	8
	Rhizophagus nitidulus	Pred	Quite rare	1
	Rhizophagus parallelocollis	Pred	Quite common	1
	Rhizophagus perforatus	Pred	Common	1
Mordellidae	*Mordella* sp.	Sapro	NA	6
	Mordellochroa abdominalis	Sapro	Common	7
	Tomoxia bucephala	Sapro	Common	22
Mycetophagidae	*Litargus connexus*	Myc	Common	227
	Mycetophagus atomarius	Myc	Quite common	3
	Mycetophagus fulvicollis	Myc	Quite rare	2
	Mycetophagus multipunctatus	Myc	Quite common	1
	Mycetophagus piceus	Myc	Quite common	1
	Mycetophagus quadriguttatus	Myc	Quite common	5
	Mycetophagus quadripustulatus	Myc	Common	3
Nitidulidae	*Carpophilus sexpustulatus*	Sap	Common	10
	Cryptarcha strigata	Sap	Common	83
	Cryptarcha undata	Sap	Common	18
	Epuraea guttata	Sap	Quite common	1
	Epuraea sp.	Sap	NA	31
	Glischrochilus quadriguttatus	Sap	Quite common	13
	Soronia grisea	Sap	Common	99
	Soronia punctatissima	Sap	Quite common	2

Appendix A (Continued)

Family	Species	Trophic group	Patrimoniality value	Abundance
Nosodendridae	*Nosodendron fasciculare*	Sap	Quite rare	17
Pyrochroidae	*Pyrochroa coccinea*	Pred	Common	6
Salpingidae	*Cariderus aeneus*	Pred	Quite rare	1
	Lissodema denticolle	Pred	Quite common	36
	Salpingus planirostris	Pred	Common	99
	Salpingus ruficollis	Pred	Common	62
	Vincenzellus ruficollis	Pred	Quite common	95
Scarabaeidae	*Cetonia aurata*	Sapro	Common	131
	Gnorimus nobilis	Sapro	Quite common	2
	Valgus hemipterus	Sapro	Common	7
Scirtidae	*Prionocyphon serricornis*	Sap	Quite common	1
Scraptiidae	*Anaspis fasciata*	Sapro	Common	56
	Anaspis frontalis	Sapro	Common	1
	Anaspis garneysi	Sapro	Common	7
	Anaspis lurida	Sapro	Common	19
	Anaspis melanopa	Sapro	Common	41
	Anaspis sp.	Sapro	Common	28
	Anaspis thoracica	Sapro	Common	4
Silvanidae	*Silvanoprus fagi*	Pred	Common	2
	Silvanus bidentatus	Pred	Common	5
	Silvanus unidentatus	Pred	Common	10
	Uleiota planatus	Pred	Common	6
Sphindidae	*Aspidiphorus orbiculatus*	Myc	Quite common	6
Tenebrionidae	*Corticeus unicolor*	Sap	Common	3
	Gonodera luperus	Sapro	Common	6
	Mycetochara axillaris	Sapro	Rare	1
	Mycetochara maura	Sapro	Common	164
	Mycetochara quadrimaculata	Sapro	Quite rare	2
	Nalassus laevioctostriatus	Sapro	Common	4
	Palorus depressus	Myc	Common	1
	Prionychus melanarius	Sapro	Common	1
Tetratomidae	*Tetratoma desmarestii*	Myc	Quite rare	1
Trogossitidae	*Nemozoma elongatum*	Pred	Common	6
	Thymalus limbatus	Myc	Quite common	4
Zopheridae	*Bitoma crenata*	Pred	Common	1
	Colobicus hirtus	Pred	Quite common	4
	Colydium elongatum	Pred	Common	2
	Coxelus pictus	Myc	Quite common	13
	Endophloeus markovichianus	Myc	Common	2
	Pycnomerus terebrans	Myc	Quite rare	3
	Synchita humeralis	Myc	Quite common	27
	Synchita separanda	Myc	Quite common	4
	Synchita undata	Myc	Quite common	6

Comparison of tree microhabitat abundance and diversity in the edges and interior of small temperate woodlands

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Highlights

1/ Microhabitat density was significantly higher in woodland edges than in their interior

2/ Bark loss, cracks, sap runs and epiphytes were significantly more abundant in woodland edges

3/ It is important to consider woodland edges for forest and non forest biodiversity conservation

Abstract

Forest edges are important features of wooded farmland. Their role for biodiversity was investigated using tree microhabitats (TMH) as an indirect indicator of forest biodiversity. Because they are managed more intensively, trees in the edges of fragmented temperate woodlands are likely to host more TMH than trees in their interior. In this study, we tested this hypothesis in relation to tree density, diameter, species composition and the structure and management of woodland edges. We selected 28 woodlands with edges differing by their structure and the adjacent fields. Eleven types of TMH were recorded in two transects set up in the edges and interior of the woodlands. TMH density was significantly higher in the woodland edges (4.67 ± 0.78) than in the interior (1.86 ± 0.23). Some TMH - patches of bark loss, cracks, sap runs and epiphytes - were significantly more abundant in the edges than in the interior. These results were accounted for by the convergence of several factors: i) significantly higher tree density in woodland edges, ii) a significantly higher proportion of TMH host trees in woodland edges, iii) a larger tree diameter on average in woodland edges and, even in the same given size class, a higher frequency of TMH host trees, iv) greater abundance in woodland edges of tree species more likely to host TMH, even with small diameters. The positive relationship found between the height of the bottom of the crown and TMH abundance may have resulted from abiotic factors (micro-climatic conditions) related to long management rotations, but we did not demonstrate any direct effect of management practices. Given the large number of forest taxa, but also farmland taxa, that depend on TMH, woodland edges should be reconsidered as zones of high potential interest for forest biodiversity conservation.

Key-words

Woodland edges, Tree microhabitat, Species composition, Structure, Management

1. Introduction

Most of Europe's forest cover is made up of fragmented woodlands (Larsson, 2001), mostly in close association with farmlands. Their fragmentation is the result of habitat destruction (Tilman *et al.*, 2001), but also of successive episodes of woodland clearance, cultivation and reforestation over historical time (Dupouey *et al.*, 2002; Pitte, 2003). Fragmented forests are characterized by: i) their small area, ii) their isolation from other forest fragments and, as a result of the above, iii) a relatively higher proportion of woodland edges compared to the total land area at any scale in small woodlands as compared to large forests.

Forest edges are defined as an abrupt transition between relatively homogeneous ecosystems, at least one of which is forest (Matlack and Litvaitis, 1999). Depending on the type of resources found in the two contiguous habitats (complementary or supplementary), different biodiversity responses are to be expected: neutral, positive or transitional (Ries *et al.*, 2004). Empirical studies on the effects of forest edges on biodiversity have shown positive as well as negative effects, depending on which side of the edge is concerned, but biodiversity in forest edges is often higher than in the interior and some authors have identified specialist forest edge species (Ries and Sisk, 2010). Regarding forest biodiversity, the edge effect equates to a reduction of the core forest area, which can have a direct effect on the loss of forest species habitats (Hanski, 2005), but also an indirect effect by exposing organisms to the conditions of the surrounding ecosystems (Murcia, 1995). The study by Salek *et al.* (2013) is one of the few suggesting that forest edges could benefit forest biodiversity as some of their characteristics are favorable to species conservation, such as the presence of large trees and a corresponding potential for the occurrence of snags and high shrubs. They argue, moreover, that exploiting forest edges for timber production is of little economic interest, and conclude that woodland edges, in temperate riparian forests, should be dedicated to conservation. In farmland, however, woodland edges are managed by farmers and/or woodland owners to prevent forest growth from interfering with crop production or livestock breeding. The main management practices are the use of herbicides that could be detrimental to plant biodiversity in field margins (Le Coeur *et al.*, 1997), or tree and/or branch cutting that could also promote biodiversity by creating tree microhabitats such as sap runs and patches of bark loss.

Tree microhabitats (TMH) are defined as structural heterogeneities on the trunks or branches of trees, such as cavities or cracks (Stokland *et al.*, 2012). They host a wide range of taxa (Speight, 1989; Winter and Möller, 2008; Michel and Winter, 2009; Larrieu *et al.*, 2012). Some taxa are highly dependent on TMH: more than 40 % of birds in French forests use tree cavities or cracks for breeding (Blondel, 2005). Nearly 25% of the species hosted by forests depend on TMH or decayed wood for at least a part of their life cycle (Stokland *et al.*, 2012). TMH are cited as relevant surrogates for taxonomic diversity assessment (Winter and Möller, 2008), at least for saproxylic beetles (Bouget *et al.*, 2013; Bouget *et al.*, 2014). Furthermore, species that depend on saproxylic TMH (i.e. which are at least partially made up of decaying wood) contribute to nutrient cycling and thus to forest soil fertility (Speight, 1989). Studies on TMH abundance in large forests are related not only to tree species and tree diameter, but also to management (Vuidot *et al.*, 2011; Larrieu *et al.*, 2012; Regnery *et al.*, 2013), but no studies have been conducted in small forests and woodland edges as considered here.

In comparing TMH in the interior and edges of forests, we tested the hypothesis that: i) woodland edges support a higher TMH density than their interior, ii) some TMH will be more abundant in woodland edges. We explored the factors potentially related to TMH density in woodland edges: tree densities and diameters, tree species composition, edge structure and management practices.

2. Methods

2.1. Study area

The study was carried out in the *Vallées et Coteaux de Gascogne*, a long-term socio-ecological research site in a rural region in Gascony, south-western France (43◦16_N, 0◦54_E). The temperate agro-forested landscape is characterized by small woodlands embedded in a mosaic of meadows (livestock farming) and crops. Woodlands cover approximately 15% of the total area and most cover less than 20 ha. The region is hilly (250–400 m a.s.l.) and has a sub-Atlantic climate with slight Mediterranean influences (mean annual temperature 12.5 ◦C; mean annual precipitation 750 mm). These climatic influences are reflected in the medio-European type flora, where oaks (*Quercus robur* L., *Quercus pubescens* Willd., *Quercus petraea* Liebl.) are the main tree species, often in combination with hornbeam (*Carpinus betulus* L.), wild cherry (*Prunus avium* L.), wild service tree (*Sorbus torminalis* (L), sweet chestnut (*Castanea sativa* Mill.) and field maple (*Acer campestre* L.) (Gonzalez *et al.*, 2009).

A previous study in the region found no permanent spatial management units in the small woodlands, where logging areas were defined according to locally prevailing conditions (Du Bus de Warnaffe *et al.*, 2006). Spatial logging patterns in these woodlands are therefore complex and hard to predict in terms of classic forestry rules. The woodland stands are characterized by coppice with standards growing from seed (ca. 30.ha). The coppices are generally assumed to be cut every 30 years by clear felling of small sections with farm machinery, mainly to produce firewood. Some of the standards may be felled as well, for sale or own use as construction timber. The study reports more frequent cutting of hedgerow trees, because of their faster growth rate and accessibility, for firewood and to manage field borders (Du Bus de Warnaffe *et al.*, 2006).

Twenty-eight woodlands were selected in this study area, varying in size from 0.87 ha to 47.44 ha (12.24 ±13.54), with the exception of one large 500 ha wood. All had at least one edge meeting the following criteria: 1) edges contiguous to agricultural land (meadows, oilseed rape or winter wheat); 2) straight edges at least 100m in length; 3) separated from each other by at least 300 m; 4) no track, bank or ditch between the wood and the adjacent field. Because the orientation of woodland edges has been shown to induce different climatic conditions (Chen *et al.*, 1993), with consequences for their biodiversity (Murcia, 1995; Ries *et al.*, 2004), north-facing edges ("cold edges") were excluded. Sharp and smooth edges were selected according to their width and general physiognomy, with adjacent meadows or crop fields.

2.2 Observation of tree microhabitats

In each of the woodlands studied, we analyzed two parallel transects 100 m in length. The first transect was set up in the woodland edge. Its outer limit was the boundary of the wood, that is to say the line joining the first trees in the wood with a diameter at breast height (DBH) of at least 5 cm, and extending for 2.5 m inside the wood. However, trees further than 2.5 m from the boundary but with branches reaching the boundary, and therefore subject to field edge management, were also included in this "edge transect".

The second transect was set up in the interior of the wood 50 m away from the first transect, but 5 m in width to compensate for the lower density of trees expected compared to the woodland edge, so that a similar number of trees could be observed in both transects. The distance of 50 m was chosen because the woods were at least 100m wide at their narrowest point.

All the standing trees having their stem in the transects thus defined and a minimum DBH of 5 cm were then examined for the presence of microhabitats on the visible part of the trunk, both beneath and within the tree crown. Snags were taken into account and examined for their microhabitats only when they were more than 1 m in height. The DBH of all these trees, alive or dead, was also recorded and approximated to the nearest centimeter. The tree microhabitats observed are listed in Table 1: all were noted as the number of occurrences per tree, except epiphytes, which were recorded in percentage classes, and carpophores as present or absent.

We recorded a set of 11 microhabitat types as follows (see Table 1 for a full description of the main associated taxa): (i) cavities excavated by woodpeckers, with an entrance wider than 3 cm: included in this category were all woodpecker breeding holes and holes made by woodpeckers when feeding and deep enough to host a vertebrate; (ii) cavities with mould and an entrance wider than 10 cm: included in this category were other natural cavities and cavities with mould with an entrance more than 10 cm in width, as well as patches of missing bark of more than 100 cm2 and wood at a decay stage of more than 3 (with reference to a 5-stage scale, see Table 1 SM); here, we differentiated cavities in contact with the ground ("base cavity") or not ("trunk cavity"); (iii) bark-lined cavities (deep cavities formed between roots) with an entrance more than 3 cm in width; (iv) cracks in the tree trunk wider than 1 cm and more than 1 m above the ground, or bark in the process of peeling and forming a shelter; dendrothelms were recorded when the entrance was wider than 3 cm., differentiating between v) rotted-bottom dendrothelms, when the bottom of the cavity was made of decayed wood, and vi) bark-lined dendrothelms when the bottom of the cavity was made of undecayed bark: in dry periods, observations of traces of water flow on the trunk allowed us to diagnose inaccessible dendrothelms; (vii) patches of bark loss with hard wood (decay stage of less than 2), covering more than 100 cm²; (viii) taxonomically unidentified sporophores of saproxylic fungi: only tough fungi were noted (polypores s.l.); (ix) crown deadwood, i.e. large dead branches more than 20 cm in diameter and 1 m in length, or dead wood accounting for more than 20% of the crown wood; (x) epiphytes covering more than 20% of the trunk surface; and (xi) active sap runs longer than 10 cm.

2.3. Woodland edge structures and management

The woodland edge structures were recorded in 2011 using two transects perpendicular to the edges. For homogeneous edges, the transects were placed at one quarter and three quarters of the total edge length. Otherwise, the two transects were set up in the middle of each main physiognomy type. Because of the difficulty of assessing the extent of the woodland part of the edge, only the length of the field part (Lfield) was recorded. The height of the canopy (h1), the height of the bottom of the crown (h2) and the type of adjacent field (meadow or crop field) were also recorded (Fig. 1). Most of the edges were managed by the farmer managing the adjacent field, in agreement with the forest owner when the two were not the same person. Data on management tools (chipper, circular saw), woodland management (only branches cut, and burned or not, or entire trees felled) and the interval between 2 cuts ("rotation" in years) were recorded using interviews and/or by sending out questionnaires (management data is missing for only two woodland edges). For one long-unmanaged edge, the rotation interval was set at 30 years, i.e. roughly the maximum coppicing interval (Bastien, 2002).

Table 1. The 11 tree microhabitats considered in this study and their related taxa in temperate forests according to the literature.

Microhabitat categories	Microhabitat types	Taxa	References
Dry cavities	Woodpecker cavities Basal cavities with mould. Bark-lined cavity	birds, bats and other mammals, arthropods, lichens, bryophytes, fungi	Ranius (2002); Le Louarn & Quéré (2003); Berniccia (2005); Blondel (2005); Tillon (2005); Radek et al. (2009); Fritz and Heilmann-Clausen (2010)
Dendrothelms	Rotted-bottom dendrothelms Bark-lined dendrothelms	insects, micro-crustaceans	Kitching (1971); Vaillant (1978); Dajoz (2007), Schmidl et al. (2008)
Cracks	Cracks	bats, spiders, birds, flat bugs	Cramp et al. (1980); Pénicaud (2000); Meschede and Heller (2003); Tillon (2005); Heiss and Pericart (2007); Stanska et al. (2010)
Deadwood	Bark loss patches	insects, fungi	Girompaire and Ballon (1992); Vane et al. (2006); Dajoz (2007)
	Crown deadwood	insects, other arthropods (Collembola, mites), fungi, bats	Unterseher & Tal (2006); Speight et al. (2010); Bouget et al. (2011); Stokland et al. (2012)
Fungi	Carpophores of saproxylic fungi	insects, fungi	Lisiewska (1992); Ellis and Ellis (1998); Bobiec et al. (2005); Dajoz (2007); Heiss and Pericart (2007)
Epiphytes	Epiphytes	birds, mammals, mosses, insects	Harrison (1977); Labrid (1986); Infante-Sanchez (2013 pers. com.) ; Valladares (2013 pers. com.)
Sap runs	Moist sap runs	insects, yeasts	Crowson (1981); Bobiec et al. (2005); Yoshimoto et al. (2005); Ricarte et al. (2009); Stokland et al. (2012)

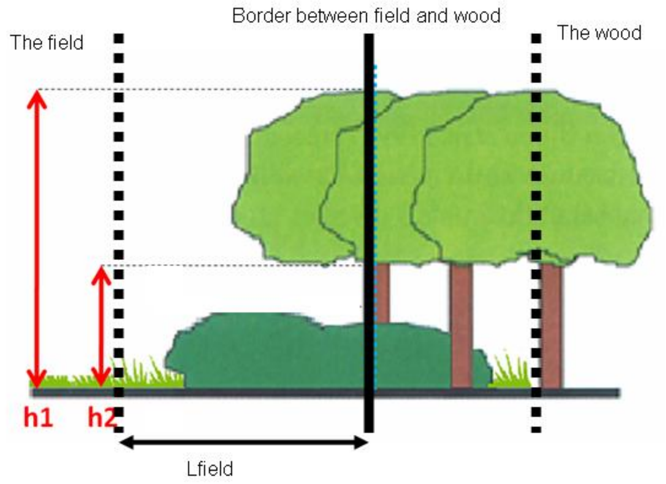

Figure 1. Woodland edge structure was described with 3 variables: length of the field part of the edge (Lfield), height of the canopy (“h1”) and height of the bottom of the crown (“h2”). The boundary between field and wood was defined as the line joining the first trees of the wood with a diameter at breast height (DBH) of at least 5 cm.

2.4. Calculation and statistical analyses

Because some edges were less than 100 m in length (in 3 cases due to the need to find rape fields for the first year of the study), tree and TMH densities were calculated as density for a 100 m^2 area. To allow comparisons between woodland edges and the interior zones, most of the data were analyzed in terms of densities (trees, TMH host trees, TMH): trees further than 2.5 m from the wood boundary were therefore not included for this purpose. However, to study the effects of woodland structure and management on TMH on woodland edges only, we considered trees further than 2.5 m from the boundary but with branches reaching the boundary, and the results are given in terms of abundance and not densities.

Comparisons between woodland edges and interior zones were made using paired permutational Student’s t-tests (Hervé, 2014). Paired tests were conducted because they control for the effect of the woodland itself on the variables studied. Non-parametric tests were chosen because most of the variables sampled did not follow a normal distribution.

Linear additive models were used to identify management and structure variables that significantly influenced TMH density and diversity in the woodland edges ("dredge" and "model.avg" functions of the "MuMIn" R package).

All analyses were performed using R software version 2.14.1 (R Development Core Team 2011).

3. Results

Altogether, we observed 1016 trees in woodland edges and 1007 in woodland interiors, belonging to 16 species (Table 3, and Table 2 SM). We identified 617 TMH in the edges and 415 in the interior zones.

3.1. Density of TMH and trees in woodland edges vs. interior zones

The density of TMH was significantly higher in woodland edges than in the interior for the whole data set as well as for live trees, but not for snags (all trees, *t* = -3.6, *df* = 27, *p* = 0.001; live trees *t* = -3.7, *df* = 27, *p* = 0.001; snags, *t* = -1.3, *df* = 27, *p* = 0.19) (Fig. 2).

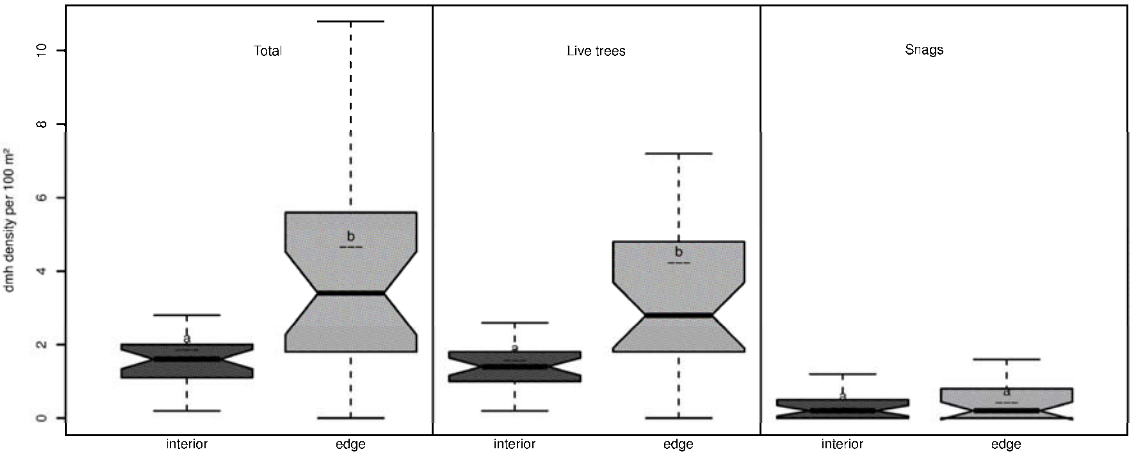

Figure 2. Microhabitat density in woodland edge and interior transects for the whole dataset, including live trees and snags. *Mean values are indicated in boxplots by dotted lines. Different letters indicate statistical differences of permutation t test at a 5% threshold.*

Some TMH contributed significantly to this pattern. Bark loss patches, cracks, sap runs and epiphytes were significantly more abundant in woodland edges than in interior zones (respectively, *t* =5.8, *df* = 27, *p* = 0.001, *t* = 2.6, *df* =27, *p* = 0.007, *t* =2.5, *df* =27, *p* =0.03, t=2.7, df=27,p = 0.007). Basal cavities with mould and crown dead wood was informative (0.05<P<0.1), with higher densities in woodland edges than in interior zones (Table 2).

Overall live tree density, whether hosting TMH or not, was significantly higher in woodland edges than in interior zones (*t = -3.0, df = 27, p = 0.002*). The difference was not significant for snags (Fig. 3).

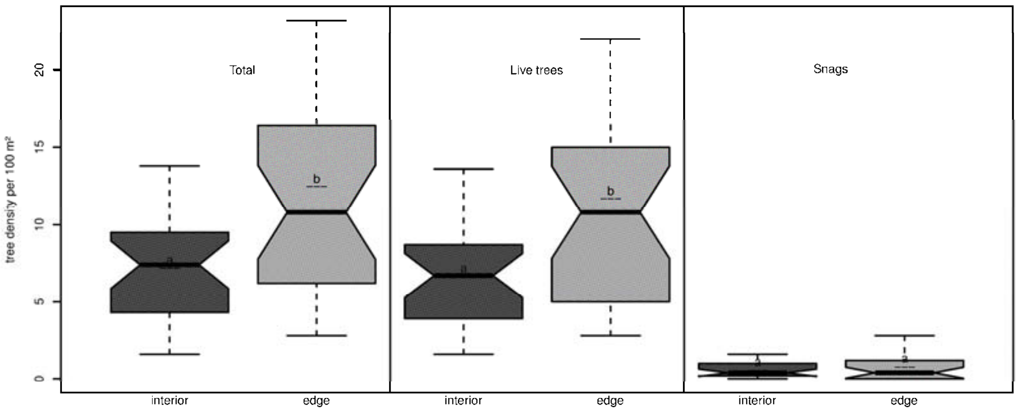

Figure 3. Tree density in woodland edge and interior transects for the whole data set, including live trees and snags. Mean values are indicated in boxplots by dotted lines. Letters indicate statistical differences of permutation t test. Different letters indicate statistical differences of permutation t test at a 5% threshold.

3.3 Effect of species composition on TMH and propensity of tree species to host TMH

Overall, roughly the same tree species were dominant in both woodland edges and interior zones, i.e. oaks and hornbeam. There were no significant differences between woodland edges and interior zones in the proportion of oaks (mainly *Q. pubescens and robur)* and most of the other species, except two: hornbeams (*Carpinus betulus*) were significantly more abundant in interior zones than in the woodland edges (*df* = 27, *p* = 0.007), while hawthorn (*Crataegus monogyna)* was significantly more abundant in the woodland edges than in the interiors (*df* = 27, *p*=0.001) (Table 3).

Overall, the proportion of TMH host trees was significantly higher in woodland edges than in the interior zones (*df* = 27 , *p* = 0.004). (Table 3). Among all the species recorded, no significant differences were found between woodland edges and interior zones in terms of tree species hosting TMH (Table 3).

Whatever the transect, some species were more likely to host TMH, such as wild cherry (*Prunus avium*) and elm (*Ulmus minor*). Some of the species included in the "other species" category, such as blackthorn (*Prunus spinosa*) and aspen *(Populus tremula)*, had a high proportion of TMH host trees (up to 30% for aspen) and were more abundant in woodland edges (see Table 2 in Additional materials for a full list). The statistical test results were not significant for these rare species because of the small number of woodlands where the species was present in both transects.

Table 2. Comparison of tree microhabitat (TMH) densities according to transect type for each TMH type. p-values are relative to paired differences; the number of transects where the microhabitat type was observed is given in brackets; '% of Woods "+"' indicates the proportion of woodlands where the microhabitat type density is higher in the woodland edge transect than in the interior transect; significant results are in bold.

TMH	TMH densities for all species / 100 m²				
	Interior	Edge	% of Woods "+"	Mean of difference	p-value
Woodpecker cavities	0.050 (6)	0.074 (5)	55 %	+ 0.02	0.59 NS
Basal cavities with mould	0.329 (18)	0.715 (15)	63 %	+ 0.39	0.07 .NS
Rot dendrothelms	0.071 (4)	0.043 (3)	43 %	- 0.03	0.70 NS
Bark losses	0.107 (11)	0.842 (21)	95 %	+0.73	0.001***
Cracks in the wood	0.064 (6)	0.276 (11)	83 %	+ 0.21	0.007 **
Deadwood in the crown	0.279 (19)	0.543 (17)	62 %	+ 0.26	0.09 .NS
Sap runs	0.021 (3)	0.129 (8)	80 %	+ 0.11	0.03 *
Basal cavities without mould	0.300 (15)	0.573 (12)	50 %	+ 0.27	0.27 NS
Bark-lined dendrothelms	0.136 (13)	0.325 (8)	46 %	+ 0.19	0.33 NS
Carpophores of saproxylic fungi	0.100 (8)	0.162 (7)	54 %	+ 0.06	0.36 NS
Epiphytes	0.400 (18)	0.982 (18)	65 %	+ 0.58	0.007 **
All TMH together	1.86 (28)	4.67 (27)	79 %	+ 2.81	0.001***

Table 3. Proportion of tree species and microhabitat-host trees in woodland edge and interior transects; in brackets, the number of transects where the species were observed.

Tree-species	% of the total number of trees		% of microhabitat host trees		
	Interior transect	Edge transect	total	Interior transect	Edge transect
Acer campestre	3.41 (7)	2.97 (7)	22.4	12.9	31.9
Carpinus betulus	12.5 (12)	4.93 (6)	18.03	20.3	13.5
Crataegus monogyna	0.43 (3)	3.53 (9)	16.5	0	22.0
Fraxinus excelsior	2.43 (5)	4.94 (5)	29.8	23.3	36.3
Prunus avium	5.55 (11)	5.56 (16)	33.6	23.0	40.9
Quercus spp.	67.8 (28)	66.4 (28)	27.3	25.3	29.3
Robinia pseudoacacia	1.96 (3)	2.59 (3)	28.0	33.3	22.8
Sorbus torminalis	3.28 (13)	2.14 (7)	20.0	19.2	21.4
Ulmus minor	1.27 (3)	4.43 (10)	34.4	33.3	34.7
Other species	1.34 (7)	2.53 (5)	54.2	35.7	80.0
Total	100	100	25.82	21.9	29.8

3.4 Oak tree diameters and TMH in woodland edges vs. interior zones

Considering only the genus *Quercus,* trees were significantly larger in the woodland edges than in the interior zones ($t = -2.6$, $df = 1231$, $p = 0.008$). In both woodland edges and interiors, TMH host trees had significantly larger diameters than trees without TMH (respectively: $df = 198$, $p = 0.005$ and $df = 296$, $p = 0.001$). For the same diameter, the proportion of TMH host trees was higher in the woodland edges than the interiors (Fig. 4).

The proportion of oaks with sap runs and patches of bark loss was significantly higher in woodland edges than interiors (respectively $df = 28$, $p = 0.02$ and $df = 34$, $p = 0.01$). Conversely, the proportion of oaks with crown deadwood was significantly higher in the interior zones than in the woodland edges ($df = 41$, $p = 0.03$).

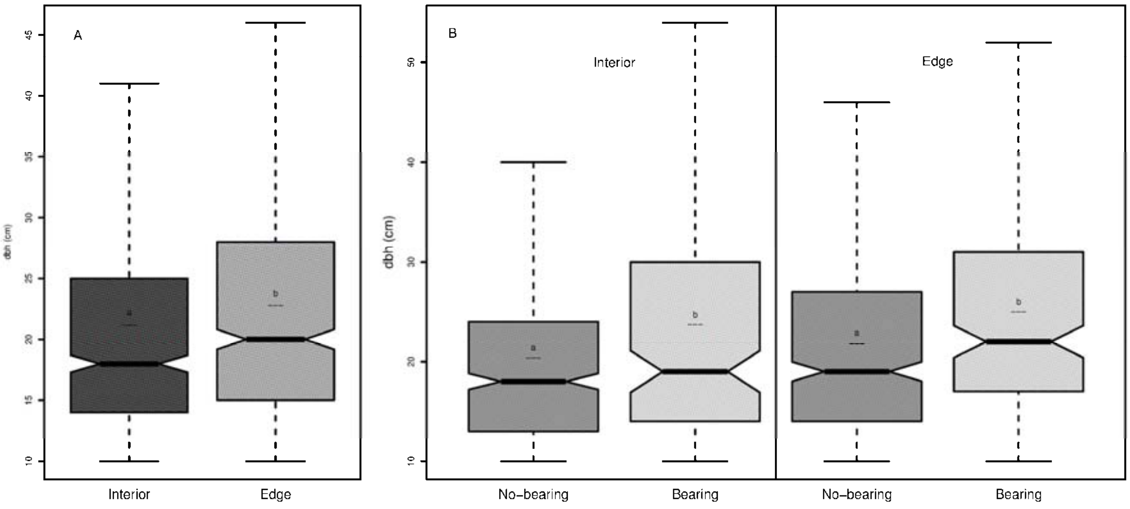

Fig. 4. Proportion of microhabitat host trees in relation to tree diameter at breast height (DBH) in woodland edge and interior transects.

3.5 Effect of woodland edge structure and management on TMH

In the linear model developed to explore the relationships between the abundance of TMH and edge structure variables, the only variable selected by the procedure and demonstrating a significant p-value was the height of the bottom of the crown (h2), which positively influenced TMH abundance (Table 4; Fig. 5). Considering the number of different types of TMH, the only variable improving the null model (h2) induced a decrease of the AIC (0.18) that was too slight to be selected.

Management variables had no effect on TMH abundance and diversity. The duration of rotations correlated positively with the height of the tree crowns (Table 5).

Table 4. Results of variable selection from the linear model testing the effects of edge-structure variables on microhabitat abundance: length of the field part of the edge (“Lfield"), mean height of the canopy top (“h1”) and of the bottom of the crown (“h2”), type of adjacent field (crop *vs.* meadow) (with AIC delta <4). (*) in the full model with shrinkage.

Model	Df	AICc	Delta	Weight	*p*-value(*)
h2	3	159.57	0.00	0.53	0.005 **
h2 + h1	4	162.37	2.79	0.13	h1: 0.87 NS
h2 + adjacent field	4	162.50	2.93	0.12	a.f. :0.90 NS
h2 + Lfield	4	162.57	3.00	0.12	L.f.: 0.94 NS
(Null model)	2	167.07	7.50	0.01	-

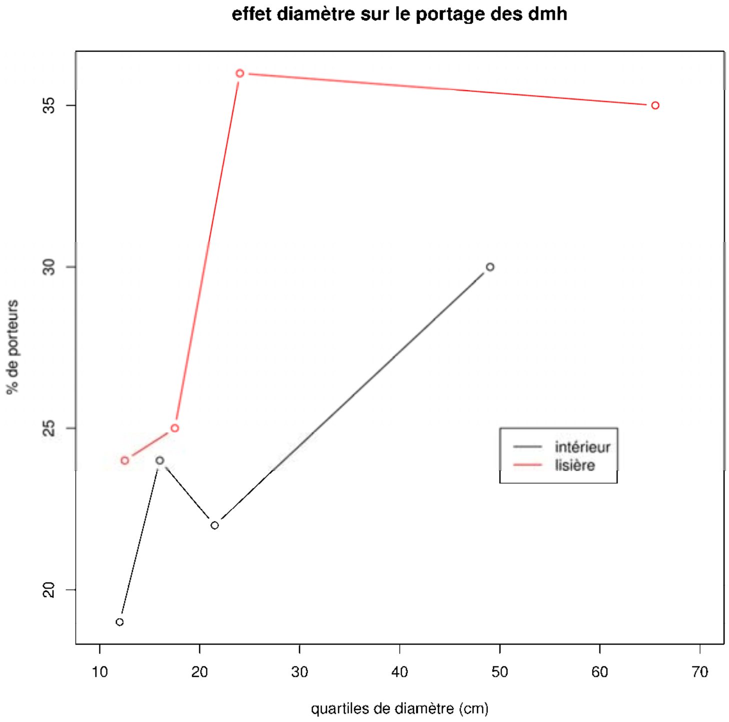

Figure 5. Number of microhabitats and proportion of microhabitat host trees in woodland edge transects, in relation to the height of the crown bottom (h2).

Table 5. Spearman correlation coefficients between numerical structure and management variables; *p*-values are given in brackets and italics, significant results are in bold; “Lfield": length of the field part of the edge; “h1”: mean height of the canopy top; “h2”: mean height of the bottom of the crown; interval between two cuts.

	h1	h2	Lfield	rotation
h1	1	0.050	0.190	0.153
h2	*(0.82)*	1	-0.213	**0.725**
Lfield	*(0.40)*	*(0.34)*	1	-0.236
rotation	*(0.50)*	***(0.0001)***	*(0.29)*	1

4. Discussion

4.1 Higher densities of TMH in woodland edges than interiors

Our results showed higher densities of TMH in woodland edges than in interior zones, thus supporting our first hypothesis. The first two hypotheses we tested to explain this positive TMH pattern in woodland edges were a higher density of trees in woodland edges than interiors, and a larger diameter (DBH). Our results showed that tree density was higher and trees were larger in the woodland edges, including within the same genus (*Quercus*).

Woodland edges are known to host larger trees because of the greater availability of light and nutrients and the lack of competition (Gehlhausen *et al.*, 2000; McDonald and Urban, 2004; Wicklein *et al.*, 2012). Salek *et al.* (2013), working in intensively managed commercial forests, also conclude that forest edges are denser with a higher standing volume than forest interiors, but other studies show the opposite trend (Harper and MacDonald, 2001). These differences could be explained by differences in management intensity in the forests studied (Salek *et al.*, 2013). Our study took place in woodlands that were intensively managed not for commercial purposes but for domestic purposes (mainly firewood) (Soudril *et al.*, 2012), which could explain the convergence with Salek's findings (2013). Considering only the genus *Quercus* (mainly *Q. pubescens and robur*), large trees hosted more TMH than smaller ones, which concurs with the results found in previous studies (Vuidot *et al.*, 2011; Regnery *et al.*, 2013) and confirms our first two hypothesis (higher density and larger diameter) on why TMH density is higher in woodland edges.

Even small diameter trees (30 cm) in the woodland edges hosted more TMH than those in the interiors. This can be accounted for by differences in species composition. First, some species are more likely to host TMH than others: e.g. *Populus tremula*, which was more frequent in woodland edges, and *Populus* spp., in which cavities are known to be frequent since they are commonly used by woodpeckers for nesting because of the soft decayed wood (Parks *et al.*, 1997). Secondly, in other species such as hawthorn (*Crataegus monogyna*), ash (*Fraxinus excelsior*), elm (U*lmus minor*) and blackthorn (*Prunus spinosa*), the proportion of TMH host trees was higher in woodland edges than in interior zones. This could indicate environmental or management conditions that applying only to woodland edges and facilitate TMH establishment. Differences in tree species composition between woodland interiors and edges, coupled with different probabilities of TMH presence depending on tree species, could also account for this finding.

Higher vascular plants were also recorded in the same woodland edges by Alignier *et al.* (2014). This study showed that species richness and diversity were generally higher in the open part of the edge (corresponding to the woodland edge definition in our study) than in open habitat, whereas no significant difference was observed between the wooded part of the edge and woodland habitats. The positive effect of woodland edges on biodiversity has often been reported in the literature as the result of two main processes: i) the mixing of open habitat and forest habitat communities (Matlack and Litvaitis, 1999) ii) and/or the presence of species preferring woodland edges (Magura, 2002). Because we studied an indirect indicator of biodiversity on trees, the first hypothesis does not apply. As regards the second, our results show that specific TMH (patches of bark loss, cracks, sap runs and epiphytes) were significantly more abundant in woodland edges than in interior zones in all the tree species considered. Regarding epiphytes, these could benefit from the greater luminosity along woodland edges, as well as from higher nutrient availability from adjacent fertilized crops and permanent meadows in some cases. Moreover, epiphytes may be more numerous in woodland edges where they are more easily disseminated by birds (Levey *et al.*, 2005). In addition, greater climatic contrasts in woodland edges than in interior zones (Ries *et al.*, 2004), with alternating summer heat and winter frosts, could produce more cracks in the trunks of trees.

4.2 No effect of woodland edge management on TMH abundance and diversity

The height of the bottom of crowns reaching into the adjacent field was the only structure variable that correlated positively with TMH abundance. Some explanations could be proposed based on microclimatic variations along woodland edges (Gehlhausen *et al.*, 2000). The absence of low limbs could expose trunks to the light and thus raise the ambient temperature. These microclimatic conditions could be favorable to epiphytes but may also induce frost cracks (Cinotti, 1990) or necrosis of the thin bark of certain tree species (Franc and Ruchaud, 1996). The height of the bottom of the crown reaching into the adjacent field could also be interpreted as a variable integrating management factors such as the rotation interval and cutting of large limbs: some woodland edges where the bottom of the crown was high were cut back every ten years with a tractor-mounted circular saw. These tools are used to cut large limbs (up to 20 cm in diameter), which heal more slowly than smaller branches, thus favoring wood-decomposing fungi (Drenou, 1999). The presence of TMH in woodland edges may thus result from abiotic factors (micro-climatic conditions) as well as from management activities.

However, our study showed no evidence of a relationship between woodland edge management and TMH abundance or diversity. The only positive relationship we found was between the rotation interval and the height of the bottom of the crown reaching into the adjacent field. We can hypothesize that management activities that raise the height of the bottom of the crown (cutting of large limbs) are not performed very frequently and may be related to long rotation intervals.

4.3 Consequences for forest and non-forest biodiversity

The TMH most frequently found in woodland edges were patches of missing bark, cracks, sap runs and epiphytes. These TMH are known to contribute to forest biodiversity with high conservation value. Many saproxylic beetle species (belonging to the families Anobiidae, Cerambycidae, Bostrichidae, Lyctidae, Buprestidae and Eucnemidae, and including endangered species), several Lepidoptera Sesidae and also Hymenoptera Siricidae are dependent for breeding on bark loss wood (Stokland *et al.*, 2012). Furthermore, this type of microhabitat is favorable to heliophilous perennial parasite polypores such as *Phellinus robustus* on *Quercus* or *Phellinus tremulae* on *Populus,* which are rare in inner forest zones because they are naturally hosted by very large trees in clearings (Corriol, pers. com.). Sap runs are used by more than 100 species belonging to a wide taxonomic range including beetles (Nitidulidae, Histeridae, Staphylinidae, Sphaeritidae, Nosodendridae), butterflies, moths, hornets and hoverflies (Yoshimoto *et al.*, 2005; Stokland *et al.*, 2012). The larvae of more than 15 hoverflies breed in this microhabitat (Speight *et al.*, 2010) and the adults contribute actively to pollination, even for trees and shrubs (Groot and Bevk, 2012). Sap runs are an essential resource for rare or endangered beetles such as *Cerambyx cerdo*, *Lucanus cervus* and *Nosodendron fasciculare*, which spends its entire life-cycle in this microhabitat (Brustel, 2014). Epiphytes can benefit woodland bird species such as the song thrush (*Turdus philomelos*) and other farmland turdidae (blackbirds, *Turdus merula*) by providing resources in winter (Cramp, 1998).

TMH can also support facultative forest species that contribute to biodiversity-based ecosystem services. For example, solitary pollinating bees breed in tree hollows used by nesting birds and in holes drilled by the larvae of saproxylic species. A significant positive influence of nearby forest cover on pollination is reported in studies made in various contexts (De Marco and Coehlo, 2004; Farwig *et al.*, 2009). Moreover, some studies have demonstrated a positive effect on pollinators (mostly *Andrena* bee species) of woodland edges near oilseed rape fields (Bailey *et al.*, 2014).

5. Conclusions

We confirmed the hypothesis that the density of TMH was higher in woodland edges than in interior zones because of the presence of large trees. We also confirmed that some TMH types were more abundant in woodland edges than in interior zones, such as bark loss patches, cracks, sap runs and epiphytes. We accounted for these results by the convergence of several factors: i) a significantly higher density of trees in woodland edges, ii) a significantly higher proportion of TMH host trees in woodland edges, iii) a larger tree diameter in woodland edges and, even for the same size class, a higher frequency of TMH host trees, iv) a greater abundance in woodland edges of tree species, even with small diameters, more likely to host TMH. The positive relationship between the height of the crown bottom and TMH abundance may have resulted from abiotic factors (micro-climatic conditions) and was related to long rotations, but we did not demonstrate any direct effect of management practices.

Because woodland edges appear to host more TMH than interior zones, they need to be considered for the conservation of woodland as well as farmland biodiversity. We recommend that tree species diversity should be maintained or improved by preserving secondary species with little or no economic value and maintaining a high proportion of trees hosting TMH, such as *Populus* spp., *Crataegus monogyna*, *Fraxinus excelsior*, *Ulmus minor* and *Prunus spinosa.* We hypothesized that management intervals of around 10 years to cut back large branches increases trunk exposure to micro-climatic variations and improves TMH abundance.

Further studies should try to elucidate the effect of the height of the crown bottom by stratifying sampling on the basis of this variable. The contribution of secondary species, even those with a small diameter, to TMH abundance should be elucidated by specifically researching these trees and observing TMH in both woodland edges and interiors to obtain a significant number of individuals to allow statistical testing.

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References

Alignier, A., Alard, D., Chevalier, R., Corcket, E., 2014. Can contrast between forest and adjacent open habitat explain the edge effects on plant diversity? Acta Botanica Gallica: Botany Letters DOI: 10.1080/12538078.2014.902771.

Bailey, S., Requier, F., Nusillard, B., Roberts, S.P.M., Potts, S.G., Bouget, C., 2014. Distance from forest edge affects bee pollinators in oilseed rape fields. Ecology & Evolution 4, 370-380.

Bastien, Y., 2002. Taillis et Taillis sous futaie. In. ENGREF, NANCY.

Blondel, J., 2005. Bois mort et cavités: leur rôle pour l'avifaune cavicole. In: Vallauri, D., et al. (Eds.), Bois morts et cavités: une clé pour des forêts vivantes. Tec et Doc Lavoisier, Paris, pp. 137-142.

Bernicchia, A., 2005. Polyporaceae s.l. Candusso, Alassio.

Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P., Laudenlayer, W.F. (eds) 2005. The afterlife of a tree. WWF Poland, Warszawa-Hajnowka.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management 261, 211-220.

Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecological Indicators 36, 656-664.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers Conserv 22, 2111-2130.

Brustel, H., 2014. Coléoptèrres saproxyliques et valeur biologique des forêts françaises. In. INP Toulouse.

Chen, J., Franklin, J.F., Spies, T.A., 1993. Contrasting microclimates among clearcut, edge, and interior of old growth Douglas-fir forest. Agricultural and Forest Meteorology 63, 219-237.

Cinotti, B., 1990. Le déterminisme de la gélivure des chênes: un nouveau bilan. Revue Forestière Française XLII, 585-598.

Cramp, S., 1998. Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Paleartic. Vol. V.

Crowson, R.A., 1981. The biology of the Coleoptera. London : Academic Press. Dublin, Ireland.

Dajoz, R. 2007. Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier, 2ème édn. Tec et Doc Lavoisier, Paris.

De Marco, P., Coehlo, F.M., 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. Biodiversity and Conservation 13, 1245-1255.

Drenou, C., 1999. La taille des arbres d’ornement ; Du pourquoi au comment. IDF, Paris.

Du Bus de Warnaffe, G., Deconchat, M., Ladet, S., Balent, G., 2006. Variability of cutting regimes in small private woods of south-western France. Annals of Forest Science 63, 915-927.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83, 2978-2984.

Ellis, M.B., Ellis, J.P., 1998. Microfungi on miscellaneous substrates. An identification handbook. Richmond Publishing, Slough, England.

Farwig, N., Bailey, D., Bochud, E., Herrmann, J.D., Kindler, E., Shüepp, C., Schmidt-Entling, M.H., 2009. Isolation from forest reduces pollination, seed predation and insect scavenging in Swiss farmland. Landscape Ecology 24, 919-927.

Franc, A., Ruchaud, F., 1996. Auto-écologie des feuillus précieux : Frêne commun, Merisier, Erable sycomore, Erable plane CEMAGREF.

Fritz, O., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (Fagus sylvatica). Biol Conserv 143:1008–1016.

Gehlhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology 147, 21-35.

Girompaire, L., Ballon, P. 1992. Conséquences de l’écorçage du cerf élaphe dans le massif des Vosges alsaciennes. Revue Forestière Française XLIV(6): 501–511.

Gonzalez, M., Deconchat, M., Balent, G., 2009. Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration. Plant Ecology 201, 305-318.

Groot, M., Bevk, D., 2012. Ecosystem services and phenology of hoverflies (Diptera: Syrphidae) in a Slovenian forest stand. Les (Ljubljana) 64, 123-128.

Hanski, I., 2005. The Shrinking World: Ecological consequences of habitat loss. International Ecology Institute, Oldendorf/Luhe.

Harrison, C., 1977. Nids, œufs et poussins d’Europe. Bordas.

Harper, K.A., MacDonald, E., 2001. Structure and composition of riparian boreal forest: new method for analyzing edge influence. Ecology 82, 649-659.

Hervé, M., 2014. Aide-mémoire de statistique appliquée à la biologie. Construire son étude et analyser les résultats à l'aide du logiciel R. In.

Heiss, E., Pericart, J. 2007. Hemiptères Aradidae Piesmatidae et Dipsocoromorphes euro-méditerranéens. Faune de France (France et régions limitrophes) 91. Fédération Française des sociétés de sciences naturelles.

Kitching, R.L., 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. Journal of Animal Ecology 40, 281-302.

Labrid, M., 1986. La Martre. Encyclopédie des carnivores de France, vol 9. SFEPM.

Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. European Journal of Forest Research 131, 773-786.

Larsson, T.B., 2001. Biodiversity evaluation tools for European forests. Ecol. Bull. 50.

Le Louarn, H., Quéré, P.J., 2003. Les rongeurs de France - Faunistique et biologie ; 2ème édition. INRA ed.

Le Coeur, D., Baudry, J., Burel, F., 1997. Field margins plant assemblages: variation partitioning between local and landscape factors. Landscape and urban planning 37, 57-71.

Levey, D., Bolker, B.M., Tewksbury, J.J., Sargent, S., Haddad, N., 2005. Effects of landscape corridors on seed dispersal by birds. Science 309, 146-148.

Lisiewska, M. 1992. Macrofungi on special substrates. In: Winterhoff W (ed) Fungi in vegetation science. Kluwer, Netherlands ,pp 151–182.

Magura, T., 2002. Carabids and forest edge: spatial pattern and edge effect. Forest ecology and management 157, 23-37.

Matlack, G.R., Litvaitis, J.A., 1999. Forest edges. In: Malcolm, L., Hunter, J.R. (Eds.), Maintaining biodiversity in forest ecosystems. Cambridge University Press, pp. 211-233.

McDonald, R.I., Urban, D.L., 2004. Forest edges and tree growth rates in the north carolina piedmont. Ecology 85, 2258-2266.

Meschede, A., Heller, KG., 2003. Ecologie et protection des chauves-souris en milieu forestier. Le Rhinolophe 16, 1-248.

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. Forest Ecology and Management 257, 1453-1464.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. TREE 10, 58-62.

Parks, C., Bull, E., Torgersen, T., 1997. Field guide for the identification of snags and logs in the interior Columbia River basin. General Technical Report - Pacific Northwest Research Station, USDA Forest Service 41.

Pénicaud, P., 2000. Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe 14:37–68.

Pitte, J.R., 2003. History of France landscapes Histoire du paysage Français. Paris: Tallandier.

Radek, K., Lucan, R., Hanak, V., Horacek, I., 2009. Long-term re-use of tree roosts by European forest bats. For Ecol Manage 258:1301–1306.

Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91.

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? Forest Ecology and Management 295, 118-125.

Ricarte, A., Jover, T., Marcos-García, M. A., Micó, E. and Brustel, H., 2009. Saproxylic beetles (Coleoptera) and hoverflies (Diptera: Syrphidae) from a Mediterranean forest: towards a better understanding of their biology for species conservation. Journal of Natural History,43:9,583 — 607.

Ries, L., Fletcher, R.J., Battin, J., Sisk, T., 2004. Ecological responses to habitat edges: mechanisms, models and variability explained. Annu. Rev. Ecol. Evol. Syst. 35, 491-522.

Ries, L., Sisk, T.D., 2010. What is an edge species? The implications of sensitivity to habitat edges. oikos 119, 1636-1642.

Salek, L., Zahradnik, D., Marusak, R., Jerabkova, L., Merganic, J., 2013. Forest edges in managed riparian forests in the eastern part of the Czech Republic. Forest Ecology and Management 305, 1-10.

Schmidl,J., Sulzer,P., Kitching,R.L., 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia 598, 285-303.

Soudril, A., Andrieu, E., Cabanettes, A., Elyakim, B., Ladet, S., 2012. How to Maintain Domesticity of Usages in Small Rural Forests? Lessons from Forest Management Continuity through a French Case Study. Ecology and Society 17, 6.

Speight, M.C.D., 1989. Saproxylic invertrebrates and their conservation. In. Concil of Europe, pp. 1-79.

Speight, M.C.D., Castella, E., Sarthou, J.P., Monteil, C., 2010. Species accounts of European Syrphidae (Diptera). Syrph the Net, the database of European Syrphidae. Syrph the Net publications, Dublin.

Stanska, M., Rozwaka, R., Kowalczyk, K. 2010. Dipoena torva (Thorell, 1875) spider living on tree stems. Lesne Prace Badawcze 71(2): 201–205.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge; UK.

Tillon, L., 2005. Biodiversité, dynamique et conservation des petits mammifères cavicoles en France. In: Vallauri D et al (eds) Bois mort et à cavités: une clé pour les forêts vivantes. Tec et Doc Lavoisier, Paris, pp 137–142.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281-284.

Unterseher, M., Tal, O., 2006. Influence of small-scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy. Mycological Research, 110, 169-178.

Vaillant, F., 1978. Les Systenus et leur habitat dendrotelme. Bull Société Ent Fr 83:73–85.

Vane, C.H., Drage, T.C. Snape, C.E., 2006. Bark decay by the white-rot fungus Lentinula edodes: Polysaccharide loss, lignin resistance and the unmasking of suberin. Inter Biodeter Biodegr 57:14–23.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144, 441-450.

Wicklein, H.F., Christopher, D., Carter, M.E., Smith, B.H., 2012. Edge effects on sapling characteristics in a small temperate deciduous forest fragment. Natural Areas Journal 32, 110-116.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251-1261.

Yoshimoto, J., Kakutani, T., Nishida, T., 2005. Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecological Research 20, 405-414.

Supplementary materials

Table 1 SM. Scale of deadwood decay stages

Decay stages	Definitions
1	Fresh deadwood (<1 year), hard and not rotten. Phloem alive or at least perceptible. More than 95% of the bark is still attached to the stem.
2	2-3 year old deadwood, still hard. Phloem dead and not perceptible. A knife blade enters only 1 or 2 cm and only parallel to the wood fiber.
3	Deadwood is starting to rot. The outer wood is soft, the interior wood still not rotten. The bark has partially fallen off. The knife blade enters 3 to 5 cm, at least parallel to the wood fiber. No material loss (v = initial volume).
4	Deadwood is clearly rotten. A knife blade enters up to the hilt. Bark is mostly missing or, if present, is soft and does not adhere to the stem. Material loss (v < initial volume).
5	Wood almost totally disintegrated, very spongy or powdery, almost formless. Large loss of material. Presence in wood of species belonging to soil-dwelling fauna.

Table 2 SM. Proportion of tree species and microhabitat-host trees per transect type for the 7 species of the “other species" categories: % of total trees and number per transect

	Number of transects encompassing the species		Number of trees		Number of microhabitat-bearing trees		% of microhabitat-bearing trees	
Tree species	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior
Betula pendula	0	1	0	4	0	0	-	0
Castanea sativa	1	0	1	0	0	0	0	-
Ilex aquifolium	0	2	0	2	0	0	-	0
Malus sylvestris	1	0	1	0	0	0	0	-
Prunus spinosa	1	0	3	0	2	0	67	-
Populus tremula	4	4	8	6	6	4	75	67
Salix caprea	0	1	0	2	0	0	-	0

Section II – Dynamiques naturelles des dendro-microhabitats et du bois mort

SECTION II - DYNAMIQUES NATURELLES DES DENDRO-MICROHABITATS ET DU BOIS MORT

Les forêts sont des écosystèmes extrêmement dynamiques, malgré le sentiment partagé par les non spécialistes de l'immuabilité des peuplements forestiers, en partie lié à la grande longévité des arbres souvent bien supérieure à celle de l'observateur. Dans le domaine tempéré, ce sentiment de stabilité est favorisé par le régime dominant de perturbation, basé sur la mortalité d'arbres isolés ou en petits groupes, qui régit la dynamique d'éco-unités de petite surface, de l'ordre de quelques centaines à quelques milliers de mètres carrés.

Les dendro-microhabitats et le bois mort participent à cette dynamique en étant des habitats évolutifs et donc temporaires, comme nous l'avons exposé dans l'introduction. Cette dynamique peut s'appréhender à deux échelles spatiales. Premièrement, celle du dendro-microhabitat lui-même (ou de la pièce de bois mort), en mesurant sa durée de vie ou en observant sa transformation progressive en dendro-microhabitat d'un autre type (ou, pour le bois mort, le passage au stade de saproxylation suivant) et le changement des communautés associées. Mais on peut également l'étudier à l'échelle du peuplement ou de la phase sylvigénétique, par le biais de l'évolution de la disponibilité globale en dendro-microhabitats et en bois mort, soit au cours du cycle sylvigénétique (Larrieu *et al.* 2014), soit après la mise en réserve de peuplements exploités (Bouget *et al.* 2014 ; Larrieu *et al.* en prép.). Dans ce travail de thèse, nous n'avons abordé que l'échelle globale, par des études synchroniques.

1 PRINCIPAUX RESULTATS

Contrairement à ce que nous attendions, nous avons observé que la disponibilité en dendro-microhabitats et en bois mort est relativement constante tout au long du cycle sylvigénétique des forêts mixtes de montagne. De plus, comme nous avions montré que le comportement des feuillus et des résineux est différent en termes de dendro-microhabitats (cf. section I), on supposait des cycles différents dans les peuplements dominés par le Hêtre ou par le Sapin pectiné, mais nos résultats n'ont pas montré de différences significatives. Nous avons également mis en évidence le rôle crucial joué par les feuillus secondaires dans la régulation de la disponibilité en bois mort (et probablement aussi en dendro-microhabitats), en complétant l'offre dans les phases où celle des essences dominantes est la plus faible.

La reconstitution des stocks de bois mort et de dendro-microhabitats dans les forêts feuillues de plaine et de collines est lente. Le type de gestion n'a pas d'effet significatif sur les volumes de bois mort laissés par l'exploitation mais un effet sur la composition dendrologique des peuplements, les stocks de dendro-microhabitats après coupe et la vitesse de reconstitution des stocks de bois mort et de dendro-microhabitats. Les peuplements non exploités depuis plus de 30 ans contiennent parfois un volume de bois mort significativement plus élevé et avec une diversité légèrement plus forte que les peuplements exploités dans les 30 dernières années. En revanche, le seuil de 30 ans n'est suffisant ni pour observer dans tous les contextes une reconstitution du stock de dendro-microhabitats, ni pour changer significativement les communautés de Coléoptères saproxyliques. Une durée de non-exploitation de 55 ans n'est pas non plus suffisante pour observer pour tous les types de gestion des valeurs significativement plus fortes que celles observées après la coupe pour, d'une part la densité et la diversité de dendro-microhabitats, et, d'autre part, le volume et la diversité de bois mort. Ces résultats en forêts feuillues planitiaires et collinéennes sont cohérents avec nos observations en hêtraie-sapinière (Larrieu *et al.* 2012, section I) où nous avions constaté que les peuplements non exploités depuis 50 ans n'avaient pas encore des caractéristiques d'hétérogénéité interne proches des peuplements sub-naturels de référence.

2 DISCUSSION ET PERSPECTIVES

Ces résultats nous montrent que pour observer des changements significatifs d'hétérogénéité structurale et de biodiversité, il faudrait sélectionner des peuplements sur un gradient temporel de non exploitation dépassant largement les 50 ans. Il serait également préférable de disposer d'effectifs de peuplements suffisants pour multiplier les classes de durée de non exploitation afin de décrire finement les phénomènes de reconstitution des stocks et des communautés. Or, il est difficile de disposer de tels peuplements : les forêts non exploitées depuis des décennies concernent essentiellement des écosystèmes de montagne et sont dans la plupart des cas situées sur des pentes escarpées et loin des axes de circulation. Cela pose des problèmes à la fois d'acquisition des données et de généricité des résultats. On se heurte également à la difficulté de recueillir des données sur l'état initial des peuplements et des communautés avant l'arrêt de l'exploitation. Ces renseignements sont d'autant plus cruciaux que la durée de non exploitation est courte.

La mise en commun de bases de données internationales permet d'augmenter la taille de l'échantillon, mais un plan d'échantillonnage réellement pertinent passerait par la réalisation concertée de mesures spécifiques, en utilisant les ressources en forêts sub-naturelles de plusieurs pays. L'étude par chronoséquence a constitué une démarche pratique pour optimiser l'acquisition de données, mais un plan d'échantillonnage diachronique affranchirait des biais inhérents à toute étude synchronique de phénomènes biologiques. Néanmoins, on connaît les difficultés à faire perdurer des dispositifs d'observation à long terme. Il serait utile, à la fois pour la généricité des résultats et pour développer simultanément une démarche pédagogique, que ce type d'étude repose dorénavant sur des dispositifs de gestion adaptative (« adaptative management », *e.g.* Wilhere 2001). Ces méthodes faciliteraient l'étude dynamique des relations entre cette hétérogénéité et la biodiversité, en d'autres termes la bio-complexité des écosystèmes, et permettraient de mieux quantifier les effets de décalage temporel dus aux dettes et aux crédits d'espèces (Jackson & Sax, 2009). Evidemment, l'acquisition des données demandera la mise en œuvre d'un partenariat à long terme avec les gestionnaires.

La recherche de forêts de références est à poursuivre. Elles doivent illustrer au maximum les processus naturels pour être en mesure de les copier, au moins en partie, dans des sylvicultures « proche de la nature » (« nature-based forest management », *e.g*. Larsen & Nielsen 2007). Nos résultats montrent que la période minimale sans intervention sylvicole doit être rallongée à minimum 100 ans, pour tamponner les effets pressentis de l'état initial (au moment de l'abandon de l'exploitation de bois) sur les observations actuelles. L'harmonisation des protocoles d'échantillonnage et l'utilisation d'une typologie de référence pour les dendro-microhabitats devraient permettre de disposer d'un plus grand nombre de ces références en couvrant une large gamme de contextes en Europe tempérée et ainsi de mieux définir les processus dynamiques naturels. Ces références sont cruciales pour établir la borne supérieure du gradient de naturalité. Charge par la suite au gestionnaire forestier de placer sa sylviculture sur le gradient, en optimisant au cas par cas ses objectifs économiques, sociaux et environnementaux, tout en gardant à l'esprit que la conservation de la biodiversité est un gage de productivité, de résistance et de résilience à long terme des écosystèmes qu'il gère (Thompson *et al*. 2009).

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22. Bouget C., Parmain G., Nusillard B., Paillet Y., Pernot C., **Larrieu** L., Gosselin F., 2014. Does a set aside conservation strategy help restore old-growth attributes and conserve saproxylic beetles in temperate forests? *Animal Conservation*, 17: 342–353

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Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity monitoring

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ABSTRACT

In forest ecosystems, conservation is often considered in the absence of any long-term dynamic perspective, yet dynamic processes extend over hundreds of years. Saproxylic taxa represent about 25% of the species diversity in temperate and boreal forests and they depend on both spatial and temporal continuity in the availability of deadwood and certain tree microhabitats. Our study focused on the dynamics of deadwood and tree microhabitats throughout the silvigenetic cycle in 32 unharvested European mountain mixed forests. Our dataset contained 178 plots classified into one of five forest development phases (regeneration, establishing, growing, culmination and disintegration). We analyzed how the amount and quality of deadwood and microhabitats varied according to the five phases. Contrary to expectations, deadwood and tree microhabitat availability remained more or less stable throughout the silvigenetic cycle, both in quantity and diversity. Furthermore, whether the forests were dominated by broadleaves or conifers, there were no significant differences in terms of deadwood or tree microhabitat dynamics. Pioneer (*Betula* spp., *Salix* spp.) and post-pioneer species (*Fraxinus exelsior*, *Sorbus* spp., *Prunus avium*) played an important role throughout the silvigenetic cycle by providing a diversity of deadwood when deadwood from the dominant species (i.e. *Abies alba*, *Fagus sylvatica*, *Picea abies*) was scarce. Understanding the dynamics of deadwood and tree microhabitats may help us provide a model for forest managers who intend to emulate natural forest dynamics and will also improve our understanding of the relationship between forest dynamics and biodiversity conservation.

1. Introduction

The scarcity of unharvested natural or near-natural reference forests across Europe (Gilg, 2005) limits our knowledge of the natural processes that affect biodiversity throughout the forest life. Thus, conservation is often considered in the absence of a dynamic perspective (i.e. without taking long-term changes in structure or composition into account), even though disturbances over time are key drivers of forest biodiversity (Larsson, 2001). Nevertheless, reference conditions can still be found in mountain forests, which were often less intensively managed in the past, display characteristic features of old-growth forests, and where forest structure is likely to be driven by natural processes.

In natural forests, disturbances as well as tree ageing and dying processes create a mosaic of different forest patches with various microclimatic conditions and deadwood resources (*silvatic mosaic*: Oldemann, 1990; Franklin et al., 2002). The smallest patches can be as small as the canopy of a single tree, whereas the biggest can encompass thousands of trees. These patches evolve over time through several developmental phases (Watt, 1947; Leibundgut, 1978) which characterize the forest life cycle (*silvigenetic cycle*: Guillaumet and Kahn, 1982). In this study, we use the term *forest development phase* (FDP, as defined by Winter and Brambach, 2011) to subdivide the *silvatic mosaic* into areas of homogeneous development steps, from regeneration to disintegration.

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Several authors have described the silvigenetic cycle, mainly in European and North American temperate forests (e.g. Korpel', 1982; Gonin, 1988; Oliver and Larson, 1996; Bobiec et al., 2000; Emborg et al., 2000; Tabaku, 2000; Franklin et al., 2002; Heurich, 2006; Kral et al., 2010b; Winter and Brambach, 2011). Five to ten phases (sometimes called "stages") have been distinguished, mainly based on forest structure variables such as tree diameter at breast height (*dbh*), or age distribution, tree density, presence of deadwood, sapling density, living biomass, maximum height of the dominant trees and vertical structure (i.e. number of strata or percentage of canopy cover).

Knowledge of the silvigenetic cycle is crucial for biodiversity conservation since characteristic species assemblages or characteristic variations in species abundances are associated with each phase (Carey and Johnson, 1995; Niemela et al., 1996; Grgic and Kos, 2005; Winter et al., 2005), possibly because of specific microclimatic conditions, but also due to resource levels, types and spatial patterns. Saproxylic taxa (i.e. whose life-cycle depends on wounded or decaying woody material from live, weakened or dead trees) represent about 25% of the species diversity in temperate and boreal forests (Stokland et al., 2012). Saproxylic species depend on the continuity, both spatial and temporal, of deadwood and specific tree microhabitats (hereafter called "microhabitats") (see e.g. Bobiec et al., 2005; Bouget and Gosselin, 2005).

"Biological legacies" (Franklin et al., 2000) such as very large deadwood items, which remain available for a long time, play an important role in the temporal continuity of deadwood habitats at the small scale. Scherzinger (1996) and André (2005) published theoretical patterns of deadwood dynamics, showing significant variations in volume throughout the silvigenetic cycle. However, the spatio-temporal availability of deadwood or microhabitats throughout natural forest cycles is still poorly documented. Burrascano et al. (2013) noticed that studies on old-growth forests generally do not include enough structural attributes to fully understand the underlying dynamics; they recommended investigating a wider set of meaningful structural attributes. Deadwood volume is typically quantified according to each FDP, but only with mean total volume. Saniga and Schutz (2002) modelled deadwood dynamics in virgin forests over a wide range of forest types, but did not take into account degree of decay or the ratio of snags to logs. Nevertheless, several studies have shown that the diversity of deadwood types is a critical feature for saproxylic taxa (e.g. Brin et al., 2011; Stokland et al., 2012; Bouget et al., 2013). Likewise, Winter and Brambach (2011) have surveyed microhabitats in beech (*Fagus sylvatica* L.) and mixed beech-spruce (*Picea abies* (L.) H.Karst.) forests and have demonstrated a significant effect of FDP on the total number of microhabitats. However, they did not analyze the relationships between FDP and the density of microhabitats per type, while different FDPs might supply different microhabitats which, in turn, might host very different species assemblages (Speight, 1989; Stokland et al., 2012).

In our chronosequence study, we aimed to describe the dynamics of both deadwood and microhabitats throughout the silvigenetic cycle in European mountain mixed forests, since deadwood and microhabitats host thousands of species and are therefore key features for biodiversity conservation (Stokland et al., 2012). We considered not only volume and diversity of deadwood, but also density and diversity of microhabitats. In mixed forests, the relative proportion of tree species should also be taken into account to assess the habitat supply for saproxylic species. Indeed, tree species composition changes throughout the forest cycle due to the varying competitive ability of species with different degrees of shade tolerance (Franklin and Van Pelt, 2004). Furthermore, contribution to microhabitat supply (Vuidot et al., 2011; Larrieu and Cabanettes, 2012) and decay rates (Stokland et al., 2004) are tree-species dependent. Finally, saproxylic assemblages in deadwood are strongly linked to tree species properties and differ considerably between broadleaved and coniferous trees (Stokland et al., 2012). Pioneer species such as *Betula* spp. seem to play a negligible role in forest dynamics (Wissel, 1992). However, Larrieu and Cabanettes (2012) showed that pioneer and post-pioneer species (such as *Fraxinus exelsior*, *Sorbus* spp., *Prunus avium*), hereafter called "secondary species", play a significant role in the microhabitat supply in montane beech-fir forests, since their proportion of microhabitat-bearing trees is over 75%.

Rather than use pre-defined phases for our FDPs, we split up the silvigenetic cycle after performing a statistical analysis of an empirical database combining datasets from France, Switzerland and Germany.

We tested whether (i) the theoretical pattern of the deadwood cycle is validated by empirical data in mountain mixed forests; (ii) microhabitat dynamics are linked to the FDP in terms of both quantity and diversity; (iii) secondary tree species play a role in deadwood dynamics; and (iv) the proportion of broadleaves and conifers impacts the availability of microhabitats.

2. Materials and methods

2.1. Forests studied and sampling design

The data we used were originally collected for different projects and make up a database encompassing 178 plots in 32 European mountain mixed forests (Larsson, 2001; Bardat et al., 2004) which have been unharvested for more than 50 years (often more than 100 years), and where both microhabitats and deadwood were recorded (see Table A1). The forests are located in the French Pyrenees (*LL* and *PG* databases), Provence (France), the French Alps, French Jura (*YP* database), Swiss Jura, the Swiss plateau, the Swiss Alps (*TL* database) and the Bavarian National Park in Germany (*SW* database) (Fig. 1).

2.2. Forest structure and calculations

The plots in the study area were set up to describe FDPs. Some of the plots were fixed-area plots: from 310 to 1000 m^2 for trees with $dbh < 30$ cm, and from 400 to 1250 m^2 for trees with $dbh > 30$ cm (Table A1). The other plots were fixed-angle plots set up with a Bitterlich relascope (Bitterlich, 1984); in this case, plot area depended on the spatial distribution of the largest trees. The assessment of the number of trees per hectare depended on the plot type. For fixed-area plots, it was calculated by multiplying the number of trees by the ratio 10,000/plot area (m^2). In the case of the fixed-angle plots, it was calculated by allocating the coefficient N_{dbh} to every tree observed in the relascope sampling, in relation to its *dbh*, as follows (Pardé and Bouchon, 1988):

$$N_{dbh} = \pi 10^8 [\mathrm{ArcTan}(1/50)/(\pi\, dbh)]^2.$$

Since the field procedures varied among the different projects, we harmonized the recorded variables at the tree level: tree species designation and type (broadleaves *vs* conifers), *dbh* (with a common minimum *dbh* fixed at 10 cm), tree status (live trees, snags and stumps, logs), deadwood decay stage (with a common scale, see Table A2) and microhabitats on the visible part of the trunk both beneath and within the tree crown (shared microhabitat types, see Table 1). We retained seven microhabitat types shared by the five databases and essential for numerous, though mainly saproxylic, taxa (Stokland et al., 2012): cavities, dendrotelms, sap runs, sporophores of saproxylic fungi, missing bark, cracks and shelter-bark, and crown deadwood (Table 1).

Logs more than 10 cm in diameter at the thinner end were either all measured over the whole plot area or sampled following

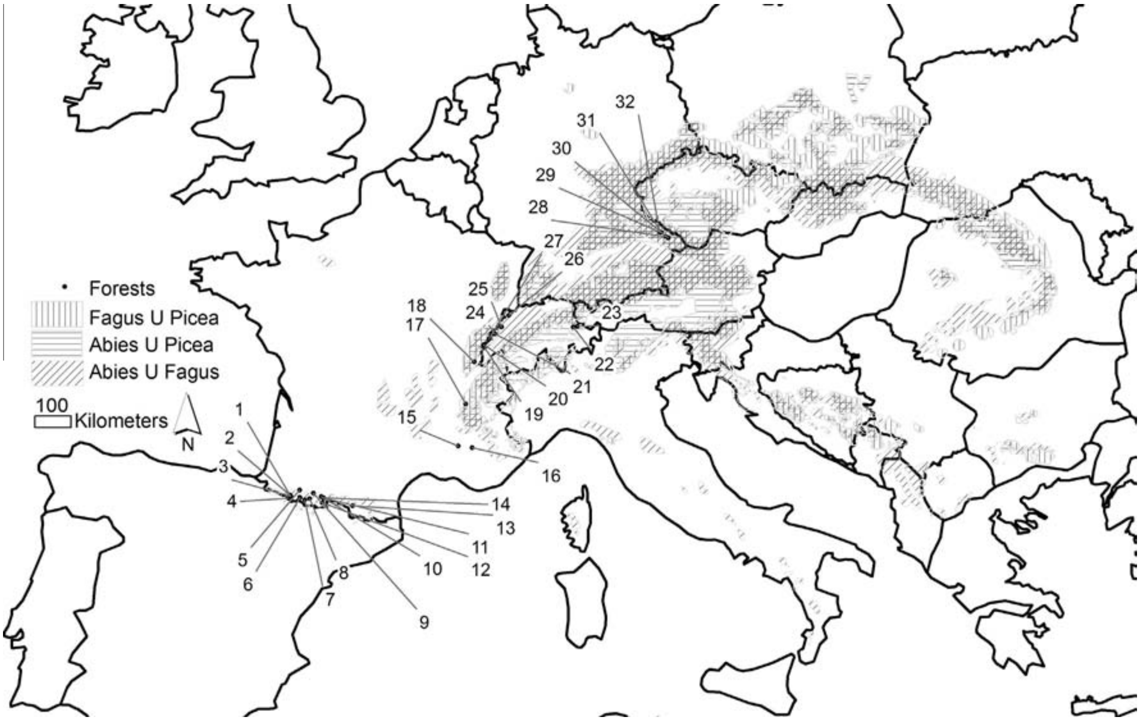

Fig. 1. European map of the natural occurrence area for mountain mixed forests (Euforgen, 2012) and localisation of the forests studied (numbers); France: 1-Sesques, 2-Arrioucaou, 3-Biscau, 4-Gouetsoule, 5-Auribareille, 6-Genie loungue, 7-Barrada, 8-Bugatet, 9-Plagnech de Ton, 10-Ouderou, 11-Es Piches, 12, Bosc nou, 13-Aston, 14-Es Tucoulets, 15-Ventoux, 16-Lure, 17-Engins, 18-Haut-Jura; Switzerland: 19-La Verrière, 20-Le Pont, 21-La Chaille, 22-Seewis, 23-Sunniwald, 24-Creux du Van, 25-Combe Biosse, 26-Bourrignon, 27-Gorges de Covatanne; Germany: 28-Rachelsee, 29-Watzlick, 30-Lusen, 31-NSG Mittelsteighütte, 32-NSG Johannisruh; U = "and".

Table 1
Tree-microhabitat types common to all five databases on mountain mixed forests (refer to Section 2.1).

Types	Cavities	Woodpecker breeding or feeding holes deep enough to host a vertebrate + Deep cavities formed between roots + Cavities with mould All positions: trunk and base cavities Entrance above 3 cm in width Inventoried on both live trees and snags
	Dendrothelms	Water-filled holes in wood All types of dendrothelms and all positions on the trunk Entrance above 3 cm in width Inventoried only on live trees
	Sap runs	Both chronic and short-lived slime fluxes Length $\geqslant$ 10 cm Inventoried only on live trees
	Saproxylic fungi	Polypores s.l. Sporophores with a diameter > 5 cm Inventoried only on live trees
	Missing bark	Bare wood patches with bark loss and wood in a decay stage of less than 2 All positions (base and trunk) Length > 5 cm Inventoried only on live trees
	Cracks and shelter bark	Cracks in the trunk wood + Peeling bark that forms a shelter Width 1–5 cm and depth > 5 cm Located more than 100 cm above the ground Inventoried on both live trees and snags
	Crown deadwood	Dead branches with a diameter > 5 cm located in the tree crown + More than 20% of the crown dead Inventoried only on live trees
Indices	Supply index (SI)	Density of observed microhabitats in the plot/number of microhabitat types predicted with the procedure used for the plot
	Diversity index (DI)	100 * (number of observed microhabitat types in the plot/maximum number of microhabitat types predicted with the procedure used for the plot) Expressed in %

the line transect method (Böhl and Brändli, 2007). In the first case, the diameter was measured at the middle of the piece and the main decay stage was assigned to the whole piece. In the second case, with three transects per plot for a total length of 34–60 m per plot, the diameter and the decay stage of all logs crossed by the transect were measured at the intersection point. The PG dataset (French Pyrenees) had no data for deadwood at the tree scale.

Volumes were calculated with the cylinder formula for items shorter than 4 m and with the truncated cone formula for items more than 4 m in length. All the variables were calculated at the plot, phase and forest scales. We distinguished broadleaved-dominated stands (where at least 50% of the live trees were broadleaves) from conifer-dominated stands. The five databases were analysed together since none of them showed any database-specific feature relative to the variables which structure FDPs (Fig A1).

2.3. Statistical procedures

2.3.1. Reconstitution of the silvigenetic cycle

Eight structure variables were measured for each plot (Table 2). These variables were used by most of the authors who have studied or defined development phases (Table 3). We used the following tree diameter classes traditionally defined by French forest managers (Bastien and Gauberville, 2011): for broadleaved species – 17.5 cm $\leqslant$ small tree (ST) $\leqslant$ 27.5 cm; medium tree (MT) $\leqslant$ 47.5 cm; large tree (LT) $\leqslant$ 67.5 cm; very large tree (VLT) > 67.5 cm and for conifers – 17.5 cm $\leqslant$ ST $\leqslant$ 27.5 cm; MT $\leqslant$ 42.5 cm; LT $\leqslant$ 62.5 cm; VLT > 62.5 cm. These classes match the significant diameter thresholds for microhabitats (Larrieu and Cabanettes, 2012). We applied a principal component analysis (PCA, R function *dudi.pca()*, *ade4* package) to the data from 169 plots (Table A1).

Next, we performed a hierarchical cluster analysis (HCA; R functions *dist()* and *hclust()*, *ade4* package; Ward method). We defined the optimal number of clusters both graphically in the HCA tree (Fig. A2), and by the proportion of inter-cluster variability in the whole variability (i.e. a gain in the explanatory value of clusters when we added new clusters). Total sums of squares (SSQtot) and those relative to clusters (SSQinter) were obtained with an ANOVA of PCA coordinates on the factor cluster on axes 1 and 2 (see Fig. A3). We interpreted the clusters as FDPs by ranking them throughout the silvigenetic cycle according to the increase in tree diameter and the deadwood structural variables used for PCA (see Figs. 2 and A5). To check that the five databases were homogeneously distributed within the 2-axed PCA plot (axis 1 and 2), they were graphically projected as clusters in this plot (R function *s.class()*, *ade4* package). To check for the relevance of the clusters at a larger scale, we projected onto the same PCA plot the five clusters obtained from all the data combined and the five clusters obtained from the *LL* + *PG* databases alone, chosen as a reference because, together, they accounted for 57% of the samples in the same

Table 2
Stand features used to reconstitute the silvigenetic cycle. Diameter at breast height (*dbh*) class: vst (very small trees) = *dbh* [10–17.5 cm]; st (small trees) = *dbh* [17.5 – 27.5 cm]; mt (medium trees) = *dbh* [27.5–42.5 cm] for conifers and [27.5–47.5 cm] for broadleaves; lt (large trees) = *dbh* [42.5–62.5 cm] for conifers and [47.4–67.5 cm] for broadleaves; vlt (very large trees) = *dbh* [62.5–97.5 cm] for conifers and [67.5–87.5 cm] for broadleaves; lst (largest trees) = *dbh* > 97.5 cm for conifers and *dbh* > 87.5 cm for broadleaves.

	Variable	Meaning
Live trees	Gliving_trees	Basal area (m^2 ha^{-1}) of living trees
	pvst	Number of *vst*/number of other trees
	pst	Number of *st*/number of other trees
	pmt	Number of *mt*/number of other trees
	pgt	Number of *lt* + *vlt* + *lst*/number of *vst* + *st* + *mt*
	plst	Number of *lst*/number of other trees
Deadwood	gsnags	Basal area (m^2 ha^{-1}) of snags
	gsnags.gliving.trees	Basal area of snags/basal area of live trees

Table 3
Review of the literature on silvigenetic cycles. *Dbh* is diameter at breast height and Hmax is the maximum height of the trees.

Author	Forest type	Time without logging	Number of stages/phases	Variables used to describe the phases
Korpel' (1982)	Montane beech-fir forest	?	3 stages subdivided into 10 phases	Tree age distribution (3 age classes), vertical structure (3 stories), trend in living volume increment
Gonin (1988)	Montane beech-fir forest	>100 years	6 phases	Tree density, *dbh* distribution, snag distribution, sapling density
Bobiec et al. (2000)	Lowland deciduous forest	?	6 phases	Tree density, *dbh* range, density of old trees, canopy cover, vertical structure pattern, deadwood amount pattern
Emborg et al. (2000)	Lowland beech forest with ash	40 years	5 phases	Stand height, plant density, presence of large trees, gap size
Tabaku (2000)	Montane beech-fir forest	Primeval forest	8 phases	*Dbh* and Hmax thresholds, proportion of deadwood in total stock volume, regeneration, canopy cover
Heurich (2006)	Mountain forests of the Bavarian Forest National Park, mainly beech, spruce-fir-beech and spruce forests	35 years	8 stages	Presence of deadwood, regeneration, *dbh* thresholds, basal area of old trees
Kral et al. (2010a)	Spruce-fir-beech forest	?	3 stages subdivided into 7 phases	*Dbh* distribution (living and dead trees), basal area per diameter class
Winter and Brambach (2011)	Beech and beech-spruce forests	Harvested stands and stands unharvested for 17–60 years	6 main phases (3 steps in the growing phase)	*Dbh* and Hmax thresholds, proportion of deadwood in total stock volume, regeneration, canopy cover

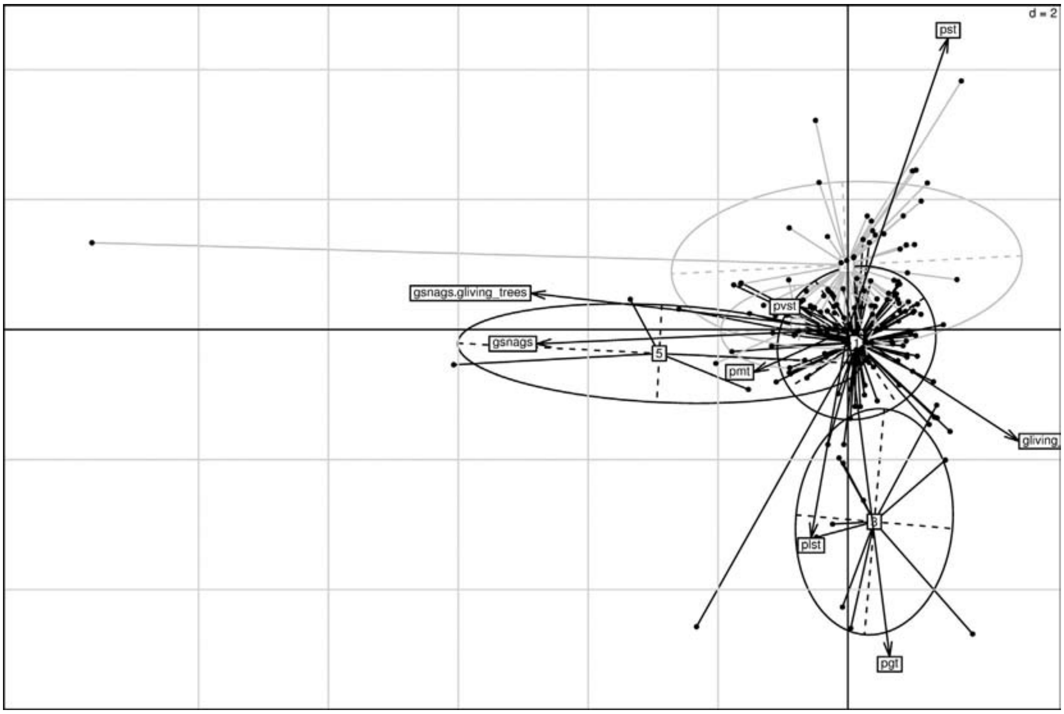

Fig. 2. Plot distribution, structuring variables and the 5 clusters resulting from HCA on the first and second PCA axes. Two clusters are drawn in grey to facilitate reading.

bio-geographical context (axis 1 and 2 of the PCA; R function *s.class()*, *ade4* package). We were thus able to visually verify that the clusters based on all five databases were not too different from those obtained from the *LL + PG* reference databases alone.

2.3.2. Density and diversity of deadwood and microhabitats

Since we used the basal area of snags (*gsnags*) and the ratio between the basal area of snags and the basal area of living trees (*gsnags.gliving.trees*) (Table 2) as global deadwood variables to distinguish the FDPs within the silvigenetic cycle, the a posteriori comparison of snag and total deadwood volume per phase was not relevant. Therefore, we did not test snag and deadwood volume variations among FDPs.

Since broadleaf and conifer proportion could influence both deadwood and microhabitat availability, we provide results for the whole dataset and for stands dominated by broadleaves or conifers. The data were sometimes unbalanced and consequently, variability was large for the FDPs represented by a small number of plots.

As suggested by Siitonen et al. (2000), we estimated deadwood diversity as the number of combinations among: (i) tree group, i.e. broadleaves vs conifers (2 categories), (ii) snags vs logs (2 categories), (iii) decay stage (5 categories), and (iv) *dbh* class (6 categories). Thus, the deadwood diversity index theoretically ranged from 0 to 120. This index was calculated per plot and was further refined to reflect tree group.

We computed a "supply index" (SI) related to microhabitat density and a "diversity index" (DI) related to the diversity of microhabitat types (Table 1). SI (per plot) was the density of microhabitats observed in the plot divided by the number of microhabitat types predicted to be observed according to the procedure used for the plot. DI (per plot, in%) was the number of microhabitat types observed in the plot divided by the maximum number of microhabitat types predicted to be observed according to the procedure used for the plot. SI and DI were averaged by cluster. To compare plots surveyed with different procedures, the total number of microhabitats per ha and per plot were weighted by the ratio Maximum number of microhabitat types (=7)/Maximum number of microhabitat types locally surveyed.

Log volume, deadwood diversity and amount and quality of microhabitats were compared with a generalized linear mixed model (GLMM) (Pinheiro and Bates, 2000) where FDP was the explanatory variable with a fixed effect and forest was a random effect (R-function *glmer()*, *lme4* package; Bates, 2010). For the number of cavities, deadwood diversity, and the supply and diversity indices, we added the interaction between FDP and broadleaves vs conifers to the models. Multiple comparisons of the means for each FDP (or each combination of FDP + broadleaves/conifers) were performed by comparing the confidence intervals of the least square means (R-function *lsmeans()*, *lmerTest* package; Kuznetsova et al., 2014). All the analyses were carried out with the R software (R Core Team v3.0.0, 2013).

3. Results

3.1. Silvigenetic cycle

From the PCA and HCA results, we considered the optimal number of clusters to be five (Figs. 2, A2 and A3). Both PCAs based on the Pyrenean (*LL + PG*) database only, or all five databases combined, gave consistent cluster patterns (Fig. A4). We then sequenced the five clusters to build the silvigenetic cycle by overlapping the clusters and the structuring variables on graphs (Figs. 2 and A5). Cluster ordination was based on the proximity of their barycentre to differences in *dbh* classes (i.e. *vst-st-mt-lst*) and proportion of deadwood (i.e. *gsnags.gliving_trees*). We first ranked cluster 4 (with the lowest *dbh* and a large amount of deadwood), then clusters 2, 1 and 3 with higher *dbh* and living-tree basal area, and finally cluster 5, much lower in living-tree basal area and higher in *gsnags/gliving_trees* ratio. Clusters 4-2-1-3-5 were respectively named as the following phases: regeneration (R), establishing (E), growing (G), culmination (C) and disintegration (D) – denomination after Winter and Brambach (2011). Axes 1 and 2 of the PCA respectively accounted for 22% and 19% of the total variance of the initial data.

3.2. Deadwood cycle

3.2.1. Deadwood volume (Fig. 3)

The general median trend (U-shaped pattern) showed the lowest availability of deadwood volume during the growing phase. The medians ranged from 56 $m^3\ ha^{-1}$ (CI = 37–74 $m^3\ ha^{-1}$) at the growing phase to 190 $m^3\ ha^{-1}$ (CI = 8–372 $m^3\ ha^{-1}$) at the disintegration phase. Values in the regeneration and disintegration phases had the greatest variability. The same general trend was observed for both broadleaved- and conifer-dominated stands; differences between broadleaved- and conifer-dominated stands were not significant at any of the phases (Fig. 3B).

The lowest availability of snags occurred during the growing phase. The medians ranged from 20 $m^3\ ha^{-1}$ (CI = 14–26 $m^3\ ha^{-1}$, 36% of total deadwood volume) during the growing phase to 94 $m^3\ ha^{-1}$ (CI = 0–247 $m^3\ ha^{-1}$, 49% of total deadwood volume) during the disintegration phase. The disintegration phase showed the greatest variability.

The availability of logs was lower during the establishing and growing phases, and higher during the disintegration phase, but the differences were not significant. The medians ranged from 32 $m^3\ ha^{-1}$ (CI = 11–53 $m^3\ ha^{-1}$, 35% of total deadwood volume, establishing phase) to 146 $m^3\ ha^{-1}$ (CI = 65–226 $m^3\ ha^{-1}$, 77% of total deadwood volume, disintegration phase). The regeneration phase displayed the greatest variability.

3.2.2. Deadwood diversity (Fig. 4)

Medians ranged from 7 to 17 deadwood categories, i.e. from 6% to 14% of the theoretical maximum. Differences between broadleaved-dominated and conifer-dominated stands were statistically significant only for the culmination phase, with higher diversity in conifer-dominated stands. Deadwood diversity reached the maximum values at the growing phase for broadleaved-dominated stands and at the culmination phase for conifer-dominated stands.

3.2.3. Role of secondary tree species in deadwood availability (Fig. 5)

While the *dead/living volume* ratio showed a general trend similar to total deadwood volume for the main tree species (beech, fir and spruce), its pattern was more complex for secondary species. Living secondary species were detected during the regeneration phase. The establishing phase was characterized by the maximum number of living trees. There was a relatively large amount of secondary-species deadwood in the establishing and growing phases. However, most of the secondary species died off during the culmination phase. Living secondary species were not detected during the disintegration phase.

3.3. Microhabitats

Because of the scarcity of certain microhabitats and the great variability of occurrences observed, only the results for cavities alone and all microhabitats combined are presented here. The microhabitat types other than cavities are included in the microhabitat diversity cycle.

3.3.1. Cavity densities (Fig. 6)

Medians of the number of cavities per ha ranged from 7 during the disintegration phase to 20 during the culmination phase, but between-phase differences were not significant. The highest variability was observed during the establishing phase. Medians of cavity densities were always lower in conifer- than in broadleaved-dominated stands but differences were not significant.

3.3.2. Microhabitat densities and diversity (Fig. 7)

The highest availability of microhabitats was measured during the regeneration, growing and culmination phases, but the differences between phases were not significant. The highest variability was observed during the growing phase. The same pattern was observed in both broadleaved- and conifer-dominated stands.

The lowest microhabitat diversity was observed during the disintegration phase, but the differences between the disintegration and the other phases were not statistically significant. Global microhabitat diversity was lower in the disintegration than in the regeneration phase, and in the establishing than in the culmination phase. In conifer-dominated stands, microhabitat diversity reached a maximum during the culmination phase. The greatest

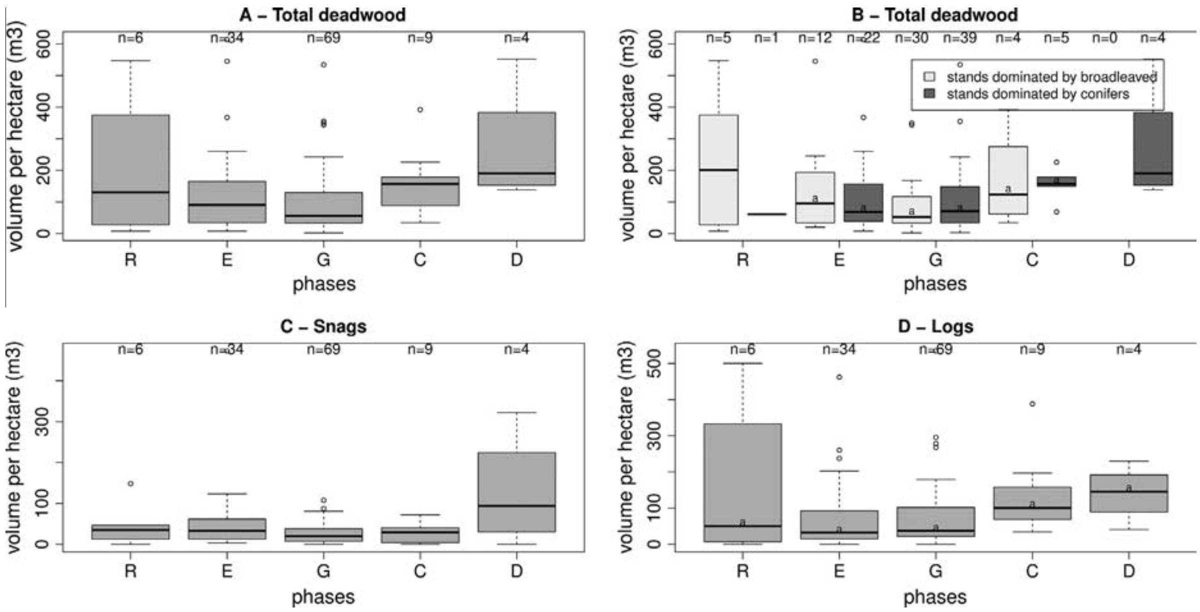

Fig. 3. Median deadwood volume and variability ($m^3\ ha^{-1}$) per forest development phase (FDP) within the silvigenetic cycle in mountain mixed forests. Panels show: A, total volume; B, total volume split into stands dominated by broadleaves or conifers; C, volume of snags; and D, volume of logs. FDPs: R = regeneration, E = establishing; G = growing; C = culmination; D = disintegration. Different letters indicate significantly different levels for the variable, assigned per FDP or per FDP + tree-group. The numbers at the top indicate the number of plots sampled per FDP.

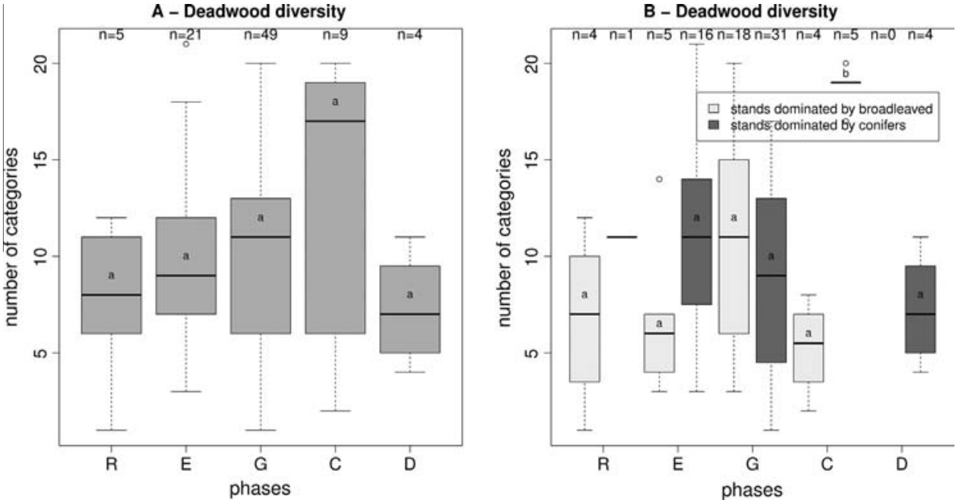

Fig. 4. Median number of deadwood categories and variability per forest development phase (FDP) within the silvigenetic cycle in mountain mixed forests. Panels show: A, diversity when all species are pooled; and B, deadwood diversity when stands dominated by broadleaves or conifers are split. FDPs: R = regeneration, E = establishing; G = growing; C = culmination; D = disintegration. Different letters indicate significantly different levels for the variable, assigned per FDP or per FDP + tree-group. The numbers at the top indicate the number of plots sampled per FDP.

variability was observed during the establishing and growing phases both for conifers and broadleaves. In broadleaved-dominated stands, microhabitat diversity was higher in the regeneration than in the establishing phase, and lower, but not significantly, in the growing than in the culmination phase.

4. Discussion

4.1. Forest dynamics

4.1.1. Forest development phases

Despite the well-known drawbacks of chronosequence analysis when dealing with ecological processes (Johnson and Miyanishi, 2008), this approach is adapted to the study of multi-century cycles (Walker et al., 2010). However, since there was no primeval forest in our dataset, the current forest dynamics we observed might have been partially influenced by past management. Moreover, a chronosequencing approach merges different contexts in terms of climate, soil fertility or biotic agents, all of which might influence the assessment of deadwood volumes or the rate of microhabitat turnover.

Although it is true that setting limits for FDPs is rather arbitrary since stand development is continuous and not a sequence of discrete stages (Franklin et al., 2002), we nonetheless statistically defined five FDPs. We used both knowledge from the literature and our field experience to construe the variables that we selected and to deduce a cycle by ordering the PCA clusters. We did not split the FDPs into sub-phases as did Winter and Brambach (2011), since neither the HCA dendrogram nor the clusters' explanatory power suggested we do so.

Our database did not allow us to balance the number of plots per phase, since their initial phase appurtenance was not known a priori. FDP variability could depend either on natural variations or on sample size. Except for the disintegration and regeneration phases which respectively occurred on only four and five plots – and which therefore should be more accurately defined, the other FDPs included enough plots to be correctly defined and positioned. Disintegration and regeneration phases are very difficult to study in Europe since most set-aside forests have been left unmanaged for a comparatively short time within the full silvigenetic cycle.

Despite these caveats, we believe that our results are relevant for most European mountain mixed forests, since adding databases did not significantly change either the number of FDPs or FDP composition.

4.1.2. Deadwood

Contrary to expectations (hypothesis (i)), deadwood volume and diversity did not significantly vary with FDP. However, our sample was somewhat unbalanced, and this lack of difference does not provide formal evidence of an overall homogeneous deadwood distribution throughout the silvigenetic cycle. In conifer-dominated forests, our results were consistent with those of Saniga and Schutz (2002): we also found small gradual changes in deadwood amount with minimum values during the growing phase. Our results were also consistent with Marage and Lemperiere (2005) who found that the *necrotic index* (i.e. 100 $*$ G snags/G living and dead trees) shows a U-shaped distribution throughout the cycle, with minimum values during the growing and culmination phases, even though the latter phase is partly characterized by scattered mortality among dominant trees. Unlike Saniga and Schutz (2002), we did not observe any different pattern when comparing broadleaved-dominated stands and those dominated by conifers, nor did we find that fir-dominated stands showed a very high ratio of dead/living volume, as did Jaworski and Paluch (2001). Since we did not observe such differences, our results do not support a shorter silvigenetic cycle for beech than for fir, as Saniga and Schutz (2002) suggested. We believe that beech and fir stands have similar longevities, in accordance with Gonin (1988) and also Rameau et al. (1993), who give roughly the same average natural lifespan for beech and fir.

Concerning hypothesis (iii), secondary species did affect the deadwood component in our forests. The cycle of secondary species revealed a complex pattern, which we interpreted in relation to species average life span (Rameau et al., 1993). Seedlings colonised during the disintegration phase but were not detected due to the minimum *dbh* threshold we used. Secondary species were abundant in the regeneration phase. Since this phase lasts 60–125 years on average (according to Gonin, 1988), the shorter-lived species such as *Salix* spp., *Populus* spp., *Ulmus glabra* or *Sorbus aucuparia* die before the end of the phase and very quickly supply diversified deadwood items. Species that have a longer life span (on average 100–200 years for *Acer platanoides*, *Sorbus aria*, *Fraxinus excelsior*, *Prunus avium*, *Alnus glutinosa*, *A. incana*) die off in great numbers during the growing phase. As a result, the

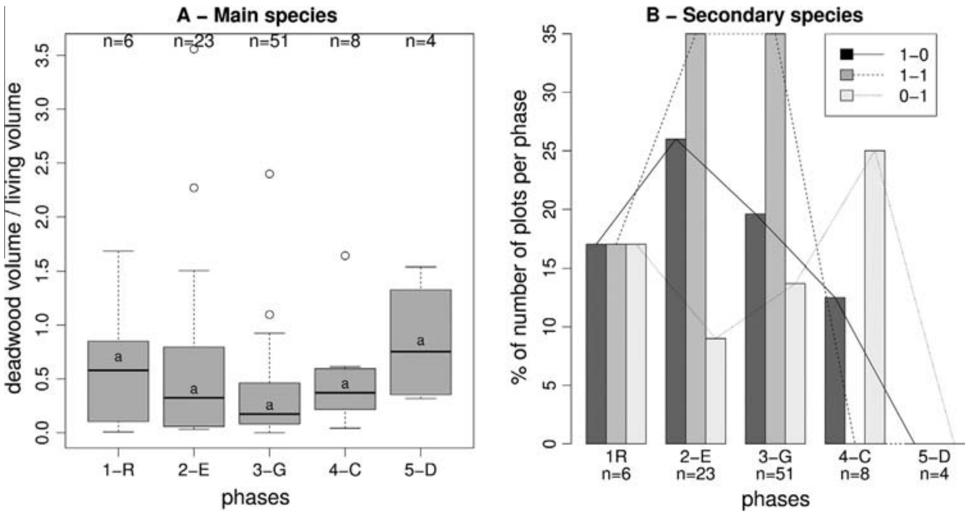

Fig. 5. Distribution of the relative occurrence of dead and living volume as a function of forest development phase (FDP). Panel A: deadwood/living volume ratio for the dominant species (beech, fir and spruce). Panel B: presence/absence of dead and living trees for secondary species; the first number (0 or 1) corresponds to living wood and the second (0 or 1) to deadwood; e.g. 1–0 indicates that only living wood is present. Proportion (%) is expressed with respect to 100% of the occurrences within the FDP. To simplify the figure, plots with no living or dead wood from secondary species are not displayed.

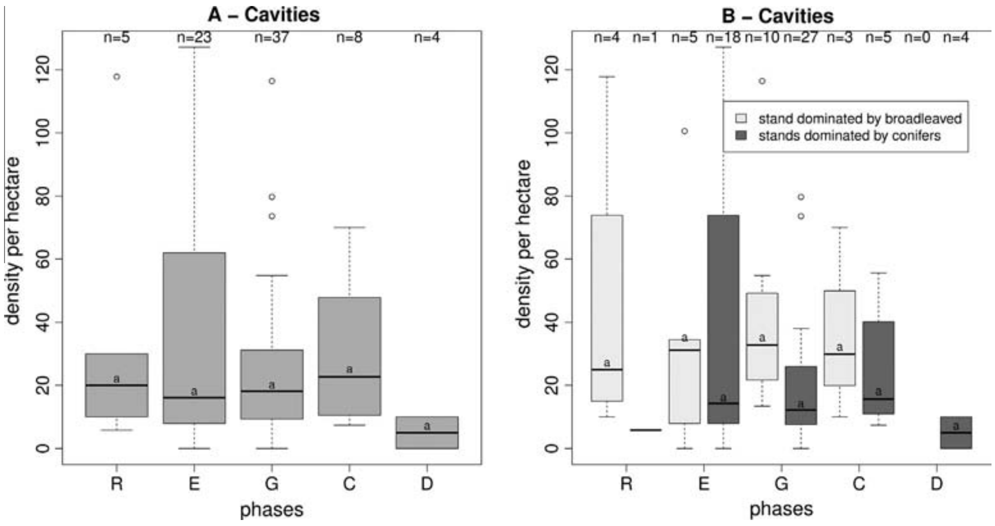

Fig. 6. Median number of cavities per hectare and variability throughout the silvigenetic cycle in mountain mixed forests. Panels show: A, cavity densities when all species are pooled; and B, cavity densities when stands dominated by broadleaves or conifers are split. Forest development phases (FDPs): R = regeneration, E = establishing; G = growing; C = culmination; D = disintegration. Different letters indicate significantly different levels for the variable, assigned per FDP or per FDP + tree-group. The numbers at the top indicate the number of plots sampled per FDP.

culmination phase is characterized by a large amount of secondary-species deadwood. Finally, some secondary species survive in open areas as very long-lived species (*Acer pseudoplatanus* (300–500 years) or *Tilia* spp. (more than 500 years)).

Stokland (2001) suggested using deadwood profiles based on tree size and decay stage as a means to evaluate naturalness and continuity in boreal forests. Our results confirm the relationship between deadwood diversity and FDP in long-unharvested mountain mixed forests, similarly to what Bobiec et al. (2005) found for lowland sub-natural forests. However, in our study, between-phase differences were often tenuous because of wide within-phase variability, possibly partly linked to the long-persisting legacies from previous phases. Stokland et al. (2012) highlighted this wide variability in a natural context.

In the context of long-unharvested forests, we expected deadwood diversity to be higher than observed (only 14% of the theoretical maximum value). This result might have been biased by our field inventory procedure where only one decay stage was attributed per item or by the small size of certain plots. However, our finding is consistent with the low deadwood diversity values (0.3–8.6%) observed by Bouget et al. (2013) in a set of lowland beech forests (with both reserves and managed stands).

4.1.3. Microhabitats

Since microhabitats were recorded differently (definitions and thresholds) for the five databases, we merged them into wide-range categories such as "cavities" (see Table 1). This procedure may have hidden differences between the FDPs. Contrary to hypothesis (ii), microhabitat availability was not higher in the disintegration phase than in the other phases – it was actually lower. The death of most of the largest trees during the disintegration phase might explain why microhabitat availability dropped in terms of density and diversity. The crucial role played by the largest trees in providing microhabitats is well known (e.g. Larrieu

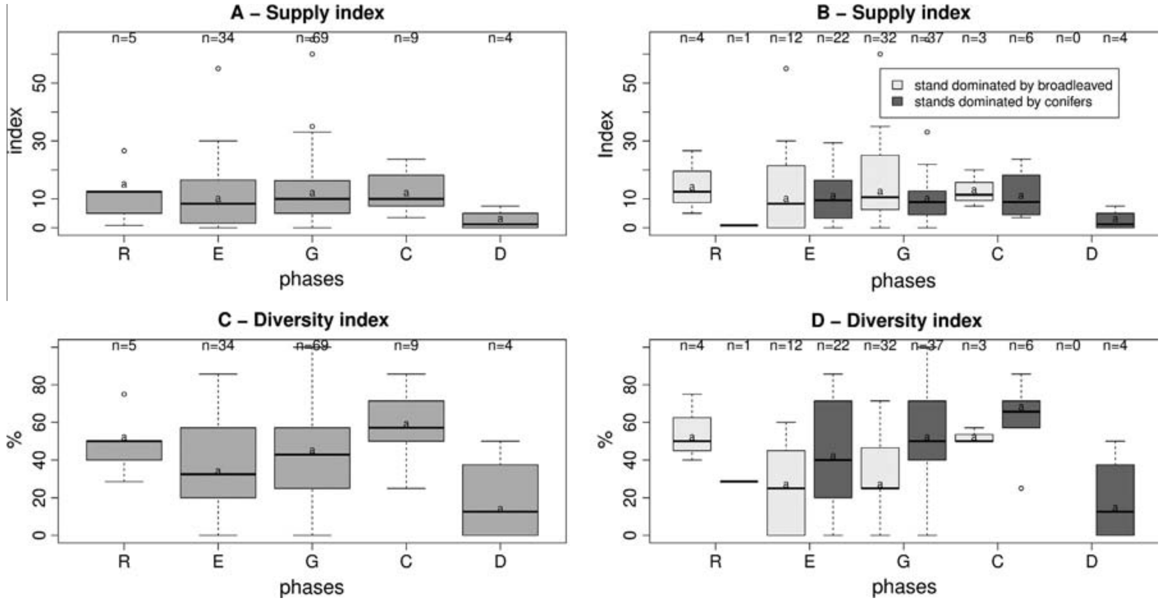

Fig. 7. Median microhabitat availability and variability throughout the silvigenetic cycle in mountain mixed forests. Panels show: A, microhabitat density index when all species are pooled; B, microhabitat density index when stands dominated by broadleaves or conifers are split; C, microhabitat diversity when all species are pooled; and D, microhabitat diversity when stands dominated by broadleaves or conifers are split. Forest development phases (FDPs): R = regeneration, E = establishing; G = growing; C = culmination; D = disintegration. Different letters indicate significantly different levels for the variable, assigned per FDP or per FDP + tree-group. The numbers at the top indicate the number of plots sampled per FDP.

et al., 2014). Furthermore, we surveyed most microhabitats only on living trees.

Conversely, Winter and Brambach (2011) demonstrated that microhabitat density was significantly higher in the disintegration than in the regeneration phase – by 80 microhabitats per ha. In a transient phase between the disintegration and regeneration phases (canopy cover <30% and saplings <50%), called the “gap phase” (Tabaku, 2000), microhabitat density was significantly and strongly lower. We might expect more cavities in the disintegration phase because of high snag volume, but tree density is low during this phase. Finally, both the higher microhabitat availability and diversity in the regeneration phase might have been favoured by the increase in pioneer species, which often bear microhabitats (Larrieu and Cabanettes, 2012).

4.2. Implications for taxa conservation and forest management

We highlight that, in long-unharvested mountain mixed forests, the availability of both deadwood and microhabitats appears to be almost continuous, in terms of both quantity and diversity. Biological legacies from the culmination and disintegration phases allow the forest to maintain features (e.g. very large trees bearing microhabitats, large pieces of deadwood) crucial to saproxylic taxa – and probably to associated species – throughout the silvigenetic cycle (Franklin et al., 2002). These legacies can persist for many decades and play an important role in structuring and facilitating the development of the next phase (Swanson et al., 2011). At the forest scale, these legacies ensure the spatio-temporal continuity of saproxylic features. Although knowledge of saproxylic species’ autecology is still insufficient (Langor et al., 2008), this continuity appears to be crucial to species with low dispersal ability and limited ecological plasticity, for example, the beetles and pseudo-scorpions living in large cavities with mould (Müller et al., 2005; Ranius et al., 2011).

The major difference between the natural silvigenetic cycle and the silvicultural cycle – other than the obvious difference related to wood removal – is the absence of the culmination and disintegration phases in managed forests (this also significantly shortens the natural cycle). Another difference is the higher structural heterogeneity, supported by deadwood and microhabitat features, observed during the regeneration and establishing phases in the silvigenetic cycle compared with young managed stands. This heterogeneity ensures a wide species diversity and complex food webs for saproxylic taxa as well as for mammals, reptiles and amphibians (Swanson et al., 2011).

Forest management should better mimic natural dynamics, especially in forests targeted for saproxylic diversity conservation. Though it is very difficult to recommend consistent ecological thresholds appropriate to all forest contexts because of the variability related both to forest type (Bouget et al., 2013) and to taxa (Müller and Bütler, 2010), we recommend conserving structural legacies in all managed stands, whatever the age or stage in the silvicultural cycle.

It is known that communities associated with broadleaves and conifers are quite dissimilar (see e.g. Nascimbene et al., 2009; Stokland et al., 2012; Mollet et al., 2013). Mixed broadleaf/conifer stands should therefore promote diversity. Furthermore, mixed stands can reduce the spread of disease or pest damage (Thompson et al., 2009). Since the life span for beech, fir and spruce seems to be similar, and since we know that all three species have roughly similar ecological requirements (Rameau et al., 1993), mixed forests with these three species should be the benchmark pattern in most montane and lower-subalpine elevations in Europe.

Secondary species impact the deadwood cycle by supplying diversified deadwood (i.e. different tree species, diameters and decay stages) when deadwood from the dominant species is the scarcest, i.e. during the growing and culmination phases. These tree species also influence microhabitat availability since they often bear microhabitats (Larrieu and Cabanettes, 2012). Furthermore, they specifically host certain beetle taxa (Möller, 2009) or fungi (Bernicchia, 2005). In managed stands, we recommend preserving secondary species (at least those with the lowest commercial values such as *Populus* spp., *Betula* spp.), since they may constitute a significant part of the broadleaved legacy. Their contribution to deadwood diversity (see also Lassauce et al., 2012) deserves further study.

5. Conclusion and perspectives

By regularly harvesting weakened trees and removing the culmination and disintegration phases from the cycle, forest management severely disrupts the availability of deadwood and microhabitats. We agree with Winter and Brambach (2011) who suggest using FDP assessment as a naturalness indicator, after including global variables to reflect deadwood and microhabitat dynamics in the FDP definitions. Recommendations to improve management practices and to decrease the impact of harvesting include legacy retention, favouring mixed stands, retaining secondary tree species, and establishing set-asides within stands. It could also be relevant to suggest more specific recommendations for each silvicultural phase, to better mimic natural features. Forest managers could reduce the scale of management units to make them coherent with FDPs to better take biodiversity into account. Subsequently, it would be easier to integrate forest dynamics into the management process, e.g. by anticipating phase shifts and their consequences on stand structure, and by setting aside areas encompassing the rarest FDPs. The management unit could also be redefined as a set combining the whole structural mosaic, as recommended by Franklin and Van Pelt (2004).

Further research is required to improve our knowledge of deadwood and microhabitats throughout the forest cycle. Only a few studies have been based on spatial observations of deadwood and microhabitats. Pinpointing the location of these features would reveal the structure of their mosaic and therefore provide a better understanding of the key drivers for saproxylic biodiversity at several scales. Furthermore, future studies should focus on (i) the rare phases of disintegration and regeneration, to better assess their variability; and (ii) the differences between broadleaved- or conifer-dominated stands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.09.007.

References

André, J., 2005. Activité et diversité des organismes hétérotrophes: les clés du bouclage des cycles biogéochimiques et sylvigénétiques. In: Vallauri, D. et al. (Eds.), Bois mort et à cavités. Une clé pour des forêts vivantes, Lavoisier, Paris, pp. 89–98.

Bardat, J., Bioret, F., Botineau, M., Boullet, V., Delpech, R., Géhu, J.M., Haury, J., Lacoste, A., Rameau, JC., Royer, J.M., Roux, G., Touffet, J., 2004. Prodrome des végétations de France MNHN, Paris.

Bastien, Y., Gauberville, C. (Coordinators), 2011. Vocabulaire forestier. Ecologie, gestion et conservation des espaces boisés. IDF, Paris, France.

Bates, D.M., 2010. Lme4: Mixed-effects modeling with R. Springer.

Bernicchia, A., 2005. Fungi Europaei. Polyporaceae. Ed. Candusso, Alassio, Italy.

Bitterlich, W., 1984. The relascope idea. Relative measurements in forestry Commonwealth Agricultural Bureaux, Farnham Royal.

Bobiec, A., van der Burgt, H., Meijer, K., Zuyderduyn, C., Haga, J., Vlaanderen, B., 2000. Rich deciduous forests in Bialowieza as a dynamic mosaic of developmental phases: premises for nature conservation and restoration management. For. Ecol. Manage. 130, 159–175.

Bobiec, A., Gutowski, J.M., Laudenslayer, W.F., Pawlaczyk, P., Zub, K. 2005. The afterlife of the tree WWF Poland, Warszawa.

Böhl, J., Brändli, U., 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. Eur. J. For. Res. 126, 449–457.

Bouget, C., Gosselin, F., 2005. Distribution spatiale du bois mort: enjeux pour la conservation des espèces cavicoles et saproxyliques. In: Vallauri, D. et al. (Eds.), Bois mort et à cavités. Une clé pour les forêts vivantes, Lavoisier, Paris, pp. 107–113.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers. Conserv. 22, 2111–2130.

Brin, A., Bouget, C., Brustel, H., Jactel, H., 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J. Insect Conserv. 15, 653–669.

Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. For. Ecol. Manage. 291, 458–479.

Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. Ecol. Appl. 5, 336–352.

Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. For. Ecol. Manage. 126, 173–189.

Euforgen, 2012. Distribution map of silver fir (*Abies alba*) Spruce (*Picea abies*) and European beech (*Fagus sylvatica*). <http://www.euforgen.org>.

Franklin, J.F., Van Pelt, R., 2004. Spatial aspects of structural complexity in old-growth forests. J. Forest. 102, 22–28.

Franklin, J.F., Lindenmayer, D., MacMahon, J.M., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. Conservat. Biol. Pract. 1, 9–16.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.

Gilg, O., 2005. Old-Growth Forests; Characteristics, conservation and monitoring. GIP ATEN, technical report n°74 bis.

Gonin, P., 1988. Contribution à l'étude de l'évolution des forêts non exploitées dans les Pyrénées. Association Forêts Pyrénéennes, St Gaudens.

Grgic, T., Kos, I., 2005. Influence of forest development phase on centipede diversity in managed beech forests in Slovenia. Biodivers. Conserv. 14, 1841–1862.

Guillaumet, J., Kahn, F., 1982. Forest structure and dynamics. Acta Amaz. 12, 61–77.

Heurich, M., 2006. Evaluierung und Entwicklung von Methoden zur automatisierten Erfassung von Waldstrukturen aus Daten flugzeuggetragener Fernerkundungssensoren. Forstl, Forschungsberichte, München, 202.

Jaworski, A., Paluch, J., 2001. Structure and dynamics of the lower mountain zone forests of primeval character in the Babia Gora Mt. National Park. J. For. Sci. 47, 60–74.

Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.

Korpel', S., 1982. Degree of equilibrium and dynamical changes of the forest on example of natural forests of Slovakia. Acta Facultatis Forestalis Zvolen 24, 9–30.

Kral, K., Janik, D., Vrska, T., Adam, D., Hort, L., Unar, P., Samonil, P., 2010a. Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. For. Ecol. Manage. 260, 2196–2203.

Kral, K., Vrska, T., Hort, L., Adam, D., Samonil, P., 2010b. Developmental phases in a temperate natural spruce-fir-beech forest: determination by a supervised classification method. Eur. J. For. Res. 129, 339–351.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2014 Package 'lmerTest', 17 p. <http://cran.rproject.org/web/packages/lmerTest/lmerTest.pdf>.

Langor, D.W., Hammond, H., Spence, J.R., Jacobs, J., Cobb, T.P., 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. Can. Entomol. 140, 453–474.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can. J. Forest Res. 42, 1433–1445.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014. Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. Eur. J. For. Res. 133, 355–367.

Larsson, T.B. (Ed.), 2001. Biodiversity evaluation tools for European forests, Ecol. Bull. p. 50.

Lassauce, A., Anselle, P., Lieutier, F., Bouget, C., 2012. Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: a case study in French deciduous forests. For. Ecol. Manage. 266, 273–285.

Leibundgut, H., 1978. Über die Dynamik europäischer Urwälder. Allg. Forstz. 24, 686–690.

Marage, D., Lemperiere, G., 2005. The management of snags: a comparison in managed and unmanaged ancient forests of the Southern French Alps. Ann. For. Sci. 62, 135–142.

Möller, G., 2009. Struktur- und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera – Käfer [Habitats and Substrates of Saproxylic Invertebrates, mainly beetles]. Dissertation Freien Universität Berlin, 284 p.

Mollet, P., Birrer, S., Pasinelli, G., 2013. Forest birds and their habitat requirements. In: Kraus, D., Krumm, F. (Eds). Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute. 284 p.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992.

Müller, J., Bussler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J., Zabransky, P., 2005. Urwald relict species – Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2, 106–113.

Nascimbene, J., Marini, L., Nimis, P.L., 2009. Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. Can. J. For. Res. 39, 785–791.

Niemela, J., Haila, Y., Punttila, P., 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19, 352–368.

Oldemann, R.A.A., 1990. Forests: Elements of silvology Springer-Verlag, New York.

Oliver, C.D., Larson, B.C., 1996. Forest stand dynamics, updated ed. John Wiley and Sons, New York, USA.

Pardé, J., Bouchon, J., 1988. Dendrométrie, 2ème ed. ENGREF, Nancy, France.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S ans S-PLUS. Springer.

R Development Core Team, 2013. R: a language and environment for statistical computing. <http://www.R-project.org>.

Rameau, JC., Mansion, D., Dumé, G., 1993. Flore Forestière Française IDF, Paris.

Ranius, T., Johansson, V., Fahrig, L., 2011. Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. Biodivers. Conserv. 20, 2027–2040.

Saniga, M., Schutz, J., 2002. Relation of dead wood course within the development cycle of selected virgin forests in Slovakia. J. For. Sci. 48, 513–528.

Scherzinger, W., 1996. Naturschutz im Wald. Qualitätsziele einer dynamischen Waldentwicklung. Ulmer Verlag, Stuttgart, 447 S.

Siitonen, J., Martikainen, P., Punttilä, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage. 128, 211–225.

Speight, M.C.D., 1989. Saproxylic invertrebrates and their conservation, Concil of Europe, p. 42.

Stokland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol. Bull. 49, 71–83.

Stokland, J., Tomter, S., Soderberg, U., 2004. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. EFI Proc., 207–226.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge, UK.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125.

Tabaku, V., 2000. Stuktur von Butchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und Wirtschafswäldern Cuvillier Verlag, Göttingen.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series n° 43, 67p.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144, 441–450.

Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.

Watt, A.S., 1947. Pattern and process in the plant community. J. Ecol. 35, 1–22.

Winter, S., Brambach, F., 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. For. Ecol. Manage. 262, 2120–2132.

Winter, S., Flade, M., Schumacher, H., Kerstan, E., Moller, G., 2005. The importance of near-natural stand structures for the biocoenosis of lowland beech forests. For. Snow Landsc. Res. 79, 127–144.

Wissel, C., 1992. Modeling the mosaic cycle of a middle european beech forest. Ecol. Model. 63, 29–43.

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Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles?

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Abstract

The decline of many saproxylic species results from the decrease in old-growth structures in European harvested forests. Among conservation tools, protected reserves withdrawn from regular harvesting and extended rotations have been employed to restore old-growth attributes in structurally simplified managed forests, even if the effects of such management actions on forest habitats and biodiversity remain largely unknown.

In this study, we compared structural stand features and saproxylic beetle assemblages in two stand classes – recently harvested stands and long-established reserves, where less or more than 30 years had elapsed since last harvest. Habitat and saproxylic beetle data were collected according to standardized protocols in 153 plots in seven lowland deciduous forests.

Tangible contrasts in stand features were found between long-established reserves and recently harvested plots. Indeed, most higher-value densities and volumes were found in unharvested areas. The difference was weaker for microhabitat-bearing tree density than for deadwood; some deadwood features, such as volume of large downed and standing deadwood showed a very pronounced difference, thus indicating a marked deleterious effect of forest harvesting on these elements. Deadwood diversity, on the other hand, was only slightly affected and the level of stand openness did not change.

The response of saproxylic beetles to delayed harvesting was weaker than the structural changes in deadwood features. Indeed even if only some guilds weakly increased in non-harvested plots, harvesting classes significantly affected the abundance of a quarter of the species tested.

Our results tend to question measures such as rotating and temporarily ageing patches. We argue in favor of permanent strict fixed-location reserves. Future work should examine how stands recover old-growth forest attributes and how the associated saproxylic fauna colonizes in the long term.

Introduction

European forest dynamics has been deeply affected by forestry and forest fragmentation for millennia (Peterken, 1996). Stand composition and structure have been greatly simplified by harvesting and other uses, even in remote areas. Several studies demonstrated the negative effects of conventional management practices on old-growth structures (e.g. Burrascano *et al*., 2013; Green & Peterken, 1997; Lombardi *et al*., 2008). Structural simplification has been shown to result in the decline of many associated saproxylic populations, but the issue has received more attention in

North America and northern Europe than in central and southern Europe (e.g. Martikainen *et al.*, 2000; Grove, 2002).

In forests subjected to structural simplification through harvesting, strategies to restore old-growth attributes may involve (1) setting aside forest plots, (2) extended rotations, (3) retention of structural features at the time of harvest and (Keeton, 2006) (4) man-made restoration of structural elements (Martikainen *et al.*, 2000). In the last 20 years, there has been an increasing focus on systematic conservation planning, that is how to select protected areas in a way that captures biodiversity as efficiently as possible (e.g. Margules & Pressey, 2000). Protected forests include different protection categories and surface areas (Schmitt *et al.*, 2009) and they are described worldwide in countless ways. Areas 'left for natural dynamics' can be found in several protection categories often as (so-called) strict forest reserves, where neither silvicultural intervention nor any other avoidable human impacts are allowed, but other denominations abound: wilderness areas, areas withdrawn from regular management, abandoned, unharvested, set-aside forest areas or unmanaged core areas in national parks. Among passive restoration strategies (Bauhus, Puettmann & Messier, 2009), small-scale management tools such as delaying harvesting, leaving unharvested patches or preserving habitat trees (Lachat & Bütler, 2009) have been employed to increase the number of old-growth structures in forests (Bauhus *et al.*, 2009). Other examples include woodland-key habitats, green-tree retention patches left in clearcuts as short-term refuges or lifeboats for many organisms during the regeneration phase in Scandinavia and North America (e.g. Vanha-Majamaa & Jalonen, 2001, Aubry *et al.*, 1999), ageing or old-growth patches kept as portions of management units in France (Lassauce *et al.*, 2013). Despite an increase in the number of empirical studies concerning the effects of forest abandonment on species diversity (see Paillet *et al.*, 2010), the relative efficiency of each management strategy in supporting biodiversity remains unknown. When harvesting activities are delayed for several decades, natural forest dynamics may bring about structural changes that restore old-growth attributes, depending on site potential (Vandekerkhove *et al.*, 2009): larger trees, heterogeneous vertical and horizontal structure with greater variations in tree size, age, spacing and species composition, increased supplies of deadwood, more large snags and fallen trees, multiple canopy layers, changes in disturbance regime, canopy gaps and understory patchiness. These structural changes have been recorded in several case studies (e.g. Lassauce *et al.*, 2012, 2013, Sitzia *et al.*, 2012) and may impact biodiversity.

In this study, we compared the habitat parameters and the diversity of saproxylic beetles (i.e. abundance, species richness and composition) in set-aside and harvested areas in seven lowland deciduous French forests. The issues were addressed in two steps: (1) How were saproxylic habitat parameters, such as the diversity and density of deadwood and tree microhabitats, affected in long-established set-aside plots compared with recently harvested plots? (2) Did saproxylic beetle assemblages (including rare species) respond to these habitat changes?

Material and methods

Study areas

The plots were located in seven lowland beech, *Fagus sylvatica* L., and oak, *Quercus robur* L and *Q. petraea* (Mattus.) Liebl., forests (Table 1) in the Atlantic or Continental biogeographic domain. Each forest was several hundred kilometers from the others: one in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). The plots in each forest were several hundred meters apart. A design of 153 plots was set up in managed stands (98) and in recently (16) or long-established (39) forest reserves. Managed forests were coppice-with-standards under conversion to high forest (33), even-aged (54) or uneven-aged (11) high forests (see Supporting Information Table S1). All plots were located in mature stands before regeneration felling or final cut. Last harvests consist of thinning operations in even-aged high forests and single tree removals in coppice-with-standards stands under conversion and uneven-aged high forests. The time elapsed from last harvest was postulated

Table 1 Sampling design layout. Among long-established reserves (L-UNH), old (> 30 years) and very old reserves (> 100 years) were not tested separately due to the small number of replicates available in the latter category. Managed plots and recently established reserves are grouped in R-HAR. Sampling year between brackets

	Beech			Oak			
		L-UNH > 30 yrs			L-UNH > 30 yrs		
	R-HAR < 30 years	30–100 years	> 100 years	R-HAR < 30 years	30–100 years	> 100 years	Total
Auberive [2009]	11	4		7	2		24
Chize [2010]	10	2		12			24
Citeaux [2010]				6	6		12
Combe-Lavaux [2010]	3	2		1	2		8
Fontainebleau [2008]	5	3	9	7			24
Rambouillet [2007]				24	6		30
Troncais [2009]				28	3		31
Total	29	11	9	85	19	0	153

for each plot based on management plans, reports or information from local managers. Unlike Christensen *et al.* (2005), we did not derive the number of years since last harvest from the official establishment date of the reserves as these do not necessarily coincide. Because the time since last harvest was not precisely known in several cases, we classified the plots into two harvesting classes based on the best estimate of the length of time without harvesting or removal of trees and deadwood (Table 1): 'recently harvested' (R-HAR < 30 years ago, $n = 114$), including harvested plots ($n = 98$) and recently established reserves ($n = 16$); or long-established reserves (L-UNH > 30 years, $n = 39$), including old (> 30 years and < 100 years, $n = 30$) and very old reserves (> 100 years, $n = 9$). Very old reserves were found in the Fontainebleau state forest only. We collected environmental and entomological data following standardized protocols.

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled by two cross-vane flight interception traps (Polytrap^{TM}, E.I. Purpan, Toulouse, France) per plot, set about 20 m from each other, for a total number of 306 traps. The unbaited traps were suspended roughly 1.5 m above ground. Active insects were collected from April to August during 1 year. For each species in all the taxa from the ±50 families recorded, we characterized degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species. All species were assigned to one saproxylic trophic group, but only the four main guilds were studied (xylomycetophagous, xylophagous, saproxylophagous and zoophagous).

Stand and deadwood variables

We used a combination of fixed-area and fixed-angle techniques to estimate (1) wood volumes for live trees, snags, logs and stumps, and (2) the basal area of live trees on 0.15 ha (Fontainebleau, Auberive, Chize, Citeaux, Combe-Lavaux) or 0.30 ha (Rambouillet, Troncais) plots. We set a minimum diameter of 7.5 cm for live trees, snags and logs.

Four variables were used to describe the deadwood: tree species, diameter (six classes: 5, 10–15, 20–25, 30–40, 50–65, > 70 cm), position (log, snag, stump), decay stage [nine classes adapted from Sippola, Siitonen & Kallio (1998) and Larjavaara & Muller-Landau (2010) and crossing three classes of remaining bark cover (from 95% of the stem still covered by attached bark to missing bark over the whole stem) and three classes of inner wood hardness assessed by 'knife penetration test' (from hard outer wood to deeply disintegrated and soft inner wood)]. A deadwood diversity index was calculated as the number of observed deadwood types, that is the number of combinations of the above four variables (tree species × diameter class × decay class × position), as suggested by Siitonen *et al.* (2000). The volume of live trees was calculated using wood volume tables based on the dbh variable, and used to estimate the deadwood volume ratio (= dead wood/(live + dead wood)), accounting for site productivity (Hahn & Christensen, 2004). Based on the deadwood surveys, we selected seven deadwood variables for analysis: (1) deadwood volume, (2) deadwood volume ratio, (3) number of deadwood types, (4) standing deadwood volume, (5) large standing deadwood (diameter > 40 cm) volume, (6) downed deadwood volume, and (7) large downed deadwood (diameter > 40 cm) volume. The thresholds defining large deadwood, large and very large trees were inspired by results in Nilsson *et al.* (2003) and Larrieu & Cabanettes (2012).

The basal area of large trees (67.5 < dbh ≤ 87.5 cm) and very large trees (dbh > 87.5 cm) were measured on 0.15–0.3 ha plots; the density of large trees was also inventoried in 1-ha circular plots. Tree microhabitat densities were inventoried during leaf-burst in 1-ha circular plots centered around the two flight traps. We recorded seven microhabitat types borne by live trees (Larrieu & Cabanettes, 2012): (1) 'empty' cavities, (2) cavities with mould, (3) fruiting bodies of saproxylic fungi, (4) sap runs, (5) dead branches, (6) tree crown deadwood, and (7) missing bark [i.e. hard patches of wood with no bark > 600 cm^2] (see Table 2 for further details on predictors). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitats, the number of microhabitat types (among the seven observed types) and the individual densities of four microhabitat types ('empty' and mould cavities pooled, dead branches and tree crown deadwood pooled, sporocarps of saproxylic fungi and sap runs) were considered for analysis. Stand openness was assessed as the total proportion of open areas (clearings, edges, stand surface with a well-developed herb layer composed of flowering plants) in a 1 ha plot. For further details on how the environmental variables were measured, see Bouget *et al.* (2013).

Data analysis

Our main objectives were to compare (1) stand structural characteristics and (2) saproxylic beetle assemblages in the two stand classes (R-HAR and L-UNH) based on the amount of time elapsed since last harvest. Because the same set of environmental variables was used for both traps in the same plot, the catches of the two traps were combined prior to analyses carried out at the plot level.

The differences in mean values of structural stand features between recently harvested and long-established reserves were analyzed with a Generalized Gaussian or Poisson Linear Mixed Model where 'forest' was a spatially implicit random effect on the intercept (lmer function in lme4 R-package).

Table 2 Effect of the harvesting class on stand characteristics (deadwood, microhabitat, large trees, openness)

	Factor	Detail	Signif	Est R-HAR	Est L-UNH	Ratio	Error distribution family
Stand features	Basal area of large trees	Basal area of large trees in a 0.3 ha plot ($67.5 < \text{dbh} \leq 87.5$ cm) ($m^2\ ha^{-1}$)	***	2.957 (1.579)	7.198 (1.663)	2.43	Gaussian
	Basal area of very large trees	Basal area of the very large trees in a 0.3 ha plot ($\text{dbh} > 87.5$ cm) ($m^2\ ha^{-1}$)	***	0.501 (0.591)	2.405 (0.628)	4.80	Gaussian
	Density of large trees	Number of large trees in a 1 ha plot ($\text{dbh} > 67.5$ cm)	***	1.389 (0.487)	2.116 (0.487)	1.52	Poisson
	Openness	Proportion in cumulative area of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants) (%) in a circular 1 ha plot	NS	12.490 (5.188)	11.667 (5.962)		Gaussian
MH features	Density of microhabitat-bearing trees	Total density of microhabitat-bearing trees in a 1 ha plot	***	2.647 (0.129)	3.046 (0.131)	1.15	Poisson
	Number of microhabitat types	Number of microhabitat types in a 1 ha plot	**	1.468 (0.061)	1.702 (0.070)	1.16	Poisson
	Density of cavity-bearing trees	Density of cavity-bearing trees in a 1 ha plot: 'empty' cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	***	1.620 (0.093)	2.208 (0.098)	1.36	Poisson
	Density of fungus-bearing trees	Density of fungus-bearing trees in a 1 ha plot: fruiting bodies of tough or pulpy saproxylic fungi, > 5 cm in diameter	***	0.397 (0.203)	0.458 (0.208)	1.15	Poisson
	Density of deadwood-bearing trees	Density of deadwood-bearing trees a 1 ha plot: crown deadwood in (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	**	1.624 (0.276)	1.824 (0.278)	1.12	Poisson
	Density of sap-run-bearing trees	Density of sap-run-bearing trees: sap runs > 10 cm in length in a 1 ha plot	NS	−1.142 (0.327)	−1.359 (0.394)		Poisson
DW features	Deadwood volume	Total volume of deadwood in a 0.3 ha plot ($m^3\ ha^{-1}$)	***	22.677 (9.539)	79.976 (10.992)	3.53	Gaussian
	Deadwood ratio	Volume ratio = deadwood /(Live trees+deadwood)	***	0.099 (0.025)	0.225 (0.030)	2.27	Gaussian
	Large downed deadwood volume	Volume of large downed deadwood (> 40 cm in diameter) in a 0.3 ha plot ($m^3\ ha^{-1}$)	***	3.052 (4.029)	27.387 (4.875)	8.97	Gaussian
	Large standing deadwood volume	Volume of large standing deadwood (> 40 cm in diameter)) in a 0.3 ha plot ($m^3\ ha^{-1}$)	***	2.123 (3.067)	18.658 (3.701)	8.79	Gaussian
	Standing deadwood volume	Volume of standing deadwood (> 10 cm in diameter) in a 0.3 ha plot ($m^3\ ha^{-1}$)	***	4.529 (2.811)	21.910 (3.572)	4.84	Gaussian
	Downed deadwood volume	Volume of downed deadwood (> 10 cm in diameter) in a 0.3 ha plot ($m^3\ ha^{-1}$)	***	16.791 (7.487)	57.373 (8.684)	3.42	Gaussian
	Number of deadwood types	Nb deadwood types (tree species*diameter*decay*position)	**	2.400 (0.243)	2.559 (0.245)	1.07	Poisson

Stands were classified as recently managed (R-HAR < 30 years ago) or long-established reserves (L-UNH > 30 years ago). Differences in stand features between the two harvesting classes were tested with a linear mixed model (NS = not significant; *$0.05 > P > 0.01$; **$0.05 > P > 0.001$; ***$P < 0.001$). Ratio = ratio dividing estimates of L-UNH by R-HAR (see Material and Methods) (SE between parentheses).

To rank the effect of the harvesting variable among structural predictors of variations in common or rare species richness, we assessed the multimodel-averaged estimates (Burnham & Anderson, 2002) determining the response of species richness to stand features. As colinearity among predictor variables may lead to unreliable parameter estimates, we implemented the strategy suggested by Zuur, Ieno & Elphick (2010) to address multicolinearity before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIFs and repeated this process until all VIFs were below a preselected threshold (Zuur *et al.*, 2010 suggest a cut off at 3). We used the 'vif.mer' function to calculate VIFs for linear mixed-effects models built using the lmer function in the 'lme4' package (Table 2). As the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen *et al.*, 2000), we used (log x+1)-transformed values for deadwood volumes. The selected variables with VIF < 3 were: harvesting class, openness, basal area of very large trees (dbh > 87.5 cm), large tree 1 ha density, density of sap-run-bearing trees, density of fungus-bearing trees, density of cavity-bearing trees, density of crown deadwood-bearing trees, number of microhabitat types, total deadwood volume, deadwood ratio, log10 (large downed deadwood volume), log10 (large standing deadwood volume). For each response variable, we generated the null model and generalized linear mixed models (Poisson error structure) with all the combinations of two explanatory variables. Using the differences in the Akaike information criterion (AICc) scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model, we calculated the model-averaged estimates. Only significant variables ($P < 0.10$ across all the models) were displayed (lme4, MuMIn, arm; R-packages).

To rank the effect of the harvesting variable among structural predictors on variations in species composition (including singletons), we performed a Canonical Analysis of Principal coordinates (vegan R-package, CAP, Anderson & Willis, 2003). Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, as colinearity among predictor variables is not considered to be a problem in CAP. We calculated total constrained inertia, the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests – 100 runs) and the relative contribution of each set of variables (deadwood, microhabitat, stand, forest, harvesting class) to constrained inertia. In addition, we used a pairwise ANOSIM procedure based on Jaccard distance matrices to test for differences in assemblage composition among predefined groups with spatially constrained permutation tests (Clarke, 1993); the grouping factor was the harvesting treatment and the spatial constraint the forest.

We also used a generalized linear mixed model, with a spatially implicit variable (forest) as a random factor on the intercept and a Poisson error distribution, to analyze the differences between the two harvesting classes in (1) mean abundance and richness per plot of rare or common species and trophic groups, and (2) mean abundance of selected species (more than 20 individuals caught and occurring in at least 10 out of the 153 plots in our data set). Since we found a close correlation between total abundance and the number of beetle species recorded on a plot, we used the number of individuals as a covariate in the richness models (Gotelli & Colwell, 2001) to separate the effects on the number of individuals from species effects. To analyze differences in occurrence per plot of selected beetle species between the two harvesting classes, we used a generalized linear mixed model with a binomial error structure and 'forest' as a spatial random effect (lmer function in lme4 R-package). In order to quantify the magnitude of significant differences between R-HAR and L-UNH treatments, we computed an index by dividing model estimates for each of the harvesting treatments (estimate L-UNH/ estimate R-HAR) with 'forest' as a random factor.

All analyses were conducted using R v2.12.0. All R-packages used are available online at http://cran.r-project.org/web/packages/available_packages_by_name.html. The 'vif.mer' function is available online at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R.

Results

Overall, the compiled dataset included 99 383 individuals in 476 beetle species (25 taxa identified at the genus level only), among which 377 common, 69 rare (15% of the total number) and 30 species with an undefined rarity status were recorded.

Habitat parameters in R-HAR plots versus L-UNH

Significant differences in stand features (deadwood, microhabitat, large trees, openness) were measured between L-UNH and R-HAR (Table 2). Values for deadwood (deadwood volume, deadwood ratio, number of deadwood types, downed deadwood volume, large standing deadwood volume, standing deadwood volume, large standing deadwood volume), microhabitats (density of microhabitat-bearing trees, number of microhabitat types, density of cavity-bearing trees, density of deadwood-bearing trees, density of fungus-bearing trees) and large tree characteristics (basal area of large trees and very large trees, density of large trees) were always considerably higher in L-UNH than in R-HAR plots. Deadwood diversity was only slightly, although significantly, higher in L-UNH. Only the density of sap-run-bearing trees and openness values remained significantly unaffected by the harvesting class.

The magnitude of the differences between R-HAR and L-UNH plots was even more pronounced with respect to certain deadwood features. These differences were characterized by a high relative increase from R-HAR to L-UNH that is the ratio dividing estimates in L-UNH by R-HAR for four variables: large downed deadwood volume (estimate ratio = 8.97), large standing deadwood volume (estimate ratio = 8.79), standing deadwood volume (estimate ratio = 4.84) and basal area of very large trees (estimate ratio = 4.80). This indicates a strong negative effect of forest harvesting on those attributes. According to the estimate ratio, the differences measured between L-UNH and R-HAR plots were even more pronounced for large deadwood volumes than for large tree characteristics. Microhabitat features were not as impacted as were deadwood and stand features by the harvesting class (Table 2).

Saproxylic beetle diversity in R-HAR plots versus L-UNH

Species composition

Variations in total inertia of saproxylic beetle assemblages were explained by geographical (35.0%), deadwood (9.0%), microhabitats (8.8%) and stand structural characteristics (7.0%) (Table 3). Only openness, microhabitat diversity, deadwood ratio and deadwood diversity had a significant ($P < 0.05$), although marginal, contribution to variations in species composition. As along with the density of fungus-bearing trees and large standing deadwood volume, the class of time elapsed since harvesting showed a non-significant trend ($P < 0.1$), accounting for only 1.7% of the constrained inertia. A spatially constrained ANOSIM test also showed slightly, but significantly, dissimilar species assemblages between the harvesting classes (1000 permutations, R: 0.168; significance: 0.002).

Species richness

The class of time elapsed since harvesting was not a key variable for saproxylic beetle species richness; it ranked fifth in explanatory value among the 12 structural stand features and was only slightly significant (Table 4). L-UNH, however, showed a higher saproxylic beetle species richness than R-HAR plots (Table 4). The best models for both rare and common species were the number of deadwood types and openness, and the best for common species was deadwood volume ratio.

Table 3 Ranked effect of the harvesting class among structural and spatial predictors on variations in species composition

	Predictors	Cumulated marginal inertia	%CI
Spatial	Forest**	7.348	34.97%
Set-aside	Harvesting class°	0.357	1.699%
Stand	Basal area of large trees, basal area of very large trees, density of large trees, openness**	1.475	7.019%
MH	Total density of microhabitats, number of microhabitat types*, density of cavity-bearing trees, of fungus-bearing trees°, of deadwood-bearing trees, of sap-run-bearing trees	1.863	8.866%
DW	log10 (Total volume deadwood), Deadwood ratio*, log10 (large downed deadwood volume), log10 (large standing deadwood volume)°, log10 (downed deadwood volume), log10 (standing deadwood volume), Number of deadwood types*	1.899	9.041%

Canonical Analysis of Principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %CI: relative contribution to constrained inertia. Significance of marginal contribution to inertia: °0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001.

Table 4 Ranked effect of the harvesting class among structural predictors on variations in species richness. Multimodel averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) and harvesting class determining the response of saproxylic beetle species richness (rare, common). Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect)

species richness	variable	Variable Model-averaged estimate (significance)	Relative contribution	Best models (DeltaAICc < 3)	
Rare	1. Number of deadwood types	1.48***	0.93	divDW+open	AICc = 596.8
	2. Openness	0.81**	0.65		
Common	1. Openness	10.02***	1.00	open+ratio	AICc = 1166.7
	2. Deadwood ratio	6.53***	0.51	divDW +open	AICc = 1167.0
	3. Number of deadwood types	10.81***	0.45		
	4. Harvesting class	3.92°	0.01		
	5. Density of cavity-bearing trees	3.70°	0.01		
	6. log10 (Volume of large downed deadwood)	3.70°	0.01		

Only significant variables (°0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001) were selected.

Table 5 Values of the estimates (s.e. between parentheses) from generalized linear mixed effect models with a Poisson error distribution for abundance and richness of ecological groups of saproxylic beetles species in 'recently harvested (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago)

		Abundance		Species richness	
		Estimate R-HAR	Estimate L-UNH	Estimate R-HAR	Estimate L-UNH
Feeding guilds	Mycophagous	4.066 (0.306)	4.201 (0.306)***	2.25 (0.099)	2.395 (0.106)*
	Saproxylophagous	2.345 (0.340)	2.533 (0.341)***	1.339 (0.172)	1.415 (0.180) NS
	Zoophagous	4.029 (0.154)	4.038 (0.155) NS	2.099 (0.119)	2.233 (0.124)*
	Xylophagous	5.056 (0.457)	4.745 (0.457)***	2.65 (0.077)	2.601 (0.084) NS
Rarity groups	Common	5.773 (0.341)	5.572 (0.341)***	3.682 (0.001)	3.776 (0.001)**
	Rare	2.073 (0.431)	2.27 (0.432)***	0.744 (0.184)	0.919 (0.1985) NS
	Total	5.859 (0.326)	5.672 (0.326)***	3.786 (0.001)	3.889 (0.001)***

Probability (*P*) of a significant difference between mean values is indicated by: NS = not significant. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. We used the abundance of a covariate in species richness models.

Guild composition

The abundance of common and xylophagous species was significantly lower in L-UNH than in R-HAR plots. Zoophagous species abundance was not sensitive to the harvesting class. In contrast, mycophagous, saproxylophagous and rare species were more abundant in L-UNH. The number of mycophagous, zoophagous and common species per plot, after accounting for abundance, was slightly, but significantly, higher in L-UNH. For saproxylophagous, xylophagous and rare species, no significant difference in species richness was observed between harvesting classes (Table 5).

Individual species responses

At the individual species level, about 25% ($n = 39.$) of the tested species had a significant response in abundance to the harvesting class. The same proportion of significantly responding species occurred in both harvesting classes: half of the species were significantly more abundant in R-HAR plots, and half were significantly more abundant in L-UNH. Two rare taxa were included among the species responding positively to L-UNH (none were found in R-HAR plots; Table 6).

Table 6 Difference in abundance per plot of selected species between 'recently harvested' (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago) plots

Abundance > in R-HAR	Abundance > in L-UNH
Ampedus quercicola	*Anaspis flava*
Anaglyptus mysticus	***Anaspis melanopa***
Anostirus purpureus	*Cis boleti*
Aulonothroscus brevicollis	*Clerus mutillarius*
Cyclorhipidion bodoanus	*Corticeus unicolor*
Ernoporicus fagi	*Cryptarcha undata*
Hemicoelus fulvicornis	*Dasytes plumbeus*
Hylecoetus dermestoides	*Dryocoetes villosus*
Leiopus femoratus	*Hylis olexai*
Litargus connexus	*Mycetochara maura*
Megatoma undata	*Mycetophagus ater*(*)
Phymatodes testaceus	*Oxylaemus cylindricus*
Platycerus caraboides	***Paromalus parallelepipedus***
Stenocorus meridianus	*Ptilinus fuscus*(*)
Taphrorychus bicolor	*Rhagium bifasciatum*
Tetratoma ancora	*Scolytus rugulosus*
Vincenzellus ruficollis	*Thanasimus formicarius*
Xyleborinus saxesenii	*Tritoma bipustulata*
Xyleborus dispar	*Trypodendron signatum*
	Xyleborus dryographus

Only significant differences are shown (*P*-value < 0.001 after a Bonferroni correction for 150 tests). Only species sampled in at least 10 plots and with more than 20 individuals were analyzed, with generalized linear mixed-effect models and a binomial error distribution; 'forest' was a random factor. Bold indicates significant in occurrence, (*) indicates rare species.

Discussion

Changes in stand structure induced by non-harvesting

In L-UNH (i.e. plots set-aside for at least 30 years) originating from managed stands, we measured tangible contrasts in stand characteristics compared with R-HAR plots. Indeed, most of the stand characteristics we studied displayed higher volume and density values in long-established set-asides than in R-HAR areas.

More than 30 years without harvesting allowed the deadwood volumes to increase significantly. Vandekerkhove *et al.* (2005) already showed that deadwood can accumulate quite fast in forest reserves, especially in terms of density. In abandoned beech forests in Germany, Meyer & Schmidt (2011) indicated a rather fast relative increase in deadwood volume: total deadwood doubled in about 9 years (standing deadwood in 7 years). Such figures are probably dependent on dominant tree species, soil fertility and the silvicultural stage of the stand at the time it was set aside. Several other studies found a similarly significant increase in deadwood volume in long-unharvested stands compared with managed ones (Kirby, Webster & Antczak, 1991; Sippola *et al.*, 1998; Motta *et al.*, 2010; Calamini *et al.*, 2011), or at least for coarse woody debris (Boncina, 2000; Marage & Lemperiere, 2005; Sitzia *et al.*, 2012). Timonen *et al.* (2011) also demonstrated that deadwood volumes are higher in woodland key habitats than in managed stands.

However, we showed that deadwood diversity only increased slightly in L-UNH (partly due to the lack of large-diameter logs in late decay stages). Nonetheless, in the data compiled by Timonen *et al.* (2011), deadwood diversity was much higher in woodland key habitats compared with managed stands, probably partly because of an initial selection effect, that is deadwood in the selected plots when they were selected as set-asides or as key habitats.

The difference between L-UNH and recently managed plots may be more pronounced with respect to certain deadwood qualities, as suggested by Siitonen *et al.* (2000). In their Finnish study in spruce forests, large dead coniferous and deciduous trees were respectively 25 and 35 times more abundant on average, in unharvested plots than in R-HAR stands. Accordingly, we found a strong impact of harvesting on large dead wood (downed and standing), with a ninefold increase in large deadwood when harvesting is delayed for at least 30 years. This increase in large deadwood was twice as high as for total deadwood volume. Boncina (2000) and Meyer & Schmidt (2011) also found a rapid accumulation of standing deadwood from unmanaged to managed stands.

Nonetheless, more deadwood was found in longer-established beech reserves (Christensen *et al.*, 2005) and in 60-year-old over-mature French coppices compared with 20-year-old mature coppice (Lassauce *et al.*, 2012). Vandekerkhove *et al.* (2009) argued that full natural restoration of deadwood characteristics (with virgin forests in Central Europe as a reference) may be quite long. Furthermore, Larrieu, Cabanettes & Delarue (2012) showed that a 50-year period of non-intervention was too short to develop complete stand maturity in beech-fir stands, even in highly productivity contexts.

Like Bauhus *et al.* (2009), we were able to detect a list of structural elements (deadwood, microhabitats, large trees) which become significantly more frequent in unharvested stands. We also showed, in accordance with the results simulated by Ball, Lindenmayer & Possingham (1999), that the increase in microhabitat-bearing tree density was weaker than the increase in deadwood density. Reaching high levels of microhabitat density requires time, since the probability of microhabitat occurrence or the number of microhabitat types increases with tree diameter (e.g. Larrieu *et al.*, 2012). In a simulation model, Ranius, Niklasson & Berg (2009) pointed out the importance of tree age for cavity formation on trees (see also empirical data in Gibbons, McElhinny & Lindenmayer, 2010). Furthermore, Fan *et al.* (2003; 2005) showed a higher frequency of cavity trees in 120-year-old forests than in younger stands, and in old-growth than in managed stands (like Bauhus *et al.*, 2009). In our results, a slightly higher density of cavity-bearing trees was measured in L-UNH than in R-HAR plots.

Across our sampling design, L-UNH and R-HAR forests did not differ in terms of stand openness, as the stands were too young to be significantly impacted by canopy gap dynamics. Gap dynamics is known to increase average sun exposure in old-growth forests compared with managed stands (Rugani, Diaci & Hladnik, 2013), and open forest habitats are required by a large number of specialized saproxylic species (Vodka, Konvicka & Cizek, 2009).

Effect of non-harvesting on saproxylic beetle assemblages

In our study, the effect of non-harvesting on biodiversity was slightly significant. The class of time elapsed since harvesting seemed to be important for 25% of the tested species, but was not as important a variable as structural parameters for saproxylic beetle assemblages in our data. Some guilds and groups were positively influenced by non-harvesting (mycophagous abundance and richness, saproxylophagous and rare species abundance), but the relationship was weak and clearly had less impact than deadwood features (see Table 2 and Table 4). Many saproxylic species may simply require a small amount of dead wood that is also available in managed forests. Or structural changes in stand characteristics may occur more quickly than the response of saproxylic organisms. Delayed responses by saproxylic beetle communities may be due to the limited ability, at least for old-growth forest specialists, to colonize favorable substrates (dispersal, habitat detection, etc.) and their density-dependence in the colonization process. Local assemblages may be deeply affected over the long term by historical deadwood supplies (Hanski & Ovaskainen, 2002). Furthermore, population levels must reach minimum thresholds for species to be detected. This interpretation is reflected in our study: the two most typically influential variables for saproxylic beetle richness – deadwood diversity and openness – did not respond strongly to more than 30 years without harvesting. Yet, deadwood diversity has been recognized as a key factor for saproxylic beetle diversity in temperate deciduous forests (Bouget *et al.*, 2013) and other studies based on similar time frames have demonstrated significant responses of saproxylic beetle diversity to setting aside forest areas (Timonen *et al.*, 2011; Lassauce *et al.*, 2013). However, Horák, Chobot & Horáková (2012) raised the question of the status of the rare species pool, deeply affected by commercial forestry in European multisecular managed forests. In our study (Table 5), rare species were more abundant (but not more species-rich) in forest reserves than in managed plots (in agreement with previous results by Lassauce *et al.*, 2013 and Hardersen, 2003 in Germany). We therefore hypothesize (1) that set-aside areas may act as incubators for rare species found in neighboring managed areas, or (2) that forest management reduces the amount of habitats available to rare species and therefore their populations, without leading them to disappear or (3) that most rare species have disappeared and only populations of a few surviving species increase with the amount of dead wood. To address these questions, it would be helpful to use very old reserves as references for species distribution and abundance. Considering the short set-aside period in our study, saproxylic beetle assemblages were probably strongly influenced by both initial forest conditions (pre-existing large trees, beetle assemblages, etc.) and the spatial isolation of the plots. The comparison between managed stands and set-asides should be deepened and a long-term monitoring strategy put in place (Djupström, Weslien & Schroeder, 2008).

Implications for forest management

Extended rotations, harvesting delays and reserves as conservation tools

In French forests, temporarily setting aside overmature stands before final harvesting, that is creating ageing and rotating islands (Lassauce *et al.*, 2013), is one of the management tools proposed to maintain saproxylic biodiversity associated with old successional stages. This approach aims to conciliate both timber production and biodiversity conservation goals. Larger trees generally have higher economic value while older stands have higher ecological value. We have shown that even a short delay in harvesting (minimum 30 years) induced significant changes in habitat conditions for saproxylic beetles, but only slightly affected saproxylic beetle assemblages. Further studies with longer harvesting delays would be necessary to analyze biodiversity responses. If longer-term habitat continuity is necessary for saproxylic beetle conservation, our results suggest that definitive strict fixed-location reserves should be favored over rotating and temporary set-asides. Moreover, the efficiency of ageing patches as temporary ecological sinks or sources has yet to be properly investigated.

Limits of management relinquishment and non-intervention: toward active restoration techniques?

Passive self-restoration of old-growth features through the abandonment of forest activities in harvestable deciduous stands takes time, at least for some features crucial for species conservation (large deadwood, tree microhabitats, etc.). Therefore, complementary active restoration techniques may be suggested to enhance the recruitment and accumulation of new substrates in conservation areas. Keeton (2006) showed that, in conventional silvicultural systems, active restoration is more successful in creating old-growth features than is delaying harvesting. For instance, standing dead trees, large downed deadwood and tree cavities can be artificially generated using cost-effective techniques like girdling trees, felling or pulling down large trees to be left on the forest floor and mechanically damaging tree trunks (with or without fungus inoculation). Costlier experiments with extreme habitat restoration have even been carried out in Italy (e.g. Cavalli & Donini, 2005). Active restoration requires an in-depth understanding of natural habitats to avoid structures inappropriate to local biodiversity; Jonsell, Nittérus & Stighäll (2004), for example, have underlined the differences between man-made and natural deadwood habitats. In any case, since most endangered saproxylic species have limited dispersal ability (e.g. Buse, 2012), the proper spatial distribution of created substrates is a prerequisite for effective restoration programs. The ecological impacts of active restoration techniques on biodiversity, but also on potential bark beetle outbreaks, should be monitored (Toivanen & Kotiaho, 2010). Thus said, active techniques should at least be considered when the restoration process must achieve the desired forest state within a relatively short time or when the species at stake are threatened by external factors.

Conclusions

Our results did not strongly support recommendations about extended rotations and reserve conservation in favor of saproxylic biodiversity. The rationale behind it would probably benefit from further studies in very old forest reserves, although they are scarce in Western Europe. In one of the study forests (Fontainebleau), despite a limited and unbalanced sampling design, we divided the class of L-UNH into old (> 30 years, $n = 3$) and very old (> 100 years, $n = 9$) reserves. From our exploratory analysis, the deadwood volume and diversity, the total beetle species richness, the rare species richness or abundance were not significantly higher in the older class. This trend deserves to be assessed by other case studies.

Forest areas left unharvested for more than 30 years show an accumulation of old-growth structures related to deadwood volumes and microhabitat diversity, but not deep changes in saproxylic beetle diversity. Restoring the old-growth-dependent community as a whole seems even slower than restoring these structural features. As suggested by Paillet *et al.* (2010), future work should examine the temporal effect of delayed harvesting at multiple time points on the same study area in order to evaluate, using a regression approach with the detailed time elapsed since harvesting, (1) how stands recover old-growth forest attributes and (2) how the associated saproxylic fauna colonize these set-asides in the long-term.

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References

Anderson, M.J. & Willis, T.J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–524.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A. & Horton, A.J. (1999). Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO Study. *Northwest Sci.* **73**, 12–26.

Ball, J.P., Lindenmayer, D.B. & Possingham, H.P. (1999). A tree hollow dynamics simulation model. *For. Ecol. Manage.* **123**, 179–184.

Bauhus, J., Puettmann, K. & Messier, C. (2009). Silviculture for old-growth attributes. *For. Ecol. Manage.* **258**, 525–537.

Boncina, A. (2000). Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. *Global Ecol. Biogeogr.* **9**, 201–211.

Bouget, C., Larrieu, L., Parmain, G. & Nusillard, B. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* **22**, 2111–2130.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*, Second edn: New York: Springer-Verlag.

Burrascano, S., Keeton, W.S., Sabatini, F.M. & Blasi, C. (2013). Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. *For. Ecol. Manage.* **291**, 458–479.

Buse, J. (2012). 'Ghosts of the past': flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J. Insect Conserv.* **16**, 93–102.

Calamini, G., Maltoni, A., Travaglini, D., Iovino, F., Nicolaci, A., Menguzzato, G., Corona, P., Ferrari, B., Di Santo, D., Chirici, G. & Lombardi, F. (2011). Stand structure attributes in potential old-growth forests in the Apennines, Italy. *Ital. For. Mount.* **66**, 365–381.

Cavalli, R. & Donini, F. (2005). Possible management actions to increase the amount of dead and marcescent wood, In *Deadwood: a key to biodiversity*: 100. Mason, F., Nardi, G. & Tisato, M. (Eds). Mantova: Sherwood, p.45–48.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005). Deadwood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manage.* **210**, 267–282.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117–143.

Djupström, L.B., Weslien, J. & Schroeder, L.M. (2008). Deadwood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *For. Ecol. Manage.* **255**, 3340–3350.

Fan, Z., Shifley, S.R., Spetich, M.A., Thompson, F.R. & Larsen, D.R. (2005). Abundance and size distribution of cavity trees in second-growth and old-growth Central Hardwood Forests. *North J. Appl. For.* **22**, 162–169.

Fan, Z.F., Larsen, D.R., Shifley, S.R. & Thompson, F.R. (2003). Estimating cavity tree abundance by stand age and basal area, Missouri, USA. *For. Ecol. Manage.* **179**, 231–242.

Gibbons, P., McElhinny, C. & Lindenmayer, D.B. (2010). What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. *For. Ecol. Manage.* **260**, 975–982.

Gotelli, N. & Colwell, R. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391.

Green, P. & Peterken, G.F. (1997). Variation in the amount of deadwood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *For. Ecol. Manage.* **98**, 229–238.

Grove, S.J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* **33**, 1–23.

Hahn, K. & Christensen, M. (2004). Dead wood in European Forest Reserves – a reference for forest management. In *Monitoring and indicators of forest biodiversity in Europe – From ideas to operationality, EFI Proceedings No. 51*: 181–191. Marchetti, M. (Ed.). Joensuu: EFI.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conserv. Biol.* **16**, 666–673.

Hardersen, S. (2003). Two lowland beech-oak forest areas abandoned for more than 30 years: what do bird and beetle communities tell us? In *Proceedings of the International Symposium: Deadwood: a key to biodiversity, Mantova, May 29th–31st 2003. Sherwood 95, Suppl. 2*: 33–36. Mason, F., Nardi, G. & Tisato, M. (Eds). Mantova: Sherwood.

Horák, J., Chobot, K. & Horáková, J. (2012). Hanging on by the tips of the tarsi: a review of the plight of the critically endangered saproxylic beetle in European forests. *Jour. Nature Conserv.* **20**, 101–108.

Jonsell, M., Nittérus, K. & Stighäll, K. (2004). Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. *Biol. Conserv.* **118**, 163–173.

Keeton, W.S. (2006). Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manage.* **235**, 129–142.

Kirby, K.J., Webster, S.D. & Antczak, A. (1991). Effects of forest management on stand structure and the quantity of fallen deadwood: some British and Polish examples. *For. Ecol. Manage.* **43**, 167–174.

Lachat, T. & Bütler, R. (2009). Identifying conservation and restoration priorities for saproxylic and old-growth forest species: a case study in Switzerland. *Environ. Manage.* **44**, 105–118.

Larjavaara, M. & Muller-Landau, H.C. (2010). Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. *Can. J. For. Res.* **40**, 2313–2321.

Larrieu, L. & Cabanettes, A. (2012). Tree species and girth are key determinants for diversity and abundance of tree microhabitats in sub-natural montane beech-fir forests. *Can. J. For. Res.* **42**, 1433–1445.

Larrieu, L., Cabanettes, A. & Delarue, A. (2012). Impact of silviculture on deadwood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *Eur. J. For. Res.* **131**, 773–786.

Lassauce, A., Anselle, P., Lieutier, F. & Bouget, C. (2012). Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: a case study in French deciduous forests. *For. Ecol. Manage.* **266**, 273–285.

Lassauce, A., Larrieu, L., Paillet, Y., Lieutier, F. & Bouget, C. (2013). The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation length in French oak high forest. *Insect Conserv. Diver.* **6**, 396–410.

Lombardi, F., Lasserre, B., Tognetti, R. & Marchetti, M. (2008). Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). *Ecosyst.* **11**, 882–894.

Marage, D. & Lemperiere, G. (2005). The management of snags: a comparison in managed and unmanaged ancient forests of the Southern French Alps. *Ann. For. Sci.* **62**, 135–142.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature* **405**, 243–253.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* **94**, 199–209.

Meyer, P. & Schmidt, M. (2011). Accumulation of deadwood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. *For. Ecol. Manage.* **261**, 343–352.

Motta, R., Berretti, R., Castagneri, D., Lingua, E., Nola, P. & Vacchiano, G. (2010). Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. *Ann. For. Sci.* **67**, 1–8.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G. & Ranius, T. (2003). Erratum to "Densities of large living and dead trees in old-growth temperate and boreal forests". *For. Ecol. Manage.* **178**, 355–370.

Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., de Bruyn, L., Fuhr, M., Grandin, U., Kana, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mézaros, I., Sebastia, M.-T., Schmidt, W., Standovar, T., Tothmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* **24**, 101–112.

Peterken, G.F. (1996). *Natural woodland: ecology and conservation in northern temperate regions*: Cambridge: Cambridge University Press.

Ranius, T., Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *For. Ecol. Manage.* **257**, 303–310.

Rugani, T., Diaci, J. & Hladnik, D. (2013). Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. *PLoS ONE* **8**, e52641.

Schmitt, C., Burgess, N., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D., Humphries, K., Kapos, V., Loucks, C., Lysenko, I., Miles, L., Mills, C., Minnemeyer, S., Pistorius, T., Ravilious, C., Steininger, M. & Winkel, G. (2009). Global analysis of the protection status of the world's forests. *Biol. Conserv.* **142**, 2122–2130.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manage.* **128**, 211–225.

Sippola, A.-L., Siitonen, J. & Kallio, R. (1998). Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scand. J. For. Res.* **13**, 204–214.

Sitzia, T., Trentanovi, G., Dainese, M., Gobbo, G., Lingua, E. & Sommacal, M. (2012). Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. *For. Ecol. Manage.* **270**, 232–238.

Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. (2011). Are woodland key habitats biodiversity hotspots in boreal forests? CEE review 09-020 (SR81). Collaboration for Environmental Evidence: www.environmentalevidence.org/SR81.html

Toivanen, T. & Kotiaho, J.S. (2010). The preferences of saproxylic beetle species for different deadwood types created in forest restoration treatments. *Can. J. For. Res.* **40**, 445–464.

Vandekerkhove, K., De Keersmaeker, L., Baeté, H. & Walleyn, R. (2005). Spontaneous re-establishment of natural structure and related biodiversity in a previously managed beech forest in Belgium after 20 years of non intervention. *For. Snow Landsc. Res.* **79**, 145–156.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde, P. (2009). When nature takes over from man: deadwood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *For. Ecol. Manage.* **258**, 425–435.

Vanha-Majamaa, I. & Jalonen, J. (2001). Green tree retention in Fennoscandian forestry. *Scand. J. For. Res.* **16**, 79–90.

Vodka, S., Konvicka, M. & Cizek, L. (2009). Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *J. Insect Conserv.* **13**, 553–562.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Bouget *et al.* ACV-05–13-OM-091. Supplementary Material

Rebuilding dynamics of tree-microhabitat and deadwood in set aside beech-oak stands

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1. Introduction

Le bois mort et les dendro-microhabitats sont des structures clés pour la biodiversité forestière (*e.g*. Speight, 1989 ; Stokland *et al.,* 2012 ; Bouget *et al*., 2014). La grande majorité des forêts Européennes sont exploitées depuis des siècles (Larsson *et al.* 2001). La gestion forestière axée sur la production rapide de bois de qualité réduit la disponibilité en bois mort et dendro-microhabitats (*e.g*. Green & Peterken, 1997 ; Lombardi *et al*., 2008 ; Burrascano *et al.,* 2013). En effet, le martelage vise à récolter les arbres dépérissants avant qu'ils ne meurent, supprimer les arbres portant des dendro-microhabitats, car ils confèrent aux grumes une faible valeur économique et réduire la part des essences jugées secondaires sur un plan économique. En liaison avec une demande environnementale d'utiliser de plus en plus de ressources renouvelables, on assiste actuellement à une demande accrue de matériau bois. Cette demande induit une réduction de la durée entre les coupes et un abaissement du diamètre d'exploitabilité et de la dimension minimale d'exploitation (i.e. le diamètre « fin bout »). Ces orientations accentuent l'effet de la gestion car (i) des passages en coupe plus fréquents permettent d'anticiper non seulement la mort des arbres mais également l'évolution des dendro-microhabitats, (ii) la réduction de la diversité dendrologique entraîne une réduction de la diversité du bois mort, et (iii) seuls les plus gros arbres portent l'ensemble des types de dendro-microhabitats (Larrieu *et al*., 2014). En conséquence, les peuplements gérés sont en règle générale peu diversifiés en essences, taille des arbres et densités (Hansen *et al.,* 1991), comportent de faibles volumes de bois mort (Gilg, 2005) et hébergent des dendro-microhabitats peu nombreux (Michel & Winter, 2009) et peu diversifiés (Larrieu et al. 2012). Au final, ils sont caractérisés par une plus faible hétérogénéité structurale (Müller *et al*., 2005) et une plus faible richesse spécifique que les peuplements inexploités depuis longtemps (Gossner *et al*., 2013).

On assiste néanmoins dans le même temps à la mise en place de mesures de gestion environnementales qui tendent à restaurer dans les massifs gérés des attributs de forêt matures par une stratégie passive (Bauhus et al., 2009), (i) en mettant en réserve définitivement des peuplements (ONF, 2009), (ii) en rallongeant les rotations dans les îlots de vieillissement (ONF, 2009), (iii) en conservant des structures lors de l'exploitation (arbres habitats) (Bütler & Lachat, 2009 ; Keeton, 2006 ; PEFC, 2011 ; FSC, 2014), ou bien active, en restaurant les éléments de structures artificiellement (e.g. Cavalli & Donini, 2005 ; Mason *et al*., 2005).

Mais la reconstitution des attributs de maturité à l'échelle du peuplement varie en fonction du potentiel du site et la restauration complète peut être très longue (Vandekerkhove *et al*., 2009). Larrieu *et al*. (2012) ont montré qu'une période sans exploitation de 50 ans était trop courte pour reconstituer une maturité complète dans une hêtraie-sapinière montagnarde, même dans un contexte très productif. En plaine, les peuplements non exploités depuis plus de 30 ans contiennent un volume de bois mort significativement plus élevé et avec une diversité légèrement plus forte que les peuplements exploités dans les 30 dernières années, mais, revanche, ce seuil de 30 ans n'est pas suffisant pour observer une reconstitution du stock de dendro-microhabitats (Bouget *et al*., 2014). Ce décalage entre le bois mort et les dendro-microhabitats a été également montré par Ball, Lindenmayer & Possingham (1999). Meyer & Schmidt (2011) ont néanmoins observé une restauration plus rapide dans des hêtraies allemandes où le volume total de bois mort doublait en 9 ans et le bois mort sur pied en seulement 7 ans. À l'échelle de l'arbre, on connaît les corrélations positives entre son diamètre et la probabilité de porter un dendro-microhabitat (Winter & Möller 2008 ; Vuidot *et al.*, 2011 ; Michel & Winter, 2009; Larrieu *et al.,* 2014 ; Regnery *et al.*, 2013). Ces relations sont seuillées pour le Hêtre et le Sapin pectiné (Larrieu et al. 2012) et il faut ainsi que les arbres atteignent ces seuils de diamètre pour porter un ou plusieurs types de dendro-microhabitats. La reconstitution du stock de dendro-microhabitats est ainsi dépendante du diamètre des arbres au moment de l'abandon des exploitations et de leur vitesse de croissance.

Le principal objectif de ce papier est d'évaluer par chronoséquence les dynamiques de reconstitution du stock de bois mort et de dendro-microhabitats après coupe, à l'échelle du peuplement et sur une amplitude de 80 ans de durée de mise en réserve, dans des peuplements de plaine dominés par les chênes ou le Hêtre. Ces forêts couvrent une grande surface en Europe de l'Ouest (Larsson *et al.,* 2001 ; Euforgen, 2012) et sont cruciales pour la filière bois en raison de la forte valeur économique du bois de ces essences. De plus, les chênes sont connus comme supports d'une forte biodiversité en général (*e.g.* Vodka *et al*., 2009) et les forêts dominées par le Hêtre constituent un habitat clé pour la conservation des Coléoptères saproxyliques car 70 % des espèces d'Europe centrale sont rencontrées dans ce type de forêt (Müller *et al*., 2013). Afin de prendre en compte l'ensemble des types de forêts existantes pour assurer un bon degré de généralisation des résultats, nous avons échantillonné des forêts : (i) publiques et aménagées suivant un document de gestion, (ii) privées et gérés suivant un document de gestion agréé, et (iii) privées et gérées sans document de gestion. L'objectif secondaire est d'apporter des éléments tangibles de réflexion pour les gestionnaires désireux de mettre en place des réseaux cohérents de conservation de la biodiversité.

2. Matériel et Méthodes

2.1 Peuplements étudiés

Deux cent quatre vingt deux placettes circulaires de 500 m² ont été installées dans 17 forêts de trois zones forestières du Sud-Ouest de la France (Tableau 1). Tous les peuplements sont des habitats potentiels de Hêtraie-chênaie collinéenne (*Quercetalia roboris* et *Fagetalia sylvaticae*, Bardat *et al*., 2004) mais l'anthropisation induit une large gamme de sylvofaciès feuillus, dominés la plupart du temps par les chênes à feuilles caduques (principalement *Quercus robur*, *Q. petraea* et *Q. pubescens*). Les peuplements ont une structure de taillis avec réserve, sauf pour le site *Tarn* où les peuplements, en cours de conversion vers la futaie régulière, ont une structure de futaie sur souche. Les peuplements sont gérés selon trois types : (i) en appliquant un document de gestion spécifique aux forêts publiques (catégorie de gestion *Public*), (ii) en appliquant un document de gestion agréé spécifique aux forêts privées (catégorie de gestion *private with PSG*), ou (iii) par le propriétaire, sans référence à un document de gestion (catégorie de gestion *private without PSG*).

Tableau 1. Distribution des effectifs d'entités observées dans les trois catégories de gestion étudiées

Management type	Site	Forest	Number of plots	Number of observed living trees	Number of observed snags	Total length of transects observed (m)	Number of observed logs
Public	Tarn	Reference	22	130	25	1260	61
		Managed	36	786	26	0	6
	Coteaux de Gascogne	BC Éoux	6	34	0	300	1
		Ref Boussan	4	108	7	240	0
		FC Lilhac	26	429	17	1500	2
Private with PSG	Rebisclou	Reference	40	878	5	2400	13
		Logged	40	209	14	2400	11
		Coppice	20	496	120	1200	15
Private without PSG	Coteaux de Gascogne	Briouant	12	263	107	720	3
		Lilhac-Pinsois	9	33	1	420	1
		Maupère	4	7	0	240	7
		St Frajou	8	40	0	420	3
		Touille	2	14	1	120	0
		La Broquère	12	300	30	600	7
		Pinsois-Esparron	15	235	30	900	21
		Bois fantôme	22	589	82	1320	7
		La Bourdasse Esparron	4	129	22	240	2
Total			282	4680	487	14280	160

2.2 Variables relevées

Toutes les mesures et observations ont été réalisées en période non feuillée pour faciliter l'observation du houppier des arbres. Tous les arbres de la placette de plus de 10 cm de diamètre à 1,3 m (dbh) ont été examinés attentivement depuis le sol et nous avons noté pour chacun : (i) son diamètre au cm arrondi, (ii) son statut (vivant, mort debout, mort au sol), (iii) les dendro-microhabitats qu'il portait sur le tronc et ses principales divisions verticales, sous et dans le houppier, à partir d'une liste de 14 types (Tableau 2).

Tableau 2. Caractéristiques des types de dendro-microhabitats observés

Type de dendro-microhabitat	Définition	Dimension de précomptage	Métrique
Bois apparent non carié	Nécrose dure, de stade de saproxylation ≤2)	surface de précomptage 100 cm²	nombre
Bois apparent carié	Nécrose altéré, de stade de saproxylation ≥3)	surface de précomptage 100 cm²	nombre
Trous de pic	Cavité creusées récemment par un pic	d≥3cm	nombre
Cavité non évolutive basse	Cavité dont les bords sont formés d'écorce, formée entre les contreforts racinaires au collet de l'arbre	d≥3cm	nombre
Cavités évolutives	Présence d'un bouchon de nécrose qui remplit la cavité (stade 2); Cavité partiellement évidée (stade 3); Cavité totalement évidée (stade 4)	d≥3cm	nombre
Fente	Fente dans le bois	Largeur>1cm, profondeur>10cm	nombre
Ecorce décollée	Formant un abri contre les intempéries	Largeur>1cm, profondeur>10cm	nombre
Dendrothelme à fond dur	Cavité dans le bois, périodiquement remplie d'eau, dont le fond est entièrement constitué d'écorce	d≥3cm	nombre
Dendrothelme à fond carié	Cavité dans le bois, périodiquement remplie d'eau, dont le fond est au moins partiellement constitué de bois nécrosé	d≥3cm	nombre
Sporophore de champignon saproxylique	Agaricale charnue ou polypore annuel et pérenne	Sporophore ≥5 cm	seulement présence/absence
Coulée de sève humide	Coulée active en période de végétation	Longueur ≥5cm	nombre
Epiphyte	Lierre (*Hedera helix*), mousses et lichens foliacés	% de recouvrement> 25%	seulement présence/absence
Galette chablis	Entrelacs de racines lié à une souche renversée	Pas de dimension seuil	seulement présence/absence

Les pièces de bois mort on été ventilées suivant trois catégories : (i) au sol ; les pièces de bois de plus de 30 cm de diamètre au milieu ont été identifiées à l'espèce quand cela était possible, mesurées et classées en 5 catégories (Tableau 3) suivant leur stade de saproxylation dominant en volume ; les pièces de bois de 2.5 à 30 cm ont été inventoriées lorsqu'elles interceptaient 2 transects perpendiculaires de 25 m chacun, et leur stade de saproxylation à l'intersection a été noté en suivant la même typologie que les plus gros bois morts au sol ; (ii) sur pied, rassemblant les chandelles avec les arbres secs sur pied, les arbres morts encroués et les souches de plus de 1 m de hauteur ; et (iii) du houppier ; ce dernier a été comptabilisé sur tous les arbres de la réserve, en estimant, depuis le sol, pour toutes les branches mortes, le diamètre au milieu (par classes de 10 cm, avec 5 cm de précomptage), la longueur (arrondie au mètre le plus proche, avec 50 cm de longueur de précomptage) et le stade de saproxylation (en 4 classes, voir Tableau 3). Un test préalable avait été réalisé pour estimer la précision d'une telle observation quand elle était réalisé par le même observateur entraîné (Burnel *et al.*, 2011).

Tableau 3. Classes de saproxylation utilisées pour caractériser le degré d'altération des pièces de bois mort

Branches	Stade de saproxylation	définition
	1	branche morte dans l'année ; présence de ramification fine ; écorce adhérente sur la majorité de la surface de la branche (équivalent du stade 1 du protocole bois mort au sol)
	2	branche morte depuis plus d'un an ; perte récente de ramification fine mais présence de ramification secondaire et la longueur d'origine persiste ; écorce adhérente sur la majorité de la surface de la branche (équivalent du stade 2 du protocole bois mort au sol)
	3	branche morte depuis plusieurs années, majoritairement sans écorce, a conservé une résistance mécanique et la quasi-intégralité de la grosseur initiale avant la mort
	4	branche morte depuis plusieurs années, une faible longueur d'origine persiste et résistance mécanique très faible avec perte partielle de matière (équivalent au stade 4 du protocole bois mort au sol)
Chandelles et bois morts au sol	1	Bois mort dans l'année, très dur, peu ou pas altéré. Écorce partout adhérente. Le liber est vivant ou au moins perceptible
	2	Bois très dur, peu altéré. Une lame de couteau s'enfonce de quelques mm seulement. Écorce quasiment partout adhérente, mais moins adhérente qu'au stade 1. Le liber n'est plus perceptible
	3	Bois altéré, plus tendre en surface. Une lame de couteau s'enfonce de 1 à quelques cm. Écorce partiellement tombée (sauf pour le Hêtre). L'essence est encore reconnaissable et le bout de bois n'a pas perdu de son volume initial
	4	Bois très altéré. Une lame de couteau s'enfonce jusqu'à la garde, au moins localement. Plus d'écorce présente. Le bout de bois a perdu du volume, mais l'essence est généralement encore reconnaissable
	5	Bois très peu cohérent et facilement dispersé par un coup de pied. Mélange d'organismes saproxyliques et du sol. Seul un examen attentif permet d'identifier l'essence

2.3 Estimation de la durée de non exploitation

Dans le cas des forêts gérées par un organisme de gestion, la donnée a été collectée directement auprès de lui, et vérifiée localement par un carottage à la tarière de Pressler d'un échantillon de 5 à 10 arbres du taillis par unité de gestion (parcelle forestière). Dans les autres cas, trois arbres du taillis ou appartenant à des essences pionnières (i.e. *Populus tremula, Betula pendula, Salix caprea*) ont été carottés sur chacune des placettes pour estimer à 5 ans près la date de la dernière coupe. Au total, 193 arbres ont été carottés à raison d'une à deux carottes par arbre. Après avoir été séché sous contrainte à l'air ambiant, les carottes ont été poncées afin de mieux révéler les cernes (Burnel 2009 ; Rozas, 2003). Les cernes ont été comptés sous stéréomicroscope Leica©. Pour les carottes ne passant pas exactement par le cœur de l'arbre, le nombre de cernes manquants situés dans l'espace séparant le cœur du bord interne du dernier cerne mesuré a été estimé en superposant la carotte à une mire transparente sur laquelle des cercles concentriques ont été tracés (Lebourgeois, 1997). Les peuplements ont été ventilés en trois catégories : (i) exploités dans les cinq dernières années (*Harv*), (ii) inexploités pendant une durée de 10 à 55 ans (*UnHarv10-55*) et (iii) inexploités pendant une durée de 55 à 80 ans (*UnHarv>55*), afin d'équilibrer le nombre de placettes par catégorie de gestion et par classe de durée de non-exploitation.

2.4 Calculs

Tous les calculs ont été réalisés sur la plateforme logicielle « R » (R Core Team v3.0.0, 2013).

Les volumes de bois mort et les quantités de dendro-microhabitats par placette ont été comparés à l'aide de modèles généralisés mixtes (GLMM, Pinheiro et Bates, 2000) dans lesquels le type de gestion et la durée de gestion sont les variables explicatives à effet fixe et susceptibles d'interaction. La variable de regroupement à effet aléatoire choisie pour les placettes est la parcelle d'exploitation (fonction *glmer* du paquet R-*lme4*). La comparaison multiple des moyennes des catégories a été réalisée après calcul des intervalles de confiance des moindres carrés réalisé à l'aide de la fonction *lsmeans* du paquet *R-lmerTest* (Kuznetsova *et al*., 2014).

La comparaison des quantités de microhabitats par espèce (chêne et hêtre) a été effectuée à l'échelle placette à l'aide du test t par permutation mis en œuvre par le paquet R-*RVAideMemoire* (Hervé, 2014).

Nous avons différencié dans les calculs les trois types de gestion, dans l'hypothèse que la gestion puisse avoir une influence sur les stocks après coupe, c'est-à-dire que le nombre et la nature des arbres conservés (réserves) et la quantité de bois mort laissée au sol puissent *a priori* différer selon ces gestions.

3. Résultats

3.1. Comportement différentiel des essences vis-à-vis des dendro-microhabitats

La relation entre le diamètre des arbres et le pourcentage d'arbres porteurs de dendro-microhabitats est quasi-similaire pour toutes les essences feuillus jusqu'au diamètre de 40 cm. Au-delà, la proportion d'arbres porteurs est plus forte pour le hêtre que pour les autres essences (Fig. 1). De surcroît, au-delà de ce diamètre de 40 cm, un arbre qui porte des dendro-microhabitats en porte en moyenne plus s'il est un hêtre que s'il est d'une autre essence (Fig. 2). Ainsi, le hêtre se comporte d'une manière différente des autres essences vis-à-vis des dendro-microhabitats.

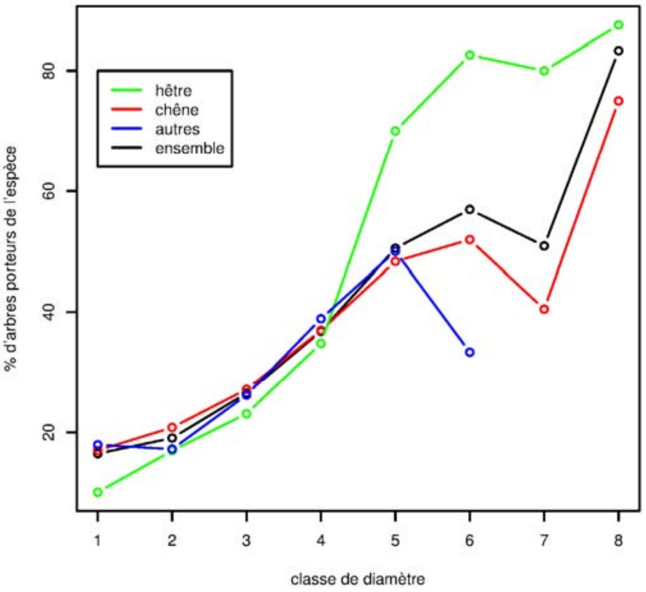

Figure 1. Pourcentage d'arbres porteurs de dendro-microhabitats en fonction de la classe de diamètre et de l'essence ; les feuillus autres que les chênes et le hêtre sont regroupés dans la catégorie « autres »

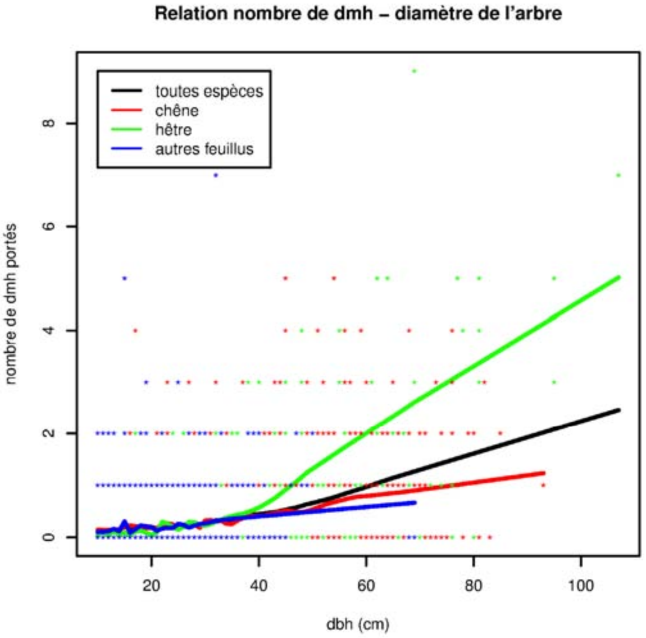

Figure 2. Relation entre le diamètre des arbres et le nombre de dendro-microhabitats portés par les arbres porteurs ; la catégorie « autres feuillus » rassemble tous les feuillus à l'exception des chênes et du hêtre

Compte tenu de ce constat, nous avons vérifié si la proportion de hêtre changeait selon les modalités de gestion et de durée de non exploitation. Il y a significativement moins de hêtre dans les catégories "gestion privé sans plan de gestion" (6.6 % de G, *p*=0.005) et « durée de non-exploitation 10-55 ans » (6.7 % de G, *p*<0.000) que dans les autres catégories. Tous diamètres et tous types de dendro-microhabitats confondus, le pourcentage global de hêtres porteurs de dendro-microhabitats ne diffère pas significativement de celui des chênes mais les dendrothelmes à fond dur sont préférentiellement portés par le hêtre (*p*=0.002) et les épiphytes (*p*=0.001) et les polypores (*p*=0.03) par les chênes (Tableau 4).

Tableau 4. Répartition des arbres vivants porteurs de dendro-microhabitats (dmh) entre le hêtre et les chênes sur les 114 placettes qui contiennent ces deux essences

Nature dmh	Nb tmh-bearing beeches	% tmh-bearing beeches	Nb tmh-bearing oaks	% tmh-bearing oaks	*p*value of % difference (paired)
bark-lined dendrotelm	**26**	**4.0**	**5**	**0.49**	**0.002 ****
rotted-bottom dendrotelm	2	0.15	6	0.50	0.25 NS
bark-lined cavity at the base of the trunk	14	4.1	29	5.8	0.38 NS
woodpecker cavity (trunk)	16	3.8	17	2.3	0.41 NS
missing bark with decayed wood	18	3.5	40	7.0	0.09 NS
cavities with mould evolving from decay wood	37	10.9	77	12.0	0.73 NS
missing bark with hard wood	51	10.9	50	9.3	0.61 NS
crack in the wood	4	2.1	4	0.5	0.35 NS
shelter under peeling bark	2	1.1	3	0.5	0.87 NS
epiphytes	**7**	**2.1**	**56**	**9.6**	**0.001*****
root-plate interlacing	0	0.00	2	0.06	1.00 NS
moist sap run	1	0.4	8	1.0	0.46 NS
pulpy agaric	0	-	0	-	-
polypore	**0**	**0.0**	**6**	**0.7**	**0.03***
TOTAL	178	43.1	303	49.8	0.42 NS

3.2 Bois mort

Le type de gestion n'a pas d'effet significatif sur les volumes de bois mort total, au sol et sur pied laissé par l'exploitation (Fig. 3). La tendance générale est une augmentation du volume de bois mort (total, au sol et sur pied) dans les peuplements inexploités par rapport aux résidus de la coupe, mais seul le volume bois mort total dans les peuplements UnHarv>55 des forêts publiques et des forêts privées sans PSG est significativement plus important que dans les peuplements Harv. On observe pour le bois mort au sol une tendance à une légère réduction du volume dans les peuplements UnHarv10-55 par rapport aux peuplements Harv (gestions publique et privée à PSG seulement), mais les différences ne sont pas significatives.

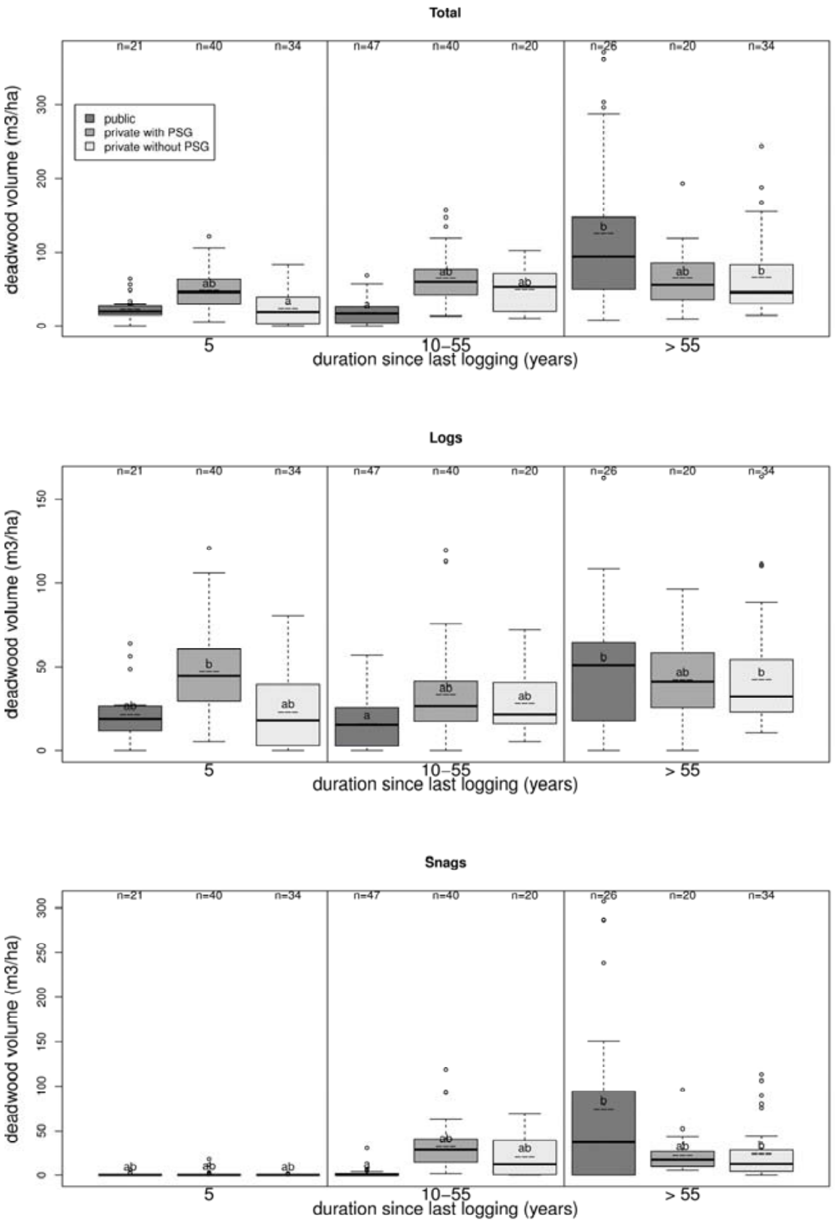

Figure 3. Boîtes à moustaches représentant les volumes de bois mort total (sur pied et au sol), au sol et sur pied, en fonction de la durée de non exploitation et du mode de gestion ; le volume moyen est indiqué par un trait pointillé horizontal ; les lettres indiquent la significativité des différences entre les moyennes

La diversité totale des types de bois mort a tendance à augmenter avec la durée de non exploitation mais la différence n’est significative que dans les forêts privées sans PSG, dès la catégorie UnHarv10-55 (Fig. 4). Dans le cas des bois morts au sol, seule la catégorie UnHarv>55 des forêts privées sans PSG montre une diversité supérieure à celle observée en Harv. Dans le cas des bois mort sur pied, on observe dès la catégorie UnHarv10-55 une diversité significativement plus forte qu'en Harv en forêt privée sans PSG, alors que la diversité n’est pas différente dans les trois classes de durée de non exploitation en forêt publique et en forêt privée à PSG. Aucune différence significative n’est observée pour la diversité du bois mort dans le houppier, quelle que soit le type de gestion ou la durée de non exploitation.

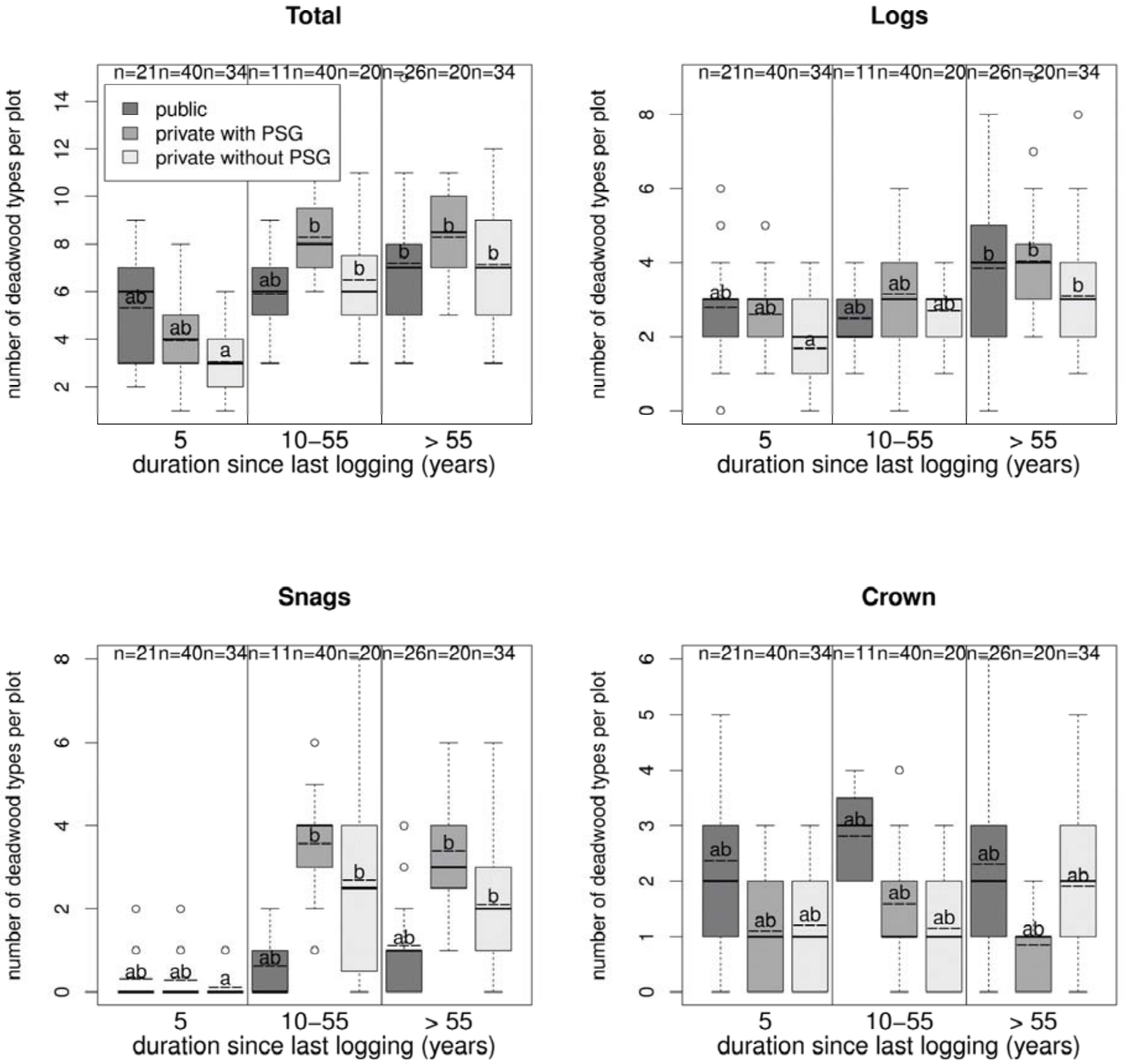

Figure 4. Boîtes à moustaches représentant la diversité des types de bois mort total (sur pied et au sol), au sol, sur pied et dans le houppier des arbres vivants, en fonction de la durée de non exploitation et du mode de gestion ; le volume moyen est indiqué par un trait pointillé horizontal ; les lettres indiquent la significativité des différences entre les moyennes

3.3 Dendro-microhabitats

La tendance générale est une augmentation rapide (dès la catégorie UnHarv 10-55) puis un maintien (dans la catégorie UnHarv>55) du nombre de dendro-microhabitats, mais la différence n'est significative que pour les forêts privées sans PSG (Fig. 5). Lorsqu'on retire le hêtre des peuplements, on observe un nombre de dendro-microhabitats par placette significativement différent dans les forêts publiques et les forêts gérées sans PSG au stade Harv.

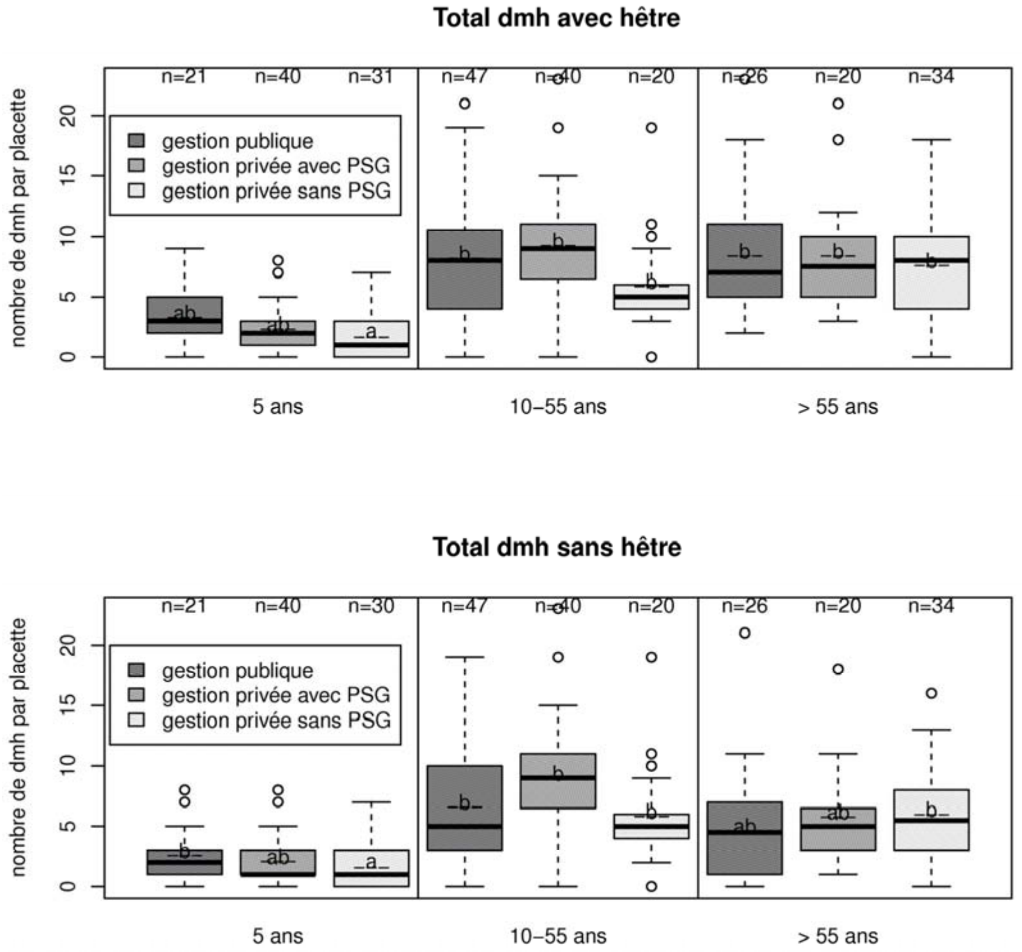

Figure 5. Boîtes à moustaches représentant les densités de dendro-microhabitats (dmh) ; la valeur moyenne est indiquée par un trait pointillé horizontal et les lettres indiquent la significativité de leurs différences ; la figure distingue le peuplement complet tel qu'il a été observé sur le terrain (Total dmh avec hêtre) et le même peuplement duquel on a retiré les hêtres (Total dmh sans hêtre)

Comme pour la densité de dendro-microhabitats, la tendance générale pour la diversité des dendro-microhabitats est une augmentation dès la catégorie UnHarv10-55 (Fig. 6), mais qui n'est significative qu'en forêt privée sans document de gestion ou en forêt privée avec document de gestion lorsque l'on prend en compte le hêtre.

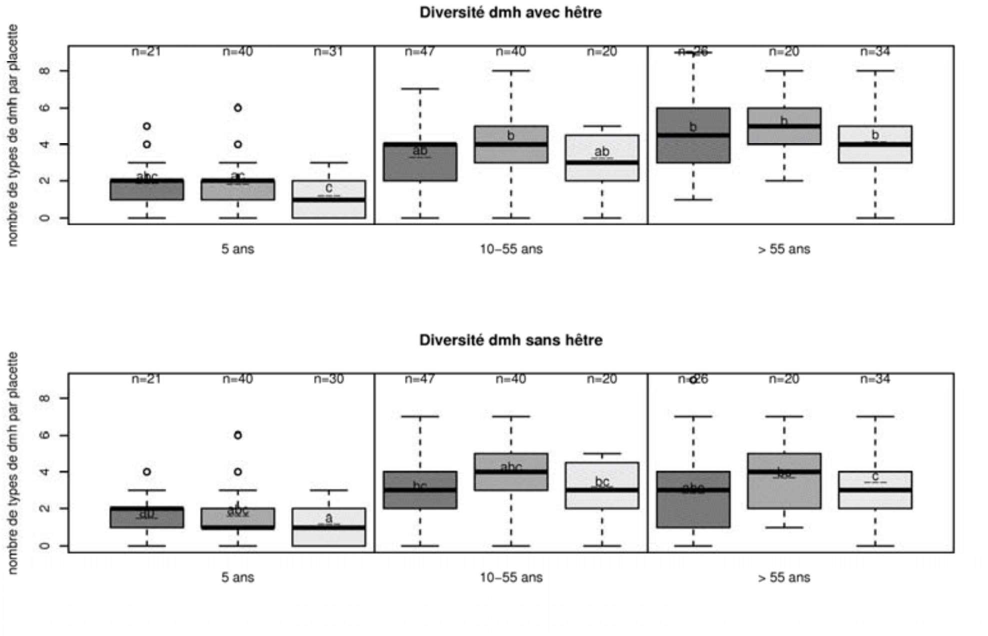

Figure 6. Boîtes à moustaches représentant la diversité des dendro-microhabitats (dmh) ; la valeur moyenne est indiquée par un trait pointillé horizontal et les lettres indiquent la significativité de leurs différences ; la figure distingue le peuplement complet tel qu'il a été observé sur le terrain (Diversité dmh avec hêtre) et le même peuplement duquel on a retiré les hêtres (Diversité dmh sans hêtre)

3.4 Synthèse

La reconstitution des stocks de bois morts et de dendro-microhabitats après exploitation semble s'effectuer principalement dans la période allant de 10 à 55 ans après la coupe. Cependant, une durée de non-exploitation de 55 ans n'est pas suffisante pour observer pour tous les types de gestion des valeurs significativement plus fortes que celles observées après la coupe pour, d'une part la densité et la diversité de dendro-microhabitats, et, d'autre part, le volume et la diversité de bois mort. Néanmoins, les amplitudes des valeurs sont grandes, probablement en liaison avec l'hétérogénéité des forêts étudiées et la grande amplitude de durée de non exploitation de la catégorie UnHarv10-55. On observe étonnamment une certaine stabilisation des stocks dans la classe 55-80 ans. Il serait intéressant de disposer de peuplements de référence non exploités depuis au moins la durée d'un cycle sylvigénétique pour relativiser les résultats obtenus après 55 ans de non exploitation. Il est possible, à l'instar de la relation seuillée entre les diamètres des arbres et les stocks de dendro-microhabitats, que la reconstitution des stocks de dendro-microhabitats ne soit pas un processus linéaire et passe séquentiellement par des phases sub-stationnaires et des phases d'augmentation rapide.

Le type de gestion n'a pas d'effet significatif sur les volumes de bois morts laissés par l'exploitation, mais semble avoir un effet à la fois sur la composition dendrologique des peuplements, les stocks de dendro-microhabitats après coupe et la vitesse de reconstitution des stocks de bois morts et de dendro-microhabitats. En forêt privée, la richesse en feuillus secondaires pourrait être la raison de la rapide reconstitution des stocks car ces essences contractent assez vite des dendro-microhabitats et ont des cycles de vie relativement courts, surtout en contexte concurrentiel.

Bibliographie

Ball J.P., Lindenmayer D.B., Possingham H.P.,1999. A tree hollow dynamics simulation model. For. Ecol. Manage. 123, 179–184.

Bauhus J., Puettmann K., Messier C., 2009. Silviculture for old-growth attributes. Forest Ecology and Management 258, 525-537.

Bouget C., Larrieu L., Brin A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecological Indicators 36, 656-664.

Burnel L., Pélissier C., 2009. Méthode de préparation d'échantillon de bois feuillus pour utilisation en dendrochronologie. Le cahier des techniques de l'INRA n°66 pp 5-12.

Burrascano S., Keeton W.S., Sabatini F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. For. Ecol. Manage. 291, 458–479.

Butler R., Lachat T., 2009. Forests without harvesting: an opportunity for the saproxylic biodiversity. Schweizerische Zeitschrift fur Forstwesen 160, 324-333.

Cavalli R., Donini F., 2005. Possible management actions to increase the amount of dead and marcescent wood, *In* Deadwood: a key to biodiversity. Mason F., Nardi G. & Tisato M. (Eds). Mantova: Sherwood , p.45–48.

EUFORGEN , 2012. Distribution map of Oaks (*Quercus robur, Q. petraea*) and European beech (*Fagus sylvatica*). http://www.euforgen.org

Forest Stewardship Council standards, 2014. https://ic.fsc.org/national-standards.247.htm

Gilg O., 2005. Old-Growth Forests; Characteristics, conservation and monitoring. GIP ATEN, technical report n°74 bis.

Gossner M., Lachat T., Brunet J., Isacsson G., Bouget C., Brustel H., Brandl R., Weisser W.W., Mueller J., 2013. Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. Conservation Biology 27, 605-614.

Green P., Peterken G.F., 1997. Variation in the amount of deadwood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. For. Ecol. Manage. 98 , 229–238.

Hervé M., 2014 Package 'RVAideMemoire' http://cran.r-project.org/web/packages/RVAideMemoire/RVAideMemoire.pdf

Keeton W.S., 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. Forest Ecology and Management 235, 129-142.

Kuznetsova A., Brockhoff P.B., Christensen R.H.B., 2014. Package `lmerTest', 17 p. <http://cran.rproject.org/web/packages/lmerTest/lmerTest.pdf>.

Larrieu L., Cabanettes A., Brin A., Bouget C., Deconchat M. 2014. Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry; *European journal of Forest Research* 133: 355–367.

Larrieu L., Cabanettes A., Delarue A., 2012. Impact of sylviculture on dead wood and on the distribution and frequency of tree microhabitats in Montane Beech-Fir forests of the Pyrenees; *European journal of Forest Research* Vol. 131 (3):773-786.

Larsson T. B., 2001. Biodiversity evaluation tools for European forests. Ecol. Bull. 50.

Lebourgeois F., 1997. La dendrochronologie. *In*: Etude dendrochronologique des 102 peuplements du réseau. Rapport RENECOFOR pp. 1-307.

Lombardi F., Lasserre B., Tognetti R., Marchetti M., 2008. Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). Ecosyst. 11, 882–894.

Mason F., Nardi G., Whitmore D., 2005. Recherches sur la restauration des habitats du bois mort : l'exemple du Life « Bosco della Fontana »(Italie). *In* Vallauri D. (ed.) : Bois mort et à cavités : Une clé pour des forêts vivantes. Ed. Tec & Doc, Lavoisier.

Meyer P., Schmidt M., 2011. Accumulation of dead wood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. Forest Ecology and Management 261, 342-352.

Michel A.K., Winter S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. Forest Ecology and Management 257, 1453-1464.

Müller J., Brunet J., Brin A., Bouget C., Brustel H., Bussler H., Förster B., Isacsson G., Köhler F., Lachat T., Gossner M., 2012. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conserv Divers 6, 162-169.

Müller J., Hothorn T., Pretzsch H., 2007. Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. Forest Ecology and Management, 242, 297–305.

Müller J., Stratz C., Hothorn T., 2005. Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. European Journal of Forest Research 124, 233-242.

ONF, 2009. Conservation de la biodiversité dans la gestion courante des forêts publiques. INS-09-T-71, Paris.

PEFC France, 2011. Cahier des charges relatif à la gestion durable de la forêt. http://www.pefc-france.org

Pinheiro J., Bates D.M., 2000. Mixed-effects models in S and S-PLUS. Statistics and computing series, Springer-Verlag, NY, USA.

R Development Core Team, 2013. R: a language and environment for statistical computing. Vienna Austria, R Foundation for Statistical Computing.

Regnery B., Paillet Y., Couvet D., Kerbiriou C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? Forest Ecology and Management 295, 118-125.

Rozas V., 2003. Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecology. 193-212.

Speight M.C.D., 1989. Saproxylic invertrebrates and their conservation. Concil of Europe. Nature and Environment Series 42, 1-79.

Stokland J. N., Siitonen J., Jonsson B. G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Vandekerkhove K., De Keersmaeker L., Menke N., Meyer P., Verschelde P., 2009. When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. Forest Ecology and Management 258, 425-435.

Vodka S., Konvicka M., Cizek L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. Journal of Insect Conservation 13, 553-562.

Vuidot A., Paillet Y., Archaux F., Gosselin F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144, 441-450.

Winter S., Möller G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251-1261.

Section III – Contribution des dendro-microhabitats et du bois mort à la diversité des espèces, à l'échelle du peuplement forestier

SECTION III - CONTRIBUTION DES DENDRO-MICROHABITATS ET DU BOIS MORT A LA DIVERSITE DES ESPECES, A L'ECHELLE DU PEUPLEMENT FORESTIER

Nous avons vu que, par le passé, la biodiversité associée aux dendro-microhabitats avait été étudiée seulement pour quelques dendro-microhabitats et toujours à l'échelle du dendro-microhabitat. Winter & Möller (2008) sont les premiers à publier en considérant les dendro-microhabitats dans un ensemble complexe de milieux de vie qui interagissent entre eux à une échelle plus vaste, et à étudier des ensembles de dendro-microhabitats au sein de peuplements forestiers. Ce changement d'échelle nécessite de choisir des modèles biologiques (i) bien connus sur le plan taxonomique, (ii) dont les différentes espèces sont liées à une large gamme de dendro-microhabitats et (iii) représentant une part non négligeable de la biodiversité taxonomique. Rappelons que l'échelle du peuplement forestier correspond à l'échelle de décision et d'action la plus couramment utilisée en gestion forestière.

Dans l'objectif d'évaluer dans quelle mesure les dendro-microhabitats et le bois mort sont des structures clés pour la biodiversité taxonomique à l'échelle du peuplement forestier, nous avons choisi dans un premier temps deux taxons qui semblent complémentaires : les Coléoptères saproxyliques (Bouget *et al.* 2013 et 2014) et les Diptères Syrphidae (Larrieu *et al.* soumis ; Herrault *et al.* soumis). Ces deux taxons partagent une grande diversité des espèces et des milieux de vie, une variabilité interspécifique des statuts de rareté, une expertise taxonomique disponible, l'existence de données sur leurs traits de vie, un échantillonnage facile et standardisé et une reconnaissance de bioindicateurs pertinents en biologie de la conservation. Les coléoptères saproxyliques représentent de surcroit 95 % de la biomasse des invertébrés saproxyliques. La complémentarité de ces deux taxons tient entre autres au fait que certains Coléoptères saproxyliques sont aptères ou peu mobiles et supposés répondre lentement aux changements alors que les Syrphidae sont pour la plupart bon voiliers (certains sont même partiellement migrateurs) et semblent aptes à recoloniser rapidement des milieux redevenant favorables. Ces derniers peuvent également révéler des structures très difficiles à observer directement, comme des nids d'hyménoptères sociaux hypogés. Conscients que certains facteurs clés pour l'occurrence de ces taxons dépassent le cadre spatial du peuplement forestier, nous avons parfois élargi le champ d'investigation en mesurant également des variables paysagères (Herrault *et al.* soumis). La dimension historique a été également finement abordée avec les Syrphidae (Herrault *et al.* soumis). Puis, dans une étude à très large échelle, nous avons élargi à la fois le champ taxonomique (neuf taxons, en différenciant pour presque tous des groupes écologiques) et le nombre de variables de structure et de composition (Larrieu *et al.* en prép.). Les dendro-microhabitats et le bois mort ont été parfois quantifiés avec un objectif de quasi-exhaustivité (Larrieu *et al.* soumis), mais dans la plupart des études (Bouget *et al.* 2013 et 2014 ; Herrault *et al.* soumis ; Larrieu *et al*. en prép.) avec un protocole simplifié emprunté à l'Indice de Biodiversité Potentielle (Larrieu & Gonin 2008) que nous présenterons en détail dans la section IV. Ces études ont porté sur une très large gamme d'écosystèmes forestiers et de type de peuplements, de la peupleraie de culture à la sapinière de montagne.

Il est trivial de dire que les insectes, poïkilothermes, sont influencés par la température ambiante et que celle-ci est un élément clé, non seulement pour leur diversité, mais aussi pour les patrons d'exploitation de l'habitat. Mais, de façon surprenante, peu d'études ont porté jusqu'alors sur les interactions entre les habitats saproxyliques et les conditions climatiques environnantes, alors que, pour les communautés d'insectes, on peut envisager d'éventuelles compensations par la température de la quantité d'habitat ou de sa qualité (Müller et al. 2014). Outre l'intérêt de réaliser ces études pour des questions de compréhension des processus écologiques, les résultats fourniraient des éléments de contextualisation des recommandations de conservation, pour optimiser leur mise en place et accroitre leur efficacité, car les mesures trop générales qui visent à appliquer partout les recommandations pour les conditions les plus défavorables sont souvent remises en cause par les gestionnaires praticiens en s'appuyant sur leur expérience locale. Nous avons investigué ces interactions avec les conditions climatiques à l'échelle du peuplement/ressource d'habitat avec les Coléoptères saproxyliques, dans un premier temps en France dans une gamme assez large de types de forêts avec le bois mort et un ensemble de dendro-microhabitats saproxyliques, en échantillonnant seulement la faune circulante (Bouget *et al.* 2013 et 2014). Les conditions de température étaient appréciées indirectement par la mesure de l'ouverture du couvert. Puis nous avons participé à une étude à l'échelle des Hêtraies européennes qui ne considérait que le bois mort et réduisait le compartiment des dendro-microhabitats au bois mort du houppier frais et de petite section (Müller *et al.* 2014). Dans ce dernier travail, les investigations ont été menées en couplant des mesures d'activité de la faune par échantillonnage avec des pièges d'interception et des mesures de densité d'espèces et d'abondance des individus par le suivi des émergences en enceinte close de pièces de bois mort pièges, et en considérant des gradients macro- et topo-climatiques.

1 PRINCIPAUX RESULTATS

A l'échelle de l'hectare autour du piège, les facteurs les plus structurants pour à la fois la composition des assemblages et la richesse spécifique des Coléoptères saproxyliques sont (i) le volume de gros bois morts, (ii) la diversité des types de bois mort, (iii) la densité d'arbres porteurs de cavités ou de sporophores de champignons lignicoles et (iv) le degré d'ouverture du couvert forestier permettant la production de fleurs. La densité de Très ou Très Très Gros Bois (respectivement d>70 cm et d> 90 cm), sans connaissance de leur caractère porteur ou non de dendro-microhabitat, n'avait pas d'effet significatif sur les assemblages de Coléoptères saproxyliques. Malheureusement pour l'élaboration de recommandations pratiques pour le gestionnaire, ces facteurs structurants ne sont pas universels pour tous les contextes forestiers et pour l'ensemble des espèces, rares ou communes. De surcroît, l'influence du bois mort et des dendro-microhabitats sur les communautés de Coléoptères saproxyliques est parfois affecté par le degré d'ouverture du peuplement. Ainsi, dans les forêts de plaine, feuillues ou résineuses, le pourcentage de milieux ouverts a un effet positif significatif sur la relation entre la densité d'arbres porteurs de cavité ou de champignon saproxylique et la richesse spécifique. Il est également corrélé *per se* à une augmentation de la richesse spécifique, probablement en raison d'un effet de complémentation en ressources florales et d'une augmentation de la température des substrats saproxyliques exposés. Dans les hêtraies, des conditions plus chaudes peuvent « compenser » un volume plus faible de bois mort. Par conséquent, les recommandations en faveur du maintien de bois mort devraient tenir compte des conditions climatiques locales, et un effort particulier devrait être fait dans les conditions les plus froides.

L'échelle de l'hectare autour du piège semble trop locale pour expliquer la variabilité des communautés de syrphes. La configuration spatiale de la forêt à l'échelle du paysage semble influer fortement sur la pertinence des variables clés pour ce taxon. Dans le cas de massif forestier continu et de grande surface, les variables les plus influentes à l'échelle du peuplement sont l'hétérogénéité de l'encombrement par le feuillage des arbres et arbustes, la présence d'une strate herbacée diversifiée et pourvoyeuse de fleurs, ainsi que la diversité des essences qui composent le peuplement. Dans le cas de petits bois morcelés dans une matrice agricole, la variable la plus explicative est la surface actuelle du bois. Néanmoins, le meilleur modèle expliquant la richesse spécifique moyenne par piège combine les variables surface actuelle du bois (88% de la variance expliquée), la densité de gros bois mort sur pied (6%) et la continuité de l'état boisé (5%). L'histoire de la dynamique paysagère autour du bois et l'évolution récente de sa connectivité semble plus influencer la richesse spécifique que la continuité de l'état boisé proprement dite.

Comme on pouvait s'y attendre, l'approche pluritaxonomique a donné des résultats complexes. On peut néanmoins en extraire les enseignements suivants. Aucune co-variation significative de la composition des assemblages n’est de sens opposé. En revanche, la variation des richesses spécifiques oppose significativement (mais avec un coefficient de corrélation <70%) les bryophytes avec les coléoptères et les champignons saproxyliques ainsi que les chiroptères avec la flore. Plusieurs effets significatifs des variables environnementales avec les variations des assemblages du taxon sont également significatifs avec les variations de richesse spécifique de ce même taxon. La richesse spécifique de certains taxons semble principalement déterminée par des variables à large échelle spatiale comme le domaine biogéographique, l’altitude ou la dominance de feuillus. Enfin, nous avons mis en évidence des seuils significatifs pour les variations de richesse spécifique : (i) plus de 5 essences autochtones augmente la richesse spécifique (RS) de la flore et des oiseaux, (ii) plus de 8 grosses (d > 40 cm) chandelles à l’hectare augmente la RS des chauves-souris et des champignons lignicoles rares, (iii) plus de 3 gros (d > 40 cm) bois morts à l’hectare augmente la RS des chauves-souris et des mousses et (iv) plus de 15 très gros (d > 70 cm) arbres vivants à l’hectare augmente la RS des chauves-souris et des champignons lignicoles rares.

2 DISCUSSION ET PERSPECTIVES

Les résultats montrent que l’on sous-estime les dimensions spatiales minimales pour appréhender correctement les communautés de Coléoptères saproxyliques et de syrphes quand on échantillonne les populations avec des pièges d’interception, parce qu’on observe alors la faune circulante dont on connaît très mal les potentialités et les modalités de déplacement. Les protocoles d’observation taxonomique devraient comporter des dispositifs à l’échelle du dendro-microhabitat (comme des pièges d’émergence) afin de minimiser le bruit lié à la mobilité des taxons, même si les échantillonnages utilisant des dispositifs locaux sont plus dispendieux que des échantillonnages réalisés seulement à l’échelle plus grossière du peuplement.

La dimension historique semblait évidente pour les Coléoptères car certains sont connus pour avoir des capacités de dispersion extrêmement faibles et d’autres sont même aptères, mais l’histoire du bois semble également importante pour les bons voiliers que sont majoritairement les syrphes.

Logiquement, les variables décrivant le bois mort apparaissent primordiales pour les taxons saproxyliques. Néanmoins, on soupçonne une redondance fonctionnelle entre certains types de bois mort et certains dendro-microhabitats qui en contiennent. Une meilleure identification des types de bois mort écologiquement calibrée et une ségrégation typologique entre les dendro-microhabitats saproxyliques et les autres devraient permettre dans le futur de réduire le bruit lié à cette redondance (cf. la typologie des dendro-microhabitats proposée en section IV). L’étude simultanée du bois mort et des dendro-microhabitats est plus contraignante qu’une étude séparée de ces deux compartiments clés pour l’hétérogénéité structurale des peuplements forestiers, mais elle nous a fortement éclairés sur la complexité du monde des saproxyliques. Il nous paraît pertinent de conserver dans les études futures cette approche simultanée.

En pratique, l’absence de facteur universel pour révéler la diversité des espèces dans tous les peuplements forestiers amène à recommander aux gestionnaires soit à contextualiser les variables clés (mais c’est vite incommode), soit un élargissement de la liste des facteurs à prendre en compte dans tous les contextes. Cette dernière option est le fondement de l’Indice de Biodiversité Potentielle (cf. section IV).

Pour explorer le maximum de la variance des communautés associées aux dendro-microhabitats, leur étude doit être multi-scalaire, de l’arbre au paysage, et doit prendre en compte la dynamique historique. La quantification de l’effet relatif de toutes ces composantes nous aidera à expliquer au gestionnaire forestier pourquoi il est préférable qu’il prenne également en compte la distribution spatiale de ses « efforts » de conservation (arbres habitats, îlots de sénescence, et.), et intégrer la dimension temporelle, comme il a l'habitude de le faire pour garantir l'équilibre des classes d'âges pour la production de bois. Sur ce dernier point, il serait pertinent que le forestier, lorsqu'il raisonne en termes de dynamique, rallonge sa perception du temps à la durée des cycles sylvigénétiques.

3 PUBLICATIONS

31. Bouget C., **Larrieu** L., Parmain G., Nusillard B., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation* 22: 2111–2130

32. Bouget C., **Larrieu** L., Brin A., 2014. Key features for saproxylic biodiversity from rapid habitat assessment in temperate forests *Ecological Indicators* 36: 656–664

33. **Larrieu** L., Cabanettes A., Sarthou JP., (en révision). Hoverfly (Diptera: Syrphidae) richness and abundance vary with stand heterogeneity: preliminary evidence from a case study in a montane beech fir forest. *European Journal of Entomology*

34. Herrault P.A., **Larrieu** L., Cordier S., Gimmi U., Lachat T., Ouin A., Sarthou J.P., Sheeren D., (soumis). Combined effects of history, connectivity and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae). *Landscape Ecology*

35. Müller J., Brustel H., Brin A., Bussler H., Bouget C., Obermaier E., Heidinger I., Lachat T., Förster B., Horak J., Schlagerhamsky J., Köhler F., **Larrieu** L., Bense U., Isacsson G., Zapponi L., Gossner M., 2014. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography* 37: 001-011

<u>Article en préparation</u>

36. **Larrieu** L., Bouget C., Deconchat M., et al., (in prep.). In search of key habitat-drivers at the stand scale for conservation of species diversity in temperate forests. *Biological conservation*?

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ORIGINAL PAPER

In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests

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Abstract Deadwood-associated species are increasingly targeted in forest biodiversity conservation. In order to improve structural biodiversity indicators and sustainable management guidelines, we need to elucidate ecological and anthropogenic drivers of saproxylic diversity. Herein we aim to disentangle the effects of local habitat attributes which presumably drive saproxylic beetle communities in temperate lowland deciduous forests. We collected data on saproxylic beetles in 104 oak and 49 beech stands in seven French lowland forests and used deadwood, microhabitat and stand features (large trees, openness) as predictor variables to describe local forest conditions. Deadwood diversity and stand openness were consistent key habitat features for species richness and composition in deciduous forests. Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. In addition, the density of cavity- and fungus-bearing

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trees had weak but significant effects. We recommend that forest managers favor the local diversification of deadwood types, especially the number of combinations of deadwood positions and tree species, the retention of large downed deadwood and microhabitat-bearing trees in order to maximize the saproxylic beetle diversity at the stand scale in deciduous forests. To improve our understanding of deadwood-biodiversity relationships, further research should be based on targeted surveys on species-microhabitat relationships and should investigate the role of landscape-scale deadwood resources and of historical gaps in continuity of key features availability at the local scale.

Keywords Microhabitat · Deadwood · Forest management · Biodiversity indicator · Oak · Beech

Introduction

Deadwood is a key component of forest ecosystems that is among the most severely affected by management in many landscapes (Fridman and Walheim 2000) and has become a focal conservation target in sustainable management. Since deadwood is one of the most species-rich components in forest ecosystems (Grove 2002a), saproxylic species have become increasingly targeted in biodiversity conservation (Stokland et al. 2012). Deadwood has often been used as a structural indicator for naturalness and biodiversity and can provide information on the intensity of past human disturbances and degree of proximity to old-growth conditions (Larsson 2001). To help define ecologically-meaningful saproxylic-friendly practices for forest managers, we need to unravel the relative importance of ecological and anthropogenic drivers on saproxylic diversity.

Multiple factors play pivotal roles in predicting both the number and distribution of saproxylic species. Species assemblage composition may result from (i) macro-ecological features (distribution area, climate), (ii) environmental characteristics at the landscape scale and at the local scale, (iii) historical events (past disruption of substrate availability, local extinctions) and (iv) species interactions (competition, predation, interactive succession) (Stokland et al. 2012). Forestry practices act at the stand and the landscape scales. Therefore the understanding of variables driving biodiversity at the stand scale seems important to improve ecological sustainability of forestry.

Beetles are an important functional (Cobb et al. 2010) and numerical (20 % of all saproxylic species, just after the fungi; Stokland et al. 2004) component of saproxylic biodiversity. Since beetles belong to relatively well-known taxonomic groups, and since most species are highly sensitive to environmental changes, have specific habitat demands and can be trapped relatively easily, they are both logistically and ecologically suitable as response indicators (Siitonen 2001).

At the local (stand) scale, habitat quality for saproxylic beetles is related to abiotic conditions (e.g. moisture and temperature conditions related to canopy closure) and available resources. Resources not only include deadwood substrates, but also more cryptic biological legacies such as microhabitats (e.g. cavities, crown deadwood), mostly found in large-diameter live trees (Larrieu and Cabanettes 2012; Winter and Möller 2008). Density and/or diversity of resources may underlie the resource-biodiversity relationship. Forest stands with a wider range of resources (resource range hypothesis) and/or a higher density of substrates (resource concentration hypothesis) may be able to support a larger number of species due to demographic, stochastic and dispersal processes affecting local population dynamics (Päivinen et al. 2003). Several studies have demonstrated a positive significant correlation between the local amount of deadwood and saproxylic beetle species richness (see Grove 2002a). Nevertheless, in a meta-analysis of available European data, Lassauce et al. (2011) found only a weak relationship between deadwood volume and species richness in temperate forests. Moreover, several studies have shown the diversity of deadwood types, rather than mere deadwood quantity, to be a critical environmental variable for saproxylic beetles (e.g. Brin et al. 2009; Stokland et al. 2004).

During the last few decades, research on saproxylic beetle habitat associations has been common in Scandinavia (Stokland et al. 2012), but has received less attention in central, western and southern Europe. By expanding this research to oak and beech forests, the two main deciduous forest types in Europe, we aimed to better understand the surrogacy patterns and environment-biodiversity relationships found there and to determine (i) relevant structural indicators of saproxylic beetle diversity and (ii) improved guidelines for sustainable forest management. We here mainly intended (i) to disentangle the effects of local habitat attributes (abiotic conditions, density or diversity of resources) which presumably drive saproxylic beetle communities in deciduous forests, and (ii) check whether key habitat features for saproxylic beetles are consistent over oak and beech forests.

Materials and methods

Study areas

We collected environmental and entomological data using standardized protocols on 153 plots in seven lowland deciduous forests (Table 1), distant of several hundred kilometers from each other: one forest in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). Two forest types were distinguished—oak and beech—according to the dominant tree species in terms of basal area. All the beech stands were associated with oak stands in the vicinity. Highland beech forests have been studied in a companion study. Inside each forest, plots were distant of hundreds of meters from each other and half of the plots were located in protected forest reserves (except in the Rambouillet and the Troncais forest, where only 20 and 10 % were in reserve stands, respectively).

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled with two cross-vane flight interception traps (Polytrap^{TM}) per plot, set about 20 m from each other, for a total number of 306 traps. The traps were suspended roughly 1.5 m above the ground. Active insects were collected from April to August, during 1 year only. The following saproxylic taxa were not identified at the species level in at least one of the seven forests and therefore removed from the compiled dataset: Cryptophagidae, Ptiliidae, Staphylinidae incl. Scaphidiinae and Pselaphinae. For the other taxa, we characterized each species' degree of geographic rarity in France according to the FRISBEE database (Bouget et al. 2010) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species of conservation concern for specific analyses.

Table 1 Description of structural (deadwood, microhabitats, large trees, openness, forest type) variables and study sites explored in the study

		Beech		Oak	
		Mean ± SE	Range	Mean ± SE	Range
Deadwood	Total volume of deadwood in a 0.3 ha plot (m^3/ha)	66.561 ± 11.771	0–371	28.131 ± 2.676	0–123
	Volume ratio = deadwood/(Live trees + deadwood)	0.213 ± 0.031	0–1	0.107 ± 0.009	0–0.5
	Nb deadwood types (tree species × diameter × decay × position)	10.122 ± 0.816	1–28	19.971 ± 1.254	1–53
	Volume of standing deadwood (>10 cm in diameter) in a 0.3 ha plot (m^3/ha)	18.284 ± 4.357	0–128	4.886 ± 0.922	0–65
	Volume of large standing deadwood (>40 cm in diameter)) in a 0.3 ha plot (m^3/ha)	14.705 ± 4.336	0–128	2.801 ± 0.818	0–65
	Volume of downed deadwood (>10 cm in diameter) in a 0.3 ha plot (m^3/ha)	48.277 ± 8.953	0–287	20.657 ± 2.379	0–111
	Volume of large downed deadwood (>40 cm in diameter) in a 0.3 ha plot (m^3/ha)	21.537 ± 5.698	0–209	4.2 ± 1.186	0–101
Microhabitat	Total density of microhabitat-bearing trees in a 1 ha plot	16.918 ± 1.744	0–52	17.663 ± 1.031	3–50
	Number of microhabitat types in a 1 ha plot	4.469 ± 0.260	0–7	4.779 ± 0.135	1–7
	Density of cavity-bearing trees in a 1 ha plot: “empty” cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	7.612 ± 0.713	0–18	5.558 ± 0.396	0–20
	Density of fungus-bearing trees in a 1 ha plot: fruiting bodies of tough or pulpy saproxylic fungi, >5 cm in diameter,	1.306 ± 0.238	0–7	0.942 ± 0.115	0–7
	Density of deadwood-bearing trees a 1 ha plot: crown deadwood in (large dead branches >20 cm in diameter and >1 m in length, crown deadwood volume >20 % of the total crown wood volume)	6.02 ± 1.052	0–37	8.096 ± 0.742	0–31
	Density of sap-run-bearing trees: sap runs >10 cm in length in a 1 ha plot	0.286 ± 0.071	0–2	0.423 ± 0.083	0–4

Table 1 continued

		Beech		Oak	
		Mean ± SE	Range	Mean ± SE	Range
Large trees	Number of very large trees in a 1 ha plot (dbh > 67. 5 cm)	4.816 ± 1.035	0–32	12.25 ± 1.181	0–51
	Basal area of very large trees in a 0.3 ha plot (67.5 < dbh ≤ 87.5 cm) (m^2/ha)	1.768 ± 0.481	0–15	5.611 ± 0.602	0–30
	Basal area of the largest trees in a 0.3 ha plot (dbh > 87.5 cm) (m^2/ha)	0.982 ± 0.361	0–14	0.753 ± 0.208	0–12
Openness	Open areas (clearings, edges, areas with a well developed herb layer composed of flowering plants) (%) in a 1 ha plot	10.792 ± 2.883	0–100	15.228 ± 2.734	0–100
	Beech or oak	49 plots, 98 traps		104 plots, 208 traps	
Forests	Auberive (AUB)	15 plots, 30 traps		9 plots, 18 traps	
	Chize (CHZ)	12 plots, 24 traps		12 plots, 24 traps	
	Citeaux (CIT)			12 plots, 24 traps	
	Combe-Lavaux (CL)	5 plots, 10 traps		3 plots, 6 traps	
	Fontainebleau (FBL)	17 plots, 34 traps		7 plots, 14 traps	
	Rambouillet (RBT)			30 plots, 60 traps	
	Troncais (TR)			31 plots, 62 traps	

Live tree and deadwood measurements

Stands were surveyed to obtain estimates of wood volumes for live trees, snags, logs and stumps and the basal area of live trees. Each plot, centered in the middle of both traps, was approximately 0.3 ha in size. We used a combination of sampling methods: fixed-angle relascope or circular plots for live trees; circular plots for stumps, large snags and large logs; line intersect sampling for small logs. We took into account minimum diameters of 7.5 cm for live trees, snags and logs. Four variables were used to describe deadwood: tree species, diameter (6 classes from 5 to >70 cm), decay stage (9 classes created by crossing 3 classes of remaining bark cover and 3 classes of inner wood hardness assessed by “knife penetration test”; Larjavaara and Muller-Landau 2010), and position (downed, standing, stump). An index of deadwood diversity was calculated as the number of observed deadwood types, i.e. the number of combinations of the above four variables (tree species × diameter class × decay class × position), as suggested by Siitonen et al. (2000). We also figured out a Shannon deadwood diversity index (Dodelin et al. 2004), accounting for the individual density (i.e. its number of pieces), and not only the occurrence, of each deadwood type. Based on these surveys, seven deadwood variables were considered for analysis (Table 1): (i) total volume, (ii) volume ratio, (iii) number of deadwood types, (iv) volume of standing deadwood, (v) volume of large standing deadwood (>40 cm in mid-diameter), (vi) volume of downed deadwood, (vii) volume of large downed deadwood (>40 cm in mid-diameter).

The basal area of very large and largest live trees was calculated for each 0.3 ha plot. The thresholds defining large trees were given by Grove (2002b), Larrieu and Cabanettes (2012) and Nilsson et al. (2002).

Very large live trees ($67.5 < \text{dbh} \leq 87.5$ cm) and tree microhabitats were inventoried during leaf-out in 1 ha circular plots centered around the two traps. We recorded seven microhabitat types borne by live trees: (i) “empty” cavities, (ii) cavities with mould, (iii) fruiting bodies of saproxylic fungi, (iv) sap runs, (v) dead branches, (vi) tree crown deadwood, (vii) missing bark (i.e. hard patches of wood with no bark >600 cm^2). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitat-bearing trees, the number of microhabitat types and the individual densities of four microhabitat types (i)“empty” and mould cavities, ii) sporocarps of saproxylic fungi, iii) dead branches and tree crown deadwood and iv) sap runs) were considered for analysis. Stand openness was defined as the total proportion of open areas in a 1 ha plot.

Data analysis

We used deadwood, microhabitat and stand features as predictor variables to describe forest conditions (Table 1), and species richness of *rare* and *common* species and species composition (incl. singletons) as response variables to describe beetle assemblages. All analyses were conducted on oak and beech datasets with R software v. 2.12.0. Since the same set of environmental variables measured within the 0.3- and 1 ha plots was used for both traps in the same plot, the catches of these two traps were combined prior to analyses carried out at the *plot* level.

To rank the effects of environmental variables on variations in species composition, we performed a Canonical Analysis of Principal Coordinates (*vegan* R-package, CAP, Anderson and Willis 2003). From Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP (Anderson and Willis 2003). We calculated total constrained inertia, the constrained inertia which was not explained by spatial factors only (NSCI), the total (intrinsic + co-explained) inertia explained by each variable (after partialling out the geographical "*forest*" effect), the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance by means of permutation tests (100 runs), and the relative contribution of each variable to NSCI.

We assessed the multi-model-averaged estimates (Burnham and Anderson 2002) determining the response of species richness to stand features. The most parsimonious model had the lowest Akaike information criterion (AICc, Burnham and Anderson 2002). For each response variable, we generated the null model and models with all the valid combinations of two explanatory variables. We calculated the differences in the AICc scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model. All models with $\Delta\text{AICc} < 2$ were used in order to figure out the model-averaged estimates weighted by the model weights. Only significant variables ($p < 0.05$ across all the models) were selected; their relative contribution, i.e. their weight of evidence across all the models, was indicated (*lme4*, *MuMIn*, *arm* R-packages). Since co-linearity among predictor variables may lead to unreliable parameter estimates, we conducted the strategy suggested by Zuur et al. (2010) for addressing the multicolinearity problem before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIF and repeated this process until all VIFs were below a pre-selected threshold (Zuur et al. (2010) suggest a cutoff of 3). The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model; a VIF = 1 indicates no co-linearity, whereas increasingly higher values suggest increasing multicolinearity. We used the "vif.mer" function (Frank 2011) to calculate VIFs for linear mixed effects models built using the lmer function in the "lme4″ package (Table 2). Since the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen et al. 2000), we used (log x + 1) transformed values for deadwood volumes. The effect on species richness of local deadwood diversity assessed by the simple index (number of deadwood types) or the Shannon index (Shannon diversity index of deadwood types, taking the local density of each deadwood type into account, using its number of pieces) was compared using AICc values of each mixed model (with forest as a random factor).

Significant relationships in generalized linear models were searched for breakpoints in species accumulation rates. Estimates of breakpoints were calculated by recursive partitioning by means of maximally selected two-sample statistics (Hothorn et al. 2006). Only primary and significant ($p < 0.001$) breakpoints are reported here. Based on 5,000 bootstrap samples, 80 % confidence intervals (to define ranges more tightly than 95 % CI) were calculated for all breakpoints (*party* and *boot* R-packages). In comparison with other models used in the study, this method does not allow to take the spatial structure of the data (at least forest location) into account.

The diversity effect was partitioned into its four basic dimensions included in the deadwood diversity index (diameter class, decay class, tree species, position). We analysed whether any of these dimensions have an outstanding importance on species richness, by comparing AICc values of linear mixed models (with forest as a random factor) including all combinations of the 4 deadwood dimensions.

Table 2 Variance inflation factor (VIF) of predictor variables selected in the linear mixed reduced models of species richness (with forest as a random effect), to be used in the model averaging approach (after sequential selection; Zuur et al. 2010), for addressing the multicollinearity problem

Predictor (covariate)	Oak	Beech
Deadwood diversity	2.26	2.24
Deadwood ratio		2.33
Volume of standing deadwood (logx + 1)	2.79	2.41
Volume of large standing deadwood (logx + 1)	2.70	
Volume of downed deadwood (logx + 1)	2.26	
Volume of large downed deadwood (logx + 1)	1.77	
Density of very large trees	1.71	
Basal area of largest trees	1.99	1.70
Density of cavity-bearing trees	2.34	2.34
Density of fungus-bearing trees	1.82	1.74
Density of deadwood-bearing trees	1.46	1.61
Density of sap-run-bearing trees	1.47	1.64
Microhabitat diversity	2.33	
Openness	1.41	1.53

The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model. A VIF = 1 indicates no collinearity. All selected VIFs were below a pre-defined cutoff of 3 (as suggested by Zuur et al. 2010)

The response to stand openness of the abundance of selected beetle species (caught in more than 10 individuals occurring in more than 10 % samples) was analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and “forest” as a spatial random effect (lmer function in lme4 R-package).

Results

Overall, the compiled dataset included 99 383 individuals and 478 saproxylic beetle species, among which 377 common, 70 rare (15 % of the total number) and 31 undefined species were recorded. On average per plot, rare species represented about 6 % of all species and 6 % of all individuals. The mean numbers of common and rare species per plot were greater in the oak than in the beech plots (49.7 ± 1.7 vs. 38.1 ± 1.9 and 3.5 ± 0.2 vs. 1.9 ± 0.1, respectively). Significant differences in several explanatory stand features were measured between oak and beech plots (Table 1).

Response of species composition to stand features

Many factors were used to describe the saproxylic environment (deadwood, microhabitats, large trees, stand openness) in order to identify the main local factors driving saproxylic beetle diversity. In oak and beech data, environmental and spatial factors respectively accounted for 45 and 52 % of variation in species composition. 31 and 23 % of the constrained inertia was explained by the intrinsic site effect in oak and beech data.

In oak and beech forests, the openness, the microhabitat diversity, the deadwood diversity and the basal area of very large trees made significant total contributions (marginal and joined) to inertia (Table 3). In the oak forests, microhabitat density also provided a significant total contribution. In the beech forests, significant total contributions were also provided by all the other deadwood descriptors (total volume, ratio, volumes of standing, large standing, downed, large downed deadwood), the density of very large trees at the 1 ha scale and the basal area of the largest trees. In oak, two environmental variables (deadwood diversity and stand openness) had a significant marginal contribution to inertia but only explained 3.5 and 3.9 % of the non-spatial constrained inertia, respectively. In beech data, although a larger proportion of the inertia was explained by the environmental predictors than in oak data, none of the tested environmental predictors made a significant intrinsic contribution to inertia. In beech and oak forests, the density of cavity-, fungus-, deadwood-, sap-run-bearing trees did not explain variations in species composition.

Response of species richness to stand features

From multi-model averaged estimates (Table 4), the stand openness was the main predictor of richness of common beetle species in oak and beech plots. The deadwood diversity and the density of fungus-bearing trees had the highest positive impacts on rare species richness in oak and beech forests, respectively. The more open the forest and the higher the local number of deadwood types, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, and with the density of fungus- and cavity-bearing trees. Overall, the influential stand features were only partially identical for rare and common species. The influence of the total volume of deadwood on the number of species was not tested, since it was collinear with other predictors in the model (Table 2).

Above the identified deflation breakpoints for significant variables, the number of species per plot kept on increasing, but more slowly. The rate of increase in rare species richness slightly slows down after the value of 1 fungus-bearing tree per ha in beech forests, and after the value of 29 deadwood types in the surrounding 0.3 ha in oak forests. The accumulation rate of common species slows down after a 17 % openness in oak stands and a 2 % openness in beech stands. In oak forests, the number of common species increased more slowly after the values of 11 deadwood types in the surrounding 0.3 ha, 1 fungus-bearing tree per ha, 46 m^3 of downed deadwood per ha.

In both beech and oak plots, the effect of deadwood diversity on species richness was partitioned into its four basic dimensions (diameter, tree species, decay, position [i.e. downed, standing or stump]). We did not measure any sharp contrasts between AICc values of linear mixed models including all combinations of the 4 deadwood dimensions for common and rare species (Fig. 1). The full model was never the most parsimonious model. The best model included (i) the number of combinations between positions and tree species, and to a lesser extent simply the diversity of deadwood positions (ΔAICc $= 1$) for rare and common species in beech forests, (ii) the diversity of tree species, and to a lesser extent of diameter classes ΔAICc $= 2$) for rare species and (iii) the number of combinations crossing tree species, diameter and decay stages for common beetle species in oak forests. Although the most structuring deadwood dimensions for species richness were not strictly consistent between oak and beech, and between common and rare species, the number of tree species was generally outstanding (Fig. 1).

Table 3 Canonical analysis of principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %NSCI: relative contribution to the non-spatial constrained inertia

		Oak plots			Beech plots		
	Variable	Total inertia	Marginal Inertia	%NSCI	Total inertia	Marginal Inertia	%NSCI
Deadwood	Volume of deadwood (logx + 1)	ns			0.589*	ns	
	Deadwood ratio	ns			0.529**		
	Deadwood diversity	0.481**	0.406*	3.5 %	0.465*		
	Volume of standing deadwood (logx + 1)	ns			0.591**		
	Volume of large standing deadwood (logx + 1)				0.548*		
	Volume of downed deadwood (logx + 1)				0.582*		
	Volume of large downed deadwood (logx + 1)				0.664*		
Microhabitat	Microhabitat density	0.404*	ns		ns	ns	
	Microhabitat diversity	0.485*			0.453°		
Large trees	Basal area of very large trees	0.420*	ns		0.723**	ns	
	Density of very large trees	ns			0.592**		
	Basal area of largest trees				0.761**		
Openness	Openness	0.663**	0.445*	3.9 %	0.513**	ns	
Spatial	Forest	11.415**	5.120**		3.392**	2.181**	

Only significant variables (** $0.01 > p > 0.001$, * $0.05 > p > 0.01$, °$0.1 > p > 0.05$) were selected

Table 4 Multi-model averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) determining the response of saproxylic beetle species richness (rare, common)

Forest type	Species richness	Predictor	Model-averaged estimate (significance)	Relative contribution	Deflation breakpoint	Best models (Delta AICc < 3)	
Oak	Rare	Deadwood diversity	1.66**	0.81	29 (19–30)	Deadwood diversity + openness	AICc = 421.1
		Openness	0.81*	0.34	No		
	Common	Openness	9.0***	0.99	17 (3–80)	Volume of downed deadwood + openness	AICc = 767.9
		Volume of downed deadwood (logx + 1)	9.4***	0.94	46 (12–47)		
		Volume of large downed deadwood (logx + 1)	7.7***	0.04	No		
		Deadwood diversity	10.0**	0.01	11 (10–17)		
		Density of fungus-bearing trees	5.4**	0.01	1 (1–3)		
		Density of cavity-bearing trees	4.3°	0.01	No		
Beech	Rare	Density of fungus-bearing trees	1.09*	0.56	1 (1–3)	Density of fungus-bearing trees	AICc = 181.5
	Common	Openness	14.38***	0.97	2 (1–10)	Deadwood diversity + openness	AICc = 378.0
		Deadwood diversity	6.27°	0.24	No		

Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect). Only significant variables (*** $p < 0.001$, ** $0.01 > p > 0.001$, * $0.05 > p > 0.01$, °$0.1 > p > 0.05$) were selected. Significant relationships in SR response were searched for breakpoints (Significance $p < 0.001$, 80 % Confidence Interval based on 5,000 bootstrap samples)

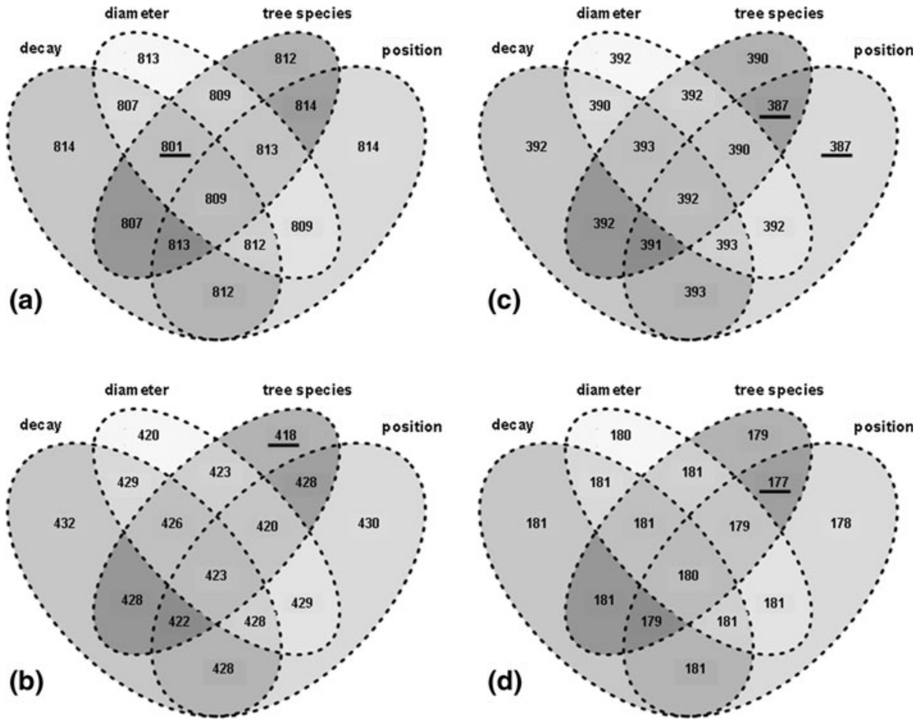

Fig. 1 Partitioning of the deadwood diversity effect on common and rare species richness into its four basic dimensions (diameter class, decay class, tree species, position) and all their combinations in beech and oak plots. All mixed models (with forest as a random factor) for all combinations of the 4 deadwood properties were compared using AICc values. The four-set Venn diagram with simple ellipses displays all 24-1 = 15 possible areas created by the interaction of 4 sets. The Venn diagram was not scaled, i.e. the graphical size of each intersecting or non-intersecting area is not proportional to the numerical AICc value. The best model is underlined. **a** and **b**: oak forests, **c** and **d**: beech forests; **a** and **c**: common species, **b** and **d**: rare species

Both deadwood diversity indices, the simple number and the Shannon diversity index of deadwood types, were similarly correlated to the deadwood volume (Spearman rho = 0.48 for the simple index, rho = 0.49 for the Shannon index). In both beech and oak data, the explanatory power of the Shannon model was only slightly better than the simple model (ΔAICc = 4).

Response of individual species to openness

30 and 36 % of tested species (102 species in beech stands, 189 species in oak stands) had a significant response to openness in beech and oak data, respectively (Table 5). In both beech and oak data, 77 % of the significant species responses related to open-preferring species, and only 23 % to shade-preferring taxa (whose abundance decreased with increasing stand openness). Among open-preferring species, 30 % species were known to have flower-visiting adults. Contrarily, we did not find any known flower-visiting species among shade-preferring taxa. Only a few species displayed contrasting responses to openness in oak and beech data (Table 5).

Table 5 Response in abundance of selected beetle species to stand openness

Shade-preferring species		Open-preferring species	
Oak stands	Beech stands	Oak stands	Beech stands
Anobium hederae***, _Hemicoelus fulvicornis_***, _Isoriphis melasoides_***, _Leiopus femoratus_***, _Melasis buprestoides_*, _Mycetophagus piceus_*, _Ochina ptinoides_*, _Orchesia undulata_*, _Pediacus dermestoides_***, _Tetratoma ancora_***, _Vincenzellus ruficollis_***, _Xyleborinus.saxesenii_***	_Aulonothroscus brevicollis_*, _Diplocoelus fagi_*, _Platystomos albinus_*	_Abdera bifasciata_**, _Agrilus_ sp***, _Alosterna tabacicolor_*, _Ampedus cinnaberinus_*, _Ampedus sanguinolentus_**, _Anaspis fasciata_*, _Anaspis frontalis_***, _Anaspis melanopa_***, _Cis boleti_**, _Clerus mutillarius_***, _Clytus arietis_*, _Colydium elongatum_***, _Cortinicara gibbosa_***, _Cortodera humeralis_***, _Cryptarcha undata_***, _Cryptolestes duplicatus_**, _Dasytes aeratus_**, _Dasytes plumbeus_***, _Dryocoetes villosus_***, _Epuraea_ sp***, _Gonodera luperus_***, _Megatoma undata_**, _Mycetochara maura_***, _Mycetophagus atomarius_*, _Pachytodes cerambyciformis_*, _Paromalus parallelepipedus_*, _Pediacus depressus_*, _Placonotus testaceus_***, _Plegaderus dissectus_**, _Prionus coriarius_**, _Ptinus bidens_***, _Ptinus subpilosus_*, _Rhagium sycophanta_**, _Rhizophagus bipustulatus_*, _Rhizophagus depressus_***, _Silvanus unidentatus_*, _Stenurella melanura_***, _Thanasimus formicarius_***, _Triplax lepida_*, _Tritoma bipustulata_***, _Tropideres albirostris_***, _Xyleborus dryographus_***	_Ampedus glycerus_***, _Corticarina similata_*, _Cyclorhipidion bodoanus_***, _Enicmus brevicornis_***, _Glischrochilus quadriguttatus_*, _Laemophloeus monilis_***, _Leptura aurulenta_**, _Melanotus villosus_*, _Microrhagus lepidus_***, _Nemozoma elongatum_***, _Platycerus caraboides_**, _Stenocorus meridianus_***, _Tomoxia bucephala_***
Hemicoelus costatus**, _Trypodendron domesticum_**, _Xyleborus dispar_***, _Xylosandrus germanus_***		_Cerambyx scopolii_***, _Cetonia aurata_***, _Cryptarcha strigata_***, _Dacne bipustulata_***, _Litargus connexus_***, _Pyrochroa coccinea_**, _Scolytus intricatus_***, _Taphrorychus bicolor_***, _Triplax russica_***, _Valgus hemipterus_**, _Xyleborus monographus_***	

Table 5 continued

Shade-preferring species		Open-preferring species	
Oak stands	Beech stands	Oak stands	Beech stands
Species with contrasting response in oak and beech data			
*Microrhagus pygmaeus** *Isoriphis marmottani**** *Salpingus planirostris**** *Ernoporicus fagi****	*Hylecoetus dermestoides***	*Hylecoetus dermestoides****	*Microrhagus pygmaeus**** *Ernoporicus fagi**** *Isoriphis marmottani**** *Salpingus planirostris***

Only species caught in more than 10 individuals and occurring in more than 10 % samples were analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and "forest" as a spatial random effect. Only significant responses were displayed (*** $p < 0.001$, ** $0.01 > p > 0.001$, * $0.05 > p > 0.01$). Species with well-known flower-visiting adults (Bouget et al. 2010) were underlined

Discussion

Local ecological drivers of saproxylic beetle diversity in temperate deciduous forests

Stand openness, a key feature

To summarize, among the diverse features describing local forest conditions for saproxylic beetles, both deadwood diversity and stand openness were consistent key habitat features for species richness and composition in oak and beech forests. The more open the deciduous forest, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. Variations in species composition were mainly determined by the openness and the deadwood diversity in the oak plots, by site and large tree predictors in the beech plots. Moreover, a high proportion of the tested species displayed a significant response to openness (30 and 36 % in beech and oak data, respectively). Our study confirms that canopy closure is clearly an outstanding attribute of the surrounding environment for saproxylic (even rare) beetles (Stokland et al. 2012). We here observed the same high proportion (77 %) of open-preferring species among significant species responses in oak and beech forests. This strong influence of openness on both species richness and composition could relate (i) to an ecological complementation effect, between neighboring deadwood for larvae and flowers for adults, (ii) to microclimatic effects on sun-exposed substrates (and therefore habitat suitability of deadwood, fungi and other microhabitats on trees), as demonstrated in temperate forests by Vodka et al. (2009), and (iii) to thermodynamic effects on beetle activity, with more flying-active species in open and sun-exposed environments. Concerning the first point, we respectively detected 30 and 0 % flower-visiting species among open- and shade-preferring taxa. Our analyses also indicated that the accumulation rate of common species slows down after a 17 % openness in oak stands and a 2 % openness in beech stands. Contrary to what we had expected, we did not observe humpback curves with two breakpoints, i.e. a decrease in richness after a second breakpoint due to the disappearance of species in extreme sun-, wind- and light-exposed substrates. The potential influence of a trappability bias (window-flight traps may be more efficient in open areas) has not been elucidated (Koch Widerberg et al. 2012).

Density and diversity of deadwood

Overall, deadwood diversity was actually a more consistent predictor of species richness than deadwood ratio and downed or standing deadwood volumes. Its co-linearity with the total deadwood volume (Spearman correlation = 0.49) prevents from disentangling their relative effects. The deadwood diversity significantly affected the species richness in beech and oak forests (as well as the species composition in oak forests). In other words, the higher the local number of deadwood types, the higher the number of common species per plot, and the number of rare species in oak stands. Our overall results confirm that the diversity of deadwood substrates plays an outstanding role in saproxylic diversity, as several previous studies have shown (e.g. Brin et al. 2009; Økland et al. 1996; Stokland et al. 2004). A wider range of resources (i.e. more various types of resource present in exploitable amounts) hosts more specialists and as many generalist species. Among the 4 dimensions describing deadwood diversity (position, decay, diameter, tree species), the local number of (deciduous) tree species was a key element for species richness.

The deadwood ratio (the proportion of deadwood in total local wood volume, alive and dead), accounting for the wide natural variability in deadwood amounts over space and time due to the productivity of the forest and stand dynamics (Siitonen 2001), did not better fit the relationship between deadwood amount and species richness than absolute deadwood volume.

Some studies have pointed out that the decline in deadwood quantity due to commercial forestry is stronger for some deadwood types, mainly snags and large logs (Sippola et al. 1998). These two components are therefore particularly at risk in managed forests. It has already been shown that oak and beech snags (Bouget et al. 2012; Brunet and Isacsson 2009) and large logs (Brin et al. 2011; Økland et al. 1996) are key deadwood types for saproxylic beetles. In our study, the volumes of downed and standing deadwood did not provide significant intrinsic contributions to assemblage composition in oak and beech plots. The best models of species richness in lowland forests never included the standing deadwood. However, it should be noted that, in a companion study (Bouget et al., in prep.), the density of large standing deadwood was the second predictor of species richness in highland beech forests. Deadwood drivers clearly depend on the forest context.

In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, both being even more influent than the deadwood diversity. Large deadwood volume did not affect the number of rare species, even though certain rare species are known to be sensitive to large log volume (Siitonen et al. 2000). Possibly the threshold we set for large deadwood (>40 cm), given for boreal forests by Nilsson et al. (2002), was too low to reflect ecological processes or should be modified for temperate contexts. Possibly species depending on large logs might be simply missing in managed forests due to the scarcity of large deadwood pieces.

Tree microhabitats as key resources?

In addition to canopy closure and deadwood resources; microhabitat features, as newly studied features, had weak but significant effects. The number of common species in oak stands and rare species in beech forests significantly increased with the density of fungus-bearing trees. Moreover the density of cavity-bearing trees had a slight positive impact on the common species richness in oak stands. However, in beech and oak forests, the density of cavity-, fungus-, deadwood-, sap-run-bearing trees did not explain variations in species composition. The role of tree microhabitats for saproxylic assemblages remains insufficiently understood (Winter and Möller 2008). Several saproxylic beetle species are known to be associated to cavities and tree holes (Ranius 2002), to sap runs (Yoshimoto et al. 2005), to crown deadwood (Bouget et al. 2011) and lignicolous fungi (Jonsell and Nordlander 2002). Microhabitats borne by live trees can occur in forests with a low total amount of deadwood. In our data, the density and diversity of microhabitats on trees and deadwood were not correlated.

Grove (2002b), Nilsson et al. (2002) and Ranius (2002) all suggested that the density of large trees could be important for certain saproxylic beetle species, since the presence of such trees reflects both habitat continuity and microhabitat supply. In our dataset, the density of large trees actually only correlated to the density of deadwood-bearing trees, but not to the density of cavity-, of fungus- and of sap-run-bearing trees. In our results, the density or basal area of large or very large trees did not explain local species richness either at a 0.3 ha scale or at a 1 ha scale. Nevertheless, variations in species composition were co-determined by site and large tree predictors in the beech plots.

The weak relationships observed between microhabitats and beetle fauna may be attributed to deficiencies (i) in beetle sampling and/or (ii) in the microhabitat surveys, and (iii) to the strong co-linearity among microhabitat variables in the modeled data. In beech data multiple joint effects between close variables or between environmental and spatial variables, made it difficult to decipher influences. In interpreting the results, we consequently should bear in mind that the present samples enable to reveal only strong effects. First, our beetle dataset is based on two window-flight traps per plot, set up during 1 year only. However, it has been demonstrated that the number of species detected at the plot level could be deeply increased by year or trap replication (Parmain et al. in press). Since the sampled assemblage may be poorly representative of the local fauna, it may weaken the analysis of the species-environment relationships. Moreover, it should be underlined that freely hanging window-flight traps are meant to catch active flying beetle species, and that (mostly rare) microhabitat-specialists, e.g. cavity-specialists, are only occasionally caught in these traps, unless a large sample size is set up. To study these groups, special kinds of targeted surveys or trapping methods are needed (Ranius and Jansson 2002). Our conclusions regarding rare species should be considered cautiously, since it is well known that (i) representative local catches of rare species require repeated sampling efforts (Martikainen and Kaila 2004), and (ii) rare species dependent on higher amounts of deadwood are difficult to model due to their low abundance in trap catches. Secondly, except for crown deadwood, the microhabitats were only measured on trunks and on live trees. The real density of cavities was probably underestimated, especially for oak with frequently-occurring cavities on large low branches within the tree crown. The density of lignicolous fungi, used as a proxy for fungal resources, was also undoubtedly underestimated since only large fruiting bodies were surveyed and one fungus at most was recorded per tree in the protocol. Moreover, the leaf cover may have hindered observations of microhabitats on the trunk; this could also have contributed to an underestimation of their number. The relationships between saproxylic and microhabitat diversity therefore require further investigations though such tree microhabitat surveys may be costly.

Perspectives

Perspectives for bio-indicator validation

Deadwood has become a centerpiece for forest monitoring in Europe. Since assessing stand structural elements is much faster and easier than inventorying species, deadwood is being widely used to indicate the conservation value of forests (Noss 1999). More precisely, deadwood volume is considered to be an important indicator of forest biodiversity (Larsson 2001) and, as such, has been selected by the European Environmental Agency as an assessment criterion for sustainable forest management practices (EEA 2007). However, a validation of deadwood indicators at a wide geographical scale is still lacking (Stokland et al. 2004). Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. Deadwood diversity provided more consistent predictive models of the local number of saproxylic beetle species than volume variables in deciduous forests. In coniferous forests, deadwood diversity has also proven to be a better predictor of species richness than volume (pine: Brin et al. 2009, fir and spruce: Bouget, pers. com.). Using diversity variables can reduce the time spent sampling deadwood since presence/absence data from each type category is sufficient (Brin et al. 2009). Other studies have demonstrated that deadwood diversity is an efficient surrogate for many forest-dwelling species presence, including taxa that are not directly dependent on deadwood (e.g. Fritz et al. 2008). Finally, when we combined deadwood diversity and microhabitat diversity (i.e. the number of both deadwood and microhabitat types) in a single additive index, there was only a negligible increase in explanatory power on beetle species richness, compared with deadwood diversity alone (from $R^2 = 0.33$ to $R^2 = 0.34$ in all deciduous plots). The validation of ecologically-relevant indirect biodiversity indicators which are easy to survey based on data from national forest inventories, would require further large-scale and multi-taxonomic analyses. These features will also serve as criteria for more effective selection of conservation areas.

Implications for forestry

Substantial evidence exists that commercial forestry has a negative impact on deadwood quantity (Fridman and Walheim 2000). Several studies have reported that the diversity of deadwood substrates is also altered by forestry (e.g. Ekbom et al. 2006). We found that deadwood diversity is a consistent key factor for saproxylic beetle diversity; we therefore suggest that forest managers favor the local diversification of deadwood types rather than any given target volume (but see below in oak forests). From our analyses, deadwood positions and tree species were key dimensions for the effect of deadwood diversity on species richness; overall, the number of tree species was outstanding. In managed forests, forestry is known to induce (i) a depleted local diversity of tree species in deadwood, due to the counter-selection of many native tree species that are not considered economically valuable, and (ii) a decreased local diversity of deadwood positions, mainly due to the elimination of standing deadwood, perceived as a safety hazard (Bishop et al. 2009). It therefore seems relevant to increase the number of combinations of positions and tree species (except introduced exotic species) to favour the local species richness of saproxylic beetles. Moreover, further ecological studies should pay more attention to mixed coniferous–deciduous forests.

Our statistical breakpoints of deadwood or microhabitat values in the accumulation rate of species can not be translated into management targets as ecologically meaningful aggregation of true species extinction thresholds. It should however be borne in mind that threshold analyses did not consider the spatial structure of the data, despite the importance of site effects. Nonetheless, they may inspire cost-effective management guidelines. For instance, the efforts to retain just 1 fungus-bearing tree per ha would significantly increase beetle species richness and would be cost-effective. In our data, the strongest increase in rare species richness in beech forests and in common species in oak forests indeed occurred from 0 to 1 fungus-bearing tree per ha. The rate of increase in species richness actually slightly slows down beyond the value of 1 tree per ha.In oak forests, an effort of downed deadwood restoration up to the target of 50 m^3 per ha would be efficient from an ecological perspective (though a bit costly in terms of forestry benefits), since the number of common species increased more slowly with deadwood volume beyond the value of 46 m^3 per ha. Nevertheless, it should be made clear that such quantitative deadwood targets would not meet the needs of all species; deadwood-dependent species are extremely numerous, and their deadwood requirements are species-specific (Müller and Bütler 2010). Finally, since stand openness strongly affected species composition, deadwood and microhabitats should be managed both under closed-canopy and open conditions (Vodka et al. 2009).

Perspectives for further approaches

One shortcoming of most of the empirical studies on saproxylic organisms is that they are typically conducted at a single, relatively small spatial scale. However, the probability of occurrence of saproxylic beetles is known to increase with the amount of dispersal sources in the surrounding landscape (e.g. Gibb et al. 2006). Moreover, habitat distribution may be more important than habitat quality in fragmented forest areas (Brunet and Isacsson 2009) like the temperate forests in Western Europe. One explanation for the lack of clear results on the relationship between deadwood or microhabitat density and biodiversity may be that resources have not been measured over an area large enough to reflect deterministic influences on local beetle assemblages, especially for aerially dispersing beetle species (Bishop et al. 2009). To date, only a few studies have shown the positive effects of deadwood volume on local saproxylic beetle species richness (Franc et al. 2007; Gibb et al. 2006; Økland et al. 1996) or deadwood-rich stands (Franc et al. 2007) in the surrounding landscape (from 100 m to 1 km). Considering the effects of regional deadwood on local assemblages might make a better spatial match between inventories and ecological processes (Turner and Tjørve 2005). Even if stand specific deadwood thresholds supply some information about the local richness and abundance of a species group, landscape-level deadwood thresholds would be necessary when considering the viability of meta-populations (Ranius and Fahrig 2006).

Local assemblages may also be considerably affected by delayed effects of past gaps in the continuity of the local deadwood supply, continuity which is critical for species long-term persistence (Jonsell and Nordlander 2002). Including more data about the history of deadwood availability would improve the explanatory power of assembly rules in saproxylic communities.

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References

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525

Bishop DJ, Majka CG, Bondrup-Nielsen S, Peck SB (2009) Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. Zookeys 22:309–340

Bouget C, Brustel H, Zagatti P, Noblecourt T (2010) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation statuts. http://frisbee.nogent.cemagref.fr/index.php/en/. Accessed 15 Jan 2013

Bouget C, Brin A, Brustel H (2011) Exploring the last biotic frontier: are temperate forest canopies special for saproxylic beetles? Forest Ecol Manag 261:211–220

Bouget C, Nusillard B, Pineau X, Ricou C (2012) Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. Insect Conserv Divers 5:264–278

Brin A, Brustel H, Jactel H (2009) Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in maritime pine plantations. Ann Forest Sci 66:1–11

Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J Insect Conserv 15:653–669

Brunet J, Isacsson G (2009) Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. J Insect Conserv 13:515–528

Burnham KP, Anderson DR (eds) (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, Berlin

Cobb TP, Hannam KD, Kishchuk BE, Langor DW, Quideau SA, Spence JR (2010) Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agric Forest Entomol 12(1):9–18

Dodelin B, André J, Wlérick L, Lempérière G (2004) Le bois mort en forêt de montagne (Alpes françaises). R. F. F. 66:507–518

EEA (2007) Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe. Luxembourg: European Environment Agency, 186 p. ISBN 978-92-9167-931-7

Ekbom B, Schroeder LM, Larsson S (2006) Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. Forest Ecol Manag 221:2–12

Franc N, Gotmark F, Okland B, Norden B, Paltto H (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biol Conserv 135:86–98

Frank AF (2011) R-hacks/mer-utils.R. https://github.com/aufrank/R-hacks/blob/master/mer-utils.R. Accessed 15 Jan 2013

Fridman J, Walheim M (2000) Amount, structure and dynamics of deadwood on managed forestland in Sweden. Forest Ecol Manag 131:23–36

Fritz O, Gustafsson L, Larsson K (2008) Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol Conserv 141:655–668

Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczanski J, Johansson T, Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography 29:1–14

Grove SJ (2002a) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Grove SJ (2002b) Tree basal area and deadwood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol Indic 1:171–188

Hothorn T, Hornik K, Zeilis A (2006) Party: a laboratory for recursive part(y)itioning (2006). http://CRAN.R-project.org/. Accessed 20 August 2012

Jonsell M, Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of deadwood. Forest Ecol Manag 157:101–118

Koch Widerberg M, Ranius T, Drobyshev I, Nilsson U, Lindbladh M (2012) Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers Conserv 21:3035–3059

Larjavaara M, Muller-Landau HC (2010) Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. Can J Forest Res 40:2313–2321

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can J Forest Res 42:1433–1445

Larsson TB (Ed) (2001) Biodiversity evaluation tools for European forests. Ecol Bull 50:1–240

Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11:1027–1039

Martikainen P, Kaila L (2004) Sampling saproxylic beetles: lessons from a 10 year monitoring study. Biol Conserv 120:171–181

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94:199–209

Müller J, Bütler R (2010) A review of habitat thresholds for deadwood: a baseline for management recommendations in European forests. Eur J Forest Res 129:981–992

Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P, Ljungberg H, Mikusinski G, Ranius T (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecol Manag 161:189–204

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. Forest Ecol Manag 115:135–146

Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers Conserv 5:75–100

Päivinen J, Ahlroth P, Kaitala V, Suhonen J (2003) Species richness and regional distribution of myrmecophilous beetles. Oecologia 134:587–595

Parmain G, Dufrene M, Brin A, Bouget C (in press) Influence of sampling effort on saproxylic beetle diversity assessment. Implications for biomonitoring studies in European temperate forests. Agric Forest Entomol 15:135–145

Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91

Ranius T, Fahrig L (2006) Targets for maintenance of deadwood for biodiversity conservation based on extinction thresholds. Scand J Forest Res 21:201–208

Ranius T, Jansson N (2002) A comparison of three methods to survey saproxylic beetles in hollow oaks. Biodivers Conserv 11:1759–1771

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms : Fennoscandian boreal forests as an example. Ecol Bull 49:11–41

Siitonen J, Martikainen P, Punttilä P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecol Manag 128:211–225

Sippola A, Siitonen J, Kallio R (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish lapland. Scand J Forest Res 13:204–214

Stokland JN, Tomter SM, Söderberg GU (2004) Development of deadwood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti M (ed) Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. European Forest Institute, EFI proceedings n°51, pp 207–226

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in deadwood. Cambridge University Press, Cambridge

Turner WR, Tjørve E (2005) Scale-dependence in species-area relationships. Ecography 28:721–730

Vodka S, Konvicka M, Cizek L (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J Insect Conserv 13:553–562

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol Manag 255:1251–1261

Yoshimoto J, Kakutani T, Nishida T (2005) Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecol Res 20:405–414

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

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Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests

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ABSTRACT

Managing and monitoring forest biodiversity is challenging and rapid habitat assessment protocols should be developed to provide us with general key features based on field data.

A rapid habitat assessment protocol was implemented over a wide forest gradient in France to analyze surrogacy patterns and performance consistency of presumed key attributes for saproxylic beetle diversity (large trees, microhabitat-bearing trees with trunk cavities, fruiting bodies of saproxylic fungi, tree crown deadwood and sap runs, large logs and snags) and of stand openness. Data compiled in this study include standardized deadwood and window-flight trapped beetle data from 313 plots in oak, lowland and highland beech, lowland pine, highland spruce–fir and mixed temperate forests throughout France.

The most structuring factors for species richness and composition of saproxylic beetles were the density of cavity- or fungus-bearing trees and of snags, as well as the degree of openness in the 1-ha surrounding the stand. These key habitat features were nevertheless inconsistent over the different types of temperate forests, and for rare species vs. all species combined. No one variable robustly explained variations in species richness in the deciduous or conifer forest types.

The influence of deadwood and "habitat trees" was affected by meso- and micro-climatic features. A significant effect of stand openness on saproxylic beetles was observed both in deciduous and in conifer forests, but only in lowlands. Effects on species richness due to an interaction between substrate availability and openness were observed in montane forests only.

Our results point toward the relevance of ecological attributes in tracking changes in saproxylic beetle biodiversity in specific forest contexts, but our study failed to identify any universal structural biodiversity indicators which could be surveyed in part with data from national forest inventories and used to track progress in sustainable forest management or in the protection of sensitive areas.

1. Introduction

1.1. Saproxylic invertebrates as indicators of sustainable forest management

As early as 1988, the Council of Europe exhorted European governments to use prioritarily saproxylic organisms, i.e. those associated to deadwood and related microhabitats, in the evaluation of forest conservation status (Recommendations R(88)10 and 11). Since the 1990s in North America, Australia and many European countries, the fate of deadwood substrates in commercial forests has become an increasing concern in conservation planning and forest management where native species conservation and ecologically sustainable resource use are valued (Grove, 2002a,b). In recent years forest managers have also become increasingly aware of the role both of trees with special characteristics ("habitat trees") and of deadwood in maintaining a declining biodiversity (Harmon, 2001). In Europe, probably the best documented part of the world, saproxylic insects have been identified as a highly threatened group (Nieto and Alexander, 2010). Saproxylic beetles are the most well-studied species group and are commonly favored as indicators of response to deadwood management (Siitonen, 2001) for logistical and ecological reasons (well-known taxonomy, inexpensive trapping, high sensitivity to changes in forest conditions, a wide range of ecological requirements). However, detailed taxonomic surveys are often prohibitively expensive and time-consuming. Therefore quick and easy direct or indirect biodiversity

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indicators to monitor saproxylic beetle biodiversity should be explored.

1.2. *Rapid forest habitat assessment*

Managing and directly monitoring forest biodiversity is challenging due to (i) the large number of species, (ii) the hardness of species identification and (iii) the wide variety of species habitat requirements. Using indirect structural characteristics to evaluate biodiversity levels may therefore be useful (Lindenmayer et al., 2000) to produce (i) relevant biodiversity indicators, (ii) better targets for sustainable forestry and (iii) more effective selection criteria for conservation areas. Tews et al. (2004) and Lindenmayer et al. (2006) suggested using keystone elements as targets to improve and monitor eco-friendly forest management. Quick and easy methods have been suggested to survey these key elements and shortly describe the habitat of forest organisms (Venier and Mackey, 1997). Presumed key attributes are already used in national environmental standards for forestry certification (FSC and PEFC). From the literature and some census data, we surveyed the rapid habitat assessment protocols where field data at stand level (e.g. indicators of High Conservation Value Forest, Jennings et al., 2003; European forest scorecards, Sollander, 2000) are used to provide us with general key features. In Belgian forests, based on available field data from the state forest inventory, a standardized practical methodology has been developed to monitor certain important aspects of biodiversity that are both easily measurable and susceptible to changes through silvicultural practices (Van Den Meersschaut and Vandekerkhove, 2000). The methodology retains aspects of forest structure, tree species composition and deadwood features as biodiversity indicators. High scores are given to very large trees (>80 cm dbh), large snags and large logs, which are usually associated with a wide variety of microhabitats and have been acknowledged as being important to diversity. All these standards result from negotiations rather than ecological research. Following the Belgian methodology, we constructed a list of potential key habitat attributes for saproxylic beetles in temperate forests which we felt were appropriate in monitoring the impact of management on saproxylic resources and biodiversity.

1.3. *Presumed key factors for saproxylic biodiversity*

Our inventory of potentially relevant habitat attributes was based on their potential surrogacy value as shown in previously published environment-biodiversity studies. The deadwood components which are particularly at stake in managed forests were included. Some studies point out that the decline in deadwood quantity due to the negative impact of commercial forestry is stronger for some deadwood types, such as snags and large logs, than for the deadwood as a whole. From Sippola et al. (1998) for instance, snag density and large log density in managed stands in Finland were respectively only 7% and 5% of their normal levels in old-growth forests. Similarly, the density of microhabitat-bearing trees, sometimes called “wildlife trees” (Hodge and Peterken, 1998) or “habitat-trees” (Bäuerle and Nothdurft, 2011), is altered by forestry (Winter and Möller, 2008), in particular for certain microhabitat types such as cavities, cracks and lignicolous fungi (Larrieu et al., 2012).

In addition, several studies have demonstrated the importance for saproxylic beetles of large logs (Økland et al., 1996; Sverdrup-Thygeson, 2001), snags, microhabitat-bearing trees (e.g. Nilsson and Baranowski, 1994), very large trees (e.g. Grove, 2002a,b) and more general forest features such as canopy closure in the immediate substrate surroundings (Stokland et al., 2012). However, the consistency of these key features had not yet been studied over a wide range of forest types (conifer vs. deciduous, lowland vs. montane. . .).

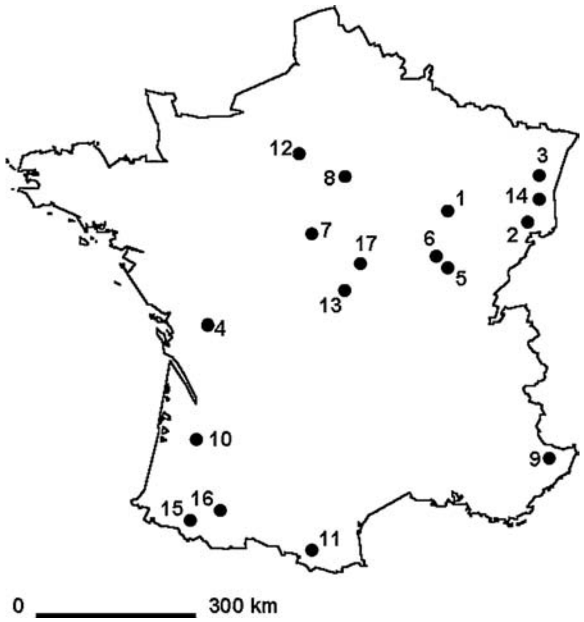

Fig. 1. Map of the 17 study forest regions in France (313 plots, 581 traps). The plots (point numbers) were part of the following datasets (between brackets is the number of plots): 1: Auberive (24), 2: Ballons-Comtois (16), 3: TaillisA (6), 4: Chize (24), 5: Citeaux (12), 6: Combe Lavaux (8), 7: Orleans (33), 8: Fontainebleau (25), 9: Mercantour (12), 10: Landes (19), 11: Orlu and Aston (18), 12: Rambouillet (60), 13: Troncais (34), 14: Ventron (8), 15: VFP (27), 16: Rebisclou (5), 17: TaillisB (20).

We used a rapid habitat assessment protocol to measure the density of large trees, microhabitat-bearing trees and large logs and snags, as well as stand openness, over a wide forest gradient in France. Analyzing the relationships between these environmental data and saproxylic beetle diversity (species richness and composition), we hoped to better understand surrogacy patterns of the presumed key attributes. From lowlands and highlands and in deciduous, coniferous and mixed forests in France, we tested the following set of questions:

1. With rapid habitat assessment, are selected key habitat features for saproxylic beetles consistent over temperate forests according to the dominant tree species?
2. Is the influence of deadwood and ‘habitat trees’ on biodiversity affected by meso-climatic (altitudinal level for beech) and micro-climatic features (stand openness)?
3. Are there critical thresholds at the stand scale in richness–environment relationships?
4. Are key habitat features consistent between rare species and all species combined?

2. Materials and methods

2.1. *Study areas, sampling design and stand characteristics*

This study is based on extensive data compiled from 17 ecological projects conducted by two French laboratories: the National Research Institute of Science and Technology for Environment and Agriculture (Irstea) and the Purpan Engineering School in a variety of French forests. We sampled 313 plots in 17 forest regions, i.e. large forests or groups of closed forests (Fig. 1). The forests in hilly regions and in plains were designated as “lowland forests” (<1000 m) and the montane and subalpine forests as “highland forests” (altitude variable). We distinguished six forest types based

Table 1
Sampling design of data compiled in this study, classified according to the main context variables: stand mixture, forest type and altitudinal level. Number of plots/traps (number of forest regions between brackets); for region number: see Fig. 1.

Stand mixture	Forest type	Highland	Lowland	Managed	Unharvested	Total	Forest regions
Coniferous dominated	Fir or spruce	31/37			31/37	31 (2)	9, 15
	Pine	2/2	27/43	27/43	2/2	29 (3)	10, 7, 9
	Total	33/39	27/43	27/43	33/39	60 (4)	
Deciduous dominated	Beech	22/36	47/94	39/72	30/58	69 (9)	1, 4, 6, 8, 17, 13, 2, 11, 15
	Oak	2/5	137/271	117/232	22/44	139 (12)	1, 4, 5, 6, 8, 10, 7, 12, 3, 17, 13, 16
	Total	24/41	184/365	156/304	52/102	208 (15)	
Mixed (coniferous and deciduous)	Beech-fir	20/37	1/2	19/37	2/2	21 (3)	14, 11, 2
	Oak-pine	1/1	23/35	23/35	1/1	24 (5)	4, 8, 10, 7, 13
	Total	21/38	24/37	42/72	3/3	45 (8)	
Total		78/118	235/445	225/419	88/144	313 (17)	

on the basal area of the dominant tree species: fir or spruce highland forests and lowland pine forests; (ii) deciduous-dominated (402 traps, 15 forest regions): beech or oak forests; (iii) mixed forests (79 traps, 9 forest regions): mainly beech-fir highland forests and oak-pine lowland forests (Table 1). Inside each forest, plots were distant of hundreds of meters from each other.

Overall, 75% of the traps were located in recently harvested plots. Eight forest regions included both managed plots and plots unharvested for more than 30 years, 3 forest regions unharvested plots only. This management factor was strongly unbalanced in coniferous-dominated (managed pine vs. unharvested spruce–fir plots) and in mixed plots (mostly managed).

2.2. *Beetle sampling and identification, species characterization*

Flying saproxylic beetles were caught in a total of 563 cross-vane flight interception traps (PolytrapTM) traps. A sampling plot was about 0.5 ha in size: 69 plots had one trap only, 239 plots had two traps, 4 plots had three traps and 1 plot had four traps. Inside each plot, multiple traps were set about 20 m from each other. The active insects were collected only one year from April to August; traps were suspended roughly 1.5 m above the ground. Saproxylic, i.e. depending "during some parts of their life cycle, upon wounded or decaying woody material from living, weakened or dead trees" (Stokland et al., 2012), beetles were identified to the lowest possible taxonomic level. The following 51 families were included in the analyses: Aderidae, Alexiidae, Anobiidae, Anthribidae, Biphyllidae, Bostrichidae, Bothrideridae, Buprestidae, Cantharidae, Cerambycidae, Cerophytidae, Cerylonidae, Ciidae, Cleridae, Corylophidae, Cucujidae, Curculionidae Scolytinae, Dermestidae, Elateridae, Endomychidae, Erotylidae, Eucinetidae, Eucnemidae, Histeridae, Laemophloeidae, Latridiidae, Leiodidae, Lucanidae, Lycidae, Lymexylidae, Melandryidae, Melyridae, Monotomidae, Mordellidae, Mycetophagidae, Nitidulidae, Nosodendridae, Oedemeridae, Prostomidae, Pyrochroidae, Salpingidae, Scarabaeidae, Scraptiidae, Silvanidae, Sphindidae, Tenebrionidae, Tetratomidae, Throscidae (Aulonothroscus only), Trogossitidae and Zopheridae. Staphylinidae and Cryptophagidae were not identified at the species level in all the elementary subsets due to the lack of available experts, and were therefore excluded before analysis. Rare species were defined as unabundant and only locally distributed, according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/).

2.3. *Live trees and deadwood measurements*

For the purpose of this study, forest conditions and potential key habitat features for saproxylic beetles were surveyed mainly during leaf-out according to a rapid stand description protocol (Larrieu and Gonin, 2008) in circular 1-ha plots centered around the traps.

We inventoried the number of large deadwood pieces (diameter >40 cm, length ≥ 1 m), distinguishing large standing deadwood pieces (LSDW) from large lying deadwood (LLDW), large live trees (LT, dbh $>$ 67.5 cm) and microhabitat-bearing live trees. We recorded four microhabitat types (Table 2): (i) "empty" cavities with or without mold (dcav), (ii) fruiting bodies of saproxylic fungi (dfun), (iii) sap runs (dsap), (iv) dead canopy branches and crown deadwood (dperdw). Microhabitats other than crown deadwood were only recorded when visible on the trunk. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. Because the leaf canopy may hinder observations of microhabitats and because microhabitats can occur on large branches as well as on the trunk, we expected an underestimation of their number for broadleaved tree species. The density of each individual microhabitat type was considered for analysis. The threshold dimensions for large trees and deadwood were inspired by results in Grove (2002b), Larrieu and Cabanettes (2012) and Nilsson et al. (2002).

We also assessed stand openness (open) as the total proportion of open areas (clearings, edges) with a well developed herb layer composed of flowering plants in the 1-ha plot.

2.4. *Data analysis*

Our analytical strategy was based on the structure of the sampling design. We divided the plots into six forest type categories: oak, lowland beech, highland beech, pine, spruce or fir, mixed, and conducted glm models for each category. We considered deadwood, microhabitats and stand features as predictor variables describing forest conditions (Table 2). Total species richness, species composition (incl. singletons), rare species richness and rare species abundance per trap were the response variables describing beetle assemblages. To avoid the deleterious effects of zero false negatives and the subsequent bio-geographical effects on our ecological investigations, the empty cells in the species-trap matrix were encoded "0" if the species was caught by at least one other trap in the same forest (i.e. the species belonged to the regional species pool). "NA" was entered in the empty cell if the species was absent from all the traps in the forest.

The influence of environmental variables on response variables was analyzed using a generalized linear mixed model, with a Poisson error distribution. Due to variations in the number of traps per plot, analyses were conducted at the trap level. Within-plot traps were not pseudo-replications, but repeated measures (Pinheiro and Bates, 2000), with spatial variables (forest region, plot) as hierarchical random factors, and with an observation-specific random

Table 2
Description of stand features (deadwood, microhabitats, large trees, stand openness) explored in the study.

Variable	Abbreviation	Meaning	Mean ± SE	Range
Large deadwood	LSDW	Number/ha of large standing deadwood (diameter > 40 cm)	2.91 ± 0.23	0–26
	LLDW	Number/ha of large lying deadwood (diameter > 40 cm)	5.74 ± 0.52	0–57
Large trees	LT	Number/ha of large trees (dbh > 67.5 cm)	8.62 ± 0.58	0–58
Microhabitats	Dcav	Number/ha of cavity-bearing trees: “empty” cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mold with an entrance above 10 cm in width	7.86 ± 0.55	0–161
	Dsap	Number/ha of sap-run-bearing trees: sap runs > 10 cm in length	0.37 ± 0.05	0–9
	Dfun	Number/ha of fungus-bearing trees: fruiting bodies of tough or pulpy saproxylic fungi, >5 cm in diameter	0.91 ± 0.08	0–10
	Dperdw	Number/ha of crown-deadwood-bearing trees (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	5.69 ± 0.56	0–37
Openness	Open	Open areas (clearings, edges, areas with a well developed herb layer composed of flowering plants) (%)	16.43% ± 1.61	0–100

intercept to account for possible overdispersion (Elston et al., 2001), and environmental variables as outer covariates. Multi-model-averaged estimates (Burnham and Anderson, 2002) determined the response of species richness or abundance to stand features. The most parsimonious model had the lowest Akaike AICc information criterion (Burnham and Anderson, 2002). For each response variable, we generated the null model and models with all the valid combinations of two explanatory variables. We calculated the differences in the AICc scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model. All models with $\Delta\text{AICc} < 2$ were used in order to figure out the model-averaged estimates weighted by the model weights. Only significant variables ($p < 0.05$) with a relative contribution (i.e. the weight of evidence across all the models) >0.05 were selected. Since co-linearity among predictor variables may lead to unreliable parameter estimates, we created correlation matrices to check for co-linearity between explanatory variables. No variables had to be removed from the modeling process. The set of non-collinear predictors used in the models included “forest.type” and eight other variables is described in Table 2.

Environmental differences between forest types expressed in mean values of the eight environmental variables were tested with a multiple comparison of means (Tukey contrasts) in a Generalized Linear Model (GLM) with a Poisson structure (R glht (multcomp) function). Between-class comparisons were conducted in separate series: (1) oak vs. beech, (2) pine vs. spruce–fir, and (3) lowland beech vs. highland beech.

Significant relationships in generalized linear models for total species richness were searched for thresholds. Threshold values were calculated by recursive partitioning and derived from estimates of breakpoints by means of maximally selected two-sample statistics (Hothorn et al., 2006). This method provides a conditional inference tree with p-values for one or more critical thresholds and a test procedure of their statistical significance. Only primary and significant ($p < 0.001$) thresholds are commented here. Based on 5000 bootstrap samples, 80% confidence intervals (to define ranges more tightly than 95% CI) were calculated for all thresholds.

Significant relationships in generalized linear models for total species richness were searched for interaction with stand openness. We performed multiplicative generalized linear mixed models, with stand openness and the density of the precise saproxylic key feature (deadwood or microhabitats) as fixed effects, with spatial variables (forest, plot) as hierarchical random factors, and with a Poisson error distribution.

A Canonical Analysis of Principal Coordinates (CAP, Anderson and Willis, 2003) was performed to investigate the effects of environmental variables on variations in species composition. The inertia was partitioned from Jaccard distance matrices on all explanatory environmental variables, since co-linearity among predictor variables is not a problem in CAP (Anderson and Willis, 2003). We calculated total constrained inertia, the constrained inertia which was not explained by spatial factors only (NSCI), the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance by means of permutation tests (100 runs), and the relative contribution of each variable to NSCI.

All analyses were carried out with R software v. 2.12.0 (lme4, vegan, MuMin, arm, party and boot packages).

3. Results

The dataset used for analyses included 149,419 individuals from 738 species. A higher mean number of species per trap was caught in deciduous (34.85 ± 0.68) than in coniferous (28.32 ± 1.38) or mixed plots (26.27 ± 1.92), in spruce–fir (33.21 ± 2.21) than in pine (24.28 ± 1.20) stands, in oak (38.54 ± 1.01) than in beech (27.06 ± 1.10) forests. A similar species richness was detected in highland (28.80 ± 3.20) and in lowland (27.06 ± 1.10) beech traps. On average per trap, the mean number of rare species was low, but higher in spruce–fir (mean = 3.67) than in other forest types (beech mean = 1.08, oak mean = 1.90, pine mean = 0.76, mixed mean = 1.0).

The ten factors used to describe the saproxylic environment (deadwood [2], microhabitats [4], large trees [1], stand openness [1], forest type [1], geography [1]) constrained 28% of the variation in species composition in oak data, 23% in lowland beech, 39% in highland beech, 36% in pine, 33% in spruce–fir and 46% in mixed data. Respectively 65%, 24% and 30% of this inertia was explained by the intrinsic effects of geographical factors in deciduous, coniferous and mixed forest data, undoubtedly due to the wide geographical range of the study. Overall, the nine non-geographical factors explained from 32% (oak) to 89% (spruce–fir) of the non-spatially constrained inertia (63% in lowland beech, 75% in pine, 76% in highland beech).

3.1. Contrasts in stand features between forest types throughout the sampling design

Contrasts in explanatory stand features were observed between forest types throughout the sampling design (Table 3). The densities of large lying and standing deadwood were higher in spruce–fir plots, than in beech and mixed plots and were strongly lower in

Table 3
Environmental differences between the main forest types investigated in the study (mean ± SE). Between-class comparisons were independently conducted in series (1) to (3).

		LLDW	LSDW	LT	dcav	dsap	dfun	dperdw	Open
Deciduous	(1) Oak	2.34 ± 0.199^{a}	1.19 ± 0.117^{a}	9.97 ± 0.668^{b}	5.70 ± 0.261^{b}	0.36 ± 0.046^{b}	0.98 ± 0.077	8.16 ± 0.436^{b}	14.72 ± 1.666^{b}
	(1) (3) Beech (lowland)	11.65 ± 1.715	3.98 ± 0.564	5.29 ± 0.796	7.06 ± 0.507^{a}	0.27 ± 0.050	1.06 ± 0.162^{a}	5.69 ± 0.740	5.96 ± 1.081
	(3) Beech (highland)	6.88 ± 0.667	4.19 ± 0.613	5.88 ± 1.587	33.81 ± 7.112^{b}	0.16 ± 0.062	1.97 ± 0.410^{b}	2.44 ± 0.465	6.57 ± 1.572
Coniferous	(2) Pine	0.62 ± 0.177^{a}	0.43 ± 0.167^{a}	0.70 ± 0.368^{a}	0.90 ± 0.368	0.16 ± 0.078	0.11 ± 0.055^{a}	1.39 ± 0.447^{a}	52.03 ± 6.950^{a}
	(2) Spruce–fir	19.92 ± 1.920^{b}	13.65 ± 1.157^{b}	16.76 ± 1.715^{b}	9.22 ± 1.374	0.57 ± 0.127	0.62 ± 0.171^{b}	2.95 ± 0.524^{b}	17.34 ± 3.653^{b}
	Mixed	6.405 ± 0.723^{b}	3.481 ± 0.446^{a,b}	7.911 ± 0.788^{a,b}	8.620 ± 0.932^{c}	0.456 ± 0.075^{a}	0.873 ± 0.176^{b}	2.785 ± 0.413^{c}	15.158 ± 3.022^{c}

Different letters a, b, c of superscript mean significant difference ($P < 0.05$), after a multiple comparison of means (Tukey contrasts) in a GLM model.

oak and then in pine plots. The openness reached higher values in pine plots, and then in spruce–fir, mixed and oak plots, than in beech plots. Values for the density of large trees were higher in spruce–fir than in oak plots, and then in mixed, beech and pine plots, in order of importance. The microhabitat attributes also differed in the different forest types. The density of cavity-bearing trees was higher in highland beech than in spruce–fir and mixed plots, and then in lowland beech, oak and pine plots in order of importance. The density of sap-run-bearing trees showed similar values in all contexts. There were more crown-deadwood-bearing trees in oak than in lowland beech plots, and then in spruce–fir, mixed and highland beech plots. The density of crown-deadwood-bearing trees was lower in pine plots. Fungus-bearing trees were more abundant in highland beech than in lowland beech, mixed and oak plots. They were scarcer in spruce–fir and then in pine plots. It should be kept in mind that pine plots were mostly located in lowland managed forests, whereas spruce–fir plots were all set in highland forest reserves (Table 1).

3.2. *Species richness*

The main environmental attributes affecting species richness differed among the forest types. The densities of large trees and sap-run-bearing trees never significantly drove species richness.

3.2.1. *Deciduous forests*

In lowland oak and beech forests the best models explaining species richness included the stand openness. In oak forests, a threshold was detected in the relationship between openness and richness ($T = 40\%$), but it had a wide 80% confidence interval [20–96%]. In beech forests, species richness was also positively influenced by the density of crown-deadwood-bearing trees. No threshold was found in the habitat-richness relationship for this habitat variable. The influential stand features for species richness were quite different in highland and lowland beech forests (Table 4). In highland beech forests, the density of cavity-bearing trees and large standing deadwood significantly affected species richness. No threshold in the deadwood-richness relationship was observed. However, the effect of cavity-bearing tree density on species richness did show a deflation threshold ($T = 21$, 80% IC = [16–28]). Nevertheless, it should be pointed out that the sample size was low to the right of the breakpoint value ($n = 10$).

3.2.2. *Coniferous forests*

In pine and spruce–fir forests species richness was positively influenced by an increasing density of cavity-bearing trees (Table 4). The significant response of species richness to cavity density showed a critical threshold at $T = 1$ (IC =]0–1]) in pine stands, which means that the number of saproxylic beetle species greatly increased as soon as there was at least one cavity-bearing tree in the 1-ha plot. In spruce–fir forests, the density of large standing and large lying deadwood and fungus-bearing trees also positively determined species richness. No thresholds were detected in habitat-richness relationships for these variables.

In mixed forests, the number of species was only influenced by the forest type (mainly oak-pine vs. beech-fir; effect estimate = 0.164, $p < 0.01$).

3.3. *Species composition*

Saproxylic beetle assemblages were driven differently by habitat features in deciduous, coniferous or mixed forests (Fig. 2). In beech forests, all habitat attributes except the density of crown-deadwood-bearing trees did significantly contribute to inertia: in

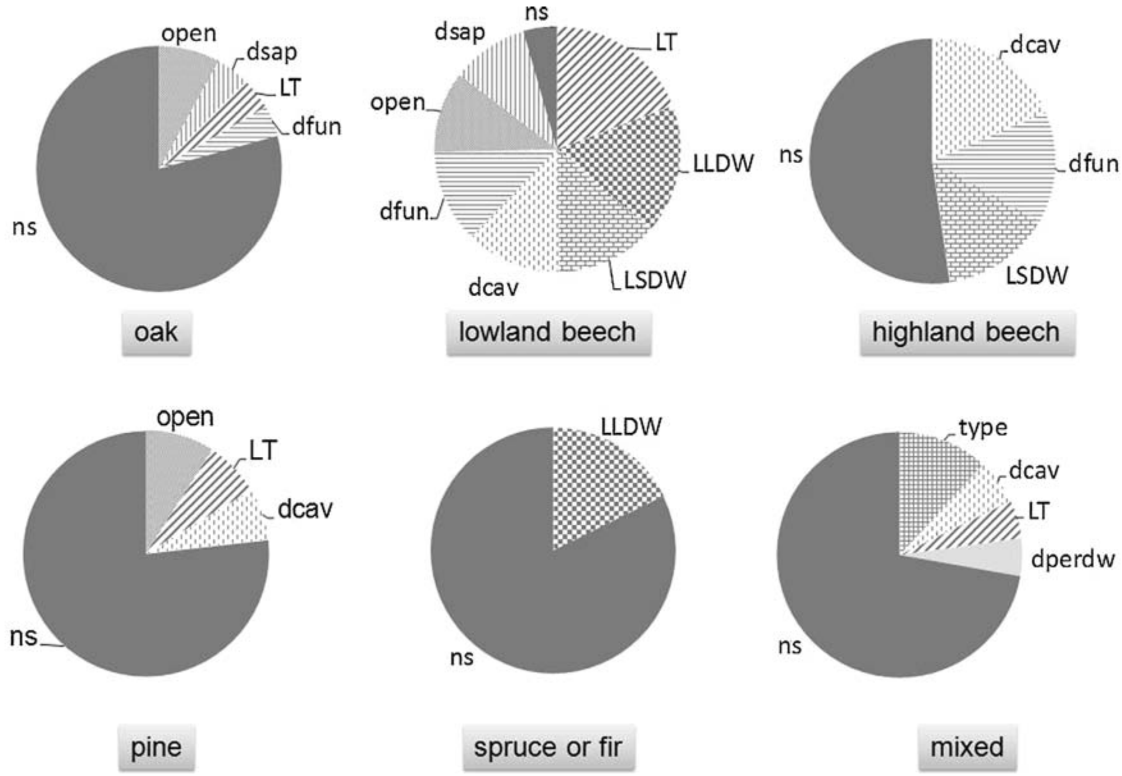

Fig. 2. Relative marginal contribution to the non-spatial constrained inertia (variation in the response species-plot matrix) of explanatory stand features (deadwood, microhabitats, large trees, openness) from Canonical Analysis of Principal coordinates (CAP). Variables: LSDW = number/ha of large standing deadwood, LLDW = number/ha of large lying deadwood, LT = number/ha of large trees, dcav = number/ha of cavity-bearing trees, dfun = number/ha of fungus-bearing trees, dperdw = number/ha of crown-deadwood-bearing trees, dsap = number/ha of sap-run-bearing trees, open = open areas (%) in a 1-ha plot; ns = variables with non-significant marginal contribution.

order of importance, density of large trees (19%), large lying deadwood (17%), large standing deadwood (13%), cavity-bearing trees (13%), fungus-bearing trees (12%), openness (11%) and sap-run-bearing trees (10%) (Fig. 2). Variations in assemblage composition were determined by openness (8%), sap-run-bearing trees (4%), large trees (4%) and fungus-bearing trees (4%) in oak plots. Only cavity-bearing trees (19%), fungus-bearing trees (15%) and large standing deadwood (15%) were significant drivers for species composition in highland beech stands. The species composition of saproxylic beetle assemblages was driven by openness (9%), large trees (7%) and cavity-bearing trees (7%) in pine stands, and by large lying deadwood (18%) in spruce–fir forests (Fig. 2). The forest type made the strongest contribution to inertia in mixed forests (12%), before cavity-bearing trees, large trees and crown-deadwood-bearing trees.

3.4. *Rare species*

Overall, inside a forest type, key habitat factors for species richness were not consistent for rare species and all species combined. In oak and highland beech forests, the density of large lying and standing deadwood positively influenced the abundance and the richness of rare species, respectively. In lowland beech and highland spruce–fir forests, the density of cavity-bearing trees positively affected the number of rare species individuals. In lowland beech plots, the density of fungus-bearing trees even significantly drove their species richness (Table 4). In lowland and highland beech forests, the density of sap-run-bearing trees was a pivotal feature for rare species abundance. An increasing density of crown-deadwood-bearing trees made the abundance of rare species increase in pine and mixed forests (Table 4).

3.5. *Interaction effects of deadwood and microhabitat variables with stand openness on species richness*

Only two microhabitat variables significantly interacted with stand openness to affect species richness. In highland beech and spruce–fir forests, the effects of cavity-bearing tree and fungus-bearing tree densities on species richness (see above) were strengthened by an increase in stand openness (interaction effect estimates +0.001, $p < 0.001$ and +0.003, $p < 0.001$, respectively).

4. Discussion

4.1. *Key factors for assemblage-habitat relationships*

Undoubtedly due to the wide geographical range of data compiled in our study – from continental to Atlantic contexts and from lowland to montane forests – most of the inertia was explained by the intrinsic effects of geographical factors. Notwithstanding this strong effect of forest regions, key habitat features for saproxylic beetles were not consistent over the different types of temperate forests. No common variable explained variations in species richness in the deciduous or conifer forest types explored in our study. Strong differences were also observed among dominant tree species. Density of cavities, presence of lignicolous fungi and snags, as well as the degree of openness in the 1-ha surroundings were the most convincing explanatory factors we found for saproxylic beetle species richness and composition in these French temperate forests.

4.1.1. *Importance of large logs*

In accordance with previous Scandinavian studies showing the importance of large logs for saproxylic beetles (Økland et al., 1996;

Table 4

Multimodel-averaged estimates for stand features (deadwood, microhabitats, large trees, openness) determining the response of saproxylic beetle species richness (SRtot), of rare species abundance (ABrare) and richness (SRrare) (mixed-effect models, with the forest as a random effect). Only significant responses (***$p < 0.001$, **$0.01 < p < 0.001$, *$0.05 < p < 0.01$) with a relative importance >0.05 were displayed. Variables: LSDW = number/ha of large standing deadwood, LLDW = number/ha of large lying deadwood, Dcav = number/ha of cavity-bearing trees, Dfun = number/ha of fungus-bearing trees, Dperdw = number/ha of crown-deadwood-bearing trees, open = open areas (%) in a 1-ha plot. The number/ha of large trees had no significant effect.

	Forest type	Deciduous			Coniferous		Mixed
		Oak	Lowland beech	Highland beech	Pine	Spruce or fir	All
Number/ha	Large lying deadwood pieces	ABrare = 0.149***				SRtot = 0.151*	
	Large standing deadwood pieces			SRtot = 0.389*** SRrare = 0.674*		SRtot = 0.295***	
	Cavity-bearing trees		ABrare = 1.205***	SRtot = 0.741***	SRtot = 0.332***	SRtot = 0.149** ABrare = 0.257*	
	Fungus-bearing trees		ABrare = 0.600*** SRrare = 0.470*			SRtot = 0.165**	
	Crown-deadwood-bearing trees		SRtot = 0.138**		ABrare = 0.846**		ABrare = 1.003***
	Sap-run-bearing trees		ABrare = 1.242***	ABrare = 1.524***			
	% open areas	SRtot = 0.171***	SRtot = 0.086*				

Sverdrup-Thygeson, 2001), we found that the local density of large logs was a significant and positive predictor of total species richness in the spruce–fir plots. Large log density also significantly affected the number of rare species in oak plots and species composition in lowland beech and spruce–fir forests. No effect of the density of large logs on local species richness was demonstrated at a 1-ha scale in our study, whereas we observed a positive and significant effect of the volume of large lying deadwood at a 0.3-ha scale in a companion study of lowland oak and beech forests only (Bouget et al., 2013). The availability of large-diameter well-decayed logs is known to affect many rare species of wood-decaying fungi (Kruys et al., 1999) and saproxylic beetles (Siitonen and Saaristo, 2000; Sverdrup-Thygeson, 2001).The ecological mechanisms underlying increased species richness in larger logs were discussed in Brin et al. (2011): substrate heterogeneity, microclimatic stability and buffering effect, life span of the deadwood piece, quantity of available resources per piece of deadwood and bark thickness.

4.1.2. *Importance of large snags*

In our study, the number of standing dead trees influenced assemblages even more than large lying logs did. Nevertheless, it should be noted that the positive effect of large snag density on richness occurred only in montane forests (beech and spruce–fir). In our montane beech plots, the density of large snags favored the number of rare species. It has already been evidenced that large standing deadwood is a key deadwood type for saproxylic beetles in Scandinavian forests (Nilsson et al., 2001; Jonsell and Weslien, 2003), with a high number of characteristic species (Brunet and Isacsson, 2009, Bouget et al., 2012). Red-listed species are often associated to large diameter deadwood, but also to snags (Stokland et al., 2012). It should be underlined that snags often bear microhabitats which are less frequent on live trees (e.g. Larrieu and Cabanettes, 2012 for fir).

4.1.3. *Importance of microhabitat density*

Even though it is well known that several saproxylic species depend more on microhabitats in habitat trees than on deadwood (Alexander, 2002), the influence of microhabitat densities on saproxylic beetle assemblages is badly known (but see Winter and Möller, 2008).

From our results, three microhabitats seem to play a pivotal role in beetle diversity. First, we found support for the important role cavity density plays in species richness in highland (beech and spruce–fir) and pine forests, but not in oakwoods. From our threshold analysis, we inferred that species richness in pine forests significantly increased as soon as the number of cavities in the neighboring ha exceeded one unit. In highland beech forests, where cavities are less scarce, the breakpoint was far higher (21 cavity-bearing trees per ha). Cavity density also positively affected the abundance of rare species in lowland beech and spruce–fir forests. Tree cavities are actually complex microhabitats which may combine several elementary microhabitats according to their volume, their exposure, their height on the tree trunk (and their connection to the soil), their type of internal decay and wood mold (Stokland et al., 2012). The higher their density, the higher their probable diversity. Secondly, in accordance with previous studies (e.g. Komonen and Kouki, 2005), we found that the density of trees bearing fruiting bodies of lignicolous fungi affected species richness in spruce–fir forests, species composition in deciduous forests (beech and oak) and abundance and richness of rare species in lowland beech forests. Thirdly, the density of crown deadwood was a significant driver for species richness in lowland beech, for species composition in pine and mixed forests, and for rare species abundance in mixed forests. This perched deadwood, more frequent in the crown of some tree species (e.g. oak) than in others (e.g. beech), is a poorly studied component of forest deadwood (Bouget et al., 2011). Finally, even though sap runs are known to provide a very specific microhabitat for sap feeders and mycophagous beetles (Yoshimoto et al., 2005), their density was here a minor factor for beetle diversity.

In our results, microhabitat-bearing trees far better explained saproxylic beetle assemblages than large trees. The density of large trees, whether or not they contain microhabitats, does not seem to be a relevant indirect surrogate for saproxylic beetle richness (contrary to Grove, 2002a,b). Tree diameter is actually an influencing factor for the frequency of cavities (Fan et al., 2003), the occurrence of certain rare microhabitats (Michel et al., 2011) and microhabitat number (Winter and Möller, 2008; Vuidot et al., 2011; Larrieu and Cabanettes, 2012) and density (Michel et al., 2011). Tree age may be a better driver for cavity occurrence (Ranius et al., 2009). Moreover, it would probably be more informative to define large trees using a variable diameter threshold according to the tree species and the soil fertility. Oak and beech trees grown on fertile soils often needs to be larger than 70 cm in diameter to be considered as mega-trees, which simultaneously host heterogeneous microhabitats and reflect ecological continuity (Nilsson and Baranowski, 1994; Kolström and Lumatjärvi, 2000).

In addition to the individual contributions of specific deadwood or habitat tree features we explored in our study, their interaction effects (neighboring or proximity effects) would be a promising field for future research.

4.2. The influence of deadwood and wildlife trees was affected by meso- and micro-climatic features

Our study confirms that canopy closure is an important attribute of the surrounding environment for saproxylic beetles (Stokland et al., 2012). Stand openness positively affected the species richness in lowland beech and oak forests. Canopy closure was also significantly structuring for species composition in lowland beech, oak and pine forests. These results were expected, as (i) numerous saproxylic beetle species live in sun-exposed dead wood (Lindhe et al., 2005) whereas others are known to prefer shady conditions (e.g. Brunet and Isacsson, 2009; Vodka et al., 2009), and (ii) open stands have generally shown higher species richness in northern nemoral (Ranius and Jansson, 2000; Brunet and Isacsson, 2009) and in temperate forests (Vodka et al., 2009; Hardersen et al., 2012).

This strong influence of openness on both species richness and composition could relate (i) to an ecological complementation effect: deadwood for larvae and nearby flowers for adults must both be present – the availability of flowers being a limiting factor; and/or (ii) to the micro-climatic effects of sun exposure on deadwood substrate quality (drier or moister, warmer or colder) or thermodynamic effects on the speed of insect development, which in turn influences habitat suitability.

It has been hypothesized that the effect of sun exposure is more structuring in northern boreal forests (Ranius and Jansson, 2000) than in temperate forests. We extended this mesoclimatic effect hypothesis to lowland vs. montane contexts; sun exposure should be more structuring in montane than in lowland forests due to sharper microclimatic effects induced by openness in colder montane conditions. This expectation was invalidated by our results, since the effect of stand openness only occurred in lowlands, even though average stand openness was only slightly higher in lowland (18%) than in montane plots (11%) in our data.

It should nevertheless be remembered that effects on species richness resulting from the interaction between substrate availability and openness were found only in montane forests. The greater the openness, the higher the positive effect of cavity and fungus density respectively on richness in highland beech stands and spruce–fir plots. In other words, in highland forests, more fungivore beetle species select sun-exposed, drier fruiting bodies (e.g. Komonen and Kouki, 2005) than they do shaded ones (e.g. Jonsell et al., 2001). Despite a raw openness effect in oak plots, we did not find any evidence of an interaction effect between canopy closure and deadwood or microhabitat density for oak. Inversely, the analyses by Widerberg et al. (2012) revealed that increased openness around large oak trees increases species richness and abundance of oak-associated beetles.

When comparing lowland and montane beech plots, we did not reveal any consistent driver for species richness. The density of crown deadwood (on average higher in lowland than in highland beech plots) or cavity-bearing beech trees (on average higher in highland than in lowland plots) actually affected species richness only in lowland or montane forests, respectively. The density of large snags did influence both species richness and the number of rare species, but only in montane forests, although average density values were the same in lowland and highland plots (contrary to Christensen et al., 2005). In agreement with Brunet and Isacsson (2010) who observed higher fungal activity in upland stands mainly due to higher precipitation, the density of polypore-bearing trees was higher in montane than in lowland beech forests. However, this parameter explained the abundance and richness of rare species in lowland plots only, where fungi were scarcer. These lowland/montane contrasts may be partly due to differences in deadwood profiles, resource scarcity and abiotic conditions in the two types of beech forests. For example,

4.3. Perspectives

From rapid habitat assessment, structuring factors for the species richness and composition of saproxylic beetle populations in French temperate forests were identified (density of cavity- and fungus-bearing trees, snags, degree of openness). These key habitat features were nevertheless inconsistent over different types of temperate forests, and for rare species vs. all species combined. No one variable robustly explained variations in species richness in the deciduous or conifer forest types.

To inspire relevant conservation measures, a rapid habitat assessment approach should be extended (i) to multi-taxonomic analyses, where other saproxylic groups (e.g. fungi) are included, and (ii) to forest types other than those explored in our study (e.g. highland larch and pine forests). More investigations could be led on mixed forests.

To improve our understanding of how key features can be used as surrogates for local biodiversity, further data should be explored.

First, more data on habitat-biodiversity relationships in naturally functioning forests is required to assess the surrogacy potential of our pre-defined key features. More reliable ‘authenticity parameters’ could be developed to evaluate ‘biological diversity potential’ rather than trying to determine precise surrogates for species richness itself (Dudley et al., 2005). Secondly, since saproxylic beetles are known to be affected by landscape structure (e.g. Økland et al., 1996), it would be useful to study how to aggregate local plot surveys, conducted at a 1-ha scale, into larger-scale parameters in order to analyze the effect of landscape-level habitat availability on local biodiversity. Thirdly, even though rapid habitat assessment only considers current habitat conditions, it would be informative to know if including data on the past continuity of the local deadwood supply strongly improves certain factors’ explanatory power.

Our results point toward ecologically-relevant indirect biodiversity indicators which can be partly surveyed using field data from updated national forest inventories. These indicators can be identified in the field without heavy reliance on specialists, and they resonate with the public and policy makers (Dudley et al., 2005). Assessing structural elements such as openness or elements related to stand maturity such as large deadwood or microhabitats, is much easier than inventorying the species themselves, and would make it easier for forest stakeholders to track progress in sustainable forest management or to monitor protected areas.

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References

Alexander, K., 2002. The Invertebrates of Living and Decaying Timber in Britain and Ireland – A Provisional Annotated Checklist. English Nature Research Reports, 467.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Bäuerle, H., Nothdurft, A., 2011. Spatial modeling of habitat trees based on line transect sampling and point pattern reconstruction. Can. J. Forest Res. 41 (4), 715–727.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the last biotic frontier: are temperate forest canopies special for saproxylic beetles? Forest Ecol. Manage. 261 (2), 211–220.

Bouget, C., Nusillard, B., Pineau, X., Ricou, C., 2012. Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. Insect Conserv. Divers. 5 (4), 264–278.

Bouget, C., Larrieu, L., Parmain, G., Nusillard, B., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers. Conserv. 22, 2111–2130.

Brin, A., Bouget, C., Brustel, H., Jactel, H., 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J. Insect Conserv. 15 (5), 653–669.

Brunet, J., Isacsson, G., 2009. Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. J. Insect Conserv. 13, 515–528.

Brunet, J., Isacsson, G., 2010. A comparison of the saproxylic beetle fauna between lowland and upland beech forests in southern Sweden. Ecol. Bull. 53, 131–139.

Burnham, K.P., Anderson, D.R. (Eds.), 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. , 2nd ed. Springer-Verlag, Berlin.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. Forest Ecol. Manage. 210, 267–282.

Dudley, N., Baldock, D., Nasi, R., Stolton, S., 2005. Measuring biodiversity and sustainable management in forests and agricultural landscapes. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360 (1454), 457–470.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X., 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology 122 (5), 563–569.

Fan, Z.F., Larsen, D.R., Shifley, S.R., Thompson, F.R., 2003. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. Forest Ecol. Manage. 179 (1–3), 231–242.

Grove, S.J., 2002a. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33, 1–23.

Grove, S.J., 2002b. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol. Indic. 1 (3), 171–188.

Hardersen, S., Toni, I., Cornacchia, P., Curletti, G., Leo, P., Nardi, G., Penati, F., Piattella, E., Platia, G., 2012. Survey of selected beetle families in a floodplain remnant in northern Italy. Bull. Insectol. 65 (2), 199–207.

Harmon, M.E., 2001. Moving towards a new paradigm for dead wood management. Ecol. Bull. 49, 269–278.

Hodge, S.J., Peterken, G.F., 1998. Deadwood in British forests: priorities and a strategy. Forestry 71, 99–112.

Hothorn, T., Hornik, K., Zeilis, A., 2006. Party: A Laboratory for Recursive Part(y)itioning, http://CRAN.R-project.org/

Jennings, S., Nussbaum, R., Judd, N., Evans, T., 2003. The High Conservation Value Forest Toolkit (Three Volumes). ProForest, Oxford.

Jonsell, M., Norlander, G., Ehnström, B., 2001. Substrate associations of insects breeding in fruiting bodies of wood decaying fungi. Ecol. Bull. 49, 173–194.

Jonsell, M., Weslien, J., 2003. Felled or standing retained wood – it makes a difference for saproxylic beetles. Forest Ecol. Manage. 175 (1–3), 425–435.

Kolström, M., Lumatjärvi, J., 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. Forest Ecol. Manage. 126, 113–120.

Komonen, A., Kouki, J., 2005. Occurrence and abundance of fungus–dwelling beetles (Ciidae) in boreal forests and clearcuts: habitat associations at two spatial scales. Anim. Biodivers. Conserv. 28 (2), 137–147.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., Ståhl, G., 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. Can. J. Forest Res. 29, 178–186.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can. J. Forest Res. 42, 1433–1445.

Larrieu, L., Cabanettes, A., Delarue, A., 2012. Impact of sylviculture on dead wood and on the distribution and frequency of tree microhabitats in Montane Beech-Fir forests of the Pyrenees. Eur. J. Forest Res. 131 (3), 773–786.

Larrieu, L., Gonin, P., 2008. L'Indice de Biodiversité Potentielle (IBP): une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. Rev. Forest. Fr. 6, 727–748.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131 (3), 433–445.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14 (4), 941–950.

Lindhe, A., Lindelöw, Å., Åsenblad, N., 2005. Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter. Biodivers. Conserv. 14, 3033–3053.

Michel, A.K., Winter, S., Linde, A., 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (Pseudotsuga menziesii var. menziesii). Can. J. Forest Res. 41 (2), 300–308.

Nieto, A., Alexander, K.N.A., 2010. European Red List of Saproxylic Beetles. Publications Office of the European Union, Luxembourg.

Nilsson, S.G., Baranowski, R., 1994. Indicators of megatree continuity – Swedish distribution of click beetles (Coleoptera: Elateridae) dependent on hollow trees. Ent. Tidskr. 115, 81–97.

Nilsson, S.G., Hedin, J., Niklasson, M., 2001. Biodiversity and its assessment in boreal and nemoral forests. Scand. J. For. Res. Suppl. 3, 10–26.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., Ranius, T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecol. Manage. 161 (1–3), 189–204.

Økland, B., Bakke, A., Hagvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers. Conserv. 5 (1), 75–100.

Pinheiro, J.C., Bates, D., 2000. Mixed-Effects Models in S and S-PLUS. Statistics and Computing Series. Springer-Verlag, New York, NY.

Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95, 85–94.

Ranius, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in penduculate oak (*Quercus robur*). Forest Ecol. Manage. 257, 303–310.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Siitonen, J., Saaristo, L., 2000. Habitat requirements and conservation of Phyto kolwensis, a beetle species of old-growth boreal forest. Biol. Conserv. 94, 211–220.

Sippola, A., Siitonen, J., Kallio, R., 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish lapland. Scand. J. Forest Res. 13, 204–214.

Sollander, E., 2000. European forest scorecards. WWF International, Gland, Switzerland.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in deadwood. Cambridge University Press, Cambridge.

Sverdrup-Thygeson, A., 2001. Can 'continuity indicator species' predict species richness or red-listed species of saproxylic beetles? Biodivers. Conserv. 10, 815–832.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31 (1), 79–92.

Van Den Meersschaut, D., Vandekerkhove, K., 2000. Development of a stand-scale forest biodiversity index based on the state forest inventory. In: Hansen, M., Burk, T. (Eds.), Integrated Tools for Natural Resources Inventories in the 21st Century. Gen. Tech. Rep. NC-212. St. Paul, MN, U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station, pp. 340–350.

Venier, L., Mackey, B.G., 1997. A method for rapid, spatially explicit habitat assessment for forest songbirds. J. Sustain. Forest 4, 99–118.

Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J. Insect Conserv. 13, 553–562.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144 (1), 441–450.

Widerberg, M., Ranius, T., Drobyshev, I., Nilsson, U., Lindbladh, M., 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers. Conserv. 21, 3035–3059.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol. Manage. 255 (3–4), 1251–1261.

Yoshimoto, J., Kakutani, T., Nishida, T., 2005. Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecol. Res. 20, 405–414.

Hoverfly (Diptera: Syrphidae) richness and abundance vary with forest stand heterogeneity: preliminary evidence from a case study in a montane beech fir forest

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Abstract

Hoverflies (Diptera, Syrphidae) are represented by 534 species in France. Members of this family provide crucial ecological services and are increasingly used as bioindicators in environmental assessment studies. Information on most Syrphidae is available regarding a wide range of life traits at the species level. However, literature on environmental requirements of forest hoverflies at the stand scale is very poor and understanding of the structure of local assemblages is weak. With the aim at exploring the "potential" key environmental requirements for hoverfly assemblages at the stand scale in montane beech-fir forest, we used French Pyrénées data from Malaise traps deployed in three stands selected to represent a wide range of structural heterogeneity, in terms of vertical structure of vegetation, tree diversity, deadwood and tree-microhabitats. We assessed hoverfly assemblages by surveying species richness, abundance and functional diversity. Malaise traps produced 2374 hoverflies belonging to 104 species. Strictly forest species were only present in the most heterogeneous stand. Species richness, abundance and functional diversity decreased dramatically in the less heterogeneous stands.

Keywords

Abies alba; deadwood; Diptera Syrphidae; *Fagus silvatica*; functional diversity; tree-microhabitats; stand heterogeneity

1-Introduction

Hoverflies (Diptera, Syrphidae) are represented by 534 species in France (Speight et al., 2013). Larvae display a large array of feeding habits and participate in deadwood recycling (Speight, 1989), and processes that regulate pests (Chambers & Adams, 1986; Tenhumberg & Poehling, 1995). Adults of all the species are floricolous and provide pollination services, even for trees and shrubs (Groot & Bevk, 2012). Preserving the highest possible species richness of such important biological groups from a functional point of view appears to be of the utmost importance in the current context of global change, given the general agreement of the insurance hypothesis (Yachi & Loreau, 1999; Tscharntke et al., 2012).

The Syrph the Net database (Speight et al., 2013) gives a wide range of life traits at the species level. However, despite the popularity of hoverflies among naturalists and their use as indicator species at the landscape scale (Sommaggio & Burgio, 2003) or for the identification of forests of conservation value (Speight, 1989; Good & Speight, 1996), literature on environmental requirements of forest hoverflies at the stand scale is very poor and understanding of the structure of local assemblages is weak (Keil & Konvicka, 2005). Notable contributions in this area have been provided by Humphrey et al (1999), who highlighted correlation between vertical stand structure and hoverfly diversity; and Fayt et al., (2006) who found that saproxylic assemblages may be constrained by occurrence of rich herb layer which provides the floral resources required for their reproduction.

Beech–fir (*Fagus silvatica* L. – *Abies alba* Mill.) forest is a dominant forest type in the bioclimatic montane level of most European mountain ranges, and cover 380,000 km^2 (4 % of the European forest area) (MCPFE, 2007; Euforgen, 2012). These forests are of great economic value, but they are also known for their key role in the conservation of forest biodiversity. Indeed, Müller et al. (2012) showed that beech-dominated forests are an umbrella habitat for central European saproxylic beetles since 70 % of these species can be found in such forests. Anthropization strongly impacts structural heterogeneity of beech-fir stands, and Metaillé (2001) showed that ancient management practices reduced their dendrological diversity by favoring beech at the expense of fir. Further, some authors have highlighted that current management (i) dramatically disturbs the structure and the dynamics of the deadwood stock (Larrieu et al., 2012), (ii) disturbs tree-microhabitat assemblages (Larrieu et al. 2012) and (iii) reduces the number of microhabitat bearing trees (Winter & Möller, 2008, Larrieu et al., 2014).

This preliminary study explores the key environmental requirements for hoverfly species at the stand scale in montane beech-fir forests. It compares hoverfly assemblages of three stands with contrasted management histories, resulting in different structural heterogeneities, in the same forest to control for the other environmental variations.

2-Materials and methods

21-Stands studied and measurement of structural features

The three stands studied are located in the same forest massif in the foothills of the central Pyrenees (WGS 84, Lat/Lon: 43 N/0.34 E). They are natural habitats of montane beech-fir forest (*Fagion sylvaticae,* Bardat et al., 2004). Since limestone is the dominant substrate, soils are rich. All the stands studied belong to ancient forest and are referred to in ancient maps “Etat major” realized during the second part of the 19th century, which corresponds in France to the period of minimum forest area (Dupouey, 2007).

We studied three stands differentiated by their structural patterns, essentially linked with management (Table 1). “UnHarv100” was the most mature beech-fir stand with no logging since 1900. ‘‘UnHarv50” was mostly dominated by beech, in a zone logged by a gravity cable technique in 1960 and unmanaged afterwards. “Harv” was mostly dominated by beech and regularly logged over the last 25 years. Observations were carried out between 2003 and 2005 on a sample of 29 plots (Table 1). All plots were set up based on an approach of relascope sampling using a Bitterlich relascope (Bitterlich, 1984). To correctly incorporate the variability of each stand, each one of them was sampled with 9–11 plots. The plot surface was 0.3 ha on average.

We finely described structural heterogeneity of the stands, in terms of vertical structure of vegetation, tree diversity, deadwood and tree-microhabitats. We used the stratiscope method (Blondel & Cuvillier, 1977) to describe the spatial heterogeneity of foliage distribution, both vertically and horizontally. Vegetation layers were surveyed on seven points separated each other from 5 m on horizontal transects centered on the plot. All foliage contacts with a virtual vertical cylinder of 50 cm of diameter were noted throughout 4 layers (<1m, 1-7m, 7-20m and ≥20m). Nine hundred thirty seven living trees and 281 dead wood objects (high stumps (0.5m<h <1m), snags (standing deadwood with h>1m) and logs) were observed individually (Table 1). All the living trees included in the relascope sampling were identified to species level and measured for the diameter on the outside of the bark, at breast height (dbh). The tree trunks were carefully examined from the ground to the top of the canopy, and eight microhabitats observed on the visible part of the trunk both beneath and within the tree crown were recorded: (1) four cavity types on living trees and snags; (2) cracks in the tree trunk, on living trees and snags; (3) dendrothelms on living trees; (4) sporophores of polypores, on living trees, snags and logs. Each tree or wood item inventoried was classed in relation to the absence or presence of sporophores, without estimating their numbers; (5) missing bark only on living trees. In addition to microhabitats, we observed dead wood. All dead wood items were identified and measured in length and in girth beyond a diameter of 20 cm at the smallest extremity. The diameter was measured in the middle for logs and snags of under 4 m, at the cut for high stumps, and at breast height for snags of over 4 m. Deadwood items were classed on a decay scale of five levels (Table 1 SI in Supporting Information). See Larrieu et al. (2012) for details.

Table 1. Main characteristics of the study stands and sampling design (CI=95% confidence interval)

Stand	Management history	Basal area G (m^2/ha) standing deadwood + living trees Mean[CI]	Studied area (ha)	Number of plots	Number of live trees observed	Numbers of dead wood items observed	Diameter at breast height (cm) mean (min-max)	
							beech	fir
UnHarv100	Not logged since 1900	40[33-48]	23	10	371	84	62.9 (15.9-127.3)	44.4 (8.0-124.1)
UnHarv50	Intensively logged in 1950 and not logged since	36.5[32-42]	20	9	286	124	42.8 (17.5-87.5)	43.3 (20.7-82.8)
Harv	Logged twice by selective logging in the last 20 years (total logged volume=50 m^3 ha^{-1})	35[31-39]	22	10	280	73	45.6 (4.8-73.2)	11.1 (11.1-11.1)

2.2-Hoverfly sampling and definition of functional groups and guilds

Hoverflies were sampled using two Malaise traps per stand. Sampling was conducted fortnightly from May to October in 2004 and 2007. All the samples were identified to the species level.

Using Syrph the Net database (Speight et al., 2013), we defined guilds relative to (1) forest dependency (strictly, optionally, or strictly not forest species for the reproduction), (2) migration behavior (strongly, weakly or non migrant) and (3) commensalism (yes or not). We added functional groupings, regarding (4) larvae feeding behavior (on living plants, on living animals, saproxylic) and (5) adult feeding behavior (pollen and nectar gathered on flowers or on leaves, Homopteran honeydew) (see details in Table 2 SI). Syrph the Net indicates quality of relationship between the life-trait and the species with a fuzzy coding system, from blank which means no association to 3 for a maximum association. In this study, we have only used the code 3.

To characterize variations in hoverfly assemblages between stands, we calculated for each of them species richness, abundance and diversity of the whole community and of guilds and functional groups. For analysis, we pooled the data from the two traps and the two sampling years per stand.

2.3-Calculations and statistical procedures

All analyses were performed using the statistical software R 3.0.2 (R Development Core Team, 2014).

Functional diversity (FD) was estimated in accordance with indications from Petchey and Gaston (2006), realising a dendrogram on the base of the life trait distance matrix (Jaccard distance, *vegan* package; Oksanen et al., 2013), for all the species observed in the study. The total length of dendrogram branches was calculated as for “phylogenetic diversity” (*picante* package, Kembel et al., 2014) for the dendrogram corresponding to all the species observed in the study (forest FD) as well as for assemblages of species observed in each stand. Results have been standardised by expressing them as percentage of the forest FD. Ratios FD/species richness (RS) have been calculated to express the functional redundancy of species belonging to the same group: the higher the ratio is, the smaller the functional redundancy.

3-Results

3.1-Stands characteristics

3.1.1- Dendrometrical structure and dendrological diversity

The dendrometrical structure of the stands studied was irregular at UnHarv100 and almost regular at the two others (Fig. 1 SI). UnHarv100 was mixed stand: beech and silver fir dominated (95 % of the standing volume), but five secondary tree species were present (*Acer campestre* L., *A. platanoides* L., *Prunus avium* L., *Taxus baccata* L. and *Tilia platyphyllos* Scop.). A species-rich herb layer was well developed, mostly in clearings. All classes of dbh were represented with 18 very large trees (VLT: dbh>70 cm) per ha. UnHarv50 was dominated by beech, with regularly sized Medium Trees (only 2 VLT/ha). Harv was almost pure beech stand, with regularly sized Medium/Large Trees (1 VLT/ha), structured in two vegetation strata since the lower layer was full of saplings and Small Trees. The average basal area (G) of the stands ranged from 23 to 38 m^2/ha.

UnHarv100 had a foliage structure (Fig. 1, left part) characterized by the four upper layers more than 70 % full and the lower layer showed an alternation of herbaceous species and litter. No vertical transect showed none contact (Fig. 1, right part), since herbaceous species filled clearings. Shrubs occupied a part of the layer 2, supplying flowers, at least in clearings. UnHarv50 and Harv had less heterogeneous structure than UnHarv100, with low cluttered state within the intermediate layer (layer 3). In these stands, the lower layer was essentially occupied by beech seedlings while shrubs were rare and the distribution of vertical contacts of vegetation showed numerous vertical transects with proportion of contacts lower than 20 %.

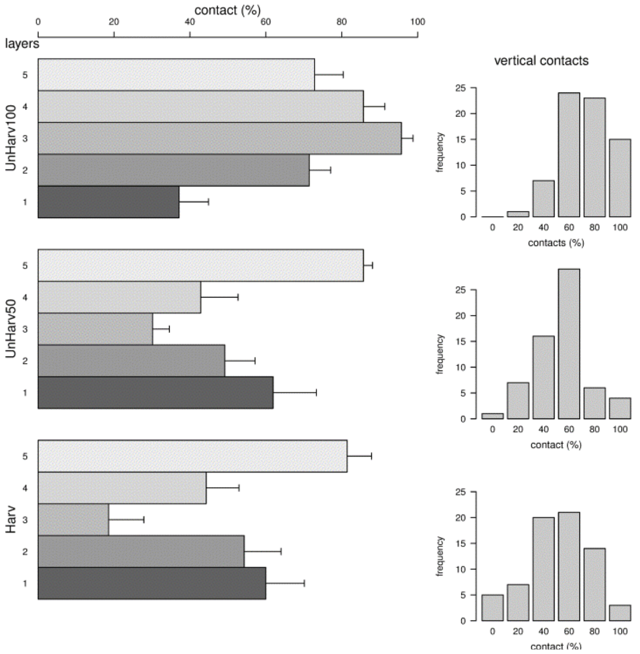

Figure 1. Foliage distribution in the three beech-fir stands studied (Harv, UnHarv50 and UnHarv100). For each stand is indicated, on the left, the % of contact per layer (layer 1: contact between ground and 1 m; 2: 1-7m; 3:7-20m; 4: over 20m) and, on the right, the distribution of the vertical contacts, all layers pooled

3.1.2- Deadwood and tree-microhabitats

The total volume of deadwood was highly lower in Harv (9 m^3 ha^{-1}, standard error SE=2.34) than in UnHarv50 (55 m^3 ha^{-1}, SE=12.73) and UnHarv100 (32 m^3 ha^{-1}, SE=8.38). In Harv, the standing dead wood was mainly represented by high stumps (96%). Patterns of volume distribution of the deadwood decay stages were very different for the three stands: the main decay stage was the 4th one at UnHarv100, the 2nd one at UnHarv50, and all decay stages were present in these stands. In Harv, only decay stages 3 and 4 occurred in the field.

The comparison of the stand types showed strong differences for microhabitat density of dendrothelms (more frequent at Harv), cracks (less frequent at Harv), saproxylic fungi (less frequent at Harv) and missing bark (more frequent at Harv and UnHarv50 than at UnHarv100) (Table 3 SI).

3.2-Hoverfly assemblages

3.2.1- Species richness and abundance

In total, 2374 hoverflies were recorded from the Malaise interception traps in the three stands during the two years (Tables 2 and 3). They were identified as belonging to 46 genera and 104 species. Fourty four species were caught at only one stand-year: 32 species only in UnHarv100, 11 only in UnHarv50, and only one species only in Harv. Eleven species were found both years in a single stand: 10 in UnHarv100, one in UnHarv50 and zero in Harv. The species strictly associated to fir, such as *Blera fallax* (Linné, 1758) and *Rhingia borealis* (Ringdahl, 1928) have not been observed in Harv.

Per stand, the highest numbers of both species and individuals were observed in UnHarv100, and the lowest in Harv, both in 2004 and 2007 (Fig. 2).

Table 2. Hoverfly assemblages in the three stands studied

Species	UnHarv100	UnHarv50	Harv	Species	UnHarv100	UnHarv50	Harv
Arctophila bombiforme	1	1	0	*Eupeodes bucculatus*	1	0	0
Arctophila superbiens	1	0	0	*Eupeodes corollae*	1	1	1
Baccha elongata	1	1	1	*Eupeodes latifasciatus*	1	1	0
Blera fallax	1	1	0	*Eupeodes luniger*	1	1	1
Brachyopa dorsata	1	1	0	*Ferdinandea cuprea*	1	1	0
Brachyopa pilosa	1	0	0	*Helophilus pendulus*	1	1	0
Brachyopa scutellaris	1	0	0	*Lapposyrphus lapponicus*	1	1	1
Brachyopa vittata	1	0	0	*Melangyna lasiophthalma*	0	1	0
Brachypalpoides lentus	1	1	0	*Melangyna umbellatarum*	1	0	0
Brachypalpus laphriformis	1	1	1	*Melanogaster hirtella*	1	0	0
Caliprobola speciosa	1	1	0	*Melanostoma mellinum*	1	1	1
Chalcosyrphus nemorum	1	1	1	*Melanostoma scalare*	1	1	1
Cheilosia aerea	1	0	0	*Meligramma cincta*	1	1	1
Cheilosia albipila	1	0	0	*Meliscaeva auricollis*	1	1	1
Cheilosia albitarsis	1	1	0	*Meliscaeva cinctella*	1	1	0
Cheilosia carbonaria	0	1	0	*Microdon analis*	1	0	0
Cheilosia fasciata	1	0	0	*Microdon mutabilis*	1	0	0
Cheilosia flavipes	1	0	0	*Myathropa florea*	1	1	1
Cheilosia fraterna	1	1	0	*Neoascia podagrica*	1	0	0
Cheilosia lenis	0	1	0	*Paragus haemorrhous*	1	0	0
Cheilosia proxima	1	0	0	*Paragus pecchiolii*	1	0	0
Cheilosia scutellata	1	0	0	*Parasyrphus punctulatus*	1	1	1
Cheilosia soror	1	1	0	*Pipiza bimaculata*	0	1	0
Cheilosia urbana	1	0	0	*Platycheirus albimanus*	1	1	1
Cheilosia variabilis	0	1	1	*Platycheirus ambiguus*	1	0	0
Cheilosia vernalis	1	0	0	*Platycheirus europaeus*	1	0	0
Cheilosia vicina	1	1	0	*Platycheirus scutatus*	1	1	0
Cheilosia vulpina	1	0	0	*Rhingia borealis*	1	0	0
Chrysotoxum bicinctum	1	1	0	*Rhingia campestris*	1	0	0

Chrysotoxum cautum	1	0	0	*Rhingia rostrata*	1	1	1
Chrysotoxum elegans	1	0	0	*Scaeva pyrastri*	0	1	0
Chrysotoxum fasciatum	0	1	0	*Scaeva selenitica*	0	1	0
Chrysotoxum festivum	1	0	0	*Sericomyia silentis*	1	1	1
Chrysotoxum vernale	1	0	0	*Sphaerophoria interrupta*	0	1	0
Criorhina asilica	1	1	0	*Sphaerophoria scripta*	1	1	1
Criorhina berberina	1	1	1	*Sphegina clunipes*	1	1	0
Criorhina floccosa	0	0	1	*Sphiximorpha subsessilis*	0	1	0
Dasysyrphus albostriatus	1	0	0	*Syrphus ribesii*	1	1	1
Dasysyrphus friuliensis	0	1	0	*Syrphus torvus*	1	1	0
Dasysyrphus venustus	1	1	0	*Syrphus vitripennis*	1	1	0
Didea fasciata	1	0	0	*Temnostoma bombylans*	1	1	1
Epistrophe eligans	1	0	0	*Temnostoma meridionale*	1	1	0
Epistrophe flava	1	1	0	*Temnostoma vespiforme*	1	1	0
Episyrphus balteatus	1	1	1	*Volucella inflata*	1	0	1
Eristalis jugorum	1	0	0	*Volucella pellucens*	1	0	1
Eristalis nemorum	1	0	0	*Xanthandrus comtus*	1	0	0
Eristalis pertinax	1	1	0	*Xanthogramma citrofasciatum*	0	1	0
Eristalis similis	1	1	0	*Xanthogramma laetum*	1	0	0
Eristalis tenax	1	0	0	*Xylota florum*	1	0	0
Eumerus flavitarsis	1	0	0	*Xylota segnis*	1	1	0
Eumerus grandis	0	1	0	*Xylota sylvarum*	1	1	0
Eumerus ornatus	1	0	0	*Xylota triangularis*	1	0	0

Table 3. Species richness and abundance of species in the three stands, in 2004 and 2007

	UnHarv100	UnHarv50	Harv
Nb of species - 2004	69	54	17
Nb of species - 2007	69	30	14
Nb of species - Total	90	60	24
Nb of individuals - 2004	911	491	52
Nb of individuals - 2007	801	82	37
Nb of individuals - Total	1712	573	89

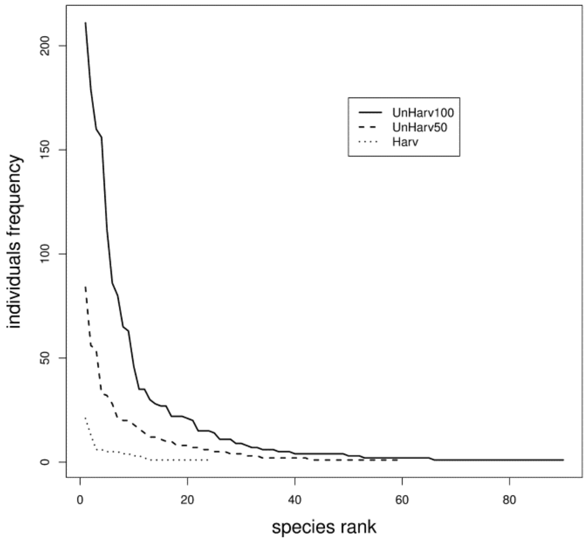

Figure 2. Abundance of hoverfly species (decreasing order) in the three beech-fir stands studied (Harv, UnHarv50 and UnHarv100)

322-Distribution of guilds and functional groups in the three stands

The species richness within the guilds and functional groups was always ranked in the following order: UnHarv100, UnHarv50, then Harv (Table 4 SI and Fig. 3). Strictly forest species were only present in UnHarv100. Further, there was a large difference in abundance between the stands, with the same rank order.

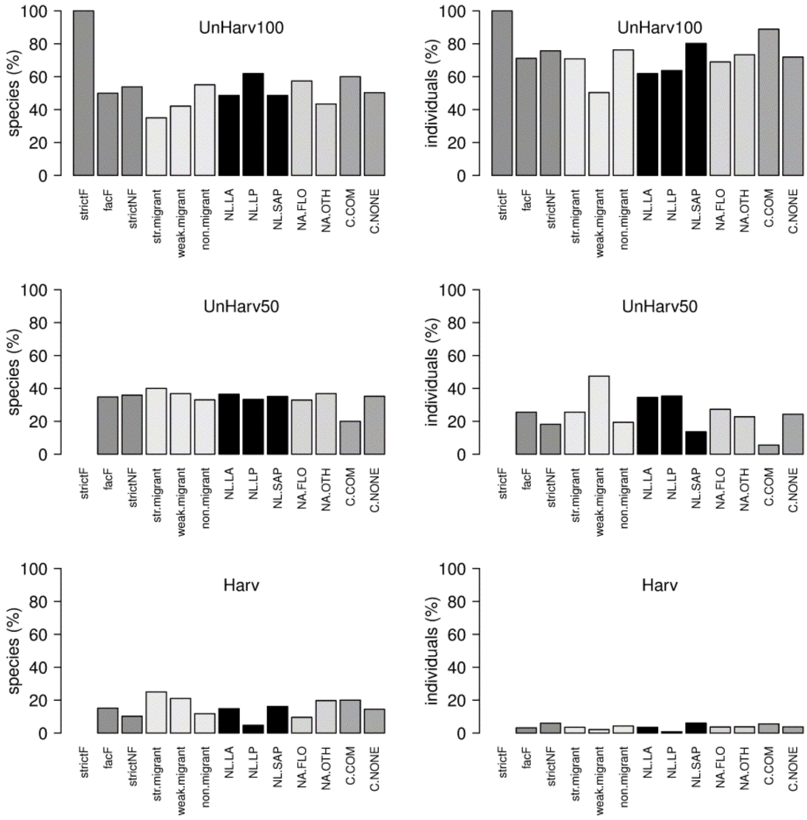

Figure 3. Distribution per stand of the number of hoverfly species (left) and individuals (right), expressed by the proportion of total amount per guild or functional group. strctF: strictly forest species for the reproduction, facF: optionally forest species for the reproduction, strctNF: strictly non forest species for the reproduction; str.migrant: strongly migrant species, weak.migrant: weakly migrant species, non.migrant: non migrant species; C.COM: commensal species, C.NONE: non commensal species; NL.LA: zoophagous larvae, NL.LP: phytophagous larvae, NL.SAP: saproxylic larvae; NA.FLO: adults feeding on pollen and nectar gathered on flowers, NA.OTH: adults feeding on pollen gathered on upper surface of leaves or feeding on sap-runs. See Table 2 SI for guild and functional group description

3.2.3-Functional diversity

FD appeared to be positively correlated to species richness (RS). Both FD and SR decreased dramatically from UnHarv100 to Harv but not in the same proportion. Indeed, FD/RS ratio increased from UnHarv100 (1.11) to UnHarv50 (1.31) then Harv (1.96) (Table 4).

Table 4. Specific richness (SR) and functional diversity (FD) for the three studied stands, expressed as percentages of the total observed for the forest

Stands	SR (%)	FD (%)
UnHarv100	86.54	95.96
UnHarv50	57.69	75.30
Harv	23.08	45.18

4-Discussion

4.1-Structural heterogeneity of the stands

Only UnHarv100 had a structural heterogeneity close to the one observed in sub-natural stands, i.e. complex vegetation structure, high dendrological diversity, numerous very large trees and typical patterns of deadwood and microhabitats (Greenberg et al., 1997; Nilsson et al., 2002; Christensen et al., 2005; Larrieu et al., 2012, 2014). UnHarv50 had a lesser complex vegetation structure and a lesser dendrological diversity with only occasional firs. Harv showed the simplest structure, with a great dominance of beech, a very low deadwood amount and a lack of several deadwood decay stages. Moreover, it showed densities of microhabitats very different than those observed in sub-natural stands (Larrieu et al., 2014). We observed in the field that beech regenerates easily in the studied context (i.e. montane level, rich soils), and abundant seedlings occur within beech-dominated stands when the basal area is lower than 35 m², which is generally the case in UnHarv50 and Harv. At UnHarv100, we also observed that fir and very large trees slackened the growth of beech seedlings, and stand maturity favored large open areas where a diversity of shrubs and herbaceous species display flowers from spring to autumn.

4.2-Hoverfly assemblages and functional diversity

All the guilds and functional groups were represented in the three stands, except the one of strictly forest species, observed only in UnHarv100. We observed a dramatically decrease of species richness and individual abundance amongst guilds and functional groups from UnHarv100 to UnHarv50 then Harv, except for the guild of strongly migrant species. Huston (1994) indicated that the first result of habitat's structural heterogeneity enhancement is an increase in the number of functional groups, then an increase in the number of species within each functional group. It seems that even at Harv, the structural heterogeneity is high enough to support roughly the same composition in functional groups or guilds than at UnHarv100. However, the diminution of structural heterogeneity from UnHarv100 to Harv is of sufficient magnitude to lead to a strong decrease in the diversity of hoverfly assemblages. In our case, an increasing anthropization remanence could have resulted in a significant reduction of stands' structural heterogeneity that could significantly have weakened functional redundancy between species and individuals. This might impair the potential resilience of the stands UnHarv50 and above all Harv in the face of perturbations, which has to be considered as a threat from the insurance hypothesis viewpoint (Yachi & Loreau, 1999). In addition, this demonstrates that, in the case of hoverflies, the consideration of only the simple composition in functional groups or guilds is inappropriate. Decrease of structural heterogeneity, by leading species disappearances, could have cascade-step consequences since these disappearances can also cause, themselves, the decrease of structural heterogeneity (Therriault & Kolasa, 2000).

UnHarv100 offered the biggest proportion of very large trees and Reemer et al. (2005) demonstrated that an increase in the average age and size of living trees plus the conservation of overmature and dead trees led to a spatial spreading of hoverfly saproxylic species. Furthermore, under-storey tree and shrub species were also more various in UnHarv100 than in UnHarv50 and above all Harv. It could explain the higher species richness of aphidophagous and foliage or root-linked hoverflies we observed there (Speight et al., 2013). Only UnHarv100 displayed a species-rich herb layer. This layer could explain on the one hand the richest and most abundant phytophagous and zoophagous hoverfly communities, and, on the other hand, the richest and most abundant flower-visiting and 'others'-visiting ones (Speight et al., 2013). In the same way, Fayt et al. (2006) found that a well developed and species-rich herb layer in open stand with large trees is the main factor supporting saproxylic hoverflies in beech and oak forests.

FD measures the functional trait diversity within assemblages and hence is a biodiversity component (Petchey & Gaston, 2006), determining ecosystem processes (e.g. Loreau et al., 2001). FD allows analyzing assemblage variations in terms of alteration of ecosystem properties (Loreau et al., 2001). Functional diversity proved to be very representative of the general trend observed between the stands through species richness and abundance, but, in our stand sample, decreased more slowly than species richness. As species richness and FD are positively correlated (Petchey & Gaston, 2006), Harv retained a medium FD despite the low species richness and abundance we observed, since most of guilds and functional groups were represented. The method we used to calculate FD does not take into account the species abundance which might partly ensure the effectiveness of ecological service provided by the functional group.

5-Conclusion

Since our results were highly contrasted, emphasizing the relevant bioindicator side of hoverflies, they encourage further biodiversity studies which should be conducted in a larger stand sample and in other forest types, e.g. in lowland and/or fragmented forest contexts. It would also be advisable to conduct such surveys using emergence traps in addition to Malaise traps. Since abundance was the most sensitive variable to structural changes in our study, we recommend that this variable be recorded in future hoverfly surveys. Furthermore, as flowers seem to be key feature, a more precise survey of the diversity of shrub and herb layers should be conducted during the hoverfly sampling period.

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References

Bardat J., Bioret F., Botineau M., Boullet V., Delpech R., Géhu J.M., Haury J., Lacoste A., Rameau J.C., Royer J.M., Roux G. & Touffet J. 2004: *Prodrome des végétations de France*. MNHN, Paris.

Bitterlich W. 1984: *The relascope idea: relative measurements in forestry.* Commonwealth Agricultural Bureaux. Farnham Royal.

Blondel J. & Cuvillier R. 1977: Une méthode simple et rapide pour décrire les habitats d'oiseaux: le stratiscope. *Oïkos* 29, 326-331.

Blondel J., Ferry C. & Frochot B. 1973: Avifaune et végétation, essai d'analyse de la diversité. *Alauda*, 41, pp. 63-84.

Chambers R.J. & Adams T.H.L. 1986: Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. *Journal of Applied Ecology,* 23, 895–904.

Christensen M., Hahn K., Mountford E., Odor P., Standovar T., Rozenbergar D., Diaci J., Wijdeven S., Meyer P., Winter S. & Vrska T. 2005: Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management,* 210, 267–282.

Dupouey J.L.., Bachacou J., Cosserat R., Aberdam S., Vallauri D., Chappart G. & Corvisier de Villèle, M.A. 2007: Vers la réalisation d'une carte géoréférencée des forêts anciennes de France. *CFC* 191: 85-98.

EUFORGEN 2012: Distribution map of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). http://www.euforgen.org.

Fayt P., Dufrene M., Branquart E., Hastir P., Pontegnie C., Henin J.M. & Versteirt V. 2006: Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. *Journal of Insect Conservation* 10, 129-150.

Good J. & Speight M.C.D. 1996: Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe: Les invertébrés saproxyliques et leur protection à travers l'Europe. Conseil de l'Europe. 16ème réunion. Strasbourg, 1996.

Greenberg C.H., McLeod D.E., Loftis D.L. 1997: An old-growth definition for Western and mixed mesophytic forest. USDA, Southern research station, Gen tech rep SRS-16. USDA Forest Service, Southern Research Station. Asheville, 14 p.

Groot M. & Bevk D. 2012: Ecosystem services and phenology of hoverflies (Diptera: Syrphidae) in a Slovenian forest stand. *Les* (Ljubljana) 64, 123-128.

Humphrey J.W., Hawes C., Peace A.J., Ferris-Kaan R. & Jukes M.R. 1999: Relationships between insect diversity and habitat characteristics in plantation forests. *Forest Ecology and Management* 113, 11-21.

Huston M.A. 1994: *Biological diversity. The coexistence of species on changing landscapes.* Cambridge University Press. 681p.

Keil P. & Konvicka M. 2005: Local species richness of Central European hoverflies (Diptera: Syrphidae): a lesson taught by local faunal lists. *Diversity and Distributions* 11, 417-426.

Kembel S.W., Ackerly D.D., Blomberg S.P., Will K. Cornwell W.K., Peter D., Cowan P.D., Helmus M.R., Morlon H. & Webb C.O. 2014: Package 'picante', 56 p. http://cran.r project.org/web/packages/picante/picante.pdf.

Larrieu L., Cabanettes A., Brin A., Bouget C. & Deconchat M. (2014) Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry. *European journal of Forest Research*, 133, 355–367. DOI 10.1007/s10342-013-0767-1.

Larrieu L., Cabanettes A. & Delarue A. 2012: Impact of sylviculture on dead wood and on the distribution and frequency of tree microhabitats in Montane Beech-Fir forests of the Pyrenees; *European journal of Forest Research,* 131 (3), 773-786. DOI 10.1007/s10342-011-0551.

Loreau M., Naeem S., Inschausti P., Bengtsson J., Grime J.P., Hector A., Hooper D.U., Huston M.A., Raffaelli D., Schmid B., Tilman D. & Wardle D.A. 2001: Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294, 804-808

Métailié J.P. 2001: Un patrimoine historico-environnemental: les forêts pastorales dans les Pyrénées. Actes du 126^{éme} congrès national des sociétés historiques et scientifiques. Paysages, territoires et aménagement dans le sud de la France. Toulouse, 33–47.

MCPFE 2007: State of Europe's forests. The MCPFE report on sustainable forest management in Europe. Ministerial conference on the protection of forests in Europe. Warsaw, Poland.

Müller J., Brunet J., Brin A., Bouget C., Brustel H., Bussler H., Förster B., Isacsson G., Köhler F., Lachat T. & Gossner M. 2012: Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. *Insect Conservation and Diversity*, 6, 162-169. DOI 10.1111/j.1752 4598.2012.00200.

Nilsson S.G., Niklasson M., Hedin J., Aronsson G., Gutowski J.M., Linder P., Ljungberg H., Mikusinnski G. & Ranius T. 2002: Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management*, 161, 189-204.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P.M., Stevens H.H., Wagner H. 2013: Package ‘vegan’. http://cran.r-project.org/web/packages/vegan/vegan.pdf.

Petchey O.L. & Gaston K.J. 2006: Functional diversity: back to basics and looking forward. *Ecology Letters,* 9, 741-758.

R Core Team 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL http://www.R-project.org/.

Reemer M. 2005: Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae). *Journal of Insect Conservation*, 9, 49-59.

Speight M.C.D. 1989: *Saproxylic invertrebrates and their conservation.* 42, 1-79. Concil of Europe. Nature and Environment Series.

Speight M.C.D., Castella E. & Sarthou J.P. 2013: StN 2013. In: Speight, M.C.D., Castella, E., Sarthou, J.-P. & Vanappelghem, C. (eds). Syrph the Net on CD, Issue 9. *The database of European Syrphidae*. ISSN 1649-1917. Syrph the Net Publications, Dublin.

Tenhumberg B. & Poehling H.M. 1995: Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agriculture, Ecosystems and* Environment, 52, 39-43.

Therriault T.W. & Kolasa J. 2000: Explicit links among physical stress, habitat heterogeneity and biodiversity. *Oikos*, 89: 387-391.

Tscharntke T., Clough Y., Wanger T.C. Jackson L., Motzke I., Perfecto I., Vandermeer J. & Whitbread A. 2012: Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151, 53-59.

Winter S. & Möller G.C. 2008: Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management*, 255(3-4), 1251–1261. DOI 10.1016/j.foreco.2007.10.029.

Yachi S. & Loreau M. 1999: Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Nat. Acad. Sci.,* 96, 1463-1468.

Combined effects of history, morphology, connectivity and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae)

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Abstract

Hoverflies (Diptera Syrphidae) play a crucial role in ecosystem functioning and are often chosen as bioindicators in evaluations of ecosystem conservation. However, little work has been undertaken to explore the relative importance of local and landscape-scale factors in addition to historical changes in habitat to explain species patterns. In this study, the joint effects of forest structural heterogeneity, morphology, connectivity and history on the species richness of hoverflies were investigated. It was also evaluated whether hoverfly exhibit a delayed response to habitat changes, and tests were undertaken on the effect of considering spatiotemporal changes in explaining species assemblages. The current species richness of the habitat specialist was sampled in 49 woodlots using 106 Malaise traps. The structural explanatory variables were derived from a rapid habitat assessment protocol. Old maps and aerial photographs were used to extract past and present spatial patterns of the woodlots. Generalised linear models showed that the current habitat area, historical continuity and average number of large lying deadwood played a significant part in explaining species richness. It was also observed that hoverfly diversity was affected by a change in patch area and connectivity since 1850, although no evidence of extinction debt was found. These results demonstrated that the richness of forest hoverflies was influenced by a combination of three factors operating on a different scale of analysis from plot to landscape. They also revealed the interest of adopting a change-oriented approach to explain the current distribution pattern of species.

Keywords

Hoverflies, woodlands, heterogeneity, morphology, connectivity, history

1- Introduction

Forests are among the most biologically diverse ecosystems on the planet (Gosselin and Laroussinie 2004). They have been exploited in Western Europe for thousands of years and their species diversity has been greatly affected by human activities (Larsson 2001). The species communities currently observed in woodlands are outcomes of local conditions applied to a pool of regional species. A hierarchy of filters determines their compositions (Belyea and Lancaster 1999; Decaëns et al 2008): (i) macroclimate, topography, species chorology and population dynamics on a large scale (*e.g.* extinction), (ii) the amount of available habitat patches, permeability of the landscape matrix, connectivity and barriers that prevent dispersion at landscape scale, and (iii) local abiotic conditions and food resources. Thus, broad spatial-scale processes, local conditions, historical factors, as well as also stochastic events greatly influence the structure of local communities (Ricklefs 1987). However, most of the studies on biodiversity in woodlands focus on just one of these filters or on just one scale. Quantifying the relative importance of each factor still presents a challenge.

Habitat loss and fragmentation are the primary causes of biodiversity decline (Fahrig 2003; Foley et al. 2005; Hanski 2005). Local extinction of populations might not be reversed by colonisation because an increase in isolation and reduction of habitat size could lead to species extinction. Some species react immediately to landscape changes while others express a time-lagged response (Hanski and Ovaskainen 2002; Lindborg and Eriksson 2004; Metzger et al. 2009; Krauss et al. 2010). This time delay in the response of certain species may lead to what is termed an extinction debt (Tilman et al. 1994; Cousins 2009; Kuussaari et al. 2009).

Extinction debts have been observed for vascular plants in temperate regions (Helm et al. 2006; Krauss et al. 2010; Guardiola et al. 2013) but also for others species with higher dispersal ability, such as pollinating insects (butterflies, hoverflies) or birds (Brooks et al. 1999; Ford et al. 2009). Even though the mechanisms involved in the delayed responses of species are still unclear, generalist species are expected to be less affected by habitat changes than specialist species (Cousins and Vanhoenacker, 2011).

Empirical evidence of extinction debt is often based on the comparison of past and present habitat characteristics (Kuussaari et al. 2009). When past habitat variables explain current species richness better than the present ones, an extinction debt is assumed (Krauss et al. 2010). Although this approach enables to detect a potential extinction debt, “past” and “current” habitat characteristics are disconnected because the state of habitats is described at one time without integrating patch history. Consequently, the temporal trajectory of habitats is mostly ignored.

Recently, some authors adopted a dynamic approach in the detection of extinction debt or the analysis of historical factors controlling the pattern of species (Metzger et al. 2009), considering habitat change as a cumulative process (Ewers et al. 2013). Metzger et al.. (2009) showed that including the rate of change of habitat area (i.e. the rate of relative change between two dates) and connectivity for several taxonomic groups (tree, bird and frog species), in addition to the present habitat characteristics, enabled to strongly improve the explanation of species richness and abundance. The rate of landscape change could influence the balance between colonization and extinction (Münzbergová et al. 2005).

Ouin et al. (2006) previously investigated the effects of landscape variables on the presence of hoverflies (Syrphidae) in a fragmented landscape of southwest France and highlighted that the current woodlot area explained roughly 30 % of the variability in the response variable. Hoverflies are known to be quite mobile and are therefore sensitive to conditions on large scales (Smith et al. 2008). This family encompasses a species diverse group in terms of trophic and habitat requirements, including saproxylic species, and has been used as an indicator of disturbance or habitat quality (Sommaggio 1999). They are also used as bioindicators to identify forests for potential conservation (Good and Speight, 1996). Adults are flower-visiting insects that provide pollination services, including for trees and shrubs (Groot & Bevk 2012).

Despite the crucial role of hoverflies in ecosystem functioning, little is known about the various factors that influence their contemporary patterns (Keil and Konvicka 2005). It might therefore be useful to know more about this to reinforce their role as bioindicators (Sommaggio 1999). In this paper, investigations were undertaken in the same fragmented woodlots as those in Ouin et al. (2006) on the combined effects of current landscape variables, their past dynamics and local structural heterogeneity variables on the species richness of hoverflies. Firstly, an assessment was undertaken of the relative importance of local and historical factors in addition to landscape variables in controlling the richness of hoverflies. It was assumed that the presence of tree microhabitats (hereafter called microhabitats) and deadwood could offer favourable habitats for certain species, namely saproxylic species. Evaluations were then undertaken as to whether hoverfly communities are subject to extinction debt in this context. Little attention has been given to this taxonomic group even though a recent study showed that hoverflies as a habitat specialist can be affected by extinction debt in relation to a habitat area (Bommarco et al. 2014). Finally, it was examined whether variables of past landscape dynamics provided a better explanation of this family's species richness.

2-Materials and methods

21-Study area

The study site is located in southwest France (43°16’28’’N, 0°51’11’’ E, WGS-84) and covers roughly 30,000 ha, including the Long-Term Ecological Research site “Vallées et Coteaux de Gascogne” (LTER_EU_FR_003) (Fig. 1). This is a hilly region (altitude 215-400 m), dissected by north-south valleys. The climate is temperate with Pyrenean Mountain and slight Mediterranean influences. Wood cover is fragmented and covers some 15 % of the area. The dominant tree species are sessile oak (*Quercus petraea* Mattus), pedunculate oak (*Quercus robur* L.) and pubescent oak (*Quercus pubescens* Willd.) for more than 80 % of the area (IFN, 2000).

In this region, small private forests are the most frequent type of woodlands. Owing to the absence of a forest management plan for approximately 90 % of the area, there is high spatial heterogeneity between woodlands. Owners generally only have empirical knowledge of forest management, which may strongly influence the spatial patterns of forest biodiversity (De Warnaffe et al. 2006; Andrieu et al. 2008).

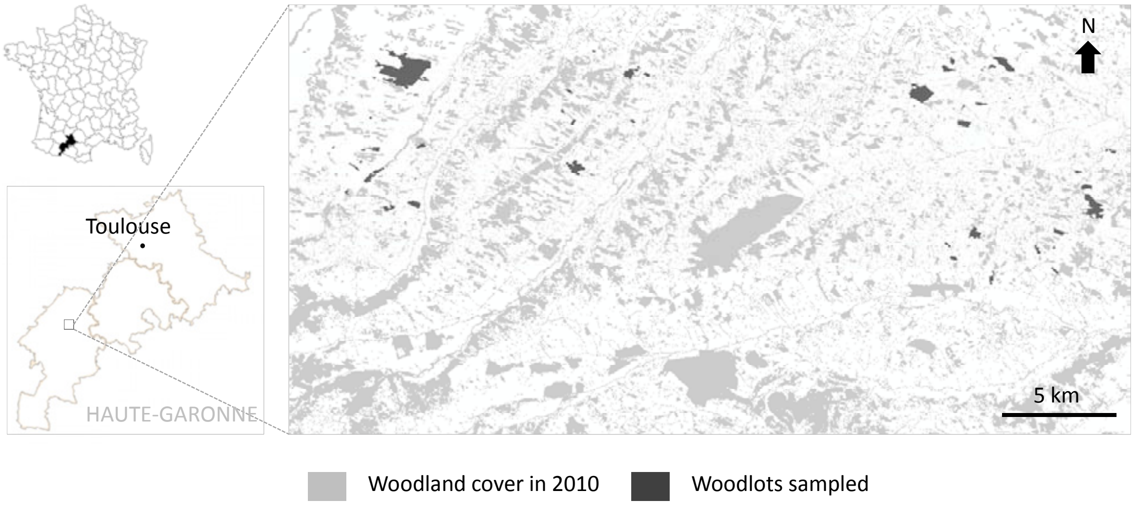

Figure1. Location of the 49 woodlots sampled in the study site in southwest France

22-Data collection

221-Biological sampling

Hoverfly (Diptera: Syrphidae) sampling was conducted by Ouin et al. (2006) using Malaise traps during two one-month periods: 10 May – 10 June (spring) and 13 September – 13 October 2000 (autumn). Collection bottles were replaced every fortnight in spring and every month in autumn. 49 woodlands were selected from Ouin et al. (2006) according to a gradient of surface area, isolation and type of management, resulting in different forest structures and compositions. The trap number per woodlot was adjusted to the patch area in order to obtain an equivalent trapping intensity for each woodlot (Table 1). The large majority of small woodlots (< 5ha) contained only one trap. For larger woodlots, more traps were added. A total of 106 Malaise traps were installed in the surveyed woodlots.

Table 1. For each woodlot area class: number of traps, number of woodlots in the class and average forest species richness per wood

Class of surface area (A)	No. of traps	No. of woodlots in the class	Average forest species richness per wood
A < 5ha	1	29	2.6
5 < A < 10ha	2	9	6.25
10 < A < 15ha	3	3	6.75
15 < A < 25ha	4	4	6.5
35 < A < 45ha	6	1	12
45 < A < 60ha	7	2	14
150 < A < 200ha	14	1	18

Species were classified according to the Syrph the Net (StN) database, which enable ecological groups to be differentiated based on the requirements of their larval stage (Speight et al. 2000). The focus was on forest species because they are more sensitive to forest characteristics and isolation (Ouin et al. 2006). For each woodlot, species richness (i.e. the number of different species) was calculated. The names of all the 27 forest species can be found in Appendix 1.

222-Structural heterogeneity variables of woodlands

Structural variables were surveyed during summer 2011 using a rapid stand description protocol (Larrieu and Gonin 2008) in a 1-ha circular plot centred around each trap. 106 hectares were therefore sampled. Eight attributes of forest structure and composition were observed that were assumed to be relevant to hoverfly assemblages: (1) the number of indigenous tree species; (2) the number of large standing deadwood (diameter at breast height (dbh)>40cm) including whole dead trees, snags or stumps taller than 1.5 m; (3) the number of large lying deadwood (diameter>40cm and length>1m); (4) the number of very large living trees (dbh>70cm); (5) the number of microhabitat-bearing trees (only living trees), a tree being counted once for each type of microhabitat carried, namely empty cavities, cavities with mould, sporophores of saproxylic fungi, dendrothelms, missing bark, cracks, broken crowns, large amount (>20 %) of deadwood in the crown; (6) a diversity index equal to the sum of microhabitat-bearing trees when considering a maximum of two trees bearing the same microhabitat type per plot; (7) the proportion (%) of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants); and (8) the number of aquatic habitats (in reference to a list). Finally the average value of each of these variables per trap in one wood was calculated in order to test the effect of structural heterogeneity on the species richness of hoverflies.

223-Historical, morphological and connectivity variables of woodlands

Aerial colour infrared orthophotos from 2010 were used to estimate the current area and connectivity of each woodlot. Connectivity was captured in terms of isolation, i.e. as the forest density in the surrounding landscape of one focal patch (Tischendorf et al. 2003; Magle et al. 2009). Forest density was measured in a circle with a 4.8 km radius (Fig. 2), which was assumed to be the relevant scale for analysing the effect of isolation on the hoverfly community (Ouin et al. 2006). Such a large scale is explained by the high dispersal capacity of hoverflies (Sarthou and Speight 2005).

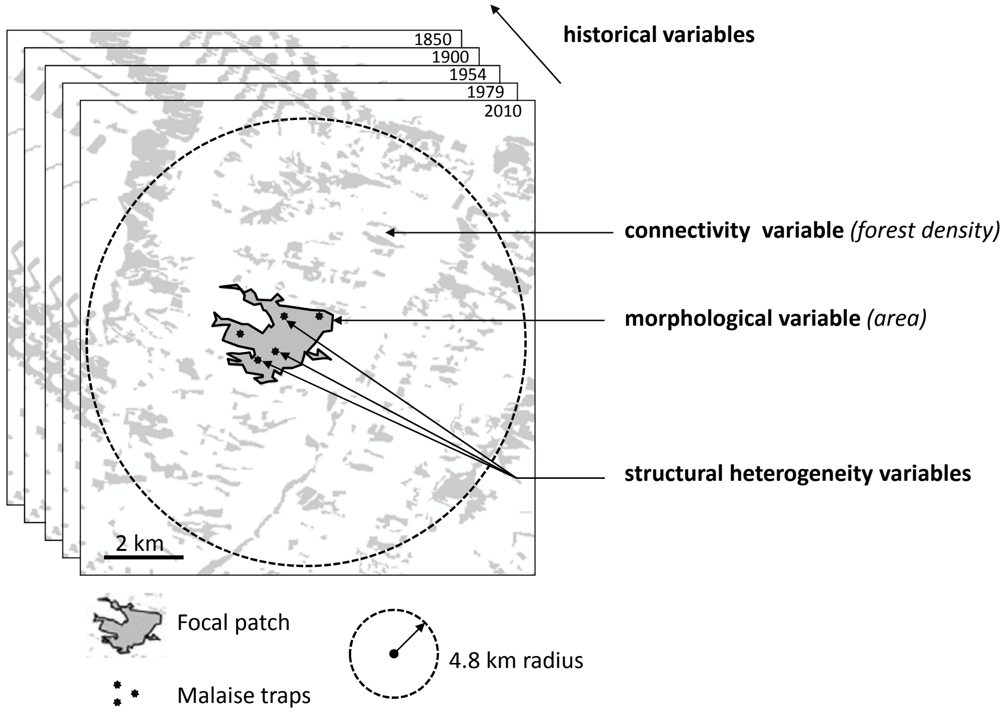

Figure 2. Structural heterogeneity, morphology, connectivity and historical continuity of woodlots: multiple variables from local to landscape-scale to explain the spatial patterns of hoverfly species richness

Historical spatial data were also used to quantify the effect of changes in woodland area and isolation on current species richness as forest continuity over time. Two historical maps were used in addition to old orthophotos from 1954 and 1979 (Fig. 3). The first historical map is a colour map from the middle of the 19th century at a scale of 1:40,000. The second map is a revised version of the first one from 1900 and produced in black and white at a scale of 1:80,000. These historical maps were geo-referenced with a 3rd order polynomial transformation (70 ground control points, root mean square error ~ 55 metres). Woodlands were digitised at 1.7-metre resolution according to a rule base defined by cartographic experts ensuring a homogeneous representation of the objects (Favre et al. 2012). Old aerial black and white photographs were ortho-rectified using a digital terrain model of 25-metre resolution and applying a linear transformation (40 ground control

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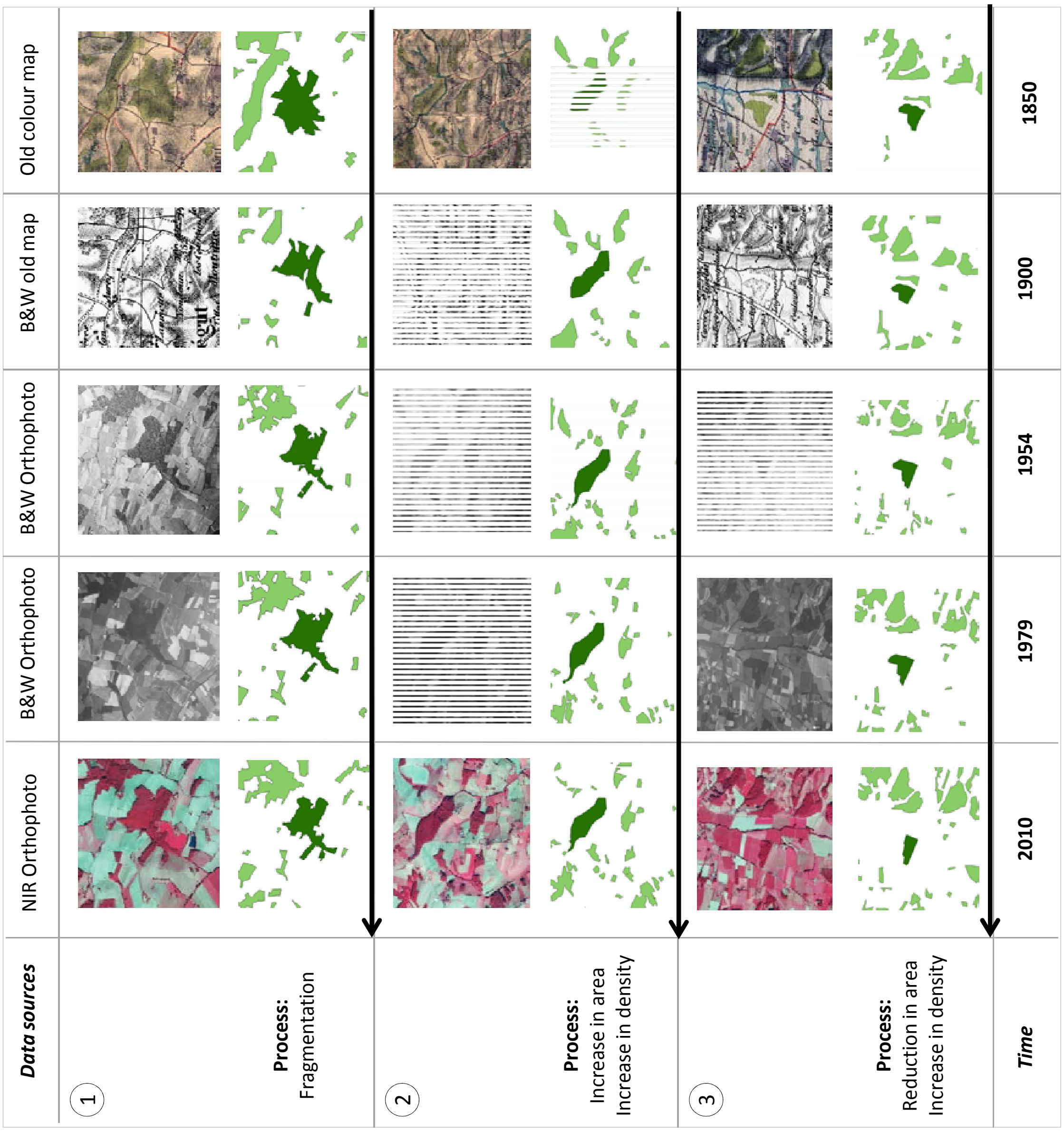

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Changes in woodlot area and connectivity were computed by retrospective analysis (i.e. looking backwards). For the current time period *t*, woodlots were always equal to one single spatial object. However, for past time periods, the current woodland could be matched to several older forest fragments because of the disappearance or aggregation processes from one period to another. In this case, when one-to-many or many-to-many matching relationships appeared between time periods, the fragmented woodlot was viewed as a complex object (or “meta-object”) composed of simple objects. The area of the complex object was defined as the sum of all the areas of the simple objects. For connectivity, the convex hull containing all the simple objects was created to represent the extent of the meta-object. A buffer was formed around this convex hull and the proportion of forest within this neighbourhood was calculated. The forest density index chosen in this study showed a strong correlation between area-weighted distance-based metrics of connectivity (*e.g.* Spearman correlation = 0.75, p-value<0.001 with Hanski's index for the 2010 dataset (Hanski and Thomas 1994; Magle et al. 2009). Finally, changes in woodlot area and connectivity between each consecutive time periods were estimated, in addition to historical area and connectivity at each date. A binary variable was also defined to provide information about whether forest continuity had been maintained over time since the first historical map in 1850. More precisely, two groups of woodlots were identified: *old* ones present in all cartographic data (continuity variable value = 0) and *recent* ones created after 1850 (continuity variable value = 1).

23-Statistical analyses

Statistical analyses were performed using R 2.3.0.1 software ("vegan" R package) (Oksanen et al. 2007). Relationships between species richness and explanatory variables were explored using generalised linear models (GLM). Poisson family distribution was used to fit the species richness models. A set of three scenarios and associated models were tested (Table 2). The contribution was measured of each explanatory variable on the current forest species richness of hoverfly per wood (scenario 1). Current area, connectivity and structural heterogeneity variables were incorporated in addition to the historical woodland continuity (11 factors). This analysis included all the woodlots surveyed (n=49). Then, the role of past and present area and connectivity in explaining current species richness patterns was compared to assess the existence of an extinction debt (scenario 2) (Kuussaari et al. 2009; Guardiola et al. 2013). These models were performed with woodlots existing at each date, i.e. having historical continuity over time (n=30). Finally, the interest of combining current area and connectivity of woods with their past dynamics was investigated (scenario 3). This analysis was carried out combining all types of woodland changes (e.g. reduction of size, increase in isolation) owing to the small sample size (n=30).

Variance inflation factors (VIF) were checked using the 'VIF' R package (Lin 2009) to prevent multicollinearity between covariates. For the first two scenarios, all VIF values were below two, suggesting that collinearity of variables did not affect the model (Zuur et al. 2010). For the third scenario, variables were more strongly correlated because of the historical change variables (VIF < 6; correlation coefficients $|r| < 0.63$), but the collinearity did not exceed the recommended thresholds of diagnostic indices (VIF < 10; correlation coefficients $|r| < 0.7$) (Dormann et al. 2013).

The most parsimonious models for the first and third scenario were also assessed on the basis of the Akaike information criterion (AIC) (Burnham and Anderson 2004). A stepwise backward selection of variables was carried out to select the "best" model with the lowest AIC. In addition, Δ-AIC (the difference in AIC values between a candidate model and the best model) was calculated to compare models using all combinations of selected variables. Models with Δ-AIC < 2 are equally likely. Variance partitioning was also calculated from the best model to measure the independent contribution of each variable to the explained variance of the response variable.

The goodness of fit of the models was quantified by examining the amount of the adjusted explained deviance (% adj-D^2), which takes into account the number of observations and explanatory variables. The predictive performance was evaluated using Spearman rank correlations (Rho) and the root mean square error (RMSE) between observed and predicted values, based on three-fold cross-validation (Shmueli 2010). Folds were generated by randomly splitting the total dataset into three groups of equal size. The model was calibrated with the first two groups and predictions were made on the third group. Cross-validation was repeated 100 times.

Table 2. The three modeling scenarios examined (A, B, C) including the list of explanatory variables.

Explanatory variables		Description	N°	Model form
A) Model with present area, connectivity, structural heterogeneity and historical continuity				
Area 2010	β_1	Present area of woodland patch (orthophoto 2010)	a_1	$E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \beta_8 + \beta_9 + \beta_{10} + \beta_{11}$
Connect 2010	β_2	Present forest density in a 4.8km buffer radius (orthophoto 2010)		
AvgNb_ATS	β_3	Present average number of indigenous tree species per wood		
AvgNb_STW	β_4	Present average number of large standing deadwood per wood		
AvgNb_LDW	β_5	Present average number of large lying deadwood per wood		
AvgNb_VLLT	β_6	Present average number of very large living trees per wood		
AvgNb_MH	β_7	Present average number of microhabitats per wood		
AvgNb_TreeMH	β_8	Present average number of trees supporting microhabitats per wood		
AvgOpen_Area	β_9	Present average size of open areas per wood		
AvgNb_Aquatic	β_{10}	Present average number of aquatic habitat per wood		
Histo_continuity	β_{11}	Historical forest continuity over time (0 = continuity; 1 = no continuity)		
B) Models with present or past area and connectivity				
Area 2010	β_1	Present area of woodland patch (orthophoto 2010)	b_1	$E(y) = \beta_0 + \beta_1 + \beta_2$
Connect 2010	β_2	Present forest density in a 4.8km buffer radius (orthophoto 2010)		
Area 1979	β_{13}	Past area of woodland patch (orthophoto 1979)	b_2	$E(y) = \beta_0 + \beta_{13} + \beta_{14}$
Connect 1979	β_{14}	Past forest density in a 4.8km buffer radius (orthophoto 1979)		
Area 1954	β_{15}	Past area of woodland patch (orthophoto 1954)	b_3	$E(y) = \beta_0 + \beta_{15} + \beta_{16}$
Connect 1954	β_{16}	Past forest density in a 4.8km buffer radius (orthophoto 1954)		
Area 1900	β_{17}	Past area of woodland patch (old map 1900)	b_4	$E(y) = \beta_0 + \beta_{17} + \beta_{18}$
Connect 1900	β_{18}	Past forest density in a 4.8km buffer radius (old map 1900)		
Area 1850	β_{19}	Past area of woodland patch (old map 1850)	b_5	$E(y) = \beta_0 + \beta_{19} + \beta_{20}$
Connect 1850	β_{20}	Past forest density in a 4.8km buffer radius (old map 1850)		
C) Models with present area and connectivity with their past dynamics				
Area 2010	β_1	Present area of woodland patch (orthophoto 2010)	c_1	$E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_{21} + \beta_{22} + \beta_{23} + \beta_{24} + \beta_{25} + \beta_{26} + \beta_{27} + \beta_{28} + \beta_{29} + \beta_{30}$
Connect 2010	β_2	Present forest density in a 4.8km buffer radius (orthophoto 2010)		
ΔArea 2010-1979	β_{21}	Change in area between 2010 and 1979		
ΔCon 2010-1979	β_{22}	Change in connectivity between 2010 and 1979		
ΔArea 1979-1954	β_{23}	Change in area between 1979 and 1954		
ΔCon 1974-1954	β_{24}	Change in connectivity between 1979 and 1954		
ΔArea 1954-1900	β_{25}	Change in area between 1954 and 1900		
ΔCon 1954-1900	β_{26}	Change in connectivity between 1954 and 1900		
ΔArea 1900-1850	β_{27}	Change in area between 1900 and 1850		
ΔCon 1900-1850	β_{28}	Change in connectivity between 1900 and 1850		
ΔArea 2010-1850	β_{29}	Change in area between 2010 and 1850		
ΔCon 2010-1850	β_{30}	Change in connectivity between 2010 and 1850		

3- Results

31-Changes in woodland spatial patterns

The current and historical spatial data showed that of the 49 woodlots surveyed, 30 have historical continuity over time (*i.e.* they exist in all cartographic data from 1850) and 20 appear from 1900 or after (Table 3). It was observed that the average woodlot area decreased over time when all woodlands were considered, whereas connectivity increased as the number of patches increased. However, for old forests with historical continuity (n=30 over time), only forest density in their neighbourhood significantly increased from 11 % in 1850 to 17 % in 2010 (Kruskall-Wallis test = 13.65, *p*<0.01), but not their area (Kruskall-Wallis test = 1.76, *p value*>0.05) (Fig. 4).

Table 3: Values of area and forest density of the woodlots per time period

	1850 (n = 30)		1900 (n = 34)		1954 (n = 47)		1979 (n = 49)		2010 (n = 49)	
	Area (ha)	Forest density (%)	Area (ha)	Forest density (%)	Area (ha)	Forest density (%)	Area (ha)	Forest density (%)	Area (ha)	Forest density (%)
min	0.50	3.23	0.39	2.77	0.18	6.48	0.23	6.56	0.13	7.72
max	180.52	39.90	206.96	41.93	196.92	25.11	182.44	25.73	186.62	31.44
mean	22.76	11.58	15.97	12.90	10.28	13.09	10.19	14.63	10.93	18.38
sd	38.34	6.99	35.18	7.64	29.17	4.51	26.63	4.90	27.61	6.84

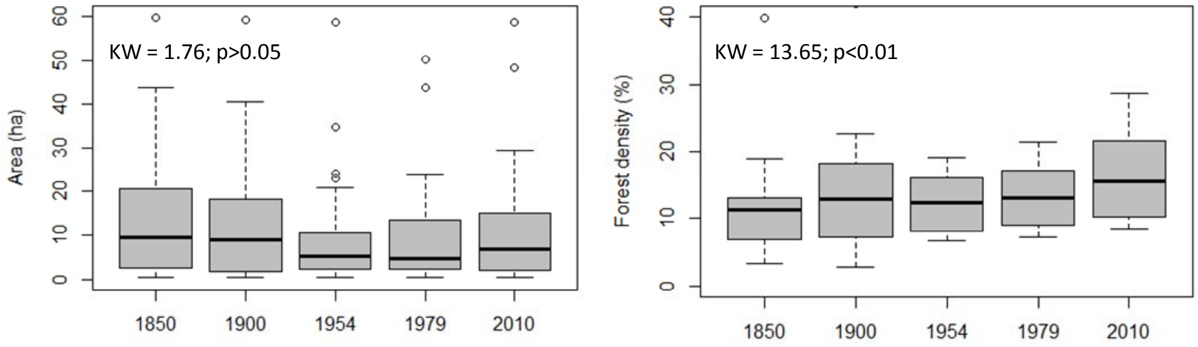

Figure 4. Distribution of woodlot area and forest density from 1850 to 2010. The boxes show medians, and 1st and 3rd quartiles. Non-parametric Kruskall-Wallis tests (KW) were designed to test for significant differences in population medians between time periods

32-Response of species richness to current area, connectivity, structural heterogeneity and historical continuity

A total of 3044 individuals belonging to hoverfly species were captured in the 106 Malaise traps set up in the 49 woodlands. Twenty-two forest species were recorded with average species richness per wood equal to 4.5 ± 3.7.

Three main predictors of species richness were retained after the analysis of AIC: current woodlot area (morphological variable), number of large lying deadwood (structural heterogeneity variable) and historical continuity over time (historical variable). These variables composed the “best model” of the first scenario, *i.e.* the model with the lowest AIC. Models considering only a subset of these variables had less support than the best model (Δ-AIC > 2; Table 4) suggesting that each of the three variables retained made a significant contribution. This was confirmed by the diagnostics of the best model (Table 5). A strong significant positive relationship was found between woodlot area and the response variable as well as a weak positive effect of the number of lying deadwood. In addition, historical continuity showed a weak but significant effect on species richness. The best model explained a good proportion of deviance ($\%D^2 = 0.37$; $\%adj\text{-}D^2 = 0.33$) with a fair predictive performance ($|r| = 0.53$) (Fig. 5, model a_1).

Table 4. Comparison between the best model, i.e. the model with the lowest AIC, and a candidate model for each scenario (A, B, C). Models are ranked according to their Δ-AIC: difference between a given model and the best model

Rank	Explanatory variables	Δ-AIC
A) Models with present area, connectivity, structural heterogeneity and historical continuity (n = 49)		
1	Area2010 (+) ; AvgNb_LDW (+) ; Histo_continuity (-)	0.00
2	Area2010 (+) ; AvgNb_LDW (+)	2.09
3	Area2010 (+); Histo_continuity (-)	2.72
4	Area2010 (+)	4.08
5	AvgNb_LDW (+) ; Histo_continuity (-)	33.83
B) Models with present or past area and connectivity (n = 29)		
1	Area2010 (+) ; Connect2010 (+)	0.00
2	Area1979 (+) ; Connect1979 (-)	0.37
3	Area1900 (+) ; Connect1900 (+)	2.22
4	Area1954 (+) ; Connect1954 (+)	2.32
C) Models with present area and connectivity with their past dynamics (n=29)		
1	Area2010 (+) ; Connect2010 ; ΔCon 2010-1979 (+) ; ΔArea1900-1850 (+)	0.00
2	Area2010 (+) ; ΔArea1900-1850 (+)	2.84
3	Area2010 (+) ; Connect2010 ; ΔCon 2010-1979 (+)	3.24
4	Area2010 (+) ; ΔCon 2010-1979 (+)	4.11
5	Area2010 (+) ; Connect2010 ; ΔArea1900-1850 (+)	4.38
6	Area2010(+) ; Connect2010	7.58
7	ΔCon 2010-1979	29.06

33-Response of species richness to current or past woodlot area and connectivity

Models including past variables had less support than the best model including current area and connectivity (Table 4, B). However, the model considering area and connectivity from 1979 was very close to the best one (Δ-AIC = 0.37), suggesting that these models are equally likely. The deviance test indicated a non-significant difference between these two models (Chi^2 = 1.96; *p value* = 0.75).

For all models, both current and past area had a positive relationship with the response variable, but not with current and past connectivity (Table 5, models b_1 to b_5). The amount of deviance explained by all the models was fair (%adj-D^2 >= 0.31), except for the model based on the variables derived from the historical map of 1850 (%adj-D^2= 0.23). Cross-validation results also showed a fairly and moderately good predictive performance (|r| > 0.4) (Fig. 5, models b_1 to b_5).

34-Response of species richness to current area and connectivity with their past dynamics

The AIC-based stepwise selection showed that the model with the lowest AIC included four explanatory variables to explain species richness with current area and connectivity and their past dynamics: area 2010, connectivity 2010, change in connectivity between 1979 and 2010, and change in area between 1850 and 1900 (Table 5, c_1). Differences in AIC between the best model and the other ranked models suggested that not considering one the four selected variables provides models with less support (Table 4, C). The inclusion of past changes greatly improved the goodness-of-fit of the model (%D^2 = 0.50; %adj-D^2 = 0.43; Table 5, C). This model, c_1, was significantly better than all the other models (Chi^2 = 52.23; $p<0.05$). Current area, change in connectivity between 1970 and 2010, as well as change in area between 1850 and 1900 had a significant and positive effect (Table 5, C). In contrast, current connectivity (Connect 2010 in Table 5) showed a significant negative effect (*p-value <0.05*). The predictive performance of this model was moderately good (Rho > 0.55) (Fig. 5, models c_1).

Table 5. Results of the GLM models explaining hoverfly species richness of forest specialists. Explanatory variables were selected on the basis of the Akaike information criterion (AIC)

Explanatory variables	Estimates	p-values	Significance level	AIC	%D^2	%D^2 adjusted	%Relative Contribution	N°
A) Model with current area, connectivity, structural heterogeneity and historical continuity (n = 49)								
Area 2010	0.008	0.000	***	243.46	0.37	0.33	86.33	a_1
AvgNb_LDW	0.121	0.023	*				4.59	
Histo_continuity	-0.296	0.042	*				9.08	
B) Models with current or past area and connectivity (n = 29)								
a 2010	0.009	0.000	***	162.93	0.38	0.34	93.85	b_1
Connect 2010	0.001	0.908	n.s				6.15	
Area 1979	0.009	0.000	***	163.30	0.38	0.34	95.56	b_2
Connect1979	-0.008	0.668	n.s				3.44	
Area 1954	0.009	0.000	***	165.25	0.36	0.31	95.33	b_3
Connect 1954	-0.000	0.983	n.s				4.66	
Area 1900	0.008	0.000	***	165.15	0.36	0.31	84.86	b_4
Connect 1900	-0.011	0.377	n.s				15.13	
Area 1850	0.007	0.001	**	172.51	0.28	0.23	69.25	b_5
Connect 1850	0.008	0.492	n.s				30.75	
C) Models with current area and connectivity with their past dynamics (n=29)								
Area 2010	0.009	0.000	***	148.77	0.50	0.43	78.26	c_1
Connect2010	-0.041	0.028	*				4.10	
ΔCon 2010-1979	0.034	0.017	*				10.30	
ΔArea 1900-1850	0.003	0.013	*				7.34	

Significance codes: ****P*< 0.001; ***P* < 0.01; **P*< 0.05.

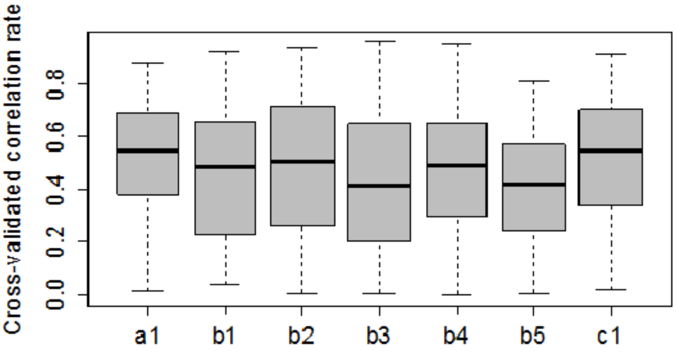

Figure 5. Cross-validated correlation values derived from six modelling settings (three scenarios). The boxes show medians and 1st and 3rd quartiles

4- Discussion

41-Woodlot area, large lying deadwood and historical continuity explained species richness of forest specialist hoverflies

These analyses indicated that the species richness of forest specialist hoverflies was mainly explained by a combination of three factors operating at different scales of analysis: the average density of large lying deadwood (local effect), the current woodlot area (patch-scale effect) and the historical continuity of wood state (temporal effect).

The density of lying deadwood with diameter>40cm and length>1m was found to be positively related to species richness. This variable could potentially be crucial for saproxylic species “that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylics” (Speight and Wainhouse, 1989). A similar result had already been observed for saproxylic beetles for which lying deadwood larger than d>50 cm allow species that prefer deadwood of large diameter to persist (Gossner et al. 2013). Since saproxylic hoverflies composed the majority (72.4% ± 21.6) of the forest specialist hoverflies, this hypothesis is quite plausible. Nevertheless, saproxylic hoverflies seemed to be more dependent on microhabitats associated with old and senescent trees than with deadwood items (Speight and Good 2003). In this study, no correlation was found between microhabitat density and hoverfly richness that might indicate that the procedure used to count microhabitats was not relevant for hoverflies or that variables related to microhabitats and deadwood were probably not the only key factors explaining saproxylic hoverfly richness. This is also suggested by Fayt et al. (2006) who found a high number of saproxylic species in woods with an open structure and large trees, providing ecological conditions for a species-rich herb layer, resources of pollen and nectar for imagoes.

The current woodlot area was the main driving factor showing a positive effect on species richness (r.c. = 86.33 %). This area effect is well-known in the habitat patch framework and consistent with previous studies (Connor and McCoy 1979; Andren 1994; Ouin et al. 2006). The increase of species richness with patch area is predicted by the equilibrium theory of island biogeography (MacArthur, 1967). It assumes that for equally isolated islands the number of individuals within a taxon increased linearly with the island area. The habitat diversity hypothesis (Root 1973; Huston 1994) is one of the hypothesis proposed to explain these positive relationships. Larger fragments are often more heterogeneous than small ones and therefore are more likely to provide critical resources for different species such as food and safety from predators. Heterogeneity relies on variability of micro-climate, structural and plant compositional variations, as well as diversity of topographic conditions (Turner 2001). This heterogeneity offers more opportunities for organisms with different requirements and tolerances to find suitable sites within the patch. In addition, larger fragments generally have a larger edge and core areas, also characterised by different environmental conditions (microclimate, moisture, wind and light). This also favours the presence of a wider collection of species, including forest core species and edge species (Harris 1984). Nevertheless, the habitat diversity hypothesis needs to be qualified in the case of this study because the increase in species number with area is also due to the sample area effect (Huston and Huston 1994). As previously observed by Ouin et al. (2006), the sample from one trap in small woodlots contained roughly the same number of species as that in large ones. Moreover, the area effect was observed with species richness but not with species density (*i.e.* the average richness per trap in one wood), which was independent of woodlot area. However, if the area effect was also due to a sampling artefact, it only affects a part of the woodlots, since 29 of the 49 woodlots surveyed contained only one trap. Furthermore, since it is assumed that Malaise traps have a limited radius of interception, using the same number of traps per woodlot whatever their size would lead to a considerable underestimation of the species richness in large woodlots.

Interestingly, this study's results showed that historical continuity was another factor positively affecting the species richness of forest specialist hoverflies. Although all hoverflies are able to fly long distances, some species such as *Criorhina floccosa*, *Doros destillatorius* or *Brachylapoides lentus*, whose microhabitat requirements of larvae are strictly linked to trees in stand (Speight 2010), might be unwilling to colonise favourable recent woodlots by crossing an unfavourable matrix such as large fields. Indeed, these species are observed outside forests very rarely (JP Sarthou, pers. com.) and they are observed far more frequently in ancient woodlots. This temporal effect could be also explained by different management strategies and cutting regimes known to be very complex and chaotic in these private woodlots (de Warnaffe et al. 2006). Forestry strategy might be more conservative in ancient woodlots, with scattered cutting of limited sized allowing for a more natural variation in vegetation structure (Reemer 2005). However, this hypothesis requires more thorough investigation because there was no evidence that structural heterogeneity in ancient woodlots was more favourable than that in recent woodlots. Indeed, significant differences were not observed in microhabitat or lying deadwood densities between the ancient and recent woodlots sampled.

42-Changes of fragment area and connectivity influenced current biodiversity patterns of hoverflies

Several studies have analysed the effects of history on plant or insect diversity in fragmented forests and grasslands, but they often estimate this effect by comparing diversity between patches with distinct dynamics (Piqueray et al. 2011; Guardiola et al. 2013). This study's results showed that including changes into the model in addition to states at one date significantly enhanced the capacity to understand and explain the species richness of hoverflies (ΔD^2adjusted = 10% between a_1 to c_1, Table 5).

It was observed that species richness was influenced by both current area and connectivity in addition to a change in connectivity between 1979 and 2010, and a change in area between 1850 and 1900. Surprisingly, current connectivity was negatively related to the species richness of hoverflies. This was in contrast to relationships highlighted between habitat connectivity and species richness. Generally, habitat connectivity has a positive effect on species diversity, in particular for specialist species with a low dispersal ability (Hanski 2005). Nevertheless, connectivity could impose negative indirect effects on certain species through the spread of invasive species Atobe et al. (2014) or pathogens (Hess 1996). Moreover, De Groot (2003) demonstrates in a case study in the surroundings of Ljubljana (Slovenia) that hoverfly species richness responds negatively to an invasive plant species, namely *Solidago canadensis*, since it homogenises plant layers by supplanting the other flowering plants. This plant species has already been observed locally in the "Vallées et Coteaux de Gascogne" area and has been described as having the ability to colonise habitat patches in fragmented landscapes quickly (Deconchat and Balent 2002). This plant was not surveyed in the present study but since the relative contribution of current connectivity in the model was very low (r.c = 4 %), this could be a credible explanation for a small number of patches surveyed.

A change in connectivity between 1979 and 2010 was positively related to the forest species diversity of hoverflies. This result showed that hoverflies may be also sensitive to "habitat continuity" that may be considered to represent connectivity over time (Hanski 2005), while "habitat connectivity" represents connectivity only in space. A meta-analysis comparing bird response to forest fragments *vs* true islands has concluded that forest fragments do not function as true islands (Brotons et al. 2003). The authors interpret this result as being a compensatory effect of the surrounding matrix in terms of availability of resources and enhanced connectivity. However, in this case, since only forest specialist hoverflies were considered, no resource was available in the matrix for larvae (flower resources could be available for adults). Connectivity between forest patches has been enhanced by the increase in the area of the existing patches. Indeed, the amount of forest habitat in the neighbourhood (4.8km) of the surveyed woodlots increased greatly between 1979 and 2010 by over 1400 ha in total. Therefore, this increase in forest density enabled the persistence of the hoverfly community in the landscape through the dispersion of insects between ancient and recent patches.

Species richness of hoverflies was also explained by the change in area between 1850 and 1900. It is widely recognised that forest area in France decreased until around 1850, and then has been increasing to the present day (Koerner et al. 2000). This increase in area leads to improved forest patch connectivity. However, this general pattern at landscape scale is not always observed at patch level. In this sample, the area of 16 woodlots decreased by more than one hectare between 1850 and 1900, while the area of the other 14 ancient woodlots stabilised (*i.e.* area loss was less than one hectare) or increased. It appeared that hoverfly species richness in the former was currently significantly lower than in the latter (n = 30; Wilcoxon test = 169; *p value*<0.05). Hoverflies could have colonised woodlots whose heterogeneity had more time to improve during this period.

These findings reinforced the conclusions of previous studies showing that not only are past or current spatial patch characteristics important for explaining present biodiversity patterns, but so are changes of patch area and connectivity (Metzger et al. 2009).

43-No extinction debt for forest hoverflies

This study's results suggested that forest specialist hoverflies did not exhibit extinction debt in relation to woodland area and isolation since present-day hoverfly distribution was better explained by current landscapes than past ones. This result may be due to the relative stability in the amount of habitat. Changes in woodland spatial patterns were not strongly pronounced. Ancient woodlots (n=30) did not show a significant change in their area over the time. In contrast, their connectivity increased slightly but significantly, which would involve a colonisation credit (Cristofoli et al. 2010).

Indication of delayed response to change in habitat area has already been observed for hoverflies in a recent study (Bommarco et al. 2014), but the analysis focuses on hoverfly generalists and specialists of semi-natural grasslands, not on forest specialists.

5- Conclusions

This study demonstrated that the current species richness of forest hoverflies was influenced by a combination of three factors operating at a different scale of analysis from plot to landscape. These findings also revealed the interest of adopting a change-oriented approach to explain the current distribution pattern of species. Although relationships between past states and present-day biodiversity were widely demonstrated, some explanation of the contemporary biodiversity patterns could be also offered by the rate of landscape changes. In this case, species richness of hoverflies was affected by a change in patch area and connectivity from 1850 as well as historical continuity, although no evidence of extinction debt was found. Methodological refinements could be performed to detect a possible extinction or colonisation credit without combining all types of woodland changes (Guardiola et al. 2013), but it would require a larger sample size to optimise samples throughout the range of structural and historical patterns of woodlots.

Incorporating historical changes in landscape ecological studies would appear to be a very promising way of obtaining a better understanding of all the factors affecting current species diversity. However, this would require an extensive spatiotemporal database incorporating a wide variety of historical data sources, the creation of which would be a challenge in itself. The availability of historical maps is often limited and the reconstruction of patch history can take a long time to complete. Recent advances in the automatic processing of digital historical maps and aerial photographs (Leyk et al. 2006; Baily et al. 2011; Herrault et al. 2013) should enable the effects of history to be considered more systematically in future. With this in mind, a closer collaboration between historical ecologists and geo-information scientists should be encouraged.

References

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 355–366.

Andrieu E, De Warnaffe GDB, Ladet S, et al (2008) Cartographier l'historique des coupes forestières dans les petits bois. Rev For Fr 60:667–676.

Atobe T, Osada Y, Takeda H, et al (2014) Habitat connectivity and resident shared predators determine the impact of invasive bullfrogs on native frogs in farm ponds. Proc R Soc B Biol Sci 281:20132621.

Baily B, Riley M, Aucott P, Southall H (2011) Extracting digital data from the First Land Utilisation Survey of Great Britain–Methods, issues and potential. Appl Geogr 31:959–968.

Deconchat M, Balent G (2002) Effets de la sylviculture et de l'exploitation forestière sur la Diversité végétale. Revue Forestière Française LIV:559566

Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. Oikos 402–416.

Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. Divers Distrib 20:591–599.

Brooks TM, Pimm SL, Oyugi JO (1999) Time lag between deforestation and bird extinction in tropical forest fragments. Conserv Biol 13:1140–1150.

Brotons L, Mönkkönen M, Martin JL (2003) Are fragments islands? landscape context and density-area relationships in boreal forest birds. Am Nat 162:343–357.

Burnham KP, Anderson DR (2004) Model selection and inference: a practical information-theoretic approach, Soc Meth and Res, 33:261–304

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 791–833.

Cousins SA (2009) Extinction debt in fragmented grasslands: paid or not? J Veg Sci 20:3–7.

Cousins SA, Vanhoenacker D (2011) Detection of extinction debt depends on scale and specialisation. Biol Conserv 144:782–787.

Cristofoli S, Piqueray J, Dufrêne M, et al (2010) Colonization credit in restored wet heathlands. Restor Ecol 18:645–655.

Decaëns T, Margerie P, Aubert M, et al (2008) Assembly rules within earthworm communities in North-Western France- a regional analysis. Appl Soil Ecol 39:321–335.

De Groot M (2003) Insect responses to invasive plant species, MSc Thesis, University of Ljubljana.

De Warnaffe GDB, Deconchat M, Ladet S, Balent G (2006) Variability of cutting regimes in small private woodlots of south-western France. Ann For Sci 63:915–927.

Dormann CF, Elith J, Bacher S, et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027–046.

Ewers RM, Didham RK, Pearse WD, et al (2013) Using landscape history to predict biodiversity patterns in fragmented landscapes. Ecol Lett 16:1221–1233.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 487–515.

Favre C, Granier E, Cosserat-Mangeot R, et al (2012) La digitalisation des cartes anciennes. Manuel pour la vectorisation de l'usage des sols et le géoréférencement de la Carte d'Etat-Major-INRA

Fayt P, Dufrêne M, Branquart E, et al (2006) Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. J Insect Conserv 10:129–150.

Foley JA, DeFries R, Asner GP, et al (2005) Global consequences of land use. science 309:570–574.

Ford HA, Walters JR, Cooper CB, et al (2009) Extinction debt or habitat change? Ongoing losses of woodland birds in north-eastern New South Wales, Australia. Biol Conserv 142:3182–3190.

Good JA, Speight MCD (1996) Saproxylic invertebrates and their conservation throughout Europe. Council of Europe, Strasbourg

Gosselin M, Laroussinie O (2004) Biodiversité et gestion forestière: connaître pour préserver, synthèse bibliographique. Cemagref

Gossner MM, Lachat T, Brunet J, et al (2013) Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. Conserv Biol 27:605–614.

Groot M, Bevk D (2012) Ecosystem services and phenology of hoverflies (Diptera: Syrphidae) in a slovenian forest stand. Les (Ljubljana) 64:123--128

Guardiola M, Pino J, Rodà F (2013) Patch history and spatial scale modulate local plant extinction and extinction debt in habitat patches. Divers Distrib 19:825–833.

Hanski I (2005) Landscape fragmentation, biodiversity loss and the societal response. EMBO Rep 6:388–392.

Hanski I, Ovaskainen O (2002) Extinction debt at extinction threshold. Conserv Biol 16:666–673.

Hanski I, Thomas CD (1994) Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biol Conserv 68:167–180.

Harris LD (1984) The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago press

Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecol Lett 9:72–77.

Herrault P-A, Sheeren D, Fauvel M, Paegelow M (2013) Automatic extraction of forests from historical maps based on unsupervised classification in the CIELab color space. Geogr. Inf. Sci. Heart Eur. Springer, pp 95–112

Hess G (1996) Disease in metapopulation models: implications for conservation. Ecology 1617–1632.

Huston MA, Huston MA (1994) Biological diversity: the coexistence of species. Cambridge University Press

Keil P, Konvicka M (2005) Local species richness of Central European hoverflies (Diptera: Syrphidae): a lesson taught by local faunal lists. Divers Distrib 11:417–426.

Koerner W, Cinotti B, Jussy J-H, Benoît M (2000) Evolution des surfaces boisées en France depuis le début du XIXe siècle: identification et localisation des boisements des territoires agricoles abandonnés. Rev For Fr 52:249–270.

Krauss J, Bommarco R, Guardiola M, et al (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol Lett 13:597–605.

Kuussaari M, Bommarco R, Heikkinen RK, et al (2009) Extinction debt: a challenge for biodiversity conservation. Trends Ecol Evol 24:564–571.

Larrieu L, Gonin P (2008) L’Indice de Biodiversité Potentielle (IBP): une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. Rev For Fr 60:727–748.

Larsson TB (2001) Biodiversity evaluation tools for European forests. Criteria Indic Sustain For Manag For Manag Unit Level 75.

Leyk S, Boesch R, Weibel R (2006) Saliency and semantic processing: Extracting forest cover from historical topographic maps. Pattern Recognit 39:953–968.

Lindborg R, Eriksson O (2004) Historical landscape connectivity affects present plant species diversity. Ecology 85:1840–1845.

Lin D (2009) VIF package (R package) http://cran.r-project.org/web/packages/VIF/index.html

MacArthur RH (1967) The theory of island biogeography. Princeton University Press

Magle SB, Theobald DM, Crooks KR (2009) A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landsc Ecol 24:267–280.

Metzger JP, Martensen AC, Dixo M, et al (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biol Conserv 142:1166–1177.

Münzbergová Z, Mildén M, Ehrlén J, Herben T (2005) Population viability and reintroduction strategies: a spatially explicit landscape-level approach. Ecol Appl 15:1377–1386.

Oksanen J, Kindt R, Legendre P, et al (2007) The vegan package. Community Ecol. Package

Ouin A, Sarthou J-P, Bouyjou B, et al (2006) The species-area relationship in the hoverfly (Diptera, Syrphidae) communities of forest fragments in southern France. Ecography 29:183–190.

Piqueray J, Cristofoli S, Bisteau E, et al (2011) Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. Landsc Ecol 26:823–836.

Reemer M (2005) Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae). J Insect Conserv 9:49–59.

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171.

Sarthou J-P, Speight M (2005) Les Diptères Syrphidés, peuple de tous les espaces. Insectes, 137:3--8

Shmueli G (2010) To explain or to predict? Stat Sci 289–310.

Smith GF, Gittings T, Wilson M, et al (2008) Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodivers Conserv 17:991–1015.

Sommaggio D (1999) Syrphidae: can they be used as environmental bioindicators? Agric Ecosyst Environ 74:343–356.

Speight MCD (2013) Species accounts of European Syrphidae (Diptera) 2010. Syrph Net Database Eur Syrphidae 72:316.

Speight MCD, Castella E, Obrdlik P (2000) Use of the Syrph the Net database 2000. Syrph Net Database Eur Syrphidae 25:99.

Speight MCD, Good JA (2003) Development of eco-friendly forestry practices in Europe and the maintenance of saproxylic biodiversity. Proc. Int. Symp. “Dead Wood Key Biodiversity” Mantova May. pp 73–77

Speight MR, Wainhouse D (1989) Ecology and management of forest insects. Clarendon Press

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371:65--66

Tischendorf L, Bender DJ, Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landsc Ecol 18:41–50.

Turner MG (2001) Landscape ecology in theory and practice: pattern and process. Springer

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14.

Supplementary material

Table 1 SM. Forest hoverfly species used to calculate the species richness variable

Ferdinandea cuprea
Brachypalpus laphriformis
Brachypalpoides lentus
Brachyopa scutellaris
Cheilosia scutellata
Caliprobola speciosa
Criorhina floccosa
Xanthandrus comtus
Criorhina berberina
Dasysyrphus venustus
Xanthogramma laetum
Xylota tarda
Epistrophe melanostoma
Criorhina asilica
Milesia crabroniformis
Cheilosia soror
Xylota sylvarum
Pipiza sp
Temnostoma meridionale
Myolepta vara
Brachyopa bicolor
Psilota anthracina
Pipiza luteitarsis
Doros destillatorius
Brachyopa pilosa
Ceriana conopsoides
Criorhina pachymera

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Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles

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Global warming and land-use change are expected to be additive threats to global diversity, to which insects contribute the highest proportion. Insects are strongly influenced by temperature but also require specific habitat resources, and thus interaction between the two factors is likely. We selected saproxylic beetles as a model group because their life cycle depends on dead wood, which is highly threatened by land use. We tested the extent to which higher temperatures compensate for the negative effects of low amounts of dead wood on saproxylic beetle species richness (Temperature–Dead wood compensation hypothesis) on both a macroclimate and a topoclimate scale (north- and south-facing slopes). We analyzed 1404 flight-interception trap catches across Europe to test for interaction effects of temperature and dead-wood amount on species richness. To experimentally test our findings from the activity trap data, we additionally reared beetles from 80 bundles of dead wood initially exposed at high and low elevations. At the topoclimate scale, we analyzed trap catches and reared beetles from dead wood exposed in 20 forest stands on south-facing and north-facing slopes in one region. On the macroscale, both temperature and dead-wood amount positively affected total and threatened species richness independently, but their interaction was significantly negative, indicating compensation. On both scales and irrespective of the method, species richness decreased with temperature decline. Our observation that increasing temperature compensates for lower amounts of dead wood has two important implications. First, managers of production forests should adapt their dead-wood enrichment strategy to site-specific temperature conditions. Second, an increase in temperature will compensate at least partially for poor habitat conditions in production forests. Such a perspective contrasts the general assumption of reinforcing impacts of global warming and habitat loss on biodiversity, but it is corroborated by recent range expansions of threatened beetle species.

Global warming has been identified as a threat to biodiversity as major as the anthropogenic destruction and fragmentation of natural habitats (IPCC 2007, Beaumont et al. 2011). Generally, the interaction of the two threats is assumed to be additive for most species (Hof et al. 2011a). Forests in Europe nowadays can be characterized as highly fragmented, and important structures that serve as habitat for many species, such as old, dead, or dying trees, are significantly reduced (Whitehouse 2006). This lack of dead-wood resources has been identified as a major weakness of the ecological integrity of production forests in Europe (Gossner et al. 2013). To effectively mitigate the loss of forest biodiversity, forest managers increasingly develop guidelines to enrich the amount of dead wood in their production forests

(Müller and Bütler 2010, Kouki et al. 2012, Angelstam et al. 2013). The most urgent concerns of forest managers now entail the type and quantity of dead wood that should be left in the forest. Threshold values for the amount of dead wood needed to maintain high biodiversity have been provided as a rule of thumb (Müller and Bütler 2010), ranging from 20 to 60 $m^3 ha^{-1}$. Such thresholds have been questioned because of the broad confidence band and the mostly continuous shape of the species richness–dead-wood resource power function (Martikainen et al. 2000, Ranius and Fahrig 2006).

Important wood-inhabiting species include saproxylic beetles. As the metabolism of insects is temperature dependent (Danks 2007, Sformo et al. 2010), temperature is assumed to be a crucial driver of the diversity of saproxylic beetles in addition to dead-wood resource (for exceptions, see Topp 2003). Allen et al. (2002) showed that species richness can generally be predicted by biochemical kinetics of metabolism as a linear function of ln(species richness) ~ $Temperature^{-1}$ with a slope of -9.0 K. Even if such a general metabolic theory of ecology (MTE) rule has been questioned by global evaluation of data (Hawkins et al. 2007), the ability to predict the kinetic effects of temperature from a basic theoretical perspective can improve the understanding of the observed variation in responses of biodiversity to other environmental factors, such as anthropogenic disturbance or dead-wood resources (Allen et al. 2002, Gillooly and Allen 2007).

Some species became extinct in the cooler temperate zone of central Europe since human settlement but survived in the warmer Mediterranean area, even though logging was historically more intense and extend further back in this area: e.g. the longhorn beetle *Cerambyx cerdo* is restricted to huge overmature oaks at its northern distribution range (Buse et al. 2007), while in the southern distribution area, the species is common and develops successfully also in dead wood of low diameter. At the local scale, an increase in diversity has been also observed for saproxylic beetle assemblages on oaks in Scandinavia after shading neighboring trees were removed (Widerberg et al. 2012). Recently, the general importance of topoclimatic (i.e. south- and north-facing slopes) or microclimatic pockets as an explanation for survival of cold-adapted species and biodiversity despite rapid climate warmings in the past has been discussed (Hof et al. 2011b). Moreover, recent studies on the effects of micro(topo)climate, macroclimate, and dead-wood resources or stand structures for diversity at a regional scale also corroborate the view of a potential interplay of climate and resources for wood-inhabiting organisms such as fungi and bryophytes (Bässler et al. 2010, Raabe et al. 2010) and forest birds (Braunisch et al. 2014).

The first strong indication of a potential interaction of dead-wood resources and temperature was provided by the meta-analysis of Lassauce et al. (2011), which showed that across Europe the positive effect of dead-wood amount on species richness of saproxylic organisms decreased in warmer temperate forests compared to cold boreal forests. This result was explained by differences in the forest management history. However, a simpler explanation for this pattern could be a compensatory interaction between temperature and low amounts of dead-wood resources, but this was not tested. Trans-biome analyses are often hindered by species turnover of the dominant tree species (conifers, broadleaves), which seriously affects the species richness of phytophagous communities (Brändle and Brandl 2001). The assumption of the increasing strength of the positive relationship between dead-wood and saproxylic beetle richness with decreasing temperatures is corroborated also by an indicator species analysis in European beech forests (Lachat et al. 2012) in which many species were statistically identified as indicators of warm forests with low and/or high amounts of dead wood, but indicators for cold beech forests were observed only in combination with high amounts of dead wood.

Improving our understanding of the interplay between resource availability (i.e. amount of dead wood) and climate (i.e. temperature) is crucial for nature conservation as it allows fine-tuning of the existing coarse recommendations for dead-wood amounts (20–60 $m^3 ha^{-1}$) depending on climate. Furthermore, this will enable recommendations that take climate warming scenarios into account. To test the hypothesis that higher temperatures compensate for lower amounts of dead wood that drive species richness (Temperature–Dead wood compensation hypothesis), we concentrated on shady forests dominated by *Fagus sylvatica*. We focused on both the macroclimate and topoclimate and used both observational and experimental approaches. We first measured the activity of flying beetles in forests across Europe by analyzing flight-interception trap catches (Activity–Macroclimate). Second, we measured the species density and abundance per dead-wood unit across Europe by rearing beetles from dead wood exposed at low and high elevations (Emergence–Macroclimate). Third, we analyzed trap catches (Activity–Topoclimate) and beetles reared (Emergence–Topoclimate) from dead wood exposed on south- and north-facing slopes in one region. Specifically, at the macroclimatic scale, we predict 1) a positive effect of dead-wood amount and temperature on species richness, and a negative effect of the interaction of both variables, which would indicate compensation, and we predict 2) a lower number of species emerging from bundles of dead-wood branches exposed to cold beech forests compared to warm beech forests. At the topoclimatic scale, we predict 3) a lower number of species in trap catches and a lower number of reared beetles from bundles of dead wood exposed to stands of north-facing slopes compared to south-facing slopes owing to less-suitable climate conditions.

Material and methods

Study areas and sites

We conducted our study at two different spatial scales: a continental (Europe) macroclimatic scale and a regional (in southern Germany) topoclimatic scale. The study at the continental scale included 1404 trap catches in 303 beech-dominated forest stands from ten European countries for assessing saproxylic beetle species richness (Fig. 1, 2A) and eight mountain and eight lowland beech forest sites in France, Switzerland, and Germany for assessing colonization of dead-wood bundles (Fig. 1, 2B). The regional study comprised ten beech forest stands situated on north-facing slopes and ten stands on south-facing slopes in the hilly Steigerwald Forest in northern Bavaria, Germany (Fig. 1, 2).

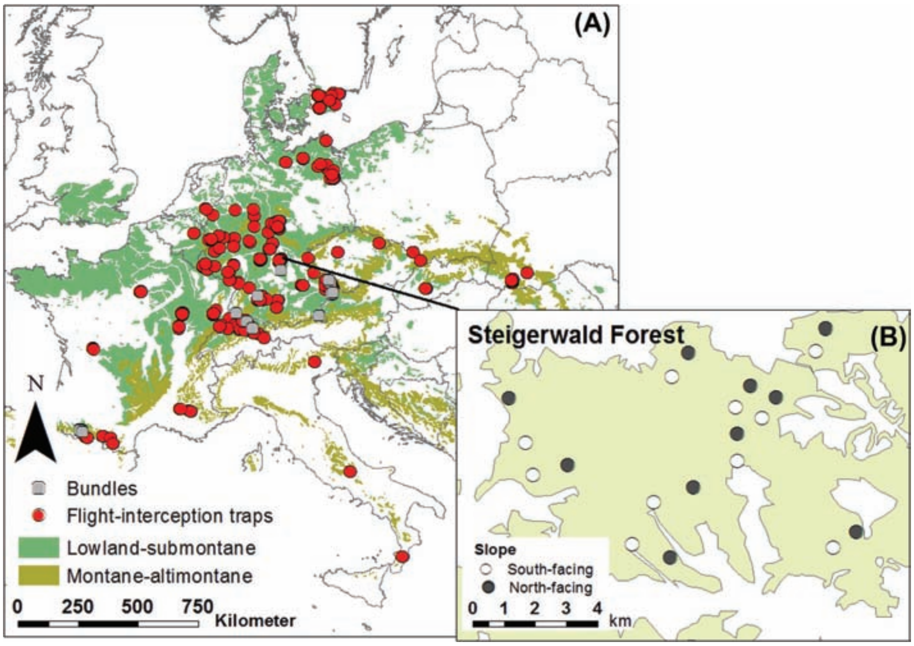

Figure 1. (A) Map showing location of 1404 flight-interception trap catches used to study the effect of dead-wood amount and macroclimate on the continental scale. Forests dominated by *Fagus sylvatica* at low and high elevations are indicated with green shadings. Bundles of dead wood branches were placed at the 16 indicated sites in low and high elevation beech forests; note that the gray dots partly overlap. (B) The 20 sites of the regional scale study, located in the Steigerwald Forest (southern Germany) on south-facing and north-facing slopes (topoclimate) where saproxylic beetles were collected from downed beech and oak trunks using flight-interception and emergence traps. The forest area is shaded green.

Figure 2. Methods used for beetle sampling. On the macroclimate scale: (A) flight-interception trap and (B) exposure of bundles of freshly cut beech branches. On the topoclimate scale: (C) three small flight-interception traps along downed tree trunks and (D) rearing of beetles from pieces of wood from oak and beech of decay stage 3 and from bundles of cut beech branches initially exposed to the environment.

Assessment of saproxylic beetles

Trap catches

Species richness of beetles at both spatial scales was assessed with flight-interception traps consisting of transparent plastic sheets, but the traps used in the subprojects differed in size and shape (vane shaped or a simple window trap with a single sheet; six types total). To control for these differences, we used trap type as a fixed factor with six levels (trap types, see Supplementary material Appendix 2, Table A1). All traps were installed near the forest floor (continental scale: randomly placed within stands 1.5 m above ground; Fig. 2A; regional scale: next to dead-wood logs; Fig. 2C), and the catch was retrieved either over one full vegetation period, varying across the climates from 5 to 7 months (continental scale) or from May to September (regional scale). At the continental scale, the trap catches (Fig. 1, 2) were sampled in one year between 1990 and 2012.

To quantify the potential effect of topoclimate on the richness of saproxylic beetles, we used a data set collected in the Steigerwald Forest in 2012. Ten closed beech-dominated forest stands on north-facing slopes and ten closed stands on south-facing slopes were studied. In each stand, one downed trunk of beech *Fagus sylvatica* and one downed trunk of the second-most admixed tree species oak *Quercus petraea*, both in decay stage 3 (advanced decomposition with soft sapwood and partly tough hardwood), were sampled, and the volume of dead wood in a 0.1 ha surrounding was measured as a control variable. In this subproject, an advanced decay stage was chosen because it is the most critical stage for saproxylic beetles in managed beech forests (Gossner et al. 2013). Along each of the trunks, we attached three small flight-interception traps (11 × 15 cm; Fig. 2).

Rearing experiments

Trap data reflect the activity of the trapped animals (in our case, the flight activity of saproxylic beetles). Despite previous studies indicating strong positive relationships between larval development and adult activity (Vodka et al. 2009), flight activity cannot be easily correlated with actual density, and such a correlation would have to be species-specific. To quantify the effect of temperature on the richness of beetles in beech on the continental scale, we therefore exposed five bundles of branches (for the sake of feasibility and standardization, branches were freshly cut) in each of 16 forest stands. The bundles, each consisting of five branches (3–6 cm in diameter, 80 cm long; Fig. 2B), were installed 1.5 m above ground with a minimum distance of 50 m between them. This set-up was replicated in eight cold beech forests (in the highest vegetation tier in which beech forms stands; mean annual temperature 4.0–6.8°C) and eight warm beech forests (in the lowest vegetation tier in which beech forms stands; 8.2–10.4°C) in France, Switzerland, and Germany (Fig. 1). To minimize effects of differences in dead-wood amount in the surroundings, we restricted our study to mature, managed beech stands with low amounts of dead wood and large distances (> 3 km) to old, unmanaged beech forest reserves. To avoid effects of heterogeneous microclimate and weather conditions, bundles were exposed in closed-canopy stands simultaneously on the west-facing side of the trees in spring 2012 and retrieved at the end of September 2012. Subsequently, the bundles were placed in plastic barrels (emergence traps), and beetle eggs and larvae contained therein were reared at the Univ. de Toulouse under suitable and standardized climate conditions to avoid effects of delayed larval development (day degree requirements) under colder climates. All emerging beetles were collected from the attached transparent collection containers monthly up to the end of September 2013.

At the regional scale, we removed a 30–40 cm segment from the same tree trunk in April 2012 for beetle rearing in the laboratory for five months (Fig. 2B). We selected downed trees in an advanced stage of decomposition (stage 3) for this analysis, as for analyses of trap catches. To control for potential effects of dead-wood volume, we measured the volume of the segments.

All collected beetle specimens were identified to the species level either by one of us (HB: rearing and some trap catches) or by taxonomic specialists recruited for the subprojects. Species were classified as saproxylic according to national lists (Gossner et al. 2013). The species richness of saproxylic beetles was considered as the number of all saproxylic beetle species found in one flight-interception trap (continental scale), in three small flight-interception traps (regional scale), in one bundle of five branches (continental scale), or in one trunk segment (regional scale). In trap catches at the continental scale, Staphylinidae (including Pselaphinae) were excluded from analysis because they had not been identified in all countries (for details, see Gossner et al. 2013). We identified species as endangered or rare according to national and Europe-wide Red Lists and similar rarity classifications (Suplementary material Appendix 1, 2).

Environmental data

At the continental scale and in line with Gossner et al. (2013), we used variables of geography, landscape composition, and stand characteristics as control variables (Table 1). As geographic variables, we used the latitudinal and longitudinal values of the ETRS 1989 projection. As landscape variables (radius 3 km), we used the proportion of human settlement, proportion of total forest, and proportion of broadleaf forest compared to forest area from the Corine database (<www.corinedfd.dlr.de>). As climate variables (radius 1 km), we used temperature and precipitation of the warmest month from the WorldClim atlas (Hijmans et al. 2005), which had been shown in a previous analysis to be more powerful than annual mean values in explaining diversity patterns in beetles (Gossner et al. 2013). Only for inspecting the slope of species richness versus temperature we used the mean annual values in line with predictions of Allen et al. (2002), but additionally give relationships with temperature of the warmest month in the Supplementary material Appendix 1, Fig. A2. As variables characterizing forest stands, we used the presence of veteran trees, years under protection, and amount of dead wood in a one hectare plot (with the trap in the center) according to Gossner et al. (2013). Dead-wood volumes were estimated in three coarse classes: 0–29 m^3 ha^{-1} was set to 15 m^3 ha^{-1}, 30–69 m^3 ha^{-1} to 50 m^3 ha^{-1}, and > 70 m^3 ha^{-1} to 100 m^3 ha^{-1}. Considering

Table 1. Summary of a generalized linear mixed Poisson model with number of saproxylic beetle species as response variable; predictors of geography, climate, landscape composition, and stand characteristics as fixed factors; and forest stand as random factor. The trap type was also included as fixed factor in the model to control for six different construction types (for estimators, see Supplementary material Appendix 2, Table A1). Variables in boldface are significant.

	Estimate	Std. error	z-value	Pr(>|z|)
(Intercept)	$-1.56\ e^{-01}$	$1.20\ e^{-00}$	−0.129	0.897
Longitude	$-2.04\ e^{-07}$	$1.52\ e^{-07}$	−1.337	0.181
Latitude	$-2.08\ e^{-08}$	$6.63\ e^{-08}$	−0.314	0.753
Forest (% cover, radius 3 km)	$1.70\ e^{-01}$	$1.18\ e^{-01}$	1.442	0.149
Settlement (% cover, radius 3 km)	$3.12\ e^{-01}$	$2.93\ e^{-01}$	1.064	0.288
Broadleaf (% cover, radius 3 km)	$1.43\ e^{-01}$	$1.18\ e^{-01}$	1.211	0.226
Veteran trees	**$-1.57\ e^{-01}$**	**$4.11\ e^{-02}$**	**−3.818**	**< 0.001*****
Time protected (years)	$2.15\ e^{-03}$	$1.26\ e^{-03}$	1.713	0.087
Precipitation (bio_18)	$-1.81\ e^{-03}$	$1.20\ e^{-03}$	−1.511	0.131
Dead wood ($m^3\ ha^{-1}$)	**$1.02\ e^{-00}$**	**$2.19\ e^{-01}$**	**4.685**	**< 0.001*****
Temperature (bio_10)	**$2.24\ e^{-02}$**	**$5.47\ e^{-03}$**	**4.100**	**< 0.001*****
Precipitation × Dead wood	$-2.01\ e^{-04}$	$2.34\ e^{-04}$	−0.859	0.390
Dead wood × Temperature	**$-5.04\ e^{-03}$**	**$1.18\ e^{-03}$**	**−4.287**	**< 0.001*****

the often observed power function of species richness versus amount of dead wood, we log-transformed the values (see above).

To quantify the topoclimatic difference between the south-facing and north-facing stands, we measured temperature with Thermochron data loggers (FA Maxim) at the logs and measured the light regime using hemispherical photos analyzed with Gap Light Analyzer ver. 2.0. Additionally, the amount of dead wood of a diameter > 12 cm in the surroundings was measured within a circle of 0.1 ha.

Species richness–temperature function and data analyses

All analyses were performed in the framework R 3.1.0 (<www.r-project.org>). For comparing the slopes of the species richness–temperature function with global results (Allen et al. 2002), we first modeled the log-transformed richness of species in a trap or dead-wood bundle in a simple linear regression model with the temperature variable 1000/mean annual temperature (Kelvin). Additionally we used temperature of the warmest month to test this relationship. To test our predictions of a positive effect of dead-wood amount and temperature on species richness, and a negative effect of the interaction of both variables, we fitted a generalized linear mixed Poisson model with the function glmer in the package lme4 with the number of species per trap as dependent variable. As explanatory variables, we used temperature, precipitation, and amount of dead wood; as main predictors, we used the interactions of both climate variables with the amount of dead wood; as covariates, we used the set of additional geographical, landscape, and forest stand variables, as well as the trap type (six levels). To account for replicated catches in one stand, we set the forest stand as a random factor. To check for robustness of our results, we additionally assigned all catches dependent on the sampling year to one of five periods and used these periods as covariates (see also Supplementary material Appendix 1, Fig. A1). However, this inclusion did not influence our results and was therefore removed from the final model.

To test our prediction of a lower number of species emerging from bundles of dead-wood branches exposed to cold beech forests compared to warm beech forests, we fitted a generalized linear mixed Poisson model with number of species and also individuals as dependent variables, elevation (high/low) as main predictor, the volume of the branches of each bundle as a control variable, and forest stand as random effect. To account for potential overdispersion in our model, we fitted an additional observation-specific random intercept for individuals (Elston et al. 2001). To test for effects of topoclimatic conditions and our predictions of a lower number of species in trap catches and a lower number of reared beetles from bundles of dead wood exposed to stands of north-facing slopes compared to south-facing slopes, we fitted generalized linear mixed Poisson models with number of species and individuals as dependent variables, tree species and aspect as main predictors, and forest stand as random factor.

Results

On the continental scale, we collected 791 saproxylic beetle species (without Staphylinidae) with the 1404 traps, ranging from 1 to 111 species per trap. Saproxylic beetles reared from bundles of beech branches consisted of 39 species and 6631 individuals, ranging from 0 to 11 species and 0 to 1338 individuals per bundle. On the topoclimatic regional scale, the small flight-interception traps yielded 2474 individuals of 190 species, ranging from 4 to 50 species (4 to 142 individuals) per trunk, and beetles reared from trunk segments yielded 250 individuals of 28 species, ranging from 0 to 45 individuals and 0 to 6 species per sample.

Despite a considerable dispersion in the species richness per trap along the temperature gradient, the confidence bands (95% CI: 8.22–12.65) of the observed slope of an ordinary linear regression model ($-10.4 \pm$ SE 2.59) included the value of -9.0 predicted by the metabolic theory for the regulation of species diversity by temperature (Fig. 3A). This pattern was not affected by the sampling periods (Supplementary material Appendix 1, Fig. A1). For

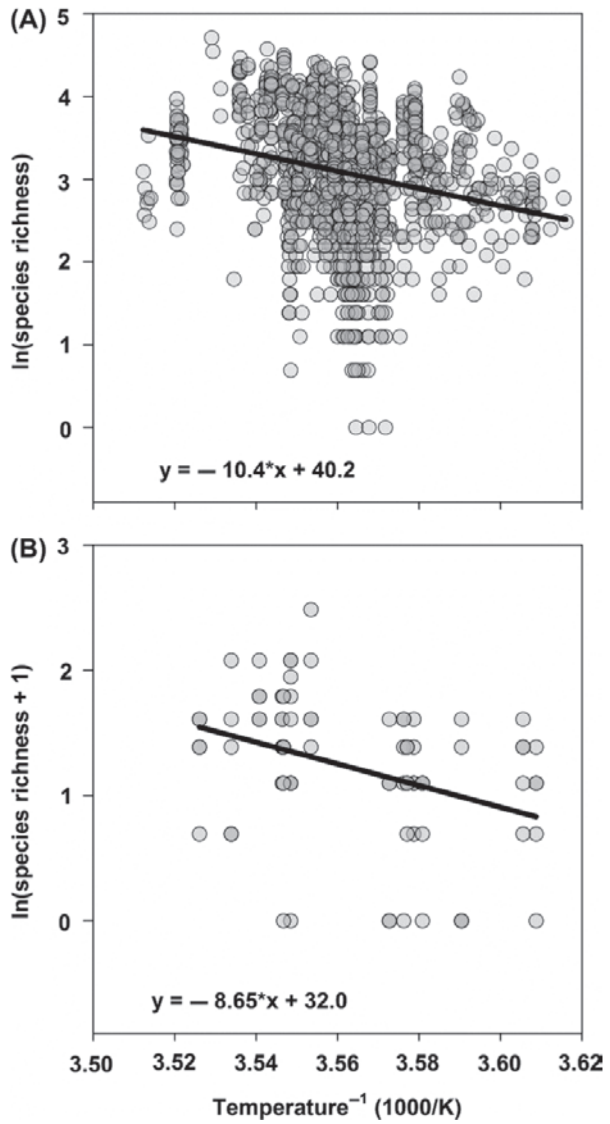

Figure 3. Number of species versus 1000/mean annual temperature based on (A) 1404 flight-interception traps across Europe, and (B) rearing of beetles from 80 bundles of branches exposed in eight high elevation and eight low elevation beech forests. 95% confidence intervals of both slopes include the predicted slope (Allen et al. 2002) of − 9.0: (A) − 12.65 to − 8.22, and (B) − 13.72 to − 3.57.

the beetles emerging from bundles of beech branches, the slope of species richness versus temperature was − 8.6 ± SE 2.59 (95% CI: 3.52–13.6), which is again within the range predicted by the metabolic theory (Fig. 3B). The pattern was similar when using the mean temperature of the warmest month (Supplementary material Appendix 1, Fig. A2). These results supported the view that temperature is a highly important driver of saproxylic beetle richness.

We observed, in line with our prediction 1), significant independent positive effects of temperature and of the amount of dead wood on the number of saproxylic species (Activity–Macroclimate), but not of precipitation, at the continental scale when we controlled for several geographical, landscape, and stand characteristics in our multiple linear model (GLMM with 1404 trap catches; Table 1). We additionally

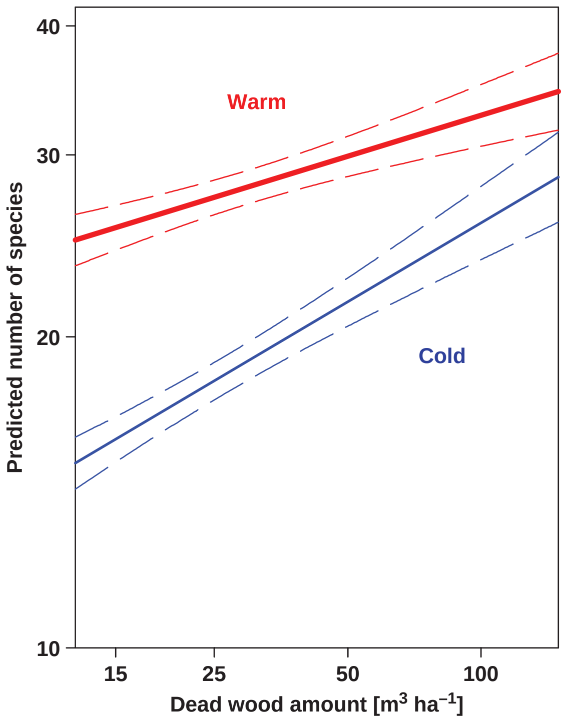

Figure 4. Linear models showing the relationship between the fitted values of the GLMM model regarding species richness based on trap catches on the continental scale (Table 1) and the amount of dead wood including 95% CI. Separate regressions are shown for high and low temperatures (threshold bio_10 = 15.78°C) to illustrate the interaction of dead-wood amount and temperature on species richness. Note the log scale of both axes.

found a negative interaction of dead-wood amount and temperature, as predicted. The full model explained 77% of the variance (R^2-equivalent for mixed effect models); when we extracted only the explanatory contribution of the fixed factors, the explained variance was 35%. A linear model of the predicted values of the GLMM under warm and cold conditions further illustrated that under cold conditions, generally fewer species occurred, but the increase in species richness as the amount of dead wood increased was steeper (Fig. 4). Both results support the hypothesis that the effect of dead wood on species richness decreases with increasing temperature (Table 1, Fig. 4). This relationship between temperature and dead wood was also confirmed when we used only the number of threatened species (for details, see Supplementary material Appendix 2, Table A2).

Significantly higher numbers of individuals and marginally significant higher numbers of species (Emergence–Macroclimate) arose from bundles exposed at lower elevations than at higher elevations, supporting our prediction of a lower number of species emerging from dead-wood branches exposed to cold beech forests compared to warm beech forests (Fig. 5, Table 2). Despite our attempt to set up standardized volumes in each bundle, the covariate 'dead-wood volume' had a significant positive effect, but only on the number of emerged beetle individuals (Table 2).

At the regional scale, the topoclimate data measured by temperature data loggers revealed a significantly lower temperature in stands on north-facing slopes compared to

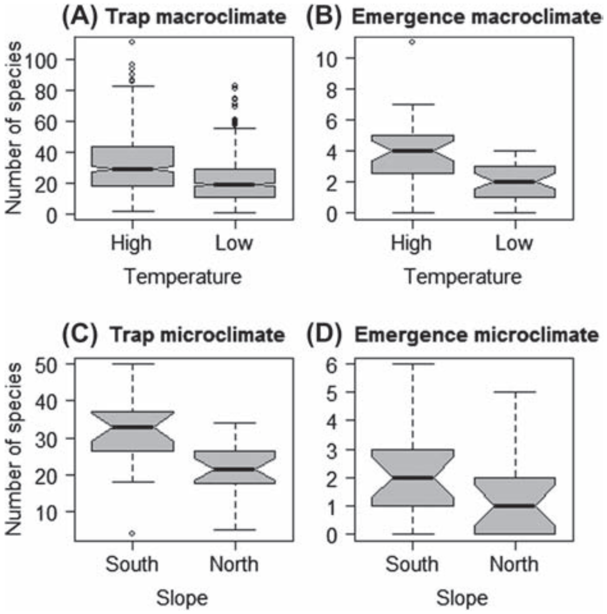

Figure 5. Notched boxplots of raw numbers of saproxylic beetle species from (A) 1404 trap catches across Europe, (B) beetles emerging from 80 bundles of dead-wood branches (volume 7283 ± SD 943 cm³) exposed in eight cold and eight warm beech forests at the continental scale (threshold bio_10 = 15.78°C), (C) trap catches along downed trunks, and (D) emergence traps with beech and oak logs (volume 7564 ± SD 3993 cm³) from beech forest stands on north-facing (cold) and south-facing (warm) slopes in the Steigerwald Forest of Germany. For explicit p-values, see Table 1–4.

south-facing slopes (Wilcoxon test $Z = -2{,}29$; $p < 0.05$), but no effect of canopy cover ($p = 0.77$). The flight-interception traps (Activity–Topoclimate) caught significantly higher numbers of species and individuals along the downed trunks in stands on south-facing slopes (Table 3, Fig. 5). Significantly more individuals but not significantly more species (Emergence–Topoclimate) emerged from collected trunk segments of downed trunks sampled on the warmer, south-facing slopes than from those sampled on the colder, north-facing slopes (Table 4). Overall, we found a robust pattern of more species at warmer temperatures on both climate scales and using both survey and experimental data (Fig. 5).

Discussion

Our main finding was that the slope of the positive relationship between dead-wood amount and saproxylic beetle richness is clearly temperature dependent (Activity–Macroclimate), with steeper slopes for colder climates (Table 1, Fig. 4). We proved this temperature dependency experimentally on both a macroclimatic scale (Emergence–Macroclimate) and a topoclimatic scale (Emergence–Topoclimate), with significant values for species or at least individuals, which suggested a scale-independent general relationship. Our results thus demonstrate that temperature needs to be considered, as an explanatory variable, much more comprehensively in studies of dead wood and diversity, independent of the spatial scale (McGill 2010). This is a prerequisite for more-effective conservation strategies.

Nevertheless, the majority of our data is based on flight interception trap catches, a type of sampling which is influenced by the flight activity of beetles. Thus, one might assume that the increase in species numbers with warmer climates is just a result of more individuals caught due to higher activity. This assumption would challenge all diversity measures, based on trap catches in different micro- (south- vs north-facing slopes, open versus closed canopy etc.) or macroclimates. We are, however, convinced that our data reflect real differences in species numbers along the temperature gradient for several reasons. First, all of our beetle data are from beech forests and all of these species have to colonize their resources by flight. These species are well adapted, using short time windows of sufficient temperatures in cold environments for colonization of new resources. This high phenotypic plasticity has recently been demonstrated for the bark beetle *Ips typographus* (Dworschak et al. 2014). Thus, concentrated activity during a short period and low activity over a longer period should both be captured well by summed trap samples over a whole vegetation period. Second, our traps do not measure pure activity of insects, because collected beetles are finally killed and not repeatedly sampled. The third and major argument for our assumption concerns the analyses of climate gradients for both, trap samples and rearing at both spatial scales (macro- and topoclimate). Rearing data reflects real densities per dead wood unit. Thus, the consistent results in both methods strongly underline the initial assumption that also trap samples well reflect the real variation in local abundances and species numbers.

The amount of dead wood has been repeatedly proven as one important surrogate for biodiversity of wood-inhabiting species, with species richness increasing with increasing dead-wood volume following a power function (Ranius and Fahrig 2006). For Europe's forests, these curves often rapidly increase between 20 and 60 m³ ha⁻¹, and these amounts are thus suggested as coarse targets in conservation strategies (Müller and Bütler 2010). Our results support this view, but additionally suggest that the relationship is highly temperature dependent and support our Temperature–Dead-wood

Table 2. Summary of two generalized linear mixed Poisson models with number of species and individuals from rearing (Fig. 1B) as response variable; elevation level and volume of dead-wood bundle as predictors; and forest stand as random factor. N = 8 sites per elevation level with five bundles each. Variables in boldface are significant. *Note that for individuals, an observation-specific random factor was added to account for overdispersion in the linear mixed model.

	Individuals*				Species			
	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Dead-wood volume	$1.04e^{-03}$	$2.40e^{-04}$	**4.32**	**< 0.001**	$9.98e^{-05}$	$9.54e^{-05}$	1.05	0.295
Elevation: low vs high	2.865	$5.48e^{-01}$	**5.23**	**< 0.001**	$7.27e^{-01}$	$3.97e^{-01}$	1.83	**0.067**

Table 3. Summary of two generalized linear mixed Poisson models for number of individuals and species caught with three small window traps along trunks of beech and oak in stands on north- and south-facing slopes with amount of local dead wood as control variable, and forest stand as random factor. N = 10 sites per slope. Variables in boldface are significant.

	Individuals				Species			
	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Slope: south vs north-facing	$3.22\ e^{-01}$	$1.45\ e^{-01}$	**2.21**	**0.027**	$3.75\ e^{-01}$	$7.30\ e^{-02}$	**5.13**	**< 0.001**
Tree species: oak vs beech	$-3.80\ e^{-01}$	$4.10\ e^{-02}$	**−9.28**	**< 0.001**	$-2.13\ e^{-01}$	$6.19\ e^{-02}$	**–3.43**	**< 0.001**
Dead-wood volume	$8.80\ e^{-02}$	$5.60\ e^{-02}$	1.585	0.113	$1.77\ e^{-01}$	$7.19\ e^{-02}$	**2.46**	**0.013**

compensation hypothesis. The temperature dependency of the relationship of dead-wood amount and saproxylic species diversity might also explain why Lachat et al. (2012) were not able to identify any indicator species for cold beech forests with low amounts of dead wood and why Lassauce et al. (2011) found weak effects of dead-wood amount on species richness of saproxylic fungi and beetles in temperate forests compared to boreal forests. Nevertheless, the question remains to which extent temperature per se plays a critical role. An ultimate prediction of species richness only from temperature, as proposed by the metabolic theory (Allen et al. 2002), has been questioned because several other variables may influence species richness as well (Huston 2003). For saproxylic species, not only dead-wood amount, but also ecological continuity and dead-wood diversity (in tree species, diameter, moisture, etc.) are well known as important drivers of the local diversity (Siitonen and Martikainen 1994, Buse 2012, Bouget et al. 2013). Our observed species richness–temperature relationship for the trap data across Europe as well as for experimental data (beetles emerging from bundles of branches exposed to warm and cold stands) (Fig. 3) yielded a slope that fits well to the prediction based on the metabolic theory of ecology (MTE). However, both plots also showed a strong scatter beyond temperature, which may be driven by confounding effects (i.e. fragmentation, habitat continuity) or by trap types (Supplementary material Appendix 2, Table A1). We want to note that the aim of our study was not to test for the general validity of the MTE (Hawkins et al. 2007), but we mention this match to underline the importance of temperature on saproxylic beetle richness within the climate variation of the major forest type in central Europe, namely beech forests.

Elevation and temperature gradients are correlated with many other environmental variables, such as precipitation and the composition of dominant tree lineages (broadleaf trees in temperate forests and coniferous trees in boreal/alpine forests) (Körner 2007, Lomolino et al. 2010). We restricted our analyses to beech-dominated forests. This potentially shortens the climate gradient, but enabled us to better control for potential effects caused by differences in regional species pools driven by the dominant tree lineage. However, the shadier canopy of beech compared to that of conifers or oak may provide one explanation why precipitation had no effect, despite the availability of water being an important environmental variable also for insects (Chown et al. 2011).

We furthermore do not believe that forest history strongly affected our results of total species richness because in our trap data set from sites across Europe, old strict reserves with a long habitat continuity occurred under different climate conditions, and the occurrence of veteran trees – as a surrogate of habitat continuity – was not positively correlated with the total number of threatened saproxylic beetle species (Tables 1, Supplementary material Appendix 2, Table A2). The even negative effect of veteran trees to total species numbers might be explained by the fact that only the presence–absence of large and over mature trees was used in our data (habitat continuity might be overestimated) and only few species (Müller et al. 2005) are really adapted to such relict habitats (dead wood amount might be more important for total species richness). Furthermore, for threatened species and despite a positive effect of time under protection, the interacting effects of dead wood and temperature on species richness was confirmed (Supplementary material Appendix 2, Table A2). The presence and furthermore the dominance of mature beech – a typical climax species – indicated the long-term spatial presence on our sampling plots of woodland habitat types crucial for organisms dependent on dead wood (Lindbladh et al. 2007). To avoid too large of a variation in dead wood surroundings, which may drive the local species communities (Økland et al. 1996), we placed the bundles of branches in common mature beech forests. Therefore, it seems highly probable that temperature is the main reason for the lower effects of dead-wood amount on species richness in warm forests.

Temperature may influence saproxylic beetles in many ways, either directly or indirectly (Ratte 1985, Jarosík et al. 2004). Indirect influences might be mediated, for instance, by shift in composition of fungi along temperature gradients (Bässler et al. 2010). The temperature threshold values at which some saproxylic species start swarming are well known (Wermelinger 2004). Furthermore, various day-degree

Table 4. Summary of two generalized linear mixed Poisson models for individuals and species reared from downed trunk segments sampled in beech forest stands on north- and south-facing slopes, with tree species (beech, oak) and segment volume as covariates and forest stand as random factor. N = 10 sites per slope. Variables in boldface are significant.

	Individuals				Species			
	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
Slope: south- vs north-facing	$9.66\ e^{-01}$	$3.62\ e^{-01}$	**2.66**	**0.007**	$3.45\ e^{-01}$	$2.43\ e^{-01}$	1.42	0.155
Tree species: oak vs beech	$-3.80\ e^{-01}$	$1.47\ e^{-01}$	**− 7.65**	**< 0.001**	$-8.48\ e^{-01}$	$2.64\ e^{-01}$	**− 3.21**	**0.001**
Dead-wood volume	$4.60\ e^{-02}$	$1.40\ e^{-01}$	0.32	0.743	$-4.00\ e^{-03}$	$1.60\ e^{-01}$	$-2.50\ e^{-02}$	0.980

requirements for individual development of numerous and different forest insect species have been reported (Topp 2003, Inward et al. 2012). For several bark beetle species, the number of generations per year increases with increasing temperature and is related to their pest status (Jönsson et al. 2007, Bussler et al. 2011). The range expansion and unprecedented outbreaks of bark beetles have been explained by global warming (Seidl et al. 2011, de la Giroday et al. 2012). However, the range of formerly threatened species has also expanded with global warming, especially in their initial stages of colonization (Horak et al. 2013). Similarly, the current expansion of the threatened jewel beetle *Coraebus florentinus* could be easily explained by climate change (Buse et al. 2013). A general range expansion of threatened saproxylic beetles and not just of single species has been documented in parts of Germany and explained by global warming (Köhler 2014). Combined with our findings, this further supports the view that warming may facilitate the survival and spreading of not only potential pest species, but also threatened saproxylic beetles.

However, the effect of temperature on the life cycle of saproxylic species or on whole communities living on dead wood and on the interactions within these communities is complex, as shown by temperature experiments with symbiotic mites and fungi associated with the southern pine beetle *Dendroctonus frontalis* in the USA (Hofstetter et al. 2007). Direct and indirect effects of temperature on the web structure of mutualistic and antagonistic relationships of this important pest species have been shown (Hofstetter et al. 2007), which underlines the difficulties of forecasts of the consequences of climate warming for saproxylic communities.

Not only macroclimate but also microclimate (exemplified in our study by topoclimate) has been identified as an important factor for wood-inhabiting species and affects the performance of saproxylic beetles in the same way as macroclimate. The higher number of species in stands of south-facing slopes compared to north-facing slopes observed in our study is in line with higher species richness observed in gaps created by disturbances (Müller et al. 2008). Similarly, Bouget et al. (2013) found openness to be the main explanatory variable for richness of saproxylic species in lowland broadleaf forest stands. On the level of a single tree, Horak and Rebl (2013) found more click beetle species in traps attached to sun-exposed trees compared to shaded veteran trees, and species richness of oak-related species increased owing to partial cutting that produced more-open canopies (Franc and Gotmark 2008). All these studies, however, used flight-interception traps, which do not allow separation of activity and density. In this respect, our study based on both trap catches and emergence data, which are recommended as complementary methods (Alinvi et al. 2007, Vodka and Cizek 2013) and which provided consistent general patterns on both macroclimatic and topoclimatic scales (Fig. 5), provided novel and generalized insights on the effect of higher temperature.

Most current published predictions on the effect of climate warming on insects in Europe are negative and predict decreased range sizes, particularly in the hot and dry Mediterranean environment at the lower altitudinal range boundaries (Thomas et al. 2004, Wilson et al. 2005). However, most reports on insect response to climate deal with Lepidoptera (Wilson and Maclean 2011), which are in their larval stage directly exposed to the environmental temperature while feeding on their host plants. In contrast, the temperature fluctuations of habitats of saproxylic beetle larvae are generally more buffered. Therefore, results of laboratory experiments showing a higher sensitivity of hermit beetle larvae *Osmoderma eremita* than of other species of the family Cetonidae are questionable with respect to real climate warming effects (Renault et al. 2005) and less supported by field surveys (Köhler 2014). One may at least expect boreal species adapted to cold environments (with a metabolism independent of temperature; Topp 2003) to be threatened by global warming. On the other hand, some saproxylic species have implemented strong inter-population plasticity for potential change of climate (Bennett et al. 2005). Moreover, even if we assume or predict negative effects of warming on the life cycle of some mountain species (Bässler et al. 2009), we have to keep in mind a second important indirect effect of global warming on saproxylic species. The increase of climate-induced disturbance events, such as windstorms and bark beetle attacks, currently increase also the amount of dead wood in most mountainous regions of Europe, also in salvage-logged forests (Seidl et al. 2011, Priewasser et al. 2013). Effectively, we observe an increase in populations of formerly rare montane saproxylic species owing to an increase of dead wood, e.g. *Ostoma ferruginea*, *Ampedus auripes*, *Danosoma fasciata* (Müller et al. 2010). Thus, it is not clear to which extent this increases in dead-wood amount overrides locally the effects of warming, as discussed also for saprophagous millipedes and woodlice (David and Handa 2010).

Our results provide an example that rising temperatures might at least to some extent compensate for anthropogenically reduced habitat conditions and might explain recent observations of range expansion of threatened species. Because many other taxa are both climate and resource restricted, a stronger focus on the interaction of the two variables seems promising to understand the current dynamics and to improve forecasts of range shifts. As all analyses of current data that consider that variation in species range shifts lead to reorganization of communities (Bässler et al. 2013) with new interactions of species, a forecast of future diversity in beech forests is still challenging, particularly when temperature exceeds our investigated range.

Independent of these uncertainties in the future, our results provide strong evidence that in Europe's temperate forests, lower amounts of dead wood are less critical under warm conditions than under cold conditions. Thus, forest managers of production forests should adapt their dead-wood enrichment strategy to the site-specific temperature conditions, with less than 40 m^3 of dead wood ha^{-1} in warm beech forests and more in cold beech forests. Based on the meta-analysis published by Lassauce et al. (2011), this strategy can probably be extrapolated to all forests in Europe.

To avoid any misinterpretation of our results by conservationists, we would like to make some cautionary final notes. First, our suggestion of lower amounts of dead wood in warm production forests does not mean that supplementation of dead wood should be renounced, but only that dead wood enrichment should be more pronounced in cold climates. Second, the amount of dead wood is only a coarse surrogate for the availability of a highly variable resource.

Very specific habitats, as hollow trees or freshly burned trees, should be provided irrespective of the temperature and deadwood amount. Recent regional studies on climate warming effects showed that particularly habitat specialists with relict occurrences in Germany, e.g. species related to hollow trees, were poorly favored by climate warming (Köhler 2014). Moreover, old veteran trees, important key habitats for the survival of some highly endangered saproxylic species, may be more susceptible to rapid climate warming than younger and more vital trees, a particularly new threat to some relict sites harboring highly threatened species. Nevertheless, we urge all conservationists, landscape managers, and ecologists studying dead wood to pay more attention to the climate gradient as one fundamental driver of saproxylic insect diversity.

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References

Alinvi, O. et al. 2007. Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. – J. Insect Conserv. 11: 99–112.

Allen, A. P. et al. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. – Science 297: 1545–1548.

Angelstam, P. et al. 2013. Evidence-based versus negotiated knowledge for assessment of ecological sustainability: the Swedish Forest Stewardship Council standard as a case study. – Ambio 42: 229–240.

Bässler, C. et al. 2009. Estimation of the extinction risk for high montane species as a consequence of global warming and assessement of their suitability as cross-taxon indicators. – Ecol. Indicators 10: 341–352.

Bässler, C. et al. 2010. Microclimate and especially resource availability are more important than macroclimate for assemblages of wood-inhabiting fungi. – J. Ecol. 98: 822–832.

Bässler, C. et al. 2013. Insects overshoot the expected upslope shift caused by climate warming. – PLoS One 8: e65842.

Beaumont, L. J. et al. 2011. Impacts of climate change on the world's most exceptional ecoregions. – Proc. Natl Acad. Sci. USA 108: 2306–2311.

Bennett, V. A. et al. 2005. Comparative overwintering physiology of Alaska and Indiana populations of the beetle *Cucujus clavipes* (Fabricius): roles of antifreeze proteins, polyols, dehydration and diapause. – J. Exp. Biol. 208: 4467–4477.

Bouget, C. et al. 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. – Biodivers. Conserv. 22: 2111–2130.

Brändle, M. and Brandl, R. 2001. Species richness of insects and mites on trees: expanding Southwood. – J. Anim. Ecol. 70: 491–504.

Braunisch, V. et al. 2014. Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. – PLoS One 9: e97718.

Buse, J. 2012. "Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. – J. Insect Conserv. 16: 93–102.

Buse, J. et al. 2007. Modelling habitat and spatial distribution of an endangered longhorn beetle – a case study for saproxylic insect conservation. – Biol. Conserv. 137: 372–381.

Buse, J. et al. 2013. Rising temperatures explain past immigration of the thermophilic oak-inhabiting beetle *Coraebus florentinus* (Coleoptera: Buprestidae) in south-west Germany. – Biodivers. Conserv. 22: 1115–1131.

Bussler, H. et al. 2011. Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. – For. Ecol. Manage. 262: 1887–1894.

Chown, S. L. et al. 2011. Water loss in insects: an environmental change perspective. – J. Insect Physiol. 57: 1070–1084.

Danks, H. V. 2007. The elements of seasonal adaptations in insects. – Can. Entomol. 139: 1–44.

David, J. F. and Handa, I. T. 2010. The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. – Biol. Rev. 85: 881–895.

de la Giroday, H.-M. C. et al. 2012. Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. – J. Biogeogr. 39: 1112–1123.

Dworschak, K. et al. 2014. Choice or constraint: plasticity in overwintering sites of the European spruce bark beetle. – For. Ecol. Manage. 328: 20–25.

Elston, D. A. et al. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. – Parasitology 122: 563–569.

Franc, N. and Gotmark, F. 2008. Openness in management: hands-off vs partial cutting in conservation forests, and the response of beetles. – Biol. Conserv. 141: 2310–2321.

Gillooly, J. F. and Allen, A. P. 2007. Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. – Ecology 88: 1890–1894.

Gossner, M. M. et al. 2013. Current "near-to-nature" forest management effects on functional trait composition of saproxylic beetles in beech forests. – Conserv. Biol. 27: 605–614.

Hawkins, B. A. et al. 2007. A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. – Ecology 88: 1877–1888.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surface for global land areas. – J. Climatol. 25: 1965–1978.

Hof, C. et al. 2011a. Additive threats from pathogens, climate and land-use change for global amphibian diversity. – Nature 480: 516–519.

Hof, C. et al. 2011b. Rethinking species' ability to cope with climate change. – Global Change Biol. 17: 2987–2990.

Hofstetter, R. W. et al. 2007. Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. – Community Ecol. 8: 47–56.

Horak, J. and Rebl, K. 2013. The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. – J. Insect Conserv. 17: 307–318.

Horak, J. et al. 2013. Changing roles of propagule, climate, and land use during extralimital colonization of a rose chafer beetle. – Naturwissenschaften 100: 327–336.

Huston, M. A. 2003. Heat and biodiversity. – Science 299: 512.

Inward, D. J. G. et al. 2012. The effect of temperature on the development and life cycle regulation of the pine weevil *Hylobius abietis* and the potential impacts of climate change – Agric. For. Entomol. 14: 348–357.

IPCC (ed.) 2007. Climate change 2007 – impacts, adaption and vulnerability, Contribution of Working Group II to the Fourth Assessment Report of the IPCC. – Cambridge Univ. Press.

Jarosík, V. et al. 2004. A general rule for the dependence of developmental rate on temperature in ectothermic animals. – Proc. R. Soc. B 271: 219–221.

Jönsson, A. M. et al. 2007. Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. – Agric. For. Meteorol. 146: 70–81.

Köhler, F. 2014. Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes – Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen. – Wald und Holz NRW, Münster.

Körner, C. 2007. The use of 'altitude' in ecological research. – Trends Ecol. Evol. 22: 569–574.

Kouki, J. et al. 2012. Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. – Divers. Distrib. 18: 348–355.

Lachat, T. et al. 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. – Ecol. Indicators 23: 323–331.

Lassauce, A. et al. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. – Ecol. Indicators 11: 1027–1039.

Lindbladh, M. et al. 2007. Forest history as a basis for ecosystem restoration – a multidisciplinary case study in a south Swedish temperate landscape. – Restor. Ecol. 15: 284–295.

Lomolino, M. V. et al. 2010. Biogeography, 4th ed. – Sinauer.

Martikainen, P. et al. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. – Biol. Conserv. 94: 199–209.

McGill, B. J. 2010. Matters of scale. – Science 328: 575–576.

Müller, J. and Bütler, R. 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations. – Eur. J. For. Res. 129: 981–992.

Müller, J. et al. 2005. Urwald relict species – saproxylic beetles indicating structural qualities and habitat tradition. – Waldökologie Online 2: 106–113.

Müller, J. et al. 2008. The European spruce bark beetle *lps typographus* (L.) in a national park – from pest to keystone species. – Biodivers. Conserv. 17: 2979–3001.

Müller, J. et al. 2010. Learning from a "benign neglect strategy" in a national park: response of saproxylic beetles to dead wood accumulation. – Biol. Conserv. 143: 2559–2569.

Økland, B. et al. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. – Biodivers. Conserv. 5: 75–100.

Priewasser, K. et al. 2013. Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. – Eur. J. For. Res. 132: 231–240.

Raabe, S. et al. 2010. Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. – For. Ecol. Manage. 260: 1956–1964.

Ranius, T. and Fahrig, L. 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. – Scand. J. For. Res. 21: 201–208.

Ratte, H. T. 1985. Temperature and insect development. – In: Hoffmann, K. H. (ed.), Environmental physiology and biochemistry of insects. Springer, pp. 31–66.

Renault, D. et al. 2005. Critical thermal maximum and body water loss in first instar larvae of three Cetoniidae species (Coleoptera). – J. Therm. Biol. 30: 611–617.

Seidl, R. et al. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. – Global Change Biol. 17: 2842–2852.

Sformo, T. et al. 2010. Deep supercooling, vitrification and limited survival to-100 C in the Alaskan beetle *Cucujus clavipes puniceus* (Coleoptera: Cucujidae) larvae. – J. Exp. Biol. 213: 502–509.

Siitonen, J. and Martikainen, P. 1994. Occurence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. – Scand. J. For. Res. 9: 89–95.

Thomas, C. D. et al. 2004. Extinction risk from climate change. – Nature 427: 145–148.

Topp, W. 2003. Phenotypic plasticity and development of cold-season insects (Coleoptera : Leiodidae) and their response to climatic change. – Eur. J. Entomol. 100: 233–243.

Vodka, S. and Cizek, L. 2013. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. – For. Ecol. Manage. 304: 33–41.

Vodka, S. et al. 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. – J. Insect Conserv. 13: 553–562.

Wermelinger, B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. – For. Ecol. Manage. 202: 67–82.

Whitehouse, N. J. 2006. Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. – Quat. Sci. Rev. 25: 1755–1789.

Widerberg, M. K. et al. 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. – Biodivers. Conserv. 21: 3035–3059.

Wilson, R. J. and Maclean, I. M. D. 2011. Recent evidence for the climate change threat to Lepidoptera and other insects. – J. Insect Conserv. 15: 259–268.

Wilson, R. J. et al. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. – Ecol. Lett. 8: 1138–1146.

Supplementary material (Appendix ECOG-00908 at <www.ecography.org/readers/appendix>). Appendix 1–2.

In search of key habitat-drivers at the stand scale for conservation of species diversity in temperate forests

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Article en préparation. Soumission prévue à *Biological Conservation*

1. Introduction

Gérer et suivre la biodiversité forestière est une tâche difficile car : (i) les forêts abritent plusieurs milliers d'espèces, même sur des petites surfaces (Rameau *et al.*, 2000), (ii) l'utilisation d'un ensemble de taxons bioindicateurs est dispendieux car il nécessite des échantillonnages de terrain souvent sur plusieurs années et l'intervention de spécialistes en taxonomie pour l'identification des espèces capturées (Puumalainen *et al.*, 2003; Nageleisen & Bouget, 2009), (iii) l'approche partielle consistant à utiliser quelques espèces comme révélateurs de la diversité globale des espèces est prometteuse (Gosselin & Gosselin, 2004) mais ces relations ne sont pas encore établies (Lindenmayer *et al.*, 2000; Mc Elhinny *et al.*, 2005; Gosselin & Dallari, 2007). Lindenmayer *et al.* (2000) ont suggéré d'utiliser des variables de structure comme indicateurs indirects de la diversité des espèces. Larsson *et al.* (2001) ont recommandé d'introduire une approche par des facteurs clés dans le suivi de la biodiversité et ont dressé une liste de facteurs clés prioritaires comprenant des facteurs de composition, de structure et de fonction. Tews *et al.* (2004) ainsi que Kraus & Krumm (2013) proposent également d'utiliser pour la gestion de la biodiversité des structures comme le bois mort ou les arbres-habitats.

Une gestion forestière multifonctionnelle devrait promouvoir la biodiversité dans son ensemble (Kraus & Krumm 2013). Mais tous les taxons vivant en forêt n'ont pas les mêmes exigences environnementales et on constate parfois des antagonismes. La plupart des publications qui ont recherché des facteurs environnementaux clés se concentraient sur les oiseaux (*e.g.* Blondel *et al.*, 1973 ; Moning & Müller 2008 ; Müller & Bütler 2010; Bütler *et al.* 2004) les champignons saproxyliques (*e.g.* Basler *et al.*, 2010) et les coléoptères saproxyliques (*e.g.* Winter & Möller 2008 ; Bouget *et al.* 2013, 2014 ; Gossner *et al.* 2013). L'approche est parfois pluritaxonomique : (i) lichens, mollusques et oiseaux (Moning & Müller, 2009), (ii) coléoptères et champignons saproxyliques (Siitonen, 2001), (iii) oiseaux et chauves-souris (Regnery *et al.*, 2013), mais focalisent seulement sur un ensemble restreint de variables environnementales (*e.g.* âge du peuplement, volume de bois mort ou encore densité de dendro-microhabitats).

En utilisant une large palette de 17 variables environnementales de structure et de composition et d'un ensemble de 9 taxons à exigences *a priori* différentes (Coléoptères saproxyliques, lichens, champignons saproxyliques, bryophytes, oiseaux, diptères Syrphidae, plantes vasculaires, Coléoptères Carabidae et chauves-souris) échantillonnés dans une large gamme de types de forêts et de contextes, cette étude avait pour objectif de déterminer les indicateurs indirects de la diversité des espèces pertinents à l'échelle du peuplement forestier et de proposer des pistes d'amélioration des itinéraires sylvicoles pour une meilleure prise en compte de la diversité des espèces. Pour cela, nous voulions répondre aux questions suivantes : (i) quelles sont les réponses des différents taxons aux variations de structure et de composition des peuplements forestiers ? (ii) les variations observées sont-elles unidirectionnelles ou observe-t-on des antagonismes, et (iii) existe-t-il des facteurs clés « universels », ou au moins consensuels pour plusieurs groupes taxonomiques ?

Compte tenu du nombre important de variables et d'une certaine hétérogénéité des données liée à une grande diversité des sources, la démarche globale était à la fois hypothéticodéductive en recherchant la validation ou l'invalidation d'hypothèses *a priori* (Tableau 1), mais aussi exploratoire, autant que les données le permettaient.

2. Matériel et méthodes

Des données environnementales et taxonomiques ont été collectées à l'aide de protocoles standardisés sur 487 placettes situées dans 19 régions forestières de France (Tableaux 1 et 2, et Fig. 1), dans le cadre de différents projets de recherche. Ce jeu de données échantillonne dans les domaines atlantique et continental, en basse altitude (étages planitiaire et collinéen) et en montagne (étages montagnard et subalpin inférieur), et dans des peuplements dominés par les feuillus ou les résineux, ou mixtes.

Tableau 1. Hypothèses de relations positives entre les variables explicatives (environnementales) et à expliquer (taxonomiques) ; les hypothèses les plus fortes apparaissent en gras ; voir la définition des variables dans les tableaux 3 et 5

Groupes de variables environnementales	Variables explicatives	Variables à expliquer supposées en lien avec la variable explicative
ambiance micro-climatique	nb.strates	rs.carab ; rs.carabopen; rs.bryo ; rs.lichen; rs.chiro; **rs.oiso;** rs.flore ; rs.florehelio; **rs.syrph**
	open	rs.colsapro ; **rs.colsaproflor**; rs.carab; **rs.carabopen**; rs.chiro ; rs.flore ; **rs.florehelio**; **rs.syrph** ; rs.syrphfor, rs.syrphsapro; rs.myco
	nb.aqua	**rs.carabhygro** ; rs.chiro; **rs.florehygro**; rs.bryo
	nb.roch	rs.carab ; rs.oiso ; rs.chiro
diversité dendrologique	nb.ess	rs.colsapro; rs.bryo ; rs.lichen ; rs.chiro ; rs.oiso ; rs.syrphfor; rs.flore; rs.myco
maturité du peuplement	nb.chand	**rs.colsapro** ; rs.colsaprorar ; rs.bryo; rs.chiro; rs.chirocav ; rs.oisofor; **rs.oisocav** ; rs.syrphsapro ; **rs.myco** ; rs.mycorar
	nb.bms	**rs.colsapro** ; rs.colsaprorar ; rs.carabfor; **rs.bryo** ; **rs.syrphsapro** ; **rs.myco** ; rs.mycorar
	nb.tgb	rs.colsapro ; rs.colsaprorar; rs.bryo; rs.lichen; rs.chiro; **rs.chirocav** ; **rs.oisofor**; **rs.oisocav** ; rs.syrphfor ; rs.syrphsapro; rs.mycorar
	nb.cav	rs.colsapro; rs.colsaprorar; **rs.chirocav ; rs.oisocav;** rs.syrphsapro
	nb.fentes	**rs.chirocav**; rs.oisocav
	nb.sap	**rs.syrphopo**
	nb.unbark	rs.colsapro ; rs.myco
	nb.fun	rs.colsapro ; rs.colsaprorar ; rs.myco; rs.mycorar
	nb.bmh	rs.colsapro ; rs.colsaprorar
	nb.epiph	rs.chiro; rs.oisofor
	div.mh	rs.colsapro ; rs.colsaprorar; rs.syrphsapro
	nb.mh	rs.colsapro ; rs.colsaprorar ; rs.syrphsapro; rs.myco
autre	conti	rs.colsaprorar ; rs.carab; rs.bryo; rs.lichen; rs.mycorar

Tableau 2. Plan d’échantillonnage des données compilées dans cette étude, classées en fonction de la zone biogéographique, de l’étage de végétation et de la dominance d’essences feuillues ou résineuses

Zone biogéographique	Étage de végétation	Nbre de placettes	Feuillus dominants	Peuplement mixte	Résineux dominants	Régions forestières
Atlantique	Basse altitude	286	230	28	28	3, 5, 7, 8, 11, 12, 13, 17, 18pp
	Montagne	57	21	10	26	4, 18pp
Continentale	Basse altitude	104	104	0	0	1, 2, 6, 9, 15, 16
	Montagne	40	6	24	10	10, 11, 14, 19
	Totaux	487	361	62	64	19 régions

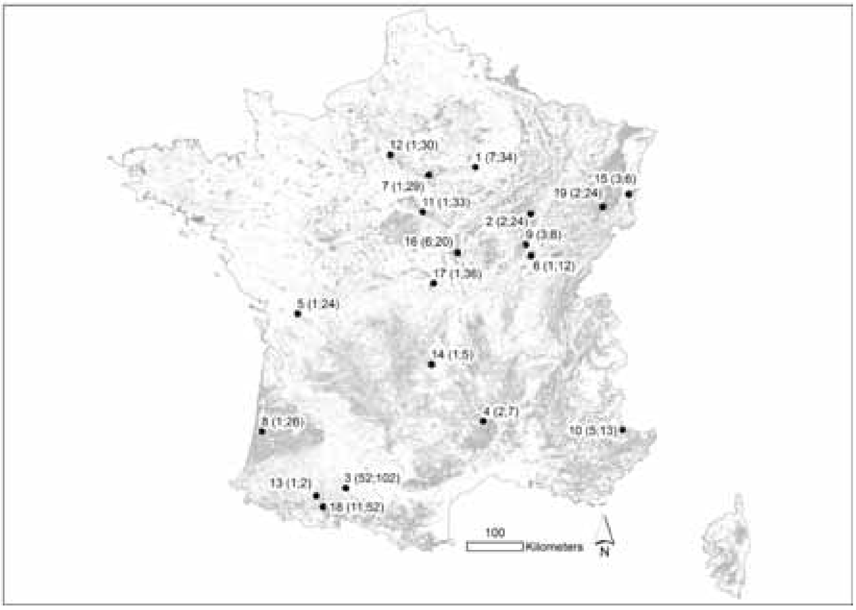


Figure 1. Carte des 19 régions forestières étudiées (entre parenthèses : le nombre de forêts inventoriées puis le nombre total de placettes pour la région); 1=Aube, 2=Auberive, 3=coteaux de Gascogne, 4=Cévennes, 5=Chizé, 6=Citeaux, 7=Fontainebleau, 8=Landes de Gascogne, 9=Lavaux, 10=Mercantour, 11=Orléans, 12=Rambouillet, 13=Rebisclou, 14=Rhue, 15=Taillis.A, 16=Taillis.B, 17=Tronçais, 18=VFP, 19=Vosges

21. Caractérisation des peuplements forestiers

Les peuplements forestiers ont été caractérisés en utilisant le protocole de notation de l'Indice de biodiversité potentielle (IBP, Larrieu & Gonin, 2008) sur des placettes circulaires centrées sur le point d'échantillonnage des taxons (piège ou surface de relevé). Ce protocole consiste à parcourir attentivement la surface de la placette en notant simultanément des variables de composition (diversité des essences), de structure (nombre de strates de végétation, bois mort, très gros arbres, arbres porteurs de dendro-microhabitats) et de texture (habitats asylvatiques associés et milieux ouverts temporaires) (Tableau 3). La continuité de l'état boisé est également prise en compte, en considérant qu'un bois présent sur la carte d'Etat Major (milieu du XIX^{e}) a une très forte probabilité de n'avoir jamais été défriché depuis (Dupouey *et al*. 2002).

Tableau 3. Description des variables de caractérisation des peuplements étudiés. Toutes les variables sont rapportées à des placettes de 1 ha. d=diamètre

Type de variables de caractérisation	Variables	Définition	Médiane	Moyenne (SE)	Min-max
Covariables géographiques	site	Région forestière			
	x	Coordonnées X de la placette (UTM, WGS 84)			
	y	Coordonnées Y de la placette (UTM, WGS 84)			
	decidconif	Peuplement dominé par les feuillus (decid), les résineux (conif) ou mixte (mixed)			
	alt	Étage bioclimatique: montagne (étages montagnard et subalpine inférieur) ou basse altitude (étages planitiaire et collinéen)			
	domain	Zone biogéographique: atlantique ou continentale			
Diversité des essences	nb.ess	Nombre d'essences autochtones (arbre vivant ou mort)	5	5.17 (0.10)	0-12
Structure verticale de la végétation	nb.strates	Nombre de strates verticales (max=4 ; herbacée, 0.5-7m, 7-20m, >20m)	4	3.70 (0.02)	2-4
Bois mort	nb.chand	Nombre de chandelles (d>37,5cm et longueur≥1m)	1	2.69 (0.21)	0-31
	nb.bms	Nombre de bois morts au sol (d>37,5cm et longueur≥1m)	1	4.66 (0.38)	0-57
Très gros arbres	nb.tgb	Nombre de très gros arbres (d>67,5cm)	2	6.54 (0.42)	0-58
Milieux ouverts	open	% de milieux ouverts avec une strate herbacée composée de plantes à fleurs	3	15.17 (1.26)	0-100
Continuité historique de l'état boisé	conti	Présence de la forêt sur la carte d'Etat Major (XIX^{e})	-	-	-
Habitats asylvatiques associés	nb.aqua	Nombre de types de milieux aquatiques	0	0.35 (0.03)	0-4
	nb.roch	Nombre de types de milieux rocheux	0	0.41 (0.04)	0-4

Type de variables de caractérisation	Variables	Définition	Médiane	Moyenne (SE)	Min-max
Dendro-microhabitats	nb.cav	Nombre d'arbres vivants portant au moins 1 cavité, avec ou sans terreau (diamètre de l'orifice>3cm)	4	6.80 (0.55)	0.161
	nb.fentes	Nombre d'arbres vivants portant au moins 1 fente ou 1 écorce décollée formant un abri	0	0.31 (0.03)	0-9
	nb.sap	Nombre d'arbres vivants portant au moins 1 coulée de sève active (longueur≥0,2m)	0	0.25 (0.02)	0-4
	nb.unbark	Nombre d'arbres vivants portant au moins 1 bois dur sans écorce (i.e. patch de bois peu altéré et de surface > 600 cm²)	1	2.36 (0.16)	0-37
	nb.fun	Nombre d'arbres vivants portant au moins 1 sporophore de polypore	0	0.63 (0.05)	0-10
	nb.bmh	Nombre d'arbres vivants ayant au moins 20% du houppier mort ou portant au moins 1 branche morte (d>20 cm et longueur>1m)	2	4.57 (0.27)	0-41
	nb.epiph	Nombre d'arbres vivants dont le tronc est couvert à plus de 30% par du lierre ou une liane	1	3.73 (0.27)	0-30
	div.mh	Nombre de types de dendro-microhabitats observés	4	3.43 (0.08)	0-7
	nb.mh	Nombre d'arbres vivants portant au moins 1 dendro-microhabitat. Les arbres portant plus d'un dendro-microhabitat d'un même type sont comptés pour 1, mais les arbres portant plusieurs types de dendro-microhabitats sont comptés pour 1 pour chaque type de dendro-microhabitat.	15	16.13 (0.66)	0-160

22. Echantillonnages taxonomiques

Un ensemble de 9 taxons a été utilisé dans cette étude. Les données taxonomiques disponibles concernaient 1 à 7 taxons par placette (Tableau 4) et des groupes écologiques ont été formés au sein de la plupart des taxons. L'ensemble constitue 21 variables taxonomiques (Tableau 5). Les protocoles d'échantillonnage sont détaillés dans le tableau 6. Afin d'analyser ensemble toutes les données disponibles pour chacun des taxons, les efforts d'échantillonnage ont été standardisés en tenant compte du nombre total d'échantillons disponibles par placette.

Tableau 4. Nombre de taxons disponibles par placette

Nombre de taxons	Nombre de régions forestières	Nombre de placettes
1	12	281
2	3	25
3	1	3
4	3	42
5	5	26
6	6	67
7	7	43
	Total	487

Tableau 5. Variables taxonomiques et groupes écologiques étudiés ; RS= richesse spécifique

Variable	Definition	Références utilisées pour la constitution des groupes
rs.colsapro	RS des coléoptères saproxyliques	FRISBEE (Bouget *et al*. 2008)
rs.colsaproflor	RS des coléoptères saproxyliques floricoles	
rs.colsaprorar	RS des coléoptères saproxyliques rares	
rs.carab	RS des coléoptères Carabidae	Coulon *et al.* (2000)
rs.carabfor	RS des coléoptères Carabidae forestiers	
rs.carabhygro	RS des coléoptères Carabidae hygrophiles	
rs.carabopen	RS des coléoptères Carabidae de milieux ouverts	
rs.bryo	RS des bryophytes	
rs.lichen	RS des lichens	
rs.chiro	RS des chauves-souris	Arthur & Lemaire (2009)
rs.chirocav	RS des chauves-souris cavicoles	
rs.oiso	RS des oiseaux	Cramps *et al*. (1981)
rs.oisocav	RS des oiseaux cavicoles	
rs.oisofor	RS des oiseaux forestiers	
rs.flore	RS des plantes vasculaires	Ellenberg (1988)
rs.florehygro	RS des plantes vasculaires hygrophiles	
rs. florehelio	RS des plantes vasculaires héliophiles	
rs.syrph	RS des diptères Syrphidae	Speight *et al*. (2013)
rs.syrphfor	RS des diptères Syrphidae forestiers	
rs.syrphopo	RS des diptères Syrphidae opophages	
rs.syrphsapro	RS des diptères Syrphidae saproxyliques	
rs.myco.d	RS des aphyllophorales	Corriol (référence non publiée)
rs.mycod.rar	RS des aphyllophorales rares	

Tableau 6. Protocoles utilisés pour les échantillonnages taxonomiques

Taxon	Région forestières	Type de piège ou surface inventoriée	Nombre d'années d'échantillonnage	Remarques
Coléoptères saproxyliques	2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19	1 à 4 PolytrapTM	1 à 3	Effort d'échantillonnage standardisé par le nombre d'échantillons disponibles (nombre d'années x nombre de pièges)
Carabes	1, 2, 5, 6, 7, 9, 11, 19	3 ou 9 Barber	1	Effort d'échantillonnage standardisé par le nombre d'échantillons disponibles (nombre de pièges x nombre de relevés pour le piège)
Bryophytes	2, 5, 6, 7, 9, 11, 12, 18, 19	Corticoles, 1250 m²	1	
Lichens	18	1 ha	1	
Chiroptères	2, 5, 6, 7, 9, 12	Enregistrement émissions ultrasoniques	1 (3 passages)	
Oiseaux	2, 5, 6, 5, 9, 19	EPS 5 mn	1 (2 passages)	
Flore	1, 2, 5, 6, 7, 9, 18, 19	Phanérogames terricoles, 200 à 1018 m²	1 (1 passage)	
Diptères Syrphidae	3, 13, 18	1 à 2 Malaise	1 à 2	Effort d'échantillonnage standardisé par le nombre d'échantillons disponibles (nombre d'années x nombre de pièges)
Champignons lignivores	2, 5, 6, 7, 9, 12, 13, 18, 19	1250 m² à 1 ha	1 à 2	

23. Analyse des données

231. Co-variation de la composition des assemblages et de la richesse spécifique

- Co-variation de la composition des assemblages

Nous avons procédé à des tests de Mantel sur la corrélation matricielle entre les matrices de dissimilarité inter-placettes pour toutes les paires de taxons qui avaient une co-occurrence supérieure à 50 placettes (Tableau 7) (distance Euclidienne, fonction *mantel.rtest*, paquet R-*ade4*, nombre de répétitions=10 000).

- Co-variation de la richesse spécifique

Nous avons calculé des coefficients de corrélation de Spearman (et leur significativité au seuil de 1%) entre richesses spécifiques pour les paires de taxons qui avaient une co-occurrence supérieure à 50 placettes (Tableau 7) (fonctions *cor* et *cor.test*, paquet R-*stats*).

Tableau 7. Nombre de placettes partageant au moins 2 taxons ; en gras apparaissent les co-occurrences supérieures à 50 placettes

Taxons	bryo	carab	chiro	colsapro	flore	lichen	myco	oiso
carab	**84**							
chiro	**90**	**83**						
colsapro	**135**	**132**	**113**					
flore	**108**	**117**	**87**	**140**				
lichen	22	0	0	23	**52**			
myco	**128**	**94**	**105**	**156**	**124**	**52**		
oiso	**84**	**115**	**85**	**116**	**119**	0	**96**	
syrph	8	0	0	9	8	8	9	0

232. Effets des variables environnementales

- Effets sur les variations de composition des assemblages taxonomiques

Les effets des variables environnementales sur les variations de composition des assemblages ont été hiérarchisés par une ordination de type “Constrained Analysis of Principal Coordinates » (CAP) sur distances non euclidiennes (Anderson & Willis 2003) (fonction *capscale*, paquet R-*Vegan*) sur des matrices de distances de Jaccard (fonction *vegdist*, paquet R-*Vegan*). Nous avons calculé pour chaque variable l’inertie totale expliquée (i.e. l’inertie intrinsèque à la variable plus l’inertie partagée avec d’autres variables) et la contribution relative de la variable à la part de variance expliquée. La significativité des résultats est estimée par un test de permutation.

- Effets sur la richesse spécifique

Après avoir sélectionné les variables par élimination séquentielle des variables colinéaires ayant un *variance inflation factor* (VIF) (fonction *vif.mer* ; Frank 2011) supérieur à 3 (Zuur *et a*l. 2010), nous avons généré le modèle nul et des modèles linéaires généralisés mixtes (fonction *glmer*, paquet R-*lme4*) en utilisant la région forestière comme variable à effet aléatoire et l’ensemble des variables explicatives non colinéaires comme variables à effet fixe. Le meilleur modèle a été sélectionné en recherchant un indice Akaike (AICc, Burnham & Anderson 2002 ; fonction *dredge*, paquet R-*MuMIn*) minimum et différent de plus de 2 unités du modèle nul (fonction *model.avg,* paquet R-*MuMIn*).

- Recherche de seuils significatifs pour les variations de richesse spécifique

Dans les cas de relations positives entre la richesse spécifique et des variables environnementales révélées par les modèles généralisés mixtes, nous avons recherché par partition récursive (Hothorn *et al*. 2006) l’existence de seuils significatifs. Seuls les seuils primaires et significatifs au seuil de p<0,001 ont été retenus. Des intervalles de confiance à 80 %, basés sur échantillonnage de type bootstrap de 5000 items, ont été calculés pour ces valeurs seuils (fonctions *ctree*, paquet R-*party*, et *boot.ci*, paquet R-*boot*), sans pouvoir prendre en compte la structure spatiale des données comme nous l’avions fait pour les analyses précédentes.

3. Résultats

31. Co-variation de la composition des assemblages et de la richesse spécifique

311. Co-variation de la composition des assemblages

Aucune covariation significative au seuil de p<0.01 n'a un estimateur négatif (Tableau 8). La composition des assemblages de (i) bryophytes covarie avec celle des carabes forestiers, de la flore et des oiseaux forestiers, (ii) carabes covarie avec celle des carabes forestiers, mais aussi avec celle des coléoptères saproxyliques, (iii) carabes forestiers covarie avec celle de la flore vasculaire et des oiseaux forestiers, (iv) chiroptères covarie avec celle des coléoptères saproxyliques et des champignons aphyllophorales, (v) coléoptères saproxyliques covarie avec celle de la flore vasculaire, des champignons aphyllophorales, des oiseaux et des oiseaux forestiers, (vi) la flore covarie avec la composition des assemblages de lichens, des champignons aphyllophorales, des oiseaux et des oiseaux forestiers.

Tableau 8. Co-variation de la composition des assemblages taxonomiques (*p*-values en dessous de la diagonale ; estimateur de Monte Carlo au-dessus) ; les co-variations significatives au seuil de p<0.01 apparaissent en gras

Taxons	bryo	carab	carabfor	chiro	sapro	flore	lichen	mycod	oiso	oisofor
bryo		0.041	**0.283**	-0.058	0.009	**0.223**		0.068	0.109	**0.176**
carab	*0.309*		**0.226**	-0.076	**0.183**	0.127		-0.014	0.157	0.108
carabfor	***0.001***	***0.002***		-0.145	-0.039	**0.273**		0.204	0.074	**0.139**
chiro	*0.799*	*0.670*	*0.95*		**0.325**	-0.084		**0.267**	0.063	0.017
sapro	*0.425*	***0.004***	*0.699*	***0.000***		**0.371**		**0.415**	**0.349**	**0.204**
flore	***9.99e-05***	*0.019*	***0.000***	*0.833*	***9.99e-05***		**0.685**	**0.205**	**0.246**	**0.222**
lichen						***9.99e-05***				
mycod	*0.161*	*0.457*	*0.033*	***0.005***	***9.99e-05***	***0.000***	***9.99e-05***		0.079	0.120
oiso	*0.038*	*0.017*	*0.135*	*0.214*	***9.99e-05***	***9.99e-05***		*0.190*		**0.9154**
oisofor	***0.001***	*0.044*	***0.008***	*0.381*	***0.000***	***9.99e-05***		*0.054*	***9.99e-05***	

312. Co-variation de la richesse spécifique

Aucune co-variation de la richesse spécifique au seuil de 0.7 (coefficient de corrélation de Spearman) et significative (*p*<0.01) n'est négative (Tableau 9). Seules des co-variations intra-taxon apparaissent : (i) la richesse spécifique des carabes forestiers avec celle des carabes, (ii) les chiroptères cavicoles avec les chiroptères, et (iii) les oiseaux forestiers avec les oiseaux. Des corrélations plus faibles inter-taxons sont toutefois significatives au seuil de 1 % : (i) les bryophytes avec les coléoptères saproxyliques, rares ou non (corrélation négative), et aussi les champignons (négative), (ii) les carabes avec les coléoptères saproxyliques (positive), (iii) les chiroptères et les chiroptères cavicoles avec les coléoptères saproxyliques (positive) et la flore (négative), (iii) les coléoptères saproxyliques avec les champignons (positif), et (iv) les coléoptères saproxyliques rares ainsi que les lichens avec les champignons et les champignons rares (positive). Sont également significatives au seuil de 1 % des co-variations intra-taxon inférieures à 70 % (toutes positives) : (i) les oiseaux et oiseaux forestiers avec les oiseaux cavicoles, (ii) les champignons avec les champignons rares, et (iii) les coléoptères saproxyliques avec les coléoptères saproxyliques rares.

Tableau 9. Co-variation de la richesse spécifique des taxons 2 à 2 ; les corrélations (Spearman) supérieures à 0.7 apparaissent en gras au-dessus de la diagonale et les co-variations significatives (p<0.01) sont soulignées ; en gras en dessous de la diagonale, les co-variations significatives au seuil de p<0.01 ; NA=donnée non disponible ; nc=non calculé car co-occurrence des taxons sur moins de 50 placettes

p\Spearman	rs.bryo	rs.carab	rs.carabfor	rs.chiro	rs.chirocav	rs.colsapro	rs.colsaprorar
rs.bryo	-	-0.214	0.101	0.126	0.038	-0.544	-0.291
rs.carab	*0.050*	-	**0.744**	0.192	0.164	0.385	0.096
rs.carabfor	*0.361*	***5 e-16***	-	0.245	0.162	0.129	0.086
rs.chiro	*0.237*	*0.082*	*0.255*	-	**0.868**	0.273	0.109
rs.chirocav	*0.720*	*0.138*	*0.136*	***2 e-16***	-	0.380	0.209
rs.colsapro	***8 e-12***	***5 e-06***	*0.141*	***0.003***	***3 e-05***	-	0.361
rs.colsaprorar	***0.000***	*0.272*	*0.318*	*0.249*	*0.026*	***1 e-09***	-
rs.flore	*0.020*	*0.186*	*0.449*	***0.000***	***5 e-05***	*0.174*	*0.873*
rs.lichen	nc	NA	NA	NA	NA	nc	nc
rs.myco.d	***9 e-08***	*0.510*	*0.187*	*0.015*	***0.000***	***0.007***	***0.000***
rs.mycorar	*0.505*	*0.359*	*0.149*	***0.008***	***0.002***	*0.297*	***0.005***
rs.oiso	*0.934*	*0.314*	*0.561*	*0.836*	*0.613*	*0.587*	*0.289*
rs.oisofor	*0.702*	*0.228*	*0.686*	*0.943*	*0.698*	*0.905*	*0.289*
rs.oisocav	*0.250*	*0.729*	*0.681*	*0.197*	*0.135*	*0.080*	*0.077*

Tableau 9. Suite

rs	rs.flore	rs.lichen	rs.myco.d	rs.mycorar	rs.oiso	rs.oisofor	rs.oisocav
rs.bryo	-0.223	nc	-0.610	0.059	0.009	0.042	0.126
rs.carab	-0.123	NA	0.069	0.096	-0.095	-0.113	0.032
rs.carabfor	-0.186	NA	0.137	0.147	-0.055	-0.037	0.038
rs.chiro	-0.347	NA	0.235	0.257	-0.023	-0.008	0.141
rs.chirocav	-0.417	NA	0.320	0.291	-0.056	-0.042	0.163
rs.colsapro	0.115	nc	0.398	-0.084	0.051	0.011	0.163
rs.colsaprorar	0.014	nc	0.305	0.222	0.099	0.099	0.164
rs.flore	-	-0.302	-0.109	-0.211	0.190	0.163	-0.022
rs.lichen	*0.133*	-	0.061	0.618	NA	NA	NA
rs.myco.d	*0.021*	***0.009***	-	0.499	-0.031	-0.004	0.104
rs.mycorar	*0.018*	***0.000***	***3 e-11***	-	0.436	-0.128	0.145
rs.oiso	*0.038*	NA	*0.599*	*0.110*	-	**0.985**	0.627
rs.oisofor	*0.076*	NA	*0.965*	*0.213*	***2 e-16***	-	0.655
rs.oisocav	*0.804*	NA	*0.319*	*0.158*	***2 e-14***	***6 e-16***	-

32. Effets des variables environnementales

321. Effets sur les variations de composition des assemblages

Les contributions des variables environnementales à l'inertie totale sont relativement faibles (0.37 à 12.83 %) mais l'ensemble des variables notées contribue de 3.6 % (pour les coléoptères saproxyliques) à près de 54 % de l'inertie totale (pour les champignons) (Tableau 10). L'effet de la continuité de l'état boisé n'a pu être testé que pour les coléoptères saproxyliques, les carabes, les carabes forestiers, les syrphes, les syrphes forestiers et les champignons, et n'est pas significatif seulement pour les carabes et les carabes forestiers. Plusieurs effets significatifs des variables environnementales avec les variations des assemblages du taxon sont également significatifs avec les variations de richesse spécifique de ce même taxon (Tableau 10) : (i) le nombre d'essences sur la flore (effet positif), (ii) le nombre de strates sur les carabes (effet négatif) et les bryophytes (effet positif), (iii) le nombre de chandelles sur les bryophytes (effet positif) et les chiroptères (effet positif), (iv) le nombre de bois mort au sol sur les carabes (effet négatif), les bryophytes (effet positif) et les oiseaux (effet positif), (v) le nombre de très gros bois sur les oiseaux (effet positif) et les oiseaux forestiers (effet positif), (vi) le pourcentage de milieux ouverts sur les coléoptères saproxyliques (effet positif), les carabes (effet positif) et la flore (effet positif), et enfin (vii) le nombre de types de milieux aquatiques sur les bryophytes (effet positif) et les lichens (effet positif).

Tableau 10. Résultats de l'ordination de type "Constrained Analysis of Principal Coordinates » (CAP) sur distances non euclidiennes, pour partitionner la variance dans la réponse de la matrice espèces/placette par rapport aux variables environnementales décrivant le peuplement. Sont indiqués la contribution totale de la variable environnementale à l'inertie totale (i.e. l'inertie intrinsèque à la variable + celle partagée avec d'autres variables) et le niveau de signification (***: p<0.001; **: 0.001<p<0.01; *: 0.01<p<0.05) ; seuls les résultats significatifs sont indiqués), ainsi que le % d'inertie expliquée par l'ensemble des variables environnementales ; les relations significatives mises en évidence également avec la richesse spécifique sont en gras

Taxons/variables environnementales	nb.ess	nb.strates	nb.chand	nb.bms	nb.tgb	nb.mh	open	conti	nb.aqua	nb.roch	total inertie expliquée
colsapro	(0.37/**)	(0.55/**)	(1.02/**)	(0.76/**)	(0.46/**)	(0.65/**)	**(0.60/**)**	(0.35/**)	(0.51/**)	(0.42/**)	3.6%
carab	ns	**(0.99/**)**	(0.76/**)	**(0.63/*)**	ns	(0.63/*)	**(0.59/*)**	ns	ns	ns	4.3%
carabfor	ns	ns	ns	(1.05/**)	ns	ns	(0.99/**)	ns	ns	ns	24.4%
bryo	ns	**(0.79/**)**	**(1.06/**)**	**(0.93/**)**	(0.71/**)	ns	(0.89/**)	untested	**(0.72/**)**	ns	5.74%
lichen	(11.61/**)	(9.73/*)	(12.83/**)	(11.28/**)	(7.32/*)	(7.81/*)	(10.86/**)	untested	**(18.52/**)**	(10.63/**)	33.78%
chiro	ns	ns	**(1.37/*)**	ns	ns	ns	ns	untested	ns	ns	7.58%
oiso	ns	(2.87/**)	(1.36/**)	**(1.69/**)**	**(1.50/**)**	(1.43/*)	(1.38/**)	untested	ns	ns	7.4%
oisofor	ns	(2.99/**)	(1.25/*)	(1.72/**)	**(1.56/**)**	(1.43/*)	ns	untested	ns	ns	59%
flore	**(1.19/**)**	(1.03/**)	(1.46/**)	(1.42/**)	(0.86/**)	(1.75/**)	**(1.59/**)**	untested	(1.82/**)	(0.75/**)	8.85%
syrph	ns	ns	(1.34/*)	ns	(1.28/*)	ns	ns	(1.58/**)	(1.19/*)	ns	8.14%
syrphfor	ns	ns	ns	ns	ns	ns	ns	(1.65/*)	ns	ns	8.20%
myco.d	(2.44/**)	(1.65/**)	(5.76/**)	(3.28/**)	(2.37/**)	(1.38/**)	ns	(1.58/**)	**(1.55/**)**	(3.84/**)	53.91%

322. Effets sur la richesse spécifique (Tableau 11)

La richesse spécifique des coléoptères saproxyliques semble principalement déterminée par des variables à large échelle spatiale : l'altitude (effet négatif) et la dominance de feuillus (effet positif). À l'échelle de la placette, le degré d'ouverture a un effet significatif ($p<0.01$) mais n'est pas retenu dans le meilleur modèle. Les facteurs à large échelle spatiale ont également un effet significatif fort sur la richesse spécifique des coléoptères saproxyliques floricoles (effet positif de la dominance des feuillus), les coléoptères saproxyliques rares (effet négatif de l'altitude), et contribuent à la richesse spécifique des bryophytes (effet négatif de l'altitude), des oiseaux cavicoles (effet négatif du domaine continental), de la flore hygrophile (effet positif du domaine continental), et des champignons rares (effet négatif de l'altitude). A l'échelle locale, les variables les plus déterminantes (au seuil de $p<0.001$) sont : (i) le nombre d'arbres porteurs de sporophores de champignons lignivores pour les coléoptères saproxyliques floricoles (effet positif), (ii) le nombre de strates pour les carabes (effet négatif), les carabes de milieux ouverts (effet négatif) et les syrphes (effet positif), (iii) le pourcentage de milieux ouverts pour les carabes de milieux ouverts (effet positif), la flore (effet positif) et la flore héliophile (effet positif), (iv) le nombre de gros bois morts au sol pour les carabes de milieux ouverts (effet négatif), les bryophytes (effet positif), (v) le nombre de chandelles sur les bryophytes (effet positif), les syrphes opophages (effet négatif) et les syrphes saproxyliques (effet négatif), (vi) le nombre d'essences autochtones sur la flore (effet positif), (vii) le nombre de types de milieux aquatiques sur la flore hygrophile (effet positif) et les champignons (effet positif), (viii) le nombre d'arbres porteurs de dendro-microhabitats sur la flore héliophile (effet positif) et les champignons (effet positif), (ix) la diversité des dendro-microhabitats pour les syrphes (effet négatif), (x) le nombre d'arbres porteurs du dendro-microhabitat « bois sans écorce » sur les champignons (effet positif), et enfin (xi) le nombre de très gros bois pour les champignons rares.

Tableau 11. Estimateurs pour les variables à large échelle spatiale et environnementales à l'échelle du peuplement, déterminantes pour la richesse spécifique de 9 taxons (modèles mixtes avec la région forestière comme variable à effet aléatoire) ; seules les réponses significatives sont présentées (***: p<0.001; **: 0.001<p<0.01; *: 0.01<p<0.05) ; apparaissent en gras les réponses significatives à p<0.01

		Large échelle spatiale		Echelle locale (placette de 1 ha)			
Taxon	Groupe écologique	Facteur à effet +	Facteur à effet -	Facteur à effet +	Facteur à effet -	Meilleur modèle (AICc)	AICc du modèle nul
Coléoptères saproxyliques	colsapro	__dediconifdecid=14.20***__	__altlow=-20.69**__	open =0.06*		altlow+decidconifdecid (2766.82)	2798.98
	colsaproflor	__dediconifdecid=3.83***__		open =0.02* __nb.roch=1.11**__ __nb.fun=0.66***__	nb.strates=-1.20*	decidconifdecid+nb.roch (1991.99)	2015.90
	colsaprorar		altlow=-0.70*	__nb.chand=0.03***__		altlow+ nb.chand (431.04)	482.26
Carabes	carab			__open=0.002**__	__nb.strates=-0.24***__ __nb.bms=-0.008**__	nb.bms+ nb.strates (214.75)	266.02
	carabfor					nb.strates (153.92)	171.14
	rs.carabhygro				__nb.strates=-0.27**__	nb.strates+open (188.17)	201.35
	rs.carabopen			__open=0.009***__	__nb.strates=-0.81***__ __nb.bms=-0.05***__	nb.bms+ nb.strates (205.36)	300.92
Bryophytes	bryo		altlow=-0.45*	__nb.strates=0.06**__ __nb.chand=0.004***__ __nb.bms=0.008***__ __nb.aqua=0.09**__	nb.fun=-0.04*	nb.aqua+nb.bms (196.86)	843.49
Lichens	lichen			nb.aqua=0.09*		nb.ess+nb.strates (25.31)	25.31
Chiroptères	chiro			nb.ess=0.07* nb.chand=0.02* nb.bms=0.01* __nb.tgb=0.01**__ div.mh=0.09* nb.cav=0.027*	nb.epiph=-0.02*	nb.ess+nb.tgb (166.63)	488.27
	chirocav					nb.chand(136.38)	406.43

		Large échelle spatiale		Echelle locale (placette de 1 ha)			
Taxon	Groupe écologique	Facteur à effet +	Facteur à effet -	Facteur à effet +	Facteur à effet -	Meilleur modèle (AICc)	AICc du modèle nul
Oiseaux	oiso			nb.ess=0.52* nb.bms=0.08* nb.tgb=0.13*		nb.ess+ nb.tgb (671.88)	678.76
	oisocav		**domainconti=-1.22****	**nb.strates=1.48**** **nb.bms=0.04**** **nb.tgb=0.06****		nb.strates+nb.tgb (509.59)	522.51
	oisofor			**gb=0.53****		nb.tgb + nb.ess (673.92)	672.65
Flore	flore			**nb.ess=0.0007***** **open=0.006*****		nb.ess+open (1128.9)	1134.44
	florehygro	**domainconti=0,32****		**nb.aqua=0.23*****		decidconif+domain+nb.aqua +nb.chand (116.93)	136.34
	florehelio			**nb.mh=0.008***** **open=0.01*****	**nb.aqua=-0.26***** nb.bms=-0.006* **nb.roch=-0.12**** **nb.strates=-0.27****	alt+decidconif+div.mh+nb.aqua +nb.bms+nb.ess+nb.mh+nb.roch +nb.strates+nb.tgb+open (124.14)	230.59
Syrphes	syrph			**nb.strates=0.32*****	**div.mh=-0.09*****	nb.strates +div.mh (617.4)	1189.00
	syrphfor			**nb.ess=0.05****	**nb.sap=-0.21****	div.mh+nb.ess (354.43)	798.95
	syrphopo			nb.fun=0.24*	**nb.chand=-0.13*****	nb.chand (140.70)	369.50
	syrphsapro			**nb.ess=0.06**** nb.strates=0.31*	**nb.sap=-0.27**** **nb.chand=-0.04*****	nb.chand+ nb.ess (317.54)	739.81
Champignons	myco.d			**nb.mh=0.005***** **nb.aqua=0.13***** **nb.unbark=0.02***** **nb.fun=0.06*****		nb.mh +nb.aqua (322.4)	947.05
	mycod.rar		altlow=-1.18*	nb.strates=0.74* **nb.chand=0.04**** **nb.tgb=0.02***** nb.roch=0.35* **nb.sap=0.30****		nb.chand+nb.roch (127.37)	139.48

Dans l’ensemble des relations significatives entre les variables environnementales à l’échelle de la placette et la richesse spécifique du taxon, on observe à la fois : (i) des relations attendues et révélées par les analyses (« au rendez-vous »), (ii) des relations attendues et qui ne sont pas révélées par les analyses, mais également (iii) des relations inattendues. Pour faciliter l’interprétation qualitative de ces relations, les variables environnementales ont été regroupées sous trois catégories. L’*ambiance micro-climatique* regroupe les variables ouverture du milieu, nombre de strates et nombre de types de milieux aquatiques ; la *diversité dendrologique* correspond seulement au nombre d’essences autochtones ; la *maturité du peuplement* regroupe le nombre de bois mort debout, au sol, de très gros bois et d’arbres porteurs de dendro-microhabitats.

- Relations attendues et « au rendez-vous » (au seuil de significativité de *p*<0.01) (Tableau 12)

Il s’agit de la confirmation par l’observation de l’hypothèse, posée *a priori*, d’une relation entre une variable environnementale et la richesse spécifique du taxon. À large échelle spatiale, les forêts dominées par les feuillus sont plus riches en coléoptères saproxyliques, floricoles ou non. À l’échelle locale, les richesses spécifiques (RS) des carabes, des carabes de milieux ouverts et des phanérogames héliophiles diminuent quand le nombre de strates augmentent. Toutes les autres relations significatives sont positives, *i.e*. la RS du taxon augmente avec la variable environnementale. Les RS des carabes, des carabes de milieux ouverts, de la flore et des phanérogames héliophiles augmentent avec le degré d’ouverture du couvert. Les RS des bryophytes et des syrphes augmentent avec le nombre de strates. La maturité du peuplement, à travers le nombre de très gros bois, l’augmentation du volume et de la diversité du bois mort, de la densité de certains dendro-microhabitats, favorise la richesse spécifique des coléoptères saproxyliques rares, des bryophytes, des champignons (rares ou non), des chiroptères et des oiseaux (forestiers ou cavicoles) (voir les détails dans le Tableau 12).

Tableau 12. Résumé des relations attendues et au rendez-vous, significatives au seuil de p<0.01, trouvées entre les facteurs environnementaux et la richesse spécifique (RS) des taxons et groupes écologiques étudiés

Groupes de variables environnementales	Variables environ.	Taxons dont la RS augmente avec la variable environnementale	Taxons dont la RS diminue quand la variable environnementale augmente
ambiance climatique	open	carab, carabopen, flore, florehelio	
	nb.strates	bryo, syrph	carab, carabopen, florehelio
	nb.aqua	bryo, florehygro	
diversité dendrologique	nb.ess	flore, syrphfor, syrphsapro	
maturité du peuplement	nb.chand	colsaprorar, bryo, mycorar	
	nb.bms	bryo	
	nb.tgb	chiro, oisocav, oisofor, mycorar	
	nb.mh	myco	
	nb.unbark	myco	
	nb.fun	myco	

- Relations inattendues (au seuil de significativité de *p*<0.01) (Tableau 13)

Les relations significatives mais inattendues ne concernent que des variables d'ambiance climatique et de maturité du peuplement. Certaines de ces relations inspirent des liens indirects comme l'ouverture du couvert et la disponibilité en fleurs quand les milieux rocheux réduisent le couvert forestier. Les carabes et les syrphes dans leur ensemble (forestiers, opophages et saproxyliques) réagissent négativement à la maturité du peuplement.

Tableau 13. Résumé des relations inattendues, significatives au seuil de p<0.01, trouvées entre les facteurs environnementaux et la richesse spécifique (RS) des taxons et groupes écologiques étudiés

Groupes de variables environnementales	Variables environnementales	Taxons dont la RS augmente avec la variable environ.	Taxons dont la RS diminue quand la variable environ. augmente
ambiance micro-climatique	nb.roch	colsaproflor	florehelio
	nb.strates	oisocav	carabhygro
	nb.aqua		florehelio
maturité du peuplement	nb.fun	colsaproflor	
	nb.mh	florehelio	
	nb.sap	mycorar	syrphfor, syrphsapro
	nb.chand		syrphopo, syrphsapro
	div.mh		syrph
	nb.bms	oisocav	carab, carabopen

Ces relations inattendues peuvent résulter de plusieurs facteurs : (i) certaines réalités biologiques nous sont méconnues ; (ii) la technique d'échantillonnage nous livre des assemblages biotiques non parfaitement représentatifs de la biodiversité locale, à notre échelle d'investigation. Par exemple, les syrphes sont dans l'ensemble très mobiles et la technique de capture à l'aide de tente Malaise vise les adultes qui sont tous floricoles, ce qui peut les éloigner des sites de pontes s'ils sont dépourvus de fleurs, comme c'est parfois le cas dans les peuplements matures mais à texture homogène ; (iii) elles sont des artefacts liés à la qualité des mesures environnementales ou (iv) elles sont infléchies par la mauvaise affectation des espèces dans les groupes écologiques (par méconnaissance de leur autécologie).

- Relations attendues et qui ne sont pas « au rendez-vous » (au seuil de significativité de *p*<0.01) (Tableau 14)

Il s'agit de relation attendue entre une variable environnementale et la richesse spécifique du taxon, mais qui n'a pas été statistiquement observée. Les plus remarquables d'entre elles sont le manque de relation entre (i) le pourcentage de milieux ouverts et la richesse spécifique des coléoptères saproxyliques floricoles et des syrphes, (ii) le nombre de strates et les oiseaux, (iii) le nombre de types de milieux aquatiques et à la fois les carabes hygrophiles et la flore hygrophile, (iii) le nombre de gros bois mort et les champignons et insectes saproxyliques, (iv) le nombre de cavités et fentes et les oiseaux et chiroptères cavicoles et (v) le nombre de coulées de sève et les syrphes opophages.

Tableau 14. Principales relations attendues mais non observées entre les variables environnementales et taxonomiques (au seuil de p<0.01) ; les non relations les plus remarquables apparaissent en gras

Groupes de variables environnementales	Variables environnementales	Variables taxonomiques
ambiance micro-climatique	open	rs.colsaproflor; rs.chiro ; rs.syrph ; rs.syrphfor, rs.syrphsapro
	nb.strates	rs.oiso
	nb.aqua	rs.carabhygro ; rs.florehygro
	nb.roch	rs.chiro
diversité dendrologique	nb.ess	rs.colsapro; rs.bryo ; rs.lichen ; rs.myco
maturité du peuplement	nb.bms	rs.colsapro ; rs.colsaprorar ; rs.syrphsapro ; rs.myco ; rs.mycorar
	nb.chand	rs.colsapro; rs.chirocav ; rs.oisocav ; rs.myco
	nb.tgb	rs.lichen; rs.chirocav ; rs.syrphfor ; rs.syrphsapro
	nb.cav	rs.colsapro; rs.colsaprorar; rs.chirocav ; rs.oisocav; rs.syrphsapro
	nb.fentes	rs.chirocav; rs.oisocav
	nb.sap	rs.syrphopo
	nb.unbark	rs.colsapro
	nb.fun	rs.mycorar
	nb.bmh	rs.colsapro
	nb.epiph	rs.oisofor
	div.mh	rs.colsapro ; rs.syrphsapro
	nb.mh	rs.colsapro ; rs.colsaprorar ; rs.syrphsapro
autre	conti	rs.colsaprorar ; rs.lichen; rs.mycorar

33. Recherche de seuils significatifs pour les variations de richesse spécifique

Nous avons mis en évidence des seuils significatifs (*p*<0.001) dans les relations positives entre la présence : (i) d'au moins 4 essences autochtones et la flore vasculaire et d'au moins 5 essences et les oiseaux, (ii) d'au moins 4 chandelles de plus de 40 cm de dbh et les chiroptères et d'au moins 8 chandelles de plus de 40 cm de dbh pour les champignons aphyllophorales rares, (iii) d'au moins 2 gros bois mort au sol de plus de 40 cm de dbh pour les chiroptères et d'au moins 3 gros bois morts au sol de plus de 40 cm de dbh pour les bryophytes, et (iv) d'au moins 11 très gros arbres vivants (dbh> 70 cm) pour les champignons aphyllophorales rares et d'au moins 15 très gros arbres vivants pour les chiroptères (Tableau 15). Au-delà de ces seuils, on observe une augmentation de la richesse spécifique.

Tableau 15. Seuils significatifs (*p*<0.001) pour les relations positives entre les caractéristiques du peuplement à l'échelle d'un hectare et la richesse spécifique (RS) du taxon (voir tableau 10) ; les intervalles de confiance à 80 % (IC 80) ont été calculés par bootstrap (5000 itérations)

Facteur	Seuils (IC 80)		Synthèse
nb.ess	flore=4 (4-5)	oiseaux=5 (3-8)	>5 essences: augmentation significative de la RS de la flore et des oiseaux
nb.chand	chiroptères=4 (0-4)	champi rares=8 (7-16)	>8 grosses chandelles /ha: augmentation significative de la RS des chauves-souris et des champignons lignicoles rares
nb.bms	chiroptères=2 (2-7)	bryophytes=3 (2-3)	>3 gros bois morts au sol/ha: augmentation significative de la RS des chauves souris et des mousses
nb.tgb	champi rares=11 (7-14)	chiroptères=15 (2-16)	>15 très gros arbres vivants /ha: augmentation significative de la RS des champignons lignicoles rares et des chauves-souris

Bibliographie

Lindenmayer D.B., Margules C.R., Botkin D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14(4): 941-950

Anderson M.J., Willis T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84, 511–525.

Blondel J., Ferry C., Frochot B., 1973. Avifaune et végétation. Essai d'analyse de la diversité. Alauda 41, 63-84.

Bouget C., Larrieu L., Brin A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecological Indicators 36, 656-664.

Bouget C., Larrieu L., Nusillard B., Parmain G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers Conserv 22, 2111-2130.

Bütler R., Angelstam P., Ekelund P., Schlaeffer R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biological Conservation 119, 305-318.

Ellenberg H., 1988. Vegetation ecology of Central Europe. Cambridge: Cambridge University Press.

Gosselin M., Laroussinie O., (coord.) 2004. Biodiversité et Gestion forestière: connaître pour préserver. Synthèse bibliographique. Cemagref , Nogent sur Vernisson France

Gosselin F., Dallari R., 2007. Des suivis "taxonomiques" de biodiversité en forêt pourquoi ? quoi ? comment ?. 1-78. 2007. CEMAGREF, Groupement de Nogent sur Vernisson.

Gossner M., Lachat T., Brunet J., Isacsson G., Bouget C., Brustel H., Brandl R., Weisser W.W., Mueller J., 2013. Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. Conservation Biology 27, 605-614.

Hothorn T., Hornik K.Z.A., 2006. *Party*: a laboratory for recursive par(y)itioning.

Kraus D., Krumm F. (eds) 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute. 284 pp.

Larsson T.B., 2001. Biodiversity evaluation tools for European forests. pp. 75-81. Ecol. Bull. 50

McElhinny C., Gibbons P., Brack C., Bauhus J., 2005. Forest and woodland stand structural complexity: Its definition and measurement. For. Ecol. Manage. 218(1-3): 1-24.

Moning C., Müller J., 2008. Environmental key factors and their thresholds for the avifauna of temperate montane forests. Forest Ecology and Management 256, 1198-1208.

Moning C., Müller J., 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. Ecological Indicators 9, 922-932.

Müller J., Bütler R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129, 981-992.

Puumalainen J, Kennedy P., Folving S., 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. J. Environ. Manage. 67(1): 5-14

Rameau J.C., Gauberville C., Drapier N. 2000. Gestion forestière et diversité biologique; identification et gestion intégrée des habitats et espèces d'intérêt communautaire. IDF , Paris

Regnery B., Paillet Y., Couvet D., Kerbiriou C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? Forest Ecology and Management 295, 118-125.

Tews J., Brose U., Grimm V., Tielborger K., Wichmann M.C., Schwager M., Jeltsch F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31(1): 79-92

Winter S., Möller G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251-1261.

Burnham K.P., Anderson D.R., 2002. Model selection and multimodel inference, Second ed.: New York: Springer-Verlag.

Zuur A.F., Ieno E.N., Elphick C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol.1, 3–14.

Larrieu L., Gonin P., 2008. L'indice de Biodiversité Potentielle (IBP) : une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. Rev. For. Fr. 06-2008 ; pp. 727-748.

Siitonen J., 2001 Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49:11–41.

Kraus D., Krumm F. (eds.) 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. EFI.

Nageleisen L.M., Bouget C.; (coord.) 2009. Forest insect studies: methods and techniques. Key considerations for standardization. An overview of the reflections of the “Entomological Forest Inventories” working group. Les dossiers forestiers n°10, ONF.

Section IV – Applications pratiques pour les gestionnaires d’espaces forestiers

SECTION IV - APPLICATIONS PRATIQUES POUR LES GESTIONNAIRES D'ESPACES FORESTIERS

Les dendro-microhabitats sont maintenant identifiés comme des éléments de structure pertinents pour suivre la diversité des espèces à l'échelle du peuplement (*e.g.* Winter et Möller 2008 ; Bouget *et al.* 2013 et 2014 en section III). Ils sont déjà utilisés à ces fins pour le suivi de biodiversité dans le land allemand de Brandebourg et sont en phase d'intégration dans des schémas de gestion durable (certifications FSC et PEFC, documents de gestion, etc.). Ils sont également inclus dans des outils de diagnostic et d'aide à la gestion intégrée comme l'Indice de Naturalité du WWF (Rossi et Vallauri 2013) ou encore l'Indice de Biodiversité Potentielle (Larrieu et Gonin 2008) que je présenterai comme exemple dans le chapitre 2.

Il est donc d'actualité de porter une attention particulière aux arbres qui portent des microhabitats et il s'avère de plus en plus nécessaire de pouvoir inventorier ces dendro-microhabitats de façon pertinente. Les acteurs ont besoin pour cela de définitions et d'une typologie commune, au moins à tous les utilisateurs du même domaine, pour pouvoir comparer les résultats de la recherche ou pour appliquer de façon cohérente les recommandations de gestion qui émanent de travaux de recherche ou de décisions politiques.

1 VERS UNE TYPOLOGIE DE REFERENCE

Nous proposons ici une typologie qui a pour objectif de construire une référence partagée par tous les utilisateurs des dendro-microhabitats, du chercheur au propriétaire forestier. Elle représente également une ébauche de base de données inédite sur la biodiversité associée aux dendro-microhabitats.

1.1 CONSTRUCTION D'UNE TYPOLOGIE A DIRE D'EXPERT

Nous voulions construire une typologie qui soit valide dans les forêts tempérées et boréales et qui réponde aux exigences suivantes :

- Écologiquement pertinente, c'est-à-dire reflétant une diversité taxonomique. Cette diversité est bien sûr potentielle car aucune mesure indirecte ne peut prendre en compte les processus historiques et les filtres environnementaux à plus petite échelle (Ricklefs 1987), les dettes d'extinction (Tilman *et al.* 1994) ou la disparition momentanée d'une partie de métapopulation (Hanski 2005).

- D'utilisation pratique, en optimisant le ratio temps d'observation sur quantité et qualité de l'information recueillie.

- Cohérente quels que soient le domaine d'utilisation et la précision demandée aux observations, et permettant le regroupement des observations pour gagner en puissance d'analyse. L'opérateur peut ainsi choisir le niveau hiérarchique de référence, en considérant ses contraintes de temps à consacrer à l'inventaire et également les contraintes physiques d'observation à distance quand on n'utilise pas des grimpeurs.

- Evolutive, c'est-à-dire permettant l'intégration de nouvelles connaissances sans remettre en cause totalement la structure.

- Différenciant dès la dichotomie initiale les dendro-microhabitats saproxyliques des autres afin de faciliter l'analyse du rôle écologique des dendro-microhabitats à des échelles supérieures à celle de l'arbre (*e.g.* redondance fonctionnelle avec le bois mort).

Nous voulions également qu'elle compile pour chaque type de dendro-microhabitat : (i) les facteurs clés pour la composition des communautés associées, (ii) les taxons caractéristiques ou spécifiques, et (iii) la littérature de référence sur ces associations habitat/taxon, afin de constituer l'ébauche d'une base de données qui rassemblerait les références bibliographiques et les dires d'experts.

La typologie prend donc la forme d'une classification hiérarchique par emboîtement, rassemblant en cascade les dendro-microhabitats en groupes et sous-groupes, puis types et sous-types (Tableaux 3 et 4). La dichotomie initiale sépare le groupe des dendro-microhabitats saproxyliques, constitués en partie de bois en cours de décomposition, du groupe des dendro-microhabitats épixyliques, seulement portés par le bois, et de celui des dendro-microhabitats formant des structures « particulières», composites et en association avec une pièce de bois mort. Dans le second niveau de classification, des grands types s'appuient sur de larges catégories morphologiques (cavités, fentes, coulées de sève, etc.), différenciées par des taxons cibles à une échelle taxonomique élevée (classe, ordre) et par leur rôle fonctionnel dominant pour le taxon considéré. Ensuite, un ensemble de variables déterminantes pour la biodiversité associée, comme la position du dendro-microhabitat ou la pérennité du carpophore de champignon, est utilisée pour discriminer des sous-types. Enfin, une segmentation ultime vise à définir des dendro-microhabitats "élémentaires", c'est-à-dire le moins composite possible, et pouvant accueillir un cortège d'espèces caractéristiques.

Cette typologie donne la priorité à la morphologie, pour faciliter son utilisation sur le terrain et le regroupement en unités hiérarchiques supérieures. Les critères morphologiques sont ceux appréhendés par la vision d'un observateur humain et non par l'arsenal multi-sensoriel d'un insecte ou d'un chiroptère. La typologie s'appuie néanmoins sur les différences des communautés associées, en utilisant les données scientifiques ou naturalistes disponibles, souvent en focalisant sur des taxons reconnus comme bioindicateurs comme les Coléoptères saproxyliques (*e.g.* Bouget 2013), les Diptères Syrphidae (*e.g.* Sommagio 1999), les chauves-souris (Van der Wijen *et al.* 2002 ; Thomas & West 1989), les oiseaux (Padoa-Schioppa *et al.* 2006), comportant souvent des espèces à statut conservatoire (listes des réseaux ZNIEFF, Natura 2000), ce qui peut augmenter la synergie des actions de gestion et de conservation. Pour être prises en compte, ces différences de communautés doivent pouvoir être traduites par une différence morphologique observable sur le terrain ; sinon, elles augmentent simplement la variabilité des communautés associées au dendro-microhabitat. Bien que reposant en grande partie sur la littérature, cette approche met en œuvre beaucoup d'expertise naturaliste et est ainsi empreinte d'une certaine subjectivité quant au regroupement des dendro-microhabitats élémentaires.

La typologie propose également l'ensemble des supports pour lesquels l'observation du dendro-microhabitat est pertinente. Il semble en effet peu utile de relever les plages d'écorce manquante sur une chandelle en décomposition car l'ensemble de la pièce de bois est un habitat saproxylique et perd graduellement et irrémédiablement son écorce. Dans ce cas, il est plus synthétique et rapide de noter le stade de décomposition dominant de la pièce de bois. Par contre, les écorces décollées sur les chandelles de sapin pectiné à un stade intermédiaire de décomposition sont des particularités qui constituent la forme la plus fréquente d'abri de type « fente » dans les hêtraies-sapinières (Larrieu et Cabanettes 2012) et méritent pour cela d'être relevées.

Tableau 3 – Liste des types de dendro-microhabitats.
Les subdivisions inférieures (sous-types, dendro-microhabitats élémentaires) et les champs complémentaires (taxons cibles, rôle fonctionnel, variables clés pour les communautés associées, valeurs seuil, taxons associés, références, support, degré de rareté et durée de vie) ne sont pas indiqués dans ce tableau

Group of tree-microhabitats	Sub-groups	Tree-microhabitat type
Saproxylic tree-microhabitats (STMh) (=tree-microhabitats which are constituted, at least partially, by decaying wood)	saproxylic cavities	cavities freshly excavated by woodpeckers
		cavities with mould evolving from decay wood
		rotted-bottom dendrotelm
		xylophagous insects gallery
	bark loss	missing bark with hard wood
		missing bark with decayed wood
	crack	crack in the wood
		shelter under peeling bark
	crown deadwood	dead branches
		broken thick branches or tree-top (ø>20cm)
	rotting tree roots	rotting tree roots
Epixylic tree-microhabitats (ETMh) (= tree-microhabitats which don't contain decay wood)	epixylic cavities	bark-lined cavity at the base of the trunk
		bark-lined dendrotelm
	Fruiting bodies of lignivorous fungi	polypore
		pulpy agaric (e;g. *Armillaria, Pleurotus, Megacollybia, Pluteus*)
		large ascomycete (*Daldinia* sp., *Hypoxylon* sp.)
	epiphytic plants	liana
		Mistletoe *(Viscum* spp., *Arceuthobium* spp., *Amyena* spp., *Loranthus* spp.)
		mosses and foliose lichens
	vertebrate nest	vertebrate nest
	"witch broom"	witch broom
	nest of *Thaumetopoea pityocampa*	nest of *Thaumetopoea pityocampa*
	wood-myxomycetes	wood-myxomycetes
	bark microsoil	bark microsoil
	moist sap run	moist sap run
Particular structures	snag bottom	snag bottom
	tree root-plate	root-plate interlacing
		root-plate pan
	ant nest	*Formica* mound
		Lasius nest in tree trunk

Tableau 4- Extrait de la typologie des dendro-microhabitats : exemple des cavités récemment creusées par les pics
Les champs concernant les supports pertinents, le degré de rareté et la durée de vie ne sont pas indiqués ici

Group of tree-microhabitats	Sub-groups	Tree-microhabitat type	Target taxa	Functional role	sub-types	Key variables for associated communities	Trends & threshold values: impact on taxa	Associated taxa ; into square brackets: [taxon weakly linked or poorly diversified]	References
Saproxylic tree-microhabitats (STMh)	**saproxylic cavities**	**cavities freshly excavated by woodpeckers**	weak excavators and secondary cavity-nesting birds	nesting place	nesting hole	entrance diameter (volume)	D=4cm/V<1l (holes digged by *Dendrocopos minor*)	Birds: Paridae; Bats: *Nyctalus leisleri, Pipistrellus pipistrellus, P. pygmaeus, Myotis nattereri*	Cramp et al. 1985; Harrison 1977; Géroudet 1980; Arthur & Lemaire 2009; Penicaud 2000; Corbet & Ovenden 1980; Le Louarn & Quéré 2003; Larrieu pers. obs. ; Ricarte et al. 2009; Prud'homme com. pers.; Blondel J 2005; Tillon L 2005; Lucan et al. 2009; Johnsson et al. 1993
			bats	breeding place ; diurnal resting place ; overwintering place			D= 5-6 cm/V=4-6l (holes digged by *Picus cinereus/P. viridis/Dendrocopos major/D. medius/D. syriacus/ D. leucotos/ Picoides tridactylus*)	Birds: *Sitta europaea, Sturnus vulgaris, Jynx torquila;* Bats: *Pipistrellus nathusii, Plecotus auritus, Myotis alcathoe, M. bechsteinii, (M. dasycneme), M. daubentonii, M. myotis, (M. mystacinus);* Rodents: *Apodemus sylvaticus, A. flavicollis, Glis glis*	
			rodents	diurnal resting place ; breeding site			D>10cm/V>15l (holes digged by *Dryocopus martius*)	Birds: *Aegolius funereus, Corvus monedula;* Bats: *(Eptesicus nilssonii), (E. serotinus), (Vespertilio murinus), Nyctalus lasiopterus, N. noctula, (Myotis capaccinii), M. daubentonii, M. emarginatus, M. myotis*	
						on broadleaved		most of bats prefer broadleaved	
			arachnids	full life-cycle		on conifer			
								Beetles: Anobiidae (*Stagetus andalusiacus*); Cetoniidae (*Cetonia aurataeformis, Potosia opaca*), Elateridae (*Elater ferrugineus*); Tenebrionidae *(Mycetochara quadrimaculata, Prionychus fairmairei, Pseudocistela ceramboides, Tenebrio obscurus*) ; Hoverflies: *Brachypalpoides lentus, B. valgus, Criorhina pachymera , Fernandinea aurea, F. cuprea, Milesia craboriformis, M. semiluctifera, Spilomyia digitata, S. saltuum, Xylota segnis*	
						hidden by ivy		bats prefer hidden cavities	
			insects (beetles, bees, hornets, hoverflies)	breeding site (=mating site + larval growth)	feeding hole	entrance diameter (volume)	d=3cm	Birds: Paridae	Arthur & Lemaire 2009; Penicaud 2000; Speight et al. 2010; Larrieu pers. obs.
						on broadleaved			
						on conifer			
						live tree			
						dead tree		most of bats prefer live trees	
						occurrence of nest of social insects	Diptera Syrphidae: Volucella spp. (without *V. inflata*)		
						height			

L’enrichissement régulier de la première version de cette typologie par l’ajout de nouveaux types, seuils ou références a montré la flexibilité du système. Les structures particulières associées exclusivement au bois mort (galettes de chablis, dômes de débris ligneux à la base de chandelles très décomposées, etc.) ne sont pas reconnues comme dendro-microhabitats par certains experts, mais la structure de la typologie permet leur exclusion sans compromettre sa cohérence. Par contre, la dichotomie initiale qui vise à regrouper les dendro-microhabitats saproxyliques pour mieux les identifier dans des études conjointes avec le bois mort soulève quelques interrogations. Premièrement, elle entraîne un éloignement des deux types de dendrothelmes, à fond dur (constitué par de l’écorce intègre) et à fond carié (constitué par du bois en décomposition), qui peut sembler artificiel car les communautés associées à ces deux types ne sont pas très différentes, et en tout cas plus semblables que celles des autres dendro-microhabitats. Deuxièmement, certains dendro-microhabitats épixyliques ne sont pas totalement déconnectés du bois en décomposition. C’est le cas des sporophores de champignons saproxyliques car les arthropodes xylomycophages qui se nourrissent des hyphes à la base du sporophore (Bouget *et al.* 2005) vivent dans un mélange intime de champignon et de bois pourrissant. C’est également le cas de certaines coulées de sève déclenchées par des blessures.

Afin d’affiner et de compléter cette typologie sur des bases empiriques solides, il nous paraît nécessaire de poursuivre la recherche “naturaliste” explorant les associations entre les dendro-microhabitats et la biodiversité taxonomique qui leur est associée. Une veille bibliographique nous permet d’intégrer les nouvelles connaissances dès qu’elles sont publiées.

Les initiatives de synthèse des connaissances acquises sur la distribution des dendro-microhabitats dans les écosystèmes forestiers souffrent de l’absence d’une typologie de référence partagée par les études scientifiques actuelles. Nous en avons fait l’expérience avec le travail sur le cycle sylvigénétique des forêts mixtes de montagne présenté en section II. Pour pallier ce problème, une publication scientifique de référence d’une typologie consensuelle s’appuyant très largement sur notre typologie est en cours de rédaction dans le cadre d’un collectif européen d’écologues experts en dendro-microhabitats et sera soumise à *Forest Ecology and Management* (Winter *et al.* en préparation). Nous espérons qu’elle permettra d’harmoniser les futurs protocoles de recherche dans les forêts tempérées et boréales. Notre typologie est d’autre part intégrée dans le récent réseau de martéloscopes européens mis en place dans le cadre du projet « Integrate + ».

Bien qu’elle soit conçue pour ne jamais être définitivement fixée, cette typologie fixe un cadre qui est l’aboutissement de plusieurs années de réflexion et de compilation de données. Par contre, les démarches exposées ci-après, c'est-à-dire la confrontation de la typologie avec des bases de données de traits de vie de taxons sélectionnés et la construction d’une typologie sur la base d’une caractérisation des dendro-microhabitats par des facteurs abiotiques, sont encore exploratoires mais nous pensons qu’elles sont utiles à son évolution.

1.2 CONFRONTATION DE LA TYPOLOGIE AVEC DES BASES DE DONNEES DE TRAITS DE VIE

Bien que l’intégration d’un dendro-microhabitat dans cette typologie soit toujours argumentée par des données taxonomiques avérées et que ma démarche typologique ne soit pas taxon-centrée, il m’a semblé intéressant de confronter notre classification (illustrée sous forme d’arbre par la figure 11) avec celles que l’on pourrait obtenir par la voie statistique en utilisant des bases de traits de vie des espèces associées aux dendro-microhabitats. L’objectif est de déceler par les assemblages des proximités de dendro-microhabitats (ou, au contraire, des mises à distances), non révélées par la simple morphologie. Cet objectif rejoint fortement la démarche initiale utilisée pour construire la typologie, mais d’une part s’appuie sur une démarche statistique et d'autre part ouvre la voie d'une explication de ces regroupements ou de ces divergences par la révélation de facteurs clés cryptiques à l'aide des autres traits de vie codés dans la base.

Il faut pour cela disposer de bases de traits pour des taxons (i) majoritairement dépendants de dendro-microhabitats, (ii) qui couvrent une large gamme de dendro-microhabitats, (iii) pour lesquels cette dépendance est suffisamment renseignée, et (iv) qui représentent une part non négligeable de la biodiversité forestière ou sont identifiés comme bio-indicateurs pertinents. Malheureusement, les bases disponibles sont, à notre connaissance, rarissimes.

La seule base publiée, Syrph the Net (Speight *et al.* 2013), concerne les Diptères Syrphidae. Il s'agit en fait d'un système expert de modélisation fonctionnelle (dit aussi « mécaniste ») qui permet d'analyser les dynamiques espèces/habitats grâce à une base de données à la fois chorologiques et écologiques disponible sous la forme d'un fichier Excel. La base couvre géographiquement la quasi-intégralité de l'Europe, de la région méditerranéenne à l'Islande et code plus de 890 espèces, ce qui représente la quasi-intégralité de la syrphido-faune connue en Europe. Les informations bioécologiques de la base sont codées sur le type « système expert à logique floue simplifié » (Castella & Speight 1999). Le codage flou permet d'exprimer la variabilité intraspécifique de certains traits de vie, et ainsi de mieux refléter la réalité écologique qu'une simple affectation binaire. Les traits biologiques traités sont : (i) les macrohabitats dans lesquels évoluent les imagos ; Syrph the Net utilise son propre système de codage des habitats, mais la correspondance avec ceux de CORINE biotopes est indiquée ; (ii) les microhabitats indispensables aux stades larvaires ; les composantes structurelles présentes dans les peuplements étudiés, comme la présence de semis, d'arbres adultes ou de vieux arbres, influent sur le codage ; (iii) les traits de vie des adultes : statut migratoire, période de vol, alimentation, etc. ; (iv) les traits biologiques des larves : exigence trophique, durée du cycle de développement, stade hivernant, etc. ; et enfin (v) le statut de rareté. Chaque variable est définie précisément dans un glossaire associé à la base. Le codage de la relation espèce/variable (en particulier les variables : types de macrohabitat et de microhabitat), se fait sur une échelle de 4 notes : (i) la note 3 indique une association extrêmement forte entre l'espèce et la variable ; (ii) la note 2 indique que l'association entre la variable et l'espèce est prédite ; (iii) la note 1 indique une association faible ; lorsqu'il s'agit des relations entre espèces et macrohabitats, l'association peut prendre une valeur supérieure à la condition qu'il y ait aussi présence d'un habitat associé nécessaire à l'espèce pour son cycle biologique ; il s'agit d'un habitat que l'on peut aussi qualifier de secondaire par rapport au principal, car facultativement présent dans ce dernier, comme par exemple une clairière herbeuse ou un ruisseau temporaire au sein d'une hêtraie-sapinière, mais ces habitats associés sont parfois indispensables pour certaines espèces qui ont une double exigence pour être présentes ; (iv) un blanc correspond à une absence de liaison. Cette base de données est mise à jour annuellement, en intégrant les données récentes. Le système expert compare la liste d'espèces observées avec une liste d'espèces prédites, dite de référence, bâtie sur le postulat d'une parfaite intégrité de l'écosystème étudié.

Pour éviter une approche mono-taxonomique, Christophe Bouget a constitué pour nous une base pour les larves de Coléoptères saproxyliques à partir des travaux de Möller (2009), en utilisant un système de codage binaire.

Une classification des dendro-microhabitats a été tentée avec ces deux bases de traits. Des matrices dendro-microhabitat/espèce on été constituées en supprimant toutes les espèces des bases de données qui n'étaient codées pour aucun des dendro-microhabitats sélectionnés, en liaison d'une absence de renseignement ou d'une mauvaise concordance entre la variable codée dans la base et notre typologie. Pour les Syrphidae, nous avons différencié les sites de développement des larves et les sites d'hivernage des adultes, et utilisé le codage flou proposé. La dissimilarité matricielle (fonction *vegdist* du package R *vegan*) a été estimée avec l'indice de Bray-Curtis pour les syrphes, en interprétant le codage flou de Syrph the Net comme un indice d'abondance, et

Jaccard pour les Coléoptères. Puis les groupes ont été constitués à l'aide d'une Classification Ascendante Hiérarchique (CAH ; fonction «agnes » du package R «*cluster* »), en utilisant la méthode UPGMA.

Malgré une concordance optimisée entre les dendro-microhabitats décrits dans les bases de traits et notre typologie, on s'attend à des divergences de classification pour les raisons suivantes : (i) l'ensemble des dendro-microhabitats décrits dans notre typologie n'est pas couvert par le taxon et le nombre maximum de clusters possibles influe sur les regroupements effectués par la CAH ; (ii) il est très probable que les insectes n'utilisent pas les mêmes variables morphologiques que nous pour rechercher leur habitat car ils n'ont pas notre souci d'être compréhensibles par les gestionnaires forestiers ; (iii) dans le cas des syrphes, le codage flou traduit une largeur de niche qui induit pour certaines espèces une forte variabilité d'affinité au dendro-microhabitat.

Figure 11. Représentation sous forme d'un arbre de la typologie des dendro-microhabitats au niveau des « types »

1.2.1 CLASSIFICATION DES DENDRO-MICROHABITATS PAR LES SYRPHES

La mise en concordance de nos types de dendro-microhabitats avec ceux codés dans Syrph the Net pour les espèces a malheureusement permis de ne conserver que sept types pour les larves (concernant 109 espèces de syrphes) et cinq types pour les adultes (121 espèces de syrphes). Pour les larves (Fig. 12), trois dendro-microhabitats bien séparés dans notre typologie, les nids d'insectes dans les cavités, les lianes et les bois sans écorce, sont discriminés fortement par la classification. Par contre, il était inattendu d'observer un regroupement des dendrothelmes avec les trous de pics car les dendrothelmes sont des milieux tellement spécifiques que plus de la moitié des espèces qu'ils hébergent régulièrement leur sont strictement inféodées au stade larvaire (Dajoz 2007) et les cavités de picidés sont généralement considérées comme des abris au sec.

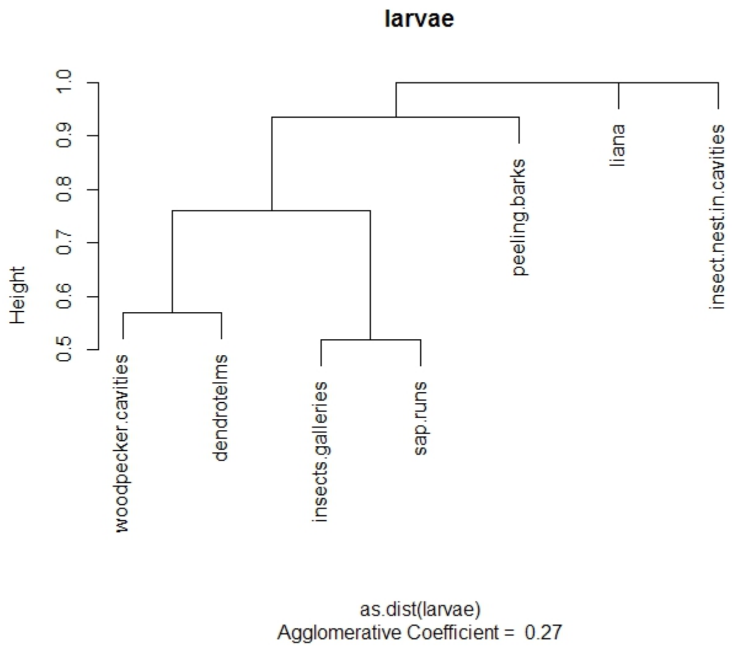


Figure 12. Classification Ascendante Hiérarchique d'une sélection de 7 dendro-microhabitats utilisés comme habitats larvaires par les Diptères Syrphidae

Comme pour les larves, la classification pour les adultes (Fig. 13) discrimine fortement les nids d'insectes dans les cavités et les bois sans écorce. Les racines en décomposition et les cavités à terreau partagent la caractéristique d'être un milieu humique évolué et sont rassemblées par la classification dans le même cluster. Les dendrothelmes tiennent une position intermédiaire, peut-être parce que les cavités à terreau et les racines en décomposition retiennent souvent une certaine humidité. Précisons que Syrph the Net ne fait pas la différence entre les dendrothelmes à fond dur et à fond carié.

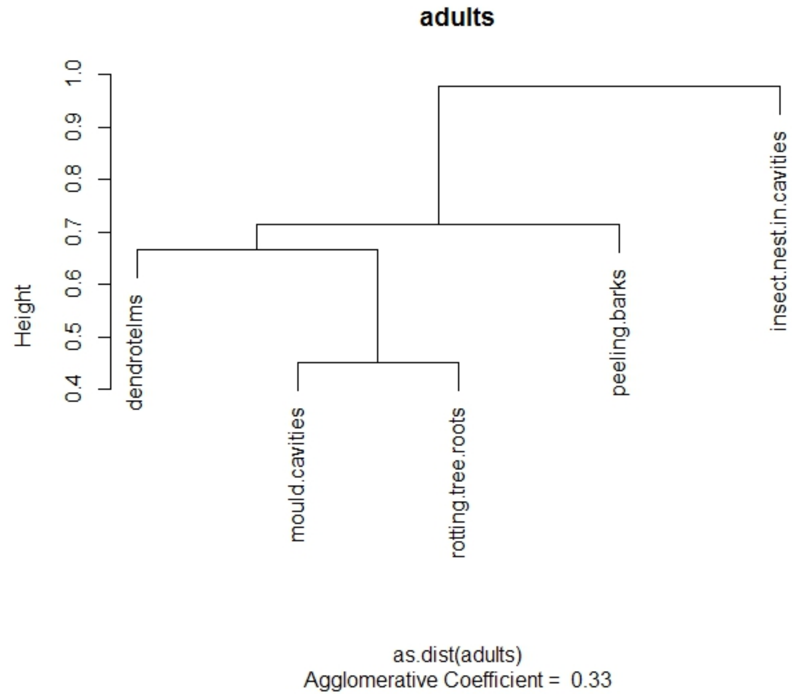


Figure 13. Classification Ascendante Hiérarchique d'une sélection de 5 dendro-microhabitats utilisés comme habitats d'hivernage par les adultes de Diptères Syrphidae

1.2.2 CLASSIFICATION DES DENDRO-MICROHABITATS PAR LES COLÉOPTÈRES SAPROXYLIQUES

La mise en forme du travail de Möller (2009) a permis d'analyser les relations entre 1584 espèces de Coléoptères saproxyliques et 13 dendro-microhabitats (Fig. 14). La classification obtenue met en évidence la spécificité des assemblages liés au bois mort racinaire (probablement plus proches des bois morts au sol que des dendro-microhabitats étudiés ici), aux nids de fourmis lignicoles, aux coulées de sève ainsi qu'aux accumulations de terreau humide au pied des arbres vivants. Il est plus inattendu de constater qu'elle ne sépare pas les dendro-microhabitats saproxyliques des autres et que les fructifications fongiques sont peu discriminées. Pour ce dernier dendro-microhabitat, il est probable qu'un codage flou aurait permis de distinguer les Coléoptères strictement liés au sporophore (*i.e.* xylomycétophages) d'autres saproxyliques plus généralistes qui fréquentent les sporophores pour d'autres ressources trophiques, comme certains prédateurs.

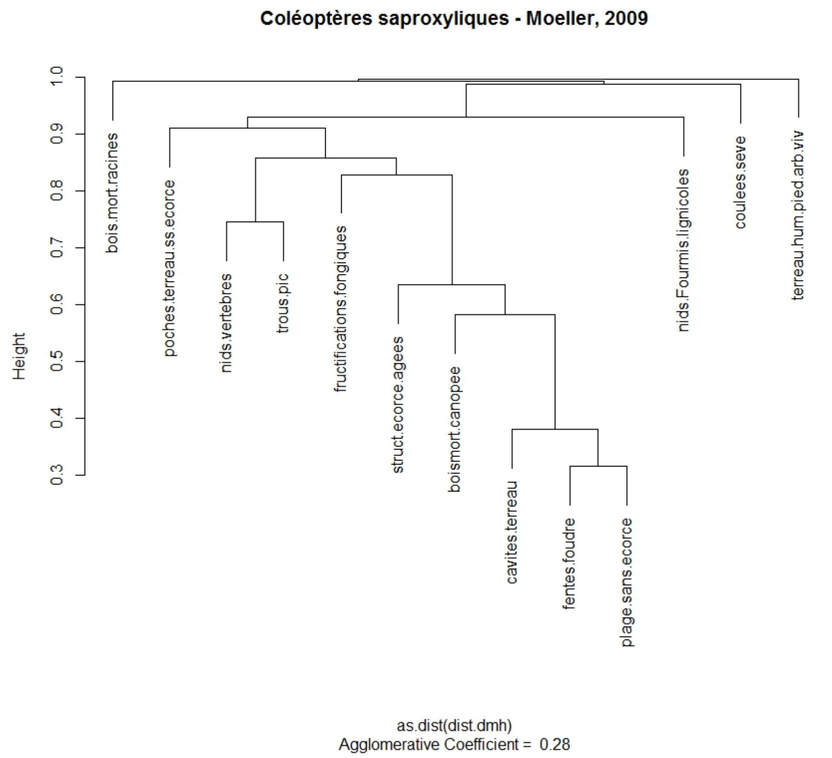


Figure 14. Classification Ascendante Hiérarchique d'une sélection de 14 dendro-microhabitats utilisés par les Coléoptères saproxyliques.

Les résultats inattendus de ces trois classifications exigeraient d'être complétés par une analyse plus fine des descriptions des dendro-microhabitats dans les bases de traits de vie des taxons et par une réflexion sur ce que sont les variables d'habitat réellement discriminantes pour les espèces.

Bien qu'elles ne soient pas particulièrement à la mode, des études naturalistes complémentaires menées par des spécialistes de la taxonomie sont primordiales pour mieux appréhender les communautés associées aux dendro-microhabitats, alimenter les bases de données de traits de vie existantes et susciter la mise en chantier de nouvelles bases pour des taxons moins emblématiques mais non moins indispensables au fonctionnement des écosystèmes, comme les mollusques ou les hyménoptères parasitoïdes.

1.3 CONSTRUCTION D'UNE TYPOLOGIE A PARTIR D'UNE BASE DE TRAITS D'HABITAT CARACTERISTIQUES

Nous avons testé également une approche réduisant la part d'expertise naturaliste dans le choix des regroupements des dendro-microhabitats. Nous l'avons conduite au niveau hiérarchique des « sous-types » de notre typologie. Elle consiste à bâtir une base (matrice de dissimilarité) de 10 caractéristiques abiotiques clés (type d'abri, présence ou non de terreau, niveau d'humidité, etc.) pouvant expliquer la composition des communautés vivant dans les dendro-microhabitats (Tableau 5), puis à regrouper ces dendro-microhabitats par une CAH sur cette matrice. Nous avons utilisé pour cela la méthode de calcul de distance de Jaccard (menée avec la fonction *vegdist* du package R *vegan*) et la méthode de regroupement UPGMA (dans la fonction *agnes* du package R *cluster*).

Tableau 5. Base de caractéristiques d’habitat des sous-types de dendro-microhabitats

	deadwood					shelter type		position on tree			humus contact	humidity			life.span		tree		vertebrate.structure	invertebrate.structure	burned.structure
tmh.types	saproxylic	epixylic	mould	snag.linked	log.linked	cavity	crack	base	trunk	crown	humus	dry	wet	water.filled	ephemeral	perenial	coniferous	deciduous	v.nest	inv.nest	burned
cavities freshly excavated by woodpeckers	1	0	0	1	0	1	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0
cavities with mould evolving from decay wood	1	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0
base cavities with mould evolving from decay wood	1	0	0	1	1	1	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0
burned base-cavities with mould evolving from decay wood	1	0	0	1	1	1	0	1	0	0	1	0	1	0	0	1	1	1	0	0	1
rotted-bottom dendrotelm	1	0	1	0	1	0	0	1	1	1	1	0	0	1	1	0	1	1	0	0	0
xylophagous insects gallery	1	0	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0
missing bark with hard wood	1	0	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0
missing bark with decayed wood	1	0	0	1	1	0	0	1	1	1	0	0	1	0	0	1	1	1	0	0	0
crack in the wood	1	0	0	1	1	0	1	0	1	1	0	1	0	0	0	1	1	1	0	0	0
shelter under peeling bark	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	1	0	0	0
dead branches	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0
broken thick branches or tree-top	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0
rotting tree roots	1	0	1	1	1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0
bark-lined cavity at the base of the trunk	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0
bark-lined dendrotelm	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0
annual polypore	0	1	0	1	1	0	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0
perenial polypore	0	1	0	1	1	0	0	1	1	1	0	1	1	0	0	1	1	1	0	0	0
pulpy agaric	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1	0	1	1	0	0	0
large ascomycete	0	1	0	1	1	0	0	1	1	1	0	1	0	0	1	0	1	1	0	0	0
liana	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0
Mistletoe	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0
mosses and foliose lichens	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	1	1	1	0	0	0
vertebrate nest	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	1	1	0	0
witch broom	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
nest of Thaumetopoea pityocampa	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0
wood-myxomycetes	0	1	0	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	0	0
bark microsoil	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	0
moist sap run	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0
snag bottom	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0
root-plate interlacing	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0
root-plate pan	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0
Formica mound	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0
Lasius nest in tree trunk	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	1	0	1	0

La proximité des dendro-microhabitats regroupés sur la base de leurs caractéristiques d’habitat peut mettre en lumière des relations cryptiques de possible substitution entre des dendro-microhabitats proches. Le résultat (Fig. 15) est assez proche de celui obtenu par l’expertise qualitative.

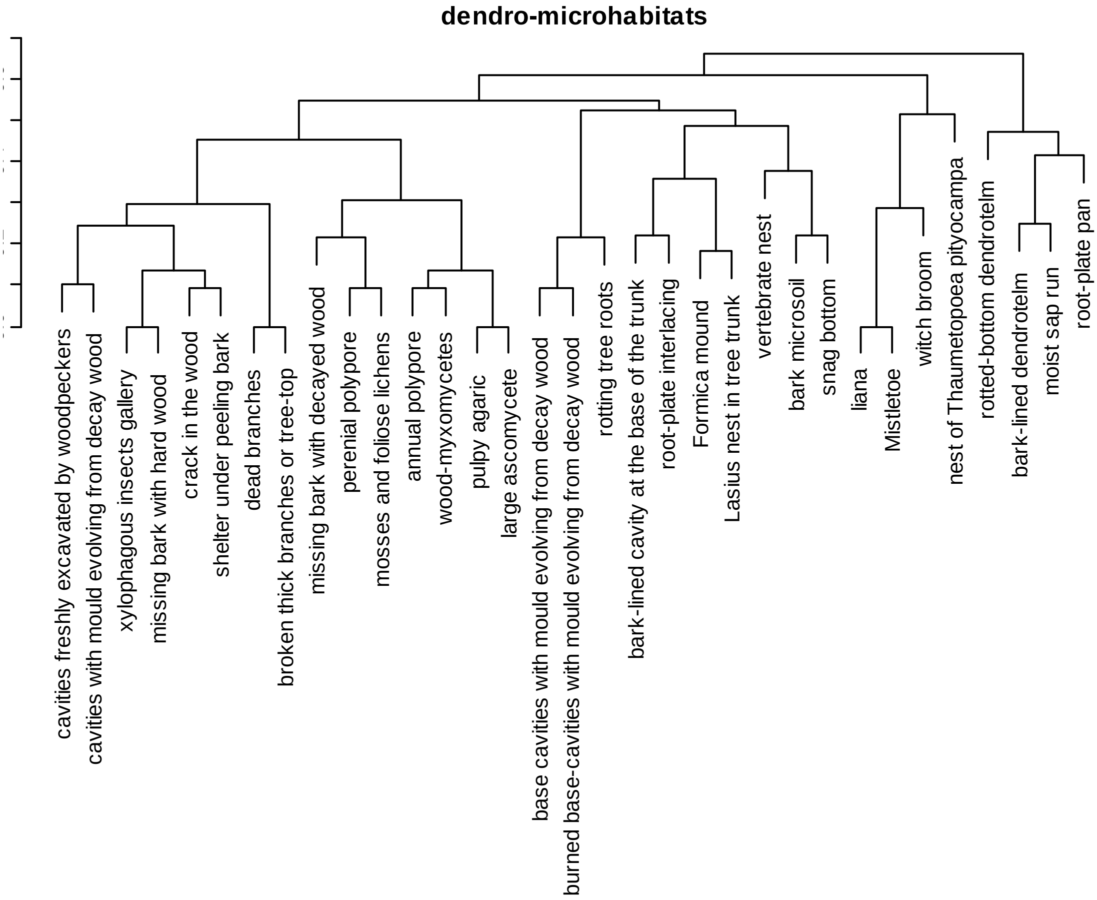


Figure 15. Arbre des dendro-microhabitats regroupés par leurs similarités de caractéristiques d'habitat

Néanmoins, les regroupements des polypores pérennes avec les mousses et les lichens foliacés, ou encore les dendrothelmes à fond dur et les coulées de sèves sont inattendus. En effet, les communautés associées à ces différents dendro-microhabitats sont très différentes, au moins pour les taxons que nous utilisons dans la typologie. Mais l'expertise comme principale approche typologique peut biaiser l'examen en focalisant l'attention sur des taxons cibles, soit parce que l'on connaît mieux leur écologie, soit parce qu'ils font l'objet d'une attention particulière en termes de conservation. D'un autre côté, l'approche par les caractéristiques clés des dendro-microhabitats est très dépendante de la qualité de la base des caractéristiques et du nombre de variables qui la compose. Elle peut mettre en évidence des proximités fonctionnelles d'habitats pour des organismes contraints par les conditions environnementales à échelle très fine (arthropodes, mollusques) ou plutôt d'ordre chimique, et l'étude de taxons microscopiques éclairerait peut être la pertinence de ces proximités fonctionnelles. Dans tous les cas, un travail supplémentaire est nécessaire pour compléter la liste des caractéristiques clés, ainsi que pour clairement différencier les caractéristiques techniquement évaluables de celles qui requièrent des mesures impossibles à réaliser en routine, comme le taux d'oxygénation de l'eau d'un dendrothelme ou le volume d'une cavité. L'utilisation d'un mode de codage flou à la place d'un simple codage binaire permettrait d'intégrer la variabilité évidente des dendro-microhabitats regroupés à ce niveau hiérarchique assez élevé du sous-type.

1.4 ÉVALUATION DE LA DIVERSITE FONCTIONNELLE DES DENDRO-MICROHABITATS

Tilman (2001) définit la diversité fonctionnelle («functional diversity », FD) d'un écosystème comme la valeur et la variabilité des traits fonctionnels des organismes qui y vivent. La FD peut être considérée soit comme un indicateur des processus gouvernant les communautés (compétition, perturbations ou gradients environnementaux) (Mouchet *et al.* 2010), soit comme un indicateur de fonctions écosystémiques (productivité, résilience et cycle biogéochimiques) (Petchey *et al.* 2004). Elle est supposée être liée positivement à l'efficacité et à la fiabilité des processus écosystémiques (Mason *et al.* 2005). S'appuyant sur un parallèle avec la diversité spécifique, Masson *et al.* (2005) puis Villéger *et al.* (2008) déclinent trois dimensions à la FD et conseillent de les considérer séparément : (i) la proportion de l'espace fonctionnel utilisée par les espèces (« functional richness »), (ii) l'équitabilité de la distribution des abondances dans cet espace (« functional evenness ») et (iii) le degré avec lequel la distribution des abondances maximise la divergence des caractères fonctionnels à travers la communauté (« functional divergence »). Les indices correspondants à ces trois dimensions sont indépendants les uns des autres, complémentaires pour décrire la FD, et permettent d'explorer plus aisément les liens entre la biodiversité et le fonctionnement de l'écosystème (Villéger *et al.* 2008). L'utilisation de ces déclinaisons permet de décrire plus finement les variations de la FD sur des gradients de contraintes environnementales (Mouchet *et al.* 2010).

Théoriquement, c'est donc l'étude des traits fonctionnels des taxons qui permet d'évaluer la FD et ainsi de traduire, entre autres, le degré d'utilisation des ressources. Mais, maintenant que nous disposons d'une typologie qui regroupe les dendro-microhabitats par des similitudes de fonction d'habitat vis-à-vis des communautés, pourquoi ne pas l'utiliser comme outil de diagnose rapide de la diversité fonctionnelle d'habitat de la population de dendro-microhabitats pour affiner le diagnostic de leur diversité ? En effet, deux dendro-microhabitats fonctionnellement proches apportent moins de diversité que deux jouant un rôle d'habitat très différent, et apportent ainsi potentiellement plus de diversité taxonomique. Il s'agirait évidemment d'une diversité « potentielle », ne préjugeant pas des effets des autres filtres, historiques ou environnementaux, ainsi que des processus stochastiques, qui impactent sur la composition des communautés observées à l'échelle locale (Bouget 2013). On pourrait aboutir au final à l'estimation de la part de diversité fonctionnelle d'habitat réalisée, correspondant à un positionnement sur une sorte de gradient « d'intégrité fonctionnelle » (« functional integrity », Woodwell 2002a). Il est vrai que, dans la littérature, l'intégrité fonctionnelle est définie avec plusieurs approches. Woodwell (2002a et b) résume l'intégrité fonctionnelle d'un paysage au taux de boisement en s'appuyant sur le fait que la forêt est la végétation climacique dans la majorité des conditions et qu'elle seule possède les attributs fonctionnels pour rendre l'ensemble des services environnementaux. Il confond ainsi l'intégrité structurale et l'intégrité fonctionnelle. Pour les écosystèmes d'eaux vives, Gessner et Chauvet (2002) pensent au contraire que les attributs structuraux ne sont pas suffisants pour juger de l'intégrité fonctionnelle et qu'il est indispensable de compléter l'analyse par des informations sur les processus. Dans un tout autre cadre, celui des fermes d'élevage, Hubert (2008) adopte une définition très large car il considère comme systèmes intègres les élevages qui maintiennent un certain équilibre entre la fertilité des sols, la production, la faune sauvage, les marchés, la compétence en termes de gestion et même les institutions humaines, mais sans toutefois définir les indicateurs pertinents pour apprécier le niveau d'intégrité. Enfin, Feio et Dolédec (2012) évaluent indirectement l'intégrité fonctionnelle d'une eau vive avec les traits de vie des espèces qui la peuplent. Nous utilisons ici la position de Woodwell : la structure de la population de dendro-microhabitats permet d'apprécier le degré d'intégrité fonctionnelle, postulant que l'ensemble des dendro-microhabitats est requis pour assurer l'ensemble des fonctions d'habitat.

Deux voies paraissent pertinentes. **La première** est de réaliser un outil généraliste, destiné à couvrir au maximum la diversité taxonomique. Nous avons construit le dendrogramme représentant la FD maximale des dendro-microhabitats en nous inspirant de Petchey et Gaston (2002, 2006 et 2007). Quelques adaptations ont été néanmoins nécessaires, par exemple pour regrouper dans l'arbre les dendrothelmes à fonds cariés de ceux à fonds durs, qui hébergent des communautés assez semblables, mais qui sont séparés très tôt dans la typologie car les fond cariés sont des dendro-microhabitats saproxyliques alors que les fonds durs sont épixyliques. De la même façon, les dendro-microhabitats « particuliers » (*e.g.* nids de fourmis, galette de chablis) qui sont souvent liés aux arbres morts, hébergent des communautés très différentes les unes des autres et doivent rester éloignés dans l'arbre, alors qu'ils sont logiquement regroupés en tête de la typologie. Pour réaliser le dendrogramme en apportant ces modifications, nous avons utilisé la fonction « *as.phylo* » du package R « *ape* ». L'arbre fonctionnel complet réunit tous les dendro-microhabitats. L'arbre de diversité fonctionnelle des dendro-microhabitats ainsi construit est assez proche de la présentation classique de la typologie (Fig. 16). Pour chaque dendro-microhabitat est calculé son score individuel de la façon suivante :

$$Score\ dmh_i = \frac{1}{n\,dmh_i} / 100 \sum_i^j \frac{1}{n\ dmh}$$

avec dmh_i le dendro-microhabitat « *i* » et *n* le nombre de nœuds du dendrogramme entre la racine et le dmh_i. Ce score correspond donc à sa participation relative à la FD maximale calculée comme la somme des contributions individuelles ramenée à 100, avec le principe que plus il y a des nœuds sur l'axe du dendro-microhabitat, plus il existe des dendro-microhabitats proches qui peuvent assurer une redondance fonctionnelle. Ce score est bien différent du score « gestion » qui sera présenté au chapitre 2.5 de la section V. La somme des scores des dendro-microhabitats réellement observés dans chaque peuplement diagnostiqué représente la FD « réalisée ». L'interprétation de la FD ainsi calculée est assez proche d'une évaluation de la diversité taxonomique. Il est possible de construire un arbre à chaque niveau hiérarchique de la typologie (la Fig. 16 illustre le niveau « sous-groupe »).

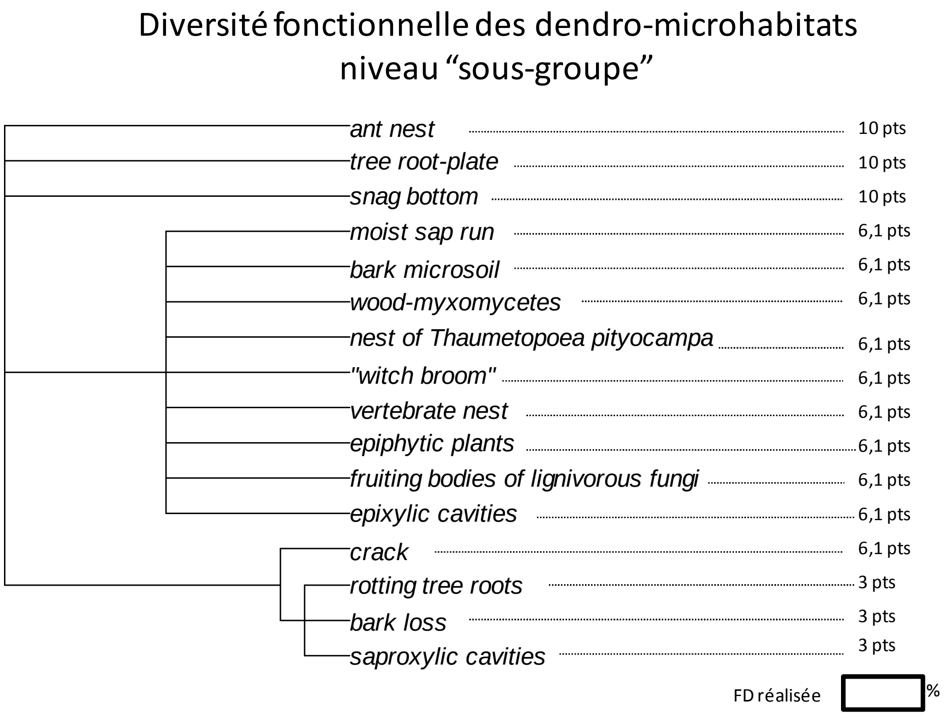


Figure 16. Grille d'évaluation de la diversité fonctionnelle d'habitat d'une population de sous-groupes de dendro-microhabitats

Cette méthode, simple, ne prend pas en compte les abondances et quantifie principalement la richesse fonctionnelle (Mouchet *et al.* 2010). Malgré ces défauts, elle est préconisée dans les cas où l'on cherche à révéler les règles de structure de la communauté sous-jacente (Mouchet *et al.* 2010), et se justifie quand le nombre d'items est inférieur au nombre de traits (Villéger *et al*. 2008). Pour simplifier encore, nous n'avons pas suivi Mouchet *et al*. (2008) qui préconisent de tester toutes les combinaisons de méthodes de calcul des distances et de clustérisation et de sélectionner le dendrogramme à plus faible dissimilarité avant d'estimer la FD. Enfin, dans le but de fournir un outil pratique d'utilisation sur le terrain, nous avons affiché les longueurs des branches sur l'arbre, pour que l'opérateur calcule *in situ* la FD réalisée du peuplement. L'ajout du compartiment bois mort élargirait la gamme des taxons concernés. En parallèle avec (i) le fait que certaines espèces ont un impact plus fort que les autres sur le fonctionnement de l'écosystème en liaison avec leur plus grande abondance (Diaz et Cabido 2001), (ii) la suggestion de Grime (1998) de pondérer l'effet de chaque espèce par son abondance pour mieux refléter sa contribution au fonctionnement, il serait judicieux de pondérer les dendro-microhabitats, par exemple par leurs densités relatives dans les écosystèmes sub-naturels. On pourrait également les pondérer par un indice de la richesse taxonomique qui leur est associée, et combiner ainsi l'originalité de l'habitat avec sa diversité. Cette approche des dendro-microhabitats par leur diversité fonctionnelle devra être approfondie, notamment en analysant les relations entre la diversité fonctionnelle et les dissimilarités biotiques dans des comparaisons inter-peuplements.

La deuxième voie est de centrer la réflexion sur un taxon cible. On pourrait dans ce cas décliner plus précisément les fonctions spécifiques pour le taxon, en différenciant les sites de repos, de reproduction, d'hivernage, etc. Dans le cas très simple de *Myotis bechsteinii* (Chiroptère Verpertillionidae), la gamme des dendro-microhabitats utilisés pour gîte couvre les cavités de pics ou les cavités à terreau pour les colonies de reproduction ou pour l'hibernation et les écorces décollées pour le repos diurne estival des mâles solitaires (Meschede et Heller 2003). Les arbres portant des manchons de lierre, devant les cavités semblent particulièrement sélectionnés par les colonies en reproduction (Prud'homme, com. pers.). La présence de ces trois types de dendro-microhabitats suffit à obtenir une FD de 100 %. Néanmoins, les chauves-souris requièrent plusieurs dendro-microhabitats du même type pour réduire les pertes de prédation, le taux de parasitisme et contrôler les conditions microclimatiques (Arthur et Lemaire 2009). Il faudrait donc compléter l'analyse avec des valeurs de densité seuils pour chacun des dendro-microhabitats mais il faut reconnaitre que ces valeurs font cruellement défaut dans la littérature, même pour des taxons communs. L'analyse peut être conduite à des niveaux hiérarchiques supérieurs (genre, famille) avec des groupes à exigences écologiques plus diversifiées, comme les Coléoptères. Dans ce cas, l'interprétation de la FD évalue la capacité du peuplement à accueillir (ou maintenir) une population du taxon cible. Il est probable qu'une valeur seuil de FD soit requise, correspondant à la présence d'au moins un de chaque dendro-microhabitat nécessaire pour couvrir l'ensemble des fonctions vitales.

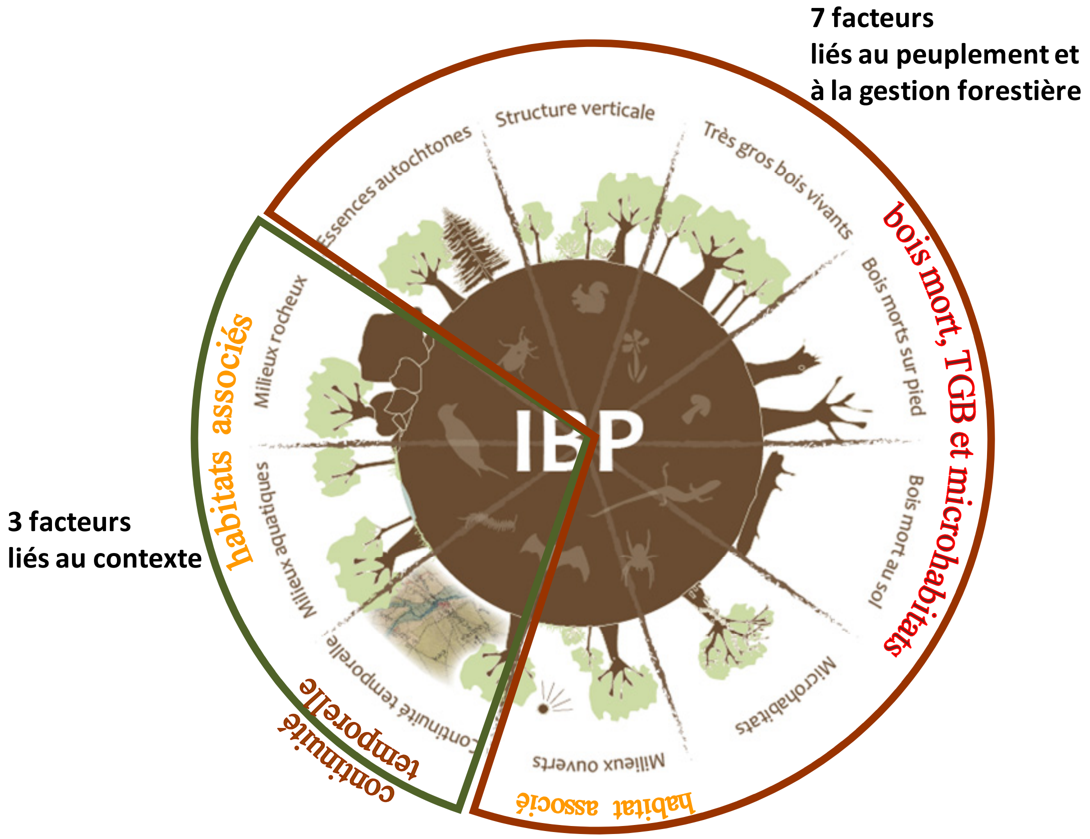
La méthode de construction d'une typologie basée sur une base de caractéristiques comme celle que nous avons présentée au chapitre précédent permet d'utiliser les techniques statistiques de calcul de la FD (par exemple en suivant Pechey et Gaston 2002).

2 LES DENDRO-MICROHABITATS INTEGRES A UN OUTIL DE GESTION

Le gestionnaire forestier détermine ses itinéraires techniques en fonction de nombreux critères, dont les impacts sur la biodiversité, car la conservation de la biodiversité fait partie des objectifs d'une foresterie multifonctionnelle. Au regard du rôle des dendro-microhabitats vis-à-vis de la diversité des espèces en forêt, nous les avons logiquement intégrés dans un outil d'aide à la gestion forestière durable : l'Indice de Biodiversité Potentielle (IBP, Larrieu et Gonin 2008).

2.1 L'IBP : UN OUTIL PERTINENT ET PRATIQUE D'AIDE A LA GESTION COURANTE

L'IBP est un indicateur indirect de la biodiversité taxonomique ordinaire des peuplements forestiers. Il ne préjuge pas de la biodiversité réellement présente, mais il évalue la capacité d'accueil en espèces en mettant en évidence des facteurs actuellement favorables à la diversité des espèces ou, au contraire, défavorables, mais améliorables par la gestion. Il a été conçu pour être utilisé à l'échelle du peuplement forestier, qui correspond à un niveau opérationnel courant. Il complète ainsi des outils de suivi de la biodiversité à des échelles plus larges et répond à une demande d'expertise de la biodiversité à l'échelle du peuplement qui était jusqu'à présent trop difficile à mettre en œuvre pour être intégrée dans le cadre de la gestion courante. Le diagnostic est simplifié par la réduction du niveau de précision, mais en altérant au minimum la pertinence de l'analyse. Pratiquement, L'IBP repose sur le diagnostic de dix facteurs (Fig. 17) pour lequel on attribue sur le terrain un score 0, 2 ou 5, en comparant les observations avec une grille de valeurs seuils (détails dans Larrieu et Gonin, 2008). Le score IBP est calculé en additionnant le score de chacun des facteurs. Ces dix facteurs ont été sélectionnés d'une part pour leur pertinence vis-à-vis de la diversité des espèces en forêt, et d'autre part pour la facilité d'observation pour des forestiers (Emberger *et al.* 2013).



CE/PG

Figure 17. Les dix facteurs qui composent l'Indice de Biodiversité Potentielle (IBP)

Conçu comme un outil de diagnostic rapide pour aider le gestionnaire forestier à prendre en compte plus aisément la diversité des espèces dans sa gestion courante, l'IBP est utilisé actuellement dans une gamme beaucoup plus large : outil pédagogique pour la sensibilisation et la formation des propriétaires, suivi de biodiversité à l'échelle territoriale (Plans de Développement de Massif), diagnostic écologique dans les martéloscopes, mise en place de trames de vieux bois, outil de discussion avec les gestionnaires dans des espaces protégés. Pour éviter d'utiliser l'IBP dans des contextes inappropriés, Larrieu *et al.* (2013) ont rappelé son domaine d'application.

L'IBP fait l'objet d'un programme de recherche et développement depuis 2009, validé par un Comité de pilotage national et financé par le ministère de l'Écologie, du Développement durable et de l'Energie et par l'INRA *via* mon poste d'interface (2009-2012) et l'appui logistique et scientifique du laboratoire Dynafor. Piloté par le Centre National de la Propriété Forestière (CNPF : IDF et CRPF), ce programme a associé de nombreux acteurs du monde forestier (chercheurs, propriétaires, professionnels de la filière bois et de l'environnement, administrations et établissements publics, enseignants...), ce qui assure une véritable co-construction de l'outil. Il a été complété par d'autres projets dans les programmes « Biodiversité et gestion forestière » (BGF), « Prise en compte de la biodiversité dans les Stratégies Locales de Développement Forestier » (SNB-SLDF) et « Biodiversité forestière et enseignement » (Biodifor) (détails dans Gonin *et al.* 2014). Je pilote et réalise en partie ce programme de recherche, qui s'articule autour de trois axes en profitant de travaux réalisés sur d'autres programmes : (i) recherche approfondie sur cinq facteurs de l'IBP : dendro-microhabitats, très gros bois, bois mort au sol et sur pied (cf. section I, II et III de ce manuscrit), continuité temporelle de l'état boisé (Cateau *et al.* sous presse ; Dupouey *et al.* soumis) ; (ii) quantification de la signification écologique de l'IBP par sa calibration taxonomique à large échelle, en confrontant des diagnostics IBP avec des données taxonomiques (cf. section III); (iii) évaluation de l'applicabilité de l'IBP en étudiant sa pertinence dans différents types de peuplements (Larrieu *et al.* 2012) et en quantifiant l'effet observateur (cf. § 2.4). Ce travail a principalement pour but d'améliorer la pertinence écologique de l'IBP en confirmant ou remettant en cause les choix initiaux (facteurs, seuils). L'IBP est donc bien un indicateur évolutif qui intègre régulièrement les nouvelles connaissances et les améliorations ergonomiques pour faciliter son utilisation par le plus grand nombre, mais dans une structure inchangée depuis son origine. Le site de la Forêt Privée Française permet à tout instant de télécharger la nouvelle version actualisée (« www.foretpriveefrancaise.com/ibp »).

2.2 PLACE DES DENDRO-MICROHABITATS DANS L'IBP

Les dendro-microhabitats constituent le facteur F de l'IBP (soit 10% du score). En parcourant attentivement le peuplement lors du diagnostic, l'observateur analyse les arbres porteurs de dendro-microhabitats. Il utilise pour cela une liste de référence comportant 12 types de dendro-microhabitats et leurs définitions précises (détails dans Emberger *et al.* 2013). Le niveau de regroupement des dendro-microhabitats que nous avons adopté dans l'IBP résulte d'un compromis entre leur pertinence à refléter une part de la diversité des espèces et la possibilité pour le plus grand nombre d'acteurs de définir sans ambigüité les types auxquels ils appartiennent lors d'un diagnostic rapide. Il correspond à une liste restreinte des « types » de notre typologie. L'observateur évalue en même temps la densité de dendro-microhabitats présents et leur diversité. En effet, le système de notation prend en compte l'importance de la diversité des dendro-microhabitats pour la diversité taxonomique en ne comptabilisant que deux dendro-microhabitats du même type par hectare. Un arbre portant plusieurs types est comptabilisé autant de fois qu'il porte de types différents. La densité d'arbres porteurs ainsi calculée permet, en confrontant ce résultat avec des valeurs seuils de densité, d'évaluer la gamme de capacité d'accueil. En considérant le détail de ses observations, l'observateur peut également appréhender la gamme des taxons concernés par cette capacité d'accueil.

Les résultats que nous avons obtenus dans les travaux présentés dans la section III (Bouget *et al*. 2013 et 2014 ; Larrieu *et al*. in prep.) valident la pertinence de (i) la densité d'arbres porteurs de dendro-microhabitats pour les variations de composition des assemblages de Coléoptères saproxyliques, de Diptères Syrphidae, de Carabes, de Lichens, d'Oiseaux et de Polypores, ainsi que pour la richesse spécifique des Polypores, (ii) la densité d'arbres porteurs de Polypores pour la richesse spécifique des Coléoptères saproxyliques, (iii) la diversité des dendro-microhabitats et la densité d'arbres porteurs de cavités pour les Chauves-souris, (iv) la densité d'arbres porteurs de Polypores pour les Syrphidae opophages (v) la densité d'arbres porteurs de bois dur sans écorce et de Polypores pour la richesse spécifique des Polypores, et enfin (vi) la densité d'arbres porteurs de coulées de sève pour la richesse spécifique des Polypores rares. Bien que spécifiques à certains taxons, les nouvelles valeurs seuils révélées par ces études seront rapidement intégrées dans l'IBP, en spécifiant bien les taxons concernés. On pourra également moduler la prise en compte de la diversité des dendro-microhabitats en intégrant dans le calcul du score les proximités de fonctions d'habitats révélées par la nouvelle typologie. Ces modifications seront certainement l'objet d'une version « expert » de l'outil, pour ne pas rebuter la majorité des utilisateurs potentiels mais fournir un diagnostic plus fin aux gestionnaires les plus exigeants.

2.3 EFFET DE L'OBSERVATEUR

Comme tous les indicateurs écologiques, l'IBP peut être dépendant de la qualité de l'observation. Elle peut être biaisée par l'observateur, c'est-à-dire constamment décalée par rapport aux observations de référence, ou plus ou moins précise d'un observateur à l'autre car bruitée par une dispersion plus grande des valeurs. La combinaison du biais et du bruit définit la justesse de l'observation (Liggins, 1997). Ces variations entre observations peuvent être dues à des différences entre observateurs en termes de sens de l'observation ou intérêt pour la mesure, et par là même difficiles à quantifier. Mais elles peuvent dépendre également de son expérience de l'observation en forêt et de l'IBP, du temps passé au diagnostic, du type de parcours utilisé pour l'observation et, dans ce cas, être analysées. D'autres variables, indépendantes de l'observateur, peuvent expliquer le niveau de qualité de l'observation, comme le contexte (peuplement dominé par les feuillus vs des résineux, observation en période feuillée ou en hiver) ou encore les conditions météorologiques. Depuis la publication de l'IBP, des protocoles d'observation ont été fixés en fonction des différents contextes rencontrés (Gonin & Larrieu 2013) et les définitions des facteurs ont été clarifiées pour réduire l'effet observateur. Tous les facteurs de l'IBP ne semblent pas, *a priori*, avoir la même sensibilité à la qualité de l'observation. Par la multiplicité des objets à observer et le système de comptage qui mélange la quantité de dendro-microhabitats et la diversité des types, le facteur F a intrinsèquement des prédispositions à être sensible. D'ailleurs, Paillet *et al.* (accepté) ont montré une grande sensibilité des dendro-microhabitats à l'effet observateur, mais en utilisant un protocole bien plus complexe que celui de l'IBP (*i.e.* plus faibles dimensions de précomptage, observation de l'ensemble de l'arbre). De nombreux tests sur le terrain comparant les observations simultanées du même peuplement par différents observateurs ont été menés, mais sans une réelle approche statistique. Ces travaux ont permis de réduire fortement les ambigüités, d'améliorer fortement l'ergonomie de l'outil IBP et de faciliter sa mise en œuvre rapide. Nous étions conscients à ce stade que la prochaine étape était de mettre en place un dispositif de grande ampleur pour évaluer la qualité de l'observation liée soit à l'observateur, soit aux conditions de terrain. C'est ce que nous avons fait au printemps et en automne 2012, grâce au concours de l'équipe EFNO de l'Irstea Nogent/Vernisson, de l'équipe enseignante du Legta accompagnée des étudiants en BTS GF de 2$^{\text{ème}}$ année. Nos principales hypothèses étaient que (i) le biais décroît et la précision augmente avec l'expérience de l'observateur à utiliser l'IBP, (ii) le biais décroît et la précision augmente quand le temps d'observation augmente et (iii) la précision décroît en période feuillée. 889 diagnostics IBP ont été réalisés par une quarantaine d'observateurs, en hiver sur un ensemble de 14 placettes circulaires de 1 ha, puis en été sur un sous-ensemble de 9 placettes, couvrant une large gamme de peuplements et de scores IBP. Le test s'est déroulé en cinq étapes : (i) une formation théorique sur la structure de l'IBP, les définitions précises de chacun des facteurs et les principales difficultés de notation, le parcours standardisé à accomplir, le système de scores et la biodiversité associée aux facteurs, (ii) un exercice de terrain supervisé, (iii) le remplissage d'un questionnaire à choix multiples pour évaluer à la fois l'intérêt du notateur à l'exercice et son niveau d'appropriation de l'outil, (iv) cinq demi-journées de notations (30 mn par placette maximum) séparées par des regroupements destinés à répondre aux difficultés rencontrées, chaque séance de notation correspondant alors à un niveau d'expérience. Les conditions météorologiques ont été optimales. Les questionnaires et les fiches d'observation étaient nominatifs et précisaient le temps d'observation. J'ai effectué des notations de référence en mode déplafonné, c'est-à-dire en consignant toutes les observations sans tenir compte des seuils qui permettent d'attribuer un score au facteur.

À l'échelle du facteur, nous avons utilisé une méthode statistique visant à modéliser la probabilité d'observer 0, 2 ou 5 – les trois niveaux possibles de la notation IBP – à partir de différents paramètres estimés à partir des données. Les paramètres étaient pour la plupart incorporés dans la modélisation d'un processus gaussien sous-jacent, dont la moyenne et la variance sont estimées. La plupart des effets étaient incorporés dans la modélisation de la moyenne, tandis que seul l'effet feuillé était incorporé dans celle de la variance. Une fois la distribution normale estimée : (i) la probabilité d'observer la note zéro était la probabilité cumulée que la variable gaussienne soit négative, (ii) la probabilité d'observer la note deux était la probabilité que la variable gaussienne soit dans l'intervalle [0 ; 1], (iii) la probabilité d'observer la note 5 était la probabilité que la variable gaussienne soit supérieure à 1. Cette manière de modéliser est *a priori* assez économe en paramètres et conserve l'ordre intrinsèque dans les notes de l'IBP. Une approche du même type avec davantage de classes a été développée pour les notes IBP cumulées, avec la différence que cette fois-ci les positions des seuils gaussiens – 0 et 1 dans le cas précédent – étaient pour certains estimés. Nous avons précédemment mis en œuvre cette approche avec un certain succès pour modéliser l'abondance-dominance de Braun-Blanquet à partir d'une distribution bêta (Herpigny & Gosselin, soumis). Les effets inclus sur la moyenne de la variable latente gaussienne étaient : (i) un décalage moyen entre les observateurs non-avertis et l'observateur de référence (biais par rapport à l'observateur de référence) ; ce biais était estimé à un niveau différent en parcelle feuillue défeuillée, (ii) une variation – évidente – du niveau moyen de la note IBP entre placettes, (iii) une variation de la note entre observateurs – une fois pris en compte le biais ci-dessus. Dans des modèles plus compliqués, les biais et variations inter-observateurs étaient modulés suivant l'expérience préalable de l'observateur, sa connaissance de l'IBP – évaluée par le questionnaire à choix multiples – et la période de mesure (début ou fin de l'exercice), mais ces résultats ne seront pas présentés ici. De même, seuls les résultats pour trois des dix facteurs, la *densité de gros (d>40 cm) bois morts sur pied* (facteur C), la *densité de gros (d>40 cm) bois morts au sol* (facteur D), et la *densité d'arbres vivants porteurs de dendro-microhabitats* (facteur F) seront présentés ci-dessous.

Tableau 6. IBP : biais et variation entre observateurs tels qu'estimés avec les modèles d'effet observateur, pour la *densité de gros (d>40 cm) bois morts sur pied* (facteur C), la *densité de gros (d>40 cm) bois morts au sol* (facteur D), et la *densité d'arbres vivants porteurs de dendro-microhabitats* (facteur F)
Les résultats sont donnés sur l'échelle latente normale, une unité étant équivalente à la frontière entre un score de 0 pour le facteur et un score de 2, ou à la frontière entre un score de 2 et un score de 5. Pour les paramètres de moyenne, on note par *, ** et NS, respectivement, une significativité (bilatérale) à 5%, 1% et non significative à 5% de la différence avec la valeur nulle.

	Facteur C	Facteur D	Facteur F
Biais entre observateurs et observateur référence – peuplement feuillu sans feuille	-0.276 (±0.197) (NS)	-0.159 (±0.131) (NS)	0.078 (±0.122) (NS)
Biais entre observateurs et observateur référence – peuplement résineux ou peuplement feuillu avec feuilles	**-0.614 (±0.214) (**)**	-0.140 (±0.130) (NS)	0.102 (±0.120) (NS)
Variation entre observateurs (écart-type)	0.130 (±0.065)	0.127 (±0.031)	0.211 (±0.035)
Variation intrinsèque (écart-type de la distribution normale) (peuplement sans feuille)	0.467 (±0.045)	0.431 (±0.027)	0.399 (±0.038)
Variation intrinsèque (écart-type de la distribution normale) (peuplement avec feuilles)	0.638 (±0.059)	0.461 (±0.029)	0.357 (±0.035)

On observe une sous-estimation systématique significative (-0.61, *p*<0.01) du score attribué au facteur *densité de gros bois morts sur pied* (facteur C) par les observateurs non-experts par rapport à la notation de référence, mais seulement dans les peuplements résineux ou feuillus lorsque ces derniers sont feuillés. Ce biais est trop faible pour entrainer systématiquement un changement de score pour le facteur. Cette sous-estimation existe encore dans les peuplements feuillus défeuillés mais est plus faible et non significative (-0.27, NS). Ce facteur montre également la plus grande incertitude sur la mesure.

Pour les facteurs *densité de gros bois morts au sol* (facteur D), et *densité d'arbres vivants porteurs de dendro-microhabitats* (facteur F), la présence des feuilles ne semble pas influer sur la notation. Contrairement à ce que l'on supposait, le facteur F n'est pas biaisé et la variation entre les observateurs non experts et l'incertitude sur la mesure sont relativement faibles.

Une publication académique est actuellement en préparation :
41. **Larrieu** L., Gonin, P., Gosselin, F. (in prep.). Estimating the observer effect on the measurement of an indirect indicator of taxonomic biodiversity: the Potential Biodiversity Index (PBI). Soumission à *Ecological Indicators*?

3 LES DENDRO-MICROHABITATS INTEGRES DANS UN MODELE DE SIMULATION DE DYNAMIQUE FORESTIERE

Une collaboration étroite avec Benoît Courbaud qui développe Samsara 2 à l'Irstea Grenoble a permis de rajouter les dendro-microhabitats aux indicateurs de biodiversité du modèle, en calibrant un modèle d'apparition de dendro-microhabitats à l'échelle de l'arbre. Ce travail fera l'objet d'une publication (Pupin *et al.*) qui sera soumise à la revue *Ecology*.

Samsara2 est un modèle de simulation de dynamique forestière adapté aux forêts mixtes de montagne à structure irrégulière (Lafond *et al.* 2014 ; Courbaud *et al.* soumis). C'est un modèle individu-centré spatialement explicite dont le moteur principal est la distribution de la lumière dans le peuplement. L'évolution du peuplement est déterminée à la fois par une vingtaine de paramètres associés aux processus démographiques de chaque essence (croissance, fécondité, survie et croissance des semis, mortalité des adultes) et une dizaine de paramètres décrivant la gestion forestière (principalement le diamètre d'exploitabilité, le volume standard d'une coupe, l'agrégation du prélèvement et la sélection préférentielle d'essences). Un certain nombre d'indicateurs de production (volume récolté par essence et par classe de diamètre) et d'indicateurs directs et indirects de biodiversité (diversité des essences, distribution des hauteurs et diamètres des arbres, arbres morts debout, bois mort au sol, très gros bois vivants, milieux ouverts, richesse spécifique de la flore du sous-bois) sont calculés par le modèle. Samsara 2 est à la fois un outil de recherche et un outil incontournable pour anticiper à long terme, en concertation avec les gestionnaires forestiers, les conséquences d'orientations de gestion. En cette période charnière de tentative d'adaptation de la gestion forestière aux changements globaux, d'orientation forte en faveur des énergies renouvelables, et d'engagements pris par les forestiers pour conserver la biodiversité, cet outil devrait prendre une place de plus en plus importante dans la réflexion sur la gestion intégrée des forêts de montagne.

Section V – Synthèse des travaux. Intégration des acquis dans des outils d'aide à la gestion forestière durable et perspectives de recherches complémentaires

SECTION V – SYNTHESE DES TRAVAUX REALISES, PROPOSITIONS POUR LA GESTION ET PERSPECTIVES DE RECHERCHE

Cette section est non seulement dédiée à résumer les principaux acquis des études menées pour cette thèse mais aussi à formuler des recommandations pour les gestionnaires d'espaces forestiers pour mieux prendre en compte les dendro-microhabitats. Nous terminerons par quelques perspectives de recherche que nous pensons utiles pour poursuivre l'exploration de ce compartiment de la biodiversité des écosystèmes forestiers.

1 SYNTHESE DES TRAVAUX REALISES

La thèse a poursuivi simultanément plusieurs objectifs : (i) explorer le monde des dendro-microhabitats du tronc et secondairement des bois morts, (ii) développer des outils et préconiser des pratiques pour intégrer ces connaissances dans la gestion forestière courante, et (iii) ébaucher des pistes de recherche complémentaires (Fig. 18).

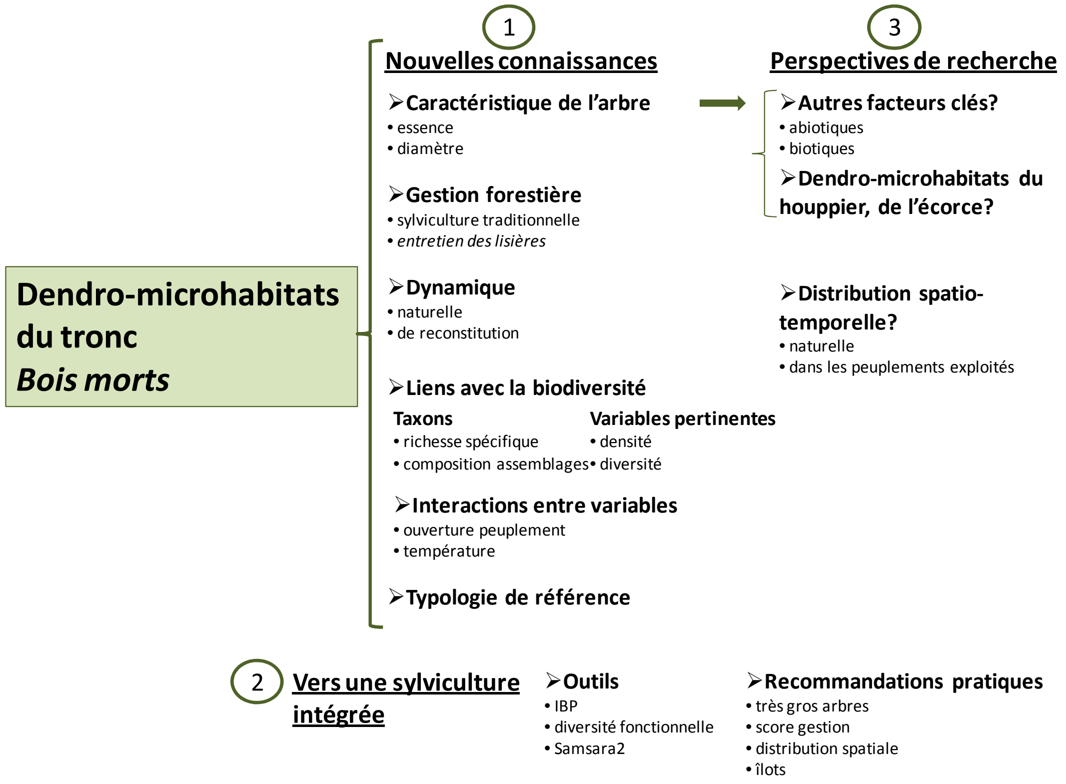


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Figure 18. Synthèse des connaissances acquises grâce à ce travail de thèse, des actions de transfert réalisées pour les gestionnaires forestiers et des perspectives de recherche déjà ébauchées
Les thèmes traités de façon secondaire apparaissent en italique

A l'échelle de l'arbre, nous avons précisé les liens déjà publiés entre l'essence ou le diamètre de l'arbre et l'occurrence des dendro-microhabitats et montré que la diversité des dendro-microhabitats est aussi corrélée à ces deux variables. Nous avons observé que ces relations sont « seuillées » et nous avons défini ces seuils pour le Hêtre et le Sapin pectiné. Nous avons modélisé ces relations, ce qui rend leur utilisation plus pratique et a permis l'amélioration d'un modèle dynamique, Samsara2 qui sera présenté succinctement dans le chapitre suivant. Un travail similaire est en cours pour d'autres essences très représentées dans les forêts françaises, comme les chênes à feuilles caduques (essentiellement *Quercus petraea*, *Q. robur* et *Q. pubescens*), le Merisier (*Prunus avium*) et le Châtaignier (*Castanea sativa*). Nos premiers résultats sur la co-occurrence des dendro-microhabitats ouvre à la fois un champ de réflexion sur les facteurs déterminant leur apparition, leur éventuelle co-évolution et, peut-être, la possibilité de simplifier la liste des dendro-microhabitats à observer dans un cadre de gestion courante. Le passage à l'échelle du peuplement nous a permis d'élaborer une liste de recommandations pratiques pour optimiser la conservation d'arbres porteurs de dendro-microhabitats dans les peuplements exploités.

Nous avons montré que la seule densité de dendro-microhabitats n'est pas suffisante pour traduire l'effet de l'exploitation forestière sur la diversité des espèces et que la diversité des dendro-microhabitats est également un facteur clé. De la même façon, pour le bois mort, le volume total ne suffit pas toujours pour discriminer les peuplements exploités des autres, mais, par contre, ils se différencient par les patrons de diversité de substrats. Une approche exploratoire de la mesure de la « diversité fonctionnelle » des dendro-microhabitats a été présentée dans le chapitre précédent.

Nous avons étudié la dynamique du bois mort et des dendro-microhabitats tout au long du cycle sylvigénétique des forêts mixtes de montagne. Elle montre un patron bien différent de celui observé dans les cycles de production mais la différence n'a pas été chiffrée dans ce travail. Elle précise, mais parfois dément, les patrons publiés jusqu'alors. Nos études synchroniques de peuplements mis hors gestion depuis des durées variables ont montré que plusieurs décennies sont nécessaires pour reconstituer les stocks de bois mort et de dendro-microhabitats et que la faune saproxylique associée réagit avec encore plus de retard.

Nous avons utilisé une approche pluritaxonomique pour mettre en évidence les facteurs clés pour la diversité spécifique ainsi que pour la composition des assemblages d'espèces. Ces facteurs diffèrent selon le groupe taxonomique ciblé, mais des relations claires ont néanmoins été révélées, en précisant les valeurs seuils. De surcroît, ces facteurs interagissent parfois et ceci limite notre capacité à définir des seuils pratiques et pertinents dans tous les contextes et nous amène également à moduler nos recommandations en fonction du contexte, en particulier climatique.

Nous avons élaboré une typologie des dendro-microhabitats qui est en bonne voie pour servir de référence internationale. Nous espérons qu'elle permettra de coordonner des actions de recherche et le développement d'outils pratiques. Les dendro-microhabitats forment une partie de l'ossature de l'Indice de Biodiversité Potentielle, un outil reconnu par la Stratégie nationale pour la biodiversité. Nos résultats ont permis d'explorer leur importance relative pour la biodiversité, de proposer des regroupements plus pertinents et de compléter leur liste. L'outil IBP et ses améliorations ont été présentés en détail dans le chapitre 2 (section IV).

Finalement, nous listerons des recommandations pratiques à destination des gestionnaires soucieux d'intégrer la diversité associée aux dendro-microhabitats dans leur gestion quotidienne. Elles concernent : (i) la conservation et le recrutement des très gros arbres, (ii) l'attribution d'un score « gestion » pour chacun des dendro-microhabitats dans un cadre de formation des praticiens, (iii) l'optimisation de la distribution spatiale des efforts de conservation et enfin (iv) la taille des îlots en libre évolution.

Il est clair que l'observation jusqu'alors non spatialisée des arbres porteurs de dendro-microhabitats et des pièces de bois mort limite notre capacité à comprendre certains processus et à formuler des recommandations plus précises. Nous avons réfléchi à un type de plan d'échantillonnage qui permettrait à la fois d'évaluer les patrons de distributions des dendro-microhabitats, d'identifier quelques facteurs déterminant leur mise en place et d'étudier leur dynamique individuelle. Il sera présenté ci-dessous dans le chapitre 3.

2 PRÉCONISATIONS POUR LA GESTION (MAINTIEN OU RESTAURATION) DES DENDRO-MICROHABITATS

Bien que beaucoup de travaux restent à réaliser pour quantifier le rôle écologique des dendro-microhabitats dans les écosystèmes forestiers et comprendre les patrons de leur dynamique naturelle (voir quelques pistes dans le chapitre 3), il nous paraît opportun, à la lumière des résultats obtenus, de formuler quelques recommandations pratiques à destination des gestionnaires forestiers.

2.1 APPROCHES SÉGREGATIVE, INTÉGRATIVE OU COMBINÉE? ("STAND SPARING" *VS* "STAND SHARING")

Pour optimiser simultanément la production de bois et la conservation de la biodiversité, l'idée générale est de définir s'il est préférable (i) de séparer les objectifs avec d'une part les espaces intensivement gérés juxtaposés aux espaces inexploités et dédiés à la conservation (« land sparing », *i.e.* gestion par sectorisation des fonctions, ségrégative) ou (ii) de protéger peut-être moins de surface et exploiter tout le reste en combinant la rétention d'éléments semi-naturels et en utilisant des itinéraires techniques prenant en compte les enjeux de conservation (« land sharing », *i.e*. gestion multifonctionnelle, intégrative) (Green *et al.* 2005). Les études ont surtout porté sur la production agricole et la protection de la biodiversité liée aux milieux forestiers ou semi-naturels.

Les études en milieux agricoles militent pour favoriser la stratégie de ségrégation (Green *et al.* 2005 ; Phalan *et al.* 2011). Ce résultat est en grande partie lié au fait que la biodiversité est beaucoup plus faible dans les cultures (même dans le cadre d'agricultures peu intensives) que les milieux semi-naturels (Green *et al.* 2005 ; Egan *et al.* 2012). Green *et al.* (2005) avancent même que la séparation géographique des objectifs permettrait, dans les pays impactés depuis très longtemps par l'agriculture, de retrouver un réseau d'habitats subnaturels. Plus étonnant sont les résultats forestiers de Edwards *et al*. (2014) qui montrent que la ségrégation est également la stratégie la plus performante pour la conservation des oiseaux, des bousiers et des fourmis en forêt tropicale d'Asie du Sud-Est, alors que la biodiversité est dans ce contexte très élevée. Mais les auteurs reconnaissent que leur plan d'échantillonnage ne prend pas en compte les effets de la fragmentation et de la perte de connectivité entre les surfaces en réserve sur la diversité taxonomique car le rôle des surfaces en réserve a été étudié dans des blocs de très grande taille (30-40 000 ha d'un seul tenant) et participant significativement aux taux de boisement total. Pour conserver la diversité des espèces forestières dans les contextes paysagers mixtes agriculture-forêt, Perfecto & Vandermeer (2012) s'appuient sur une approche métapopulationnelle et des données empiriques pour préconiser à la fois la conservation de fragments forestiers et un accroissement de la diversité structurale de la matrice agricole exploitée et l'élimination des produits agrochimiques (approche « land sharing »). Les pays scandinaves qui exploitent leurs forêts essentiellement par des coupes rases ont mis en place depuis plusieurs décennies une stratégie de conservation de la biodiversité forestière basée en grande partie sur la conservation d'habitats clés (« key woodland habitats ») comme les bordures du réseau hydrographique ou les habitats azonaux. Mais ces surfaces en libre évolution ne représentent en Finlande au total qu'environ 0,5 % de la surface des forêts et, surtout, les blocs conservés font seulement 0,5 ha en moyenne. Ces dispositions semblent insuffisantes à Hanski (2005) pour conserver réellement les taxons forestiers à cause de l'isolement des populations vivant dans ces blocs protégés ainsi que des effets négatifs de la proximité aux lisières pour les espèces de cœur de forêt. Ces craintes de perte des espèces forestières spécialistes sont étayées par des données empiriques sur les polypores à l'échelle des fragments conservés (Gu *et al.* 2000) mais aussi à l'échelle régionale pour les Coléoptères saproxyliques (Siitonen *et al.* 2001). Junninen & Kouki (2005 et 2006) montrent également que ces fragments sont peu pertinents pour la conservation des polypores menacés et Sippola & Halonen (2005) précisent que des études sont nécessaires pour s'assurer que les lichens présents dans ces fragments de petite taille perdurent bien. Plusieurs auteurs craignent donc des dettes d'extinction liées à ces fragments trop petits, c'est-à-dire le fait que les populations de certaines espèces soient encore observées mais ne se maintiennent pas à long terme (Tilman *et al.* 1994). La concentration de la biodiversité sur les réserves représente un danger en cas de future exploitation de celles-ci suite à un changement de stratégie politique (Edwards *et al.* 2014) ou à des évènements stochastiques (tempête, incendie) d'ampleur spatiale équivalente à la taille des fragments.

En fait, la meilleure solution semble être dépendante du contexte. Pour les plantes en milieu agricole, les gains obtenus par l'approche ségrégative sont plus importants dans des paysages avec un taux faible de milieux non cultivés - car la majorité des espèces est cantonnée aux milieux non cultivés - et l'approche intégrative se révèle la meilleure solution quand le paysage est plus complexe (Egan *et al.* 2012). De surcroît, la réflexion doit être générale et (i) prendre en compte une large gamme d'échelles spatiales (Grau *et al*. 2013), (ii) ne pas se contenter de ne regarder que la biodiversité et la production, mais élargir le champ de réflexion à d'autres enjeux comme la disponibilité et le potentiel de production des terres dédiées à la production ou encore le contexte socio-économique local (Fisher *et al*. 2011 et 2014).

La transposition de cette réflexion sur la conservation des habitats naturels à celle des dendro-microhabitats semble pertinente pour la conservation des communautés qui leur sont intimement liées. La question est posée de comment disposer spatialement les arbres porteurs de dendro-microhabitats que l'on conserve dans une matrice gérée. En d'autres termes, la mise en place d'îlots de vieux bois concentrant les arbres porteurs suffit-elle ou faut-il également disperser ces arbres porteurs dans le peuplement géré ? Les études de Ranius (2000 et 2006) sur *Osmoderma eremita* et Gouix (2011) sur *Limoniscus violaceus*, deux Coléoptères saproxyliques inféodés aux cavités à terreau, montrent un effet positif de l'agrégation en bouquet des arbres portant ce type de cavités. En effet, la proportion de cavités habitées par *Limoniscus violaceus* chute drastiquement avec l'éloignement à la cavité occupée la plus proche. Les mesures de dispersion menées par télémétrie et capture-recapture sur *Osmoderma eremita* montrent le même patron. Dans les deux études, la probabilité d'observer l'espèce est très faible dès que l'on s'éloigne de plus de 200 m d'une cavité occupée. Certes, ces Coléoptères sont inféodés à un habitat relativement stable, et bon nombre d'espèces liées à des environnements moins stables ont des capacités de dispersion beaucoup plus fortes, mais Ranius (2002) considère *Osmoderma eremita* comme une espèce parapluie et sa conservation permet la conservation d'un grand nombre d'espèces. Il signale dans le même article que certains Coléoptères vivant dans le même milieu (comme le Tenebrionidae *Tenebrio opacus* et l'Elateridae *Elater ferrugineus*), sont encore plus sensibles à la fragmentation qu'*Osmoderma*. Ces résultats militent pour une approche intégrative. Cependant, certains taxons ont des exigences environnementales quasiment impossibles à intégrer à la gestion forestière, comme le Champignon saproxylique *Antrodiella citrinella* qui nécessite pour sa conservation un minimum de 140 m^3 de bois mort résineux par hectare (Bässler et Müller 2010). Leur conservation exige donc le maintien de forêts en libre évolution.

À l'inverse, les oiseaux forestiers liés à de grands espaces ouverts comme l'Engoulevent d'Europe (*Caprimulgus europaeus*) profitent largement des jeunes plantations ou de coupes rases de grande surface (Rameau *et al.* 2000) alors qu'il est socialement et économiquement difficile de conserver dans les forêts gérées les grandes clairières issues de perturbations de grande ampleur comme de vastes chablis suite à des tempêtes qui constitueraient à la fois l'habitat de l'Engoulement et de bon nombre de saproxyliques thermo-héliophiles, bien entendu si on conserve le bois mort en place.

En conclusion, une approche seulement ségrégative ne paraît pas actuellement acceptable par la société car, pour être efficace en termes de conservation, elle soustrairait une trop grande partie des forêts à l'exploitation. Néanmoins, une approche exclusivement intégrative ne peut répondre aux objectifs de fournir partout des milieux favorables aux espèces très exigeantes et permettre l'expression de dynamiques naturelles de grande amplitude spatiale, comme par exemple les écroulements, sur plusieurs milliers d'hectares d'un seul tenant, de pessières subalpines liés au Coléoptère Scolitidae *Ips typographus* (Müller *et al.* 2008). La solution semble passer par une double stratégie combinant à la fois des outils pour la conservation ségrégative, c'est-à-dire des forêts en libre évolution dans les parcs nationaux, des réserves intégrales de grande surface et des corridors, et des outils de gestion intégrée comme les îlots de sénescence, la rétention de pièces de bois mort et d'arbres habitats (Lindenmayer & Franklin 2002 ; Bollmann & Braunisch 2013). On ne connaît pas actuellement quelle serait la disposition spatiale optimale des arbres habitats quand leur densité est de l'ordre de quelques unités par hectare, comme c'est actuellement le cas en respectant les normes négociées par les gestionnaires. Leur agrégation bénéficierait localement aux espèces de cavités à terreau dont on a parlé précédemment, mais aussi à des Coléoptères mycétophages (Kehler & Bondrup-Nielsen 1999). Mais leur dispersion dans le peuplement favorise la diversité des situations microclimatiques qui influence le rôle du dendro-microhabitat sur la biodiversité (Bouget *et al.* 2014) et limite le risque de disparition simultanée de tous les arbres porteurs du peuplement suite à une perturbation localisée.

La conservation d'arbres habitats serait facilitée par le remplacement de la sylviculture de masse couramment employée et visant à homogénéiser la conformation moyenne des arbres composant le peuplement par une sylviculture « d'arbres » qui concentre la production du revenu sur quelques dizaines d'arbres de haute qualité marchande à l'hectare, à la fois les mieux conformés et les plus performants en termes de croissance. Cette stratégie fait coïncider l'échelle de gestion (l'arbre) avec l'échelle de la biodiversité (le dendro-microhabitat) et permet d'allouer une partie du peuplement au fonctionnement du système en conservant des arbres qui boucleront leur cycle de vie entièrement et alimenteront le compartiment bois mort après avoir joué leur rôle d'arbres vivants porteurs de dendro-microhabitats. Certes, le volume de bois récolté diminue, mais le rendement économique net peut théoriquement rester au même niveau, voire augmenter, compte tenu des économies réalisées lors des exploitations et des travaux de régénération. Cette logique sylvicole laisse sur pied des arbres de piètre qualité marchande qui ont une valeur très faible à négative une fois retirés les frais de marquage et d'exploitation, en tout cas dans les secteurs à topographie difficile. Des études économiques telles que celles réalisées sur les placettes de l'Association futaie irrégulière (AFI) sont à même de mieux préciser, pour des types de peuplements variés, le coût ou l'économie réalisée en fonction des différents contextes rencontrés.

Dans l'optique de conserver la biodiversité dans son ensemble, il conviendrait également de considérer l'effet de cette approche combinée vis-à-vis de la conservation de la diversité génétique.

Fahrig (1998) indique que toutes les populations survivent pour des taux de couverture d'habitats de plus de 20%, quelle que soit la fragmentation de cet habitat. Harris (1984) fixe à 25 % la part minimale de forêt mature (« old growth forest ») à conserver en permanence dans le massif boisé, mais insiste sur la nécessité de connecter ces taches de forêt mature entre elles. Un seuil de même grandeur est suggéré par Wiktander *et al.* (2001) pour le Pic épeichette (*Dendrocopos minor*). Wegge et Rolstad (1986) augmentent ce seuil à 30 % de forêts matures pour le Grand tétras (*Tetrao urogallus*). Plus récemment, Gustafsson *et al.* (2012) établissent ce seuil à 5-10 %. Ces seuils correspondent à la proportion d'habitat en dessous de laquelle la fragmentation peut remettre en cause la persistance du taxon (Andren 1994; Fahrig 1998). Les seuils d'extinction définis comme la quantité minimale d'habitat en dessous de laquelle la population s'éteint irrémédiablement dépendent, eux, de l'espèce concernée et de la qualité de la matrice (Fahrig 2001; Ranius & Fahrig 2006). À l'échelle de l'arbre, Nilsson *et al*. (2001) recommandent de maintenir dans les forêts exploitées 20 % de la densité originelle d'arbres à cavité pour conserver la biodiversité associée et Bütler *et al.* (2004) suggèrent, pour le Pic tridactyle (*Picoides tridactylus*), de conserver un minimum de 5 % des arbres morts sur pied sur des surfaces supérieures à 100 ha. On constate que densité, niveau d'agrégation et quantité totale d'arbres habitat sont des variables à envisager de façon complémentaire dans un dispositif de gestion intégrée. Mais des recommandations précises sont difficiles à formuler car nous connaissons malheureusement très mal les patrons de distribution et la dynamique des dendro-microhabitats dans les forêts naturelles. Nous aborderons ci-dessous les avantages à mener ces études de distribution spatiale.

2.2 SURFACE MINIMALE DES ÎLOTS EN LIBRE EVOLUTION

La surface minimale d'habitat à dynamique naturelle nécessaire à la survie à long terme d'une espèce est assurément taxon-dépendante, les espèces les plus grosses étant les plus exigeantes en surface (mais aussi les plus ubiquistes) (Hanski 2005). La littérature est assez pauvre sur le sujet. *Osmoderma eremita* n'est pas systématiquement présent dans les peuplements de moins de 10 ha, même s'ils contiennent des arbres à cavités favorables (Ranius 2000). Nous avons montré que dans les sapinières-hêtraies montagnardes, une surface minimale de 10 ha en libre évolution depuis plus de 100 ans est nécessaire pour observer au moins un exemplaire de chaque type de dendro-microhabitats (Larrieu *et al.* 2014). Jakoby *et al.* (2010) ont montré par modélisation qu'une surface minimale de 1 ha était nécessaire aux îlots en libre évolution pour assurer à long terme la diversité des types de bois mort.

Il ne semble donc pas pertinent d'avoir des surfaces inférieures à 1 ha et plus les îlots seront grands et connectés pour les espèces cibles, mieux la conservation se fera.

2.3 CONSERVATION ET RECRUTEMENT DE TRES GROS ARBRES

Les très gros arbres jouent un rôle significatif pour les dendro-microhabitats car ils cumulent les propriétés suivantes : (i) ils sont souvent porteurs, (ii) quand ils portent, c'est souvent plusieurs dendro-microhabitats, (iii) ils portent des dendro-microhabitats qui leur sont endémiques, comme ceux liés aux écorces crevassées ou aux grosses charpentières, (iv) ils sont capables de porter tous les types de dendro-microhabitats. Les seuils traditionnels utilisés en foresterie pour les catégories de diamètre (d) « gros bois » (GB : [50-65 cm] pour les feuillus et [45-60 cm] pour les résineux) et « très gros bois » (TGB : d≥70 cm pour les feuillus et d≥65 pour les résineux) (Bastien et Gauberville 2012) font partie des intervalles de confiance à 80 % des diamètres seuils que nous avons mis en évidence pour le Hêtre et le Sapin pectiné dans la relation entre le diamètre de l'arbre et les dendro-microhabitats. En attendant d'avoir à disposition ces valeurs seuils pour l'ensemble des essences françaises, on considère que le Hêtre est représentatif des feuillus et le Sapin pectiné des essences résineuses. Tenant compte de la tendance généralisée d'abaisser les diamètres d'exploitabilité, la catégorie TGB est malheureusement souvent regroupée avec la catégorie GB. Mais comme elle a une signification écologique *via* sa relation avec les dendro-microhabitats, il serait judicieux de la conserver. Pour la même raison, il serait également pertinent de créer et d'utiliser une catégorie de diamètre supérieure, les « très très gros bois » (TTGB), dont les seuils se situent à 90 cm de diamètre pour les feuillus et 100 cm pour les résineux. Suite à une collaboration avec le WWF, le concept de TTGB est d'ores et déjà intégré dans l'Indice de naturalité (Rossi et Vallauri 2013).

2.4 RECRUTEMENT DE FUTURS ARBRES PORTEURS

Il est nécessaire de prévoir le recrutement de futurs arbres habitats pour compenser les pertes dues à leur exploitation ou à leur disparition naturelle (mort ou chablis). Dans le contexte des forêts d'Eucalyptus, Gibbons *et al*. (2010) recommandent de recruter deux fois plus d'arbres que l'objectif de conservation des arbres à cavités. De plus, lors du recrutement, on devrait tenir compte de l'évolution plus ou moins rapide des types de dendro-microhabitats : dans les forêts boréales, les cavités creusées par les pics ne persistent pas aussi longtemps que les cavités issues de blessures (Cooke & Hannon 2012).

La conservation d'arbres habitats et le recrutement de leurs successeurs devrait également assurer à minima la mixité de la population d'arbres porteurs (dans les écosystèmes naturellement mixtes, bien entendu), et, mieux, la diversité des essences.

Cette problématique de la dynamique dans le temps des qualités des arbres ou îlots de conservation est une question scientifique peu abordée et totalement oubliée par les gestionnaires. Elle est pourtant clé dans les forêts françaises, à la fois du fait de la pauvreté en arbres habitat ou en peuplements matures (dans la majorité des cas on travaille plus pour restaurer que pour maintenir un existant) et du fait des évolutions climatiques à venir face auxquelles les arbres habitat et les îlots de conservation auront un rôle d'autant plus important pour soutenir la conservation de la biodiversité.

2.5 ATTRIBUTION DE SCORES « GESTION » AUX DENDRO-MICROHABITATS

Dans un objectif de conserver la biodiversité taxonomique dans son ensemble, il est très délicat de hiérarchiser l'importance relative des dendro-microhabitats. En effet, faut-il donner plus de crédit aux cavités à terreau qui hébergent des communautés très diversifiées comportant des espèces à statut de protection, mais qui partagent de nombreuses espèces avec d'autres types de dendro-microhabitats, ou bien aux dendrothelmes qui hébergent en Europe moins de 20 espèces d'insectes, mais dont plus de la moitié sont strictement dépendants de ce dendro-microhabitats ?

Il est tentant néanmoins de faire prendre conscience aux gestionnaires forestiers que l'acte de martelage impacte différemment les populations des différents types de dendro-microhabitats, en regard de leur occurrence naturelle dans les forêts et de leur dynamique spécifique.

Il est possible de le faire assez aisément par le biais d'un indice synthétique : le « score gestion ». La méthode consiste à donner du poids aux types de dendro-microhabitats qui, d'une part, sont rares et d'autre part sont créés de façon discontinue et imprévisible, ou bien demandent de longues durées pour se développer (Tableau 7). En guise d'illustration, une fente profonde dans le bois d'un arbre vivant qui est rare dans les forêts même sub-naturelles (Larrieu *et al.* 2012) et créée occasionnellement par des évènements stochastiques tels qu'un vent violent ou un gel intense (Penicaud 2000), recevra un score maximum. La méthode intègre le fait que plus l'habitat est éphémère, moins la fragmentation aura un effet sur les communautés associées (Fahrig 1998) et que la perte d’un dendro-microhabitat qui a une forte probabilité de création rapide est moins dommageable que celle d’un dendro-microhabitat lié à des événements rares. Elle occulte néanmoins l’idée d’une densité minimale de chaque type de dendro-microhabitat indispensable pour soutenir une métapopulation pérenne.

On peut choisir d’utiliser comme référence l’occurrence observée dans les forêts sub-naturelles ou bien dans les peuplements exploités. Dans ce dernier cas, les dendro-microhabitats qui ont des densités supérieures en contexte exploité, comme les dendrothelmes et les *bois durs sans écorce*, changeront de rang. Dans le cadre d’un martelage réel, l’occurrence dans les forêts exploitées est plus conforme avec le contexte de travail. Dans le cadre d’un exercice réalisé sur un martéloscope, il préférable de compléter la formation de l’observateur en utilisant plutôt l’occurrence naturelle. Le but est bien de donner un outil au marteleur pour juger de l’effet à court et moyen termes de son martelage sur l’offre du peuplement en microhabitat (densité et diversité) et pas d’orienter des choix de biodiversité. Cet indice est en cours d’incorporation dans le réseau des martéloscopes, aussi bien en France qu’en Europe (projet « Integrate + »).

Tableau 7. Notes de « gestion » attribuées aux dendro-microhabitats en fonction de leur densité dans les peuplements, de leur probabilité d'apparition et de leur durée d'évolution
(voir détails dans le texte)

1- Scarcity gradient		
	context of subnatural beech-fir forest	**context of managed beech-fir forest**
woodpecker cavities	fairly rare	rare
bark-lined cavity at the base of the trunk	common	common
missing bark with hard wood	fairly rare	very common
cavities with mould evolving from decay wood, on the tree trunck	common	rare
cavities with mould evolving from decay wood, on the tree base	common	very rare
dendrothelms (water-filled holes)	fairly rare	from common to very common (higher the proportion of broadleaved with hardwood increases, especially beech, more common this microhabitat is)
cracks and shelter barks	rare	very rare
conk of saproxylic fungi	rare	very rare
moist sap runs	rare	very rare
broken thick branches or tree-top	common	fairly rare
crown deadwood	common	fairly rare
liana and Mistletoe	common (depending on forest habitat)	common (depending on forest habitat)

2- Reconstitution speed in unmanaged stands (the "slowness" can be related to infrequent stochastic events or a necessary long time evolution)	
woodpecker cavities	speedy (if woodpecker occurrence, they dig each year several breeding and feeding cavities)
bark-lined cavity at the base of the trunk	slow (linked to the growth of the tree base)
missing bark with hard wood	fairly slow (linked to the fall of neighbouring trees, or stones from cliffs)
cavities with mould evolving from decay wood, on the tree trunck	fairly speedy to very slow (the earlier stages can be created from "missing bark with hard wood" in only several years , but the latest stages which contain large amount of mould, require several decades)

Tableau 7 (suite). Notes de « gestion » attribuées aux dendro-microhabitats en fonction de leur densité dans les peuplements, de leur probabilité d'apparition et de leur durée d'évolution
(voir détails dans le texte)

cavities with mould evolving from decay wood, on the tree base	fairly speedy to very slow (the earlier stages can be created from "missing bark with hard wood" in only several years , but the latest stages which contain large amount of mould, require several decades)
dendrothelms (water-filled holes)	slow (require particular growing structure such as fork (bark-lined dendrothelm) or evolving of cavity collecting water flowing on the trunk (rotted-bottom dendrothelm))
cracks and shelter barks	very slow (linked to windstorm, lightening, or evolving of large linear wounds)
conk of saproxylic fungi	slow (linked to weak and senescent trees)
moist sap runs	from fairly slow (linked to simple wound, so flowing only in spring) to slow (linked to wound colonized by anaerobic bacteria: permanent flow)
broken thick branches or tree-top	slow (linked to windstorm or the fall of neighbouring trees)
crown deadwood	slow (linked to physiological stress, senescence, competition with neighbouring trees)
liana and Mistletoe	fairly speedy (but depending on liana occurrence: forest habitat)
Score scales	
scarcity	1=very common
	2=common
	3=fairly rare
	4=rare
	5=very rare
reconstitution speed	
	1=speedy
	2=fairly speedy
	3=fairly slow
	4=slow
	5=very slow

3 PERSPECTIVES DE RECHERCHE

Notre recherche finalisée considère les dendro-microhabitats comme des objets sylvicoles utiles au diagnostic indirect de la diversité des espèces vivant dans les forêts et à leur conservation. Plusieurs champs d'investigation nous sembleraient essentiels pour compléter cette approche et nous allons ci-dessous inventorier les principaux. Mais les dendro-microhabitats ne peuvent-ils pas également être des mini-systèmes utiles aux sciences écologiques ?

3.1 DES ETUDES FINALISEES COMPLEMENTAIRES

Les études finalisées qui seraient complémentaires aux travaux publiés jusqu'alors concernent la distribution spatiale et la dynamique des dendro-microhabitats ou l'étude des parties de l'arbre-support peu investiguées jusqu'à présent. Elles peuvent également examiner les possibilités d'ingénierie écologique pour suppléer l'impact de l'exploitation forestière ou pour accélérer la dynamique d'hétérogénéisation de la structure de peuplements récemment mis en libre évolution.

3.1.1 SPATIALISATION DES OBSERVATIONS DE DENDRO-MICROHABITATS

Jusqu'alors, les études sur les dendro-microhabitats à l'échelle du peuplement se limitaient aux relations arbre/dendro-microhabitat, densité et diversité des dendro-microhabitats et co-occurrence des types de dendro-microhabitats sur le même arbre. Aucune étude générale sur les dendro-microhabitats n'a spatialisé les observations. Seuls quelques auteurs étudiant des communautés particulières l'ont fait pour leur objet d'étude (*e.g.* Martin *et al.* 1999 ; Hanski *et al*. 2000 ; Ranius 2000 ; Gouix 2011). Pourtant, la spatialisation des dendro-microhabitats (et des arbres non porteurs) à l'échelle de la placette et de la forêt ouvre tout un champ d'investigations :

- Compte tenu de la grande variabilité des capacités de dispersion des espèces liées aux dendro-microhabitats, les patrons de distribution spatiale des dendro-microhabitats seraient utiles pour étudier de façon plus fine leurs relations avec les communautés associées en facilitant le choix de l'échelle spatiale la plus pertinente pour le processus écologique étudié (Dunning *et al.* 1992) ou encore en optimisant la position et la densité de dispositifs (pièges, détecteurs) utilisés pour l'observation des taxons.
- La spatialisation du bois mort sur les mêmes sites formerait un ensemble facilitant l'étude de la redondance/complémentarité du bois mort avec les dendro-microhabitats saproxyliques.
- On sait que l'exploitation forestière perturbe les populations de dendro-microhabitats en modifiant les densités absolues et les proportions relatives et en réduisant leur diversité (Winter et Möller 2008 ; Larrieu *et al.* 2012 et 2013). Mais dans quelle mesure l'exploitation modifie-t-elle les patrons de distribution spatiale ? Cette connaissance permettrait d'adapter les recommandations de conservation de dendro-microhabitats dans les peuplements exploités en les complétant par des aspects spatiaux afin de limiter au maximum les modifications de l'habitat.
- La spatialisation simultanée de certaines variables environnementales topographiques ou géomorphologiques à l'échelle de la placette (falaise, couloir d'avalanche, crête ventée ou souvent foudroyée, éboulis, clairière), couplée avec des données à une plus large échelle sur les facteurs

biotiques connus pour créer des dendro-microhabitats (diversité spécifique des Picidae, présence d'*Ursus arctos*) fournirait des informations sur les facteurs explicatifs des quelques 70 % de la variance non expliquée par les modèles construits avec seulement l'essence et le diamètre de l'arbre (Larrieu *et al.* 2014).

- La co-occurrence des dendro-microhabitats pourrait être étudiée dans sa dynamique (co-évolution de dendro-microhabitats indépendants à leur origine ?), reliée à des facteurs de création communs et faciliterait, si des relations statistiques fortes sont établies, la simplification des outils de gestion utilisant les dendro-microhabitats, par la réduction du nombre d'objets à observer.
- La pérennisation de ces placettes d'observation permettrait de suivre dans le temps l'évolution des dendro-microhabitats, leur « temps de passage » dans le cas des types évolutifs comme les cavités à terreau, et leur durée de vie. Ces observations diachroniques sont moins biaisées que les chronoséquences (Johnson et Miyanishi 2008) habituellement utilisées quand le phénomène a une durée dépassant celle de l'observateur (Walker *et al.* 2010).
- Cette approche faciliterait l'incorporation des dendro-microhabitats dans des modèles d'habitats spatialement explicites (Fahrig 1998), plus réalistes pour étudier les effets de la fragmentation sur les communautés associées (Fahrig et Merriam 1994).
- Enfin, la spatialisation fournirait le cadre pour planifier des études sur les stratégies adaptatives développées par les espèces pour tenir compte de la distribution spatiale et temporelle des dendro-microhabitats et permettrait l'utilisation des modèles de métapopulation (« Incidence Function Models » IFM ; *e.g*. Ovaskainen et Hanski 2003).

Nous proposons ici les grandes lignes d'un patron de plan d'échantillonnage pour la spatialisation des observations de dendro-microhabitats, élaboré par un groupe de travail de Dynafor que j'ai réuni pour l'occasion et rassemblant des statisticiens (M. Goulard, A. Cabanettes), une géomaticienne (S. Ladet) et des personnels de terrain (L. Burnel, J. Willm) (Fig. 19). Il découle également d'un travail d'analyse de données déjà acquises dans des peuplements de hêtraie-sapinière non exploités, réalisé par Pavel Sebek (PhD à l'Université de Bohème, Tchéquie) pour optimiser l'échantillonnage, en termes de temps passé/information récoltée. Les observations devront être menées à la fois en forêt exploitée et non exploitée depuis longtemps (dans l'idéal, au moins 100 ans). À partir d'un point de départ tiré au hasard, les distances et les angles des arbres les plus proches voisins seront mesurés, en suivant un parcours excluant la possibilité de reprendre les arbres cibles et voisins déjà utilisés. Tous les arbres de diamètre à 1,3 m supérieur à 50 cm seront identifiés à l'espèce et observés en caractérisant leur état (vivant, mort sur pied, dépérissant) ainsi que tous les dendro-microhabitats visibles depuis le sol sur le tronc et les principales divisions verticales. Suite à un test comparatif de trois modèles de GPS que nous avons réalisé sur un gradient de difficulté d'acquisition du signal, nous croyons que l'utilisation d'un GPS haut de gamme pourra réduire dans la plupart des sites le temps d'observation sur la placette.

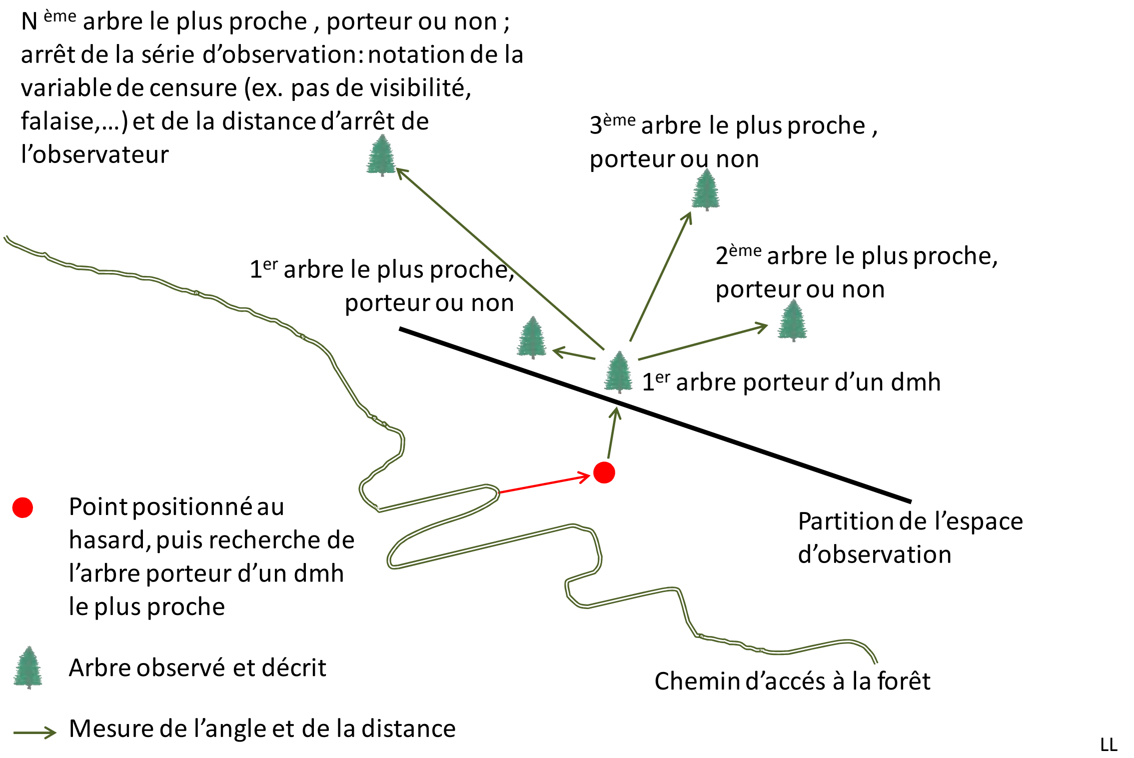

Figure 19. Patron d'un plan d'échantillonnage pour l'étude spatialisée des dendro-microhabitats, illustré à l'échelle de la placette.

Les distances mesurées entre arbres voisins seront utilisées dans un premier temps pour estimer les intensités (nombre de cas par unité de surface) des processus étudiés (arbre porteur d'un dendro-microhabitat, de plusieurs dendro-microhabitats, ou non-porteur) et pour tester si des interactions existent entre les occurrences qui sont étudiées (« Statistical analysis of spatial point patterns », Diggle 1983). Si des interactions sont repérées, nous essaierons une estimation de modèle d'interaction pour affiner les échantillonnages ultérieurs. Au final, on recherchera si l'occurrence des dendro-microhabitats est spatialement corrélée avec les facteurs pressentis, non corrélée mais non-aléatoire, ou totalement aléatoire. On tentera une modélisation spatiale de la répartition combinée des arbres, des dendro-microhabitats, et des facteurs pressentis.

3.1.2 DENDRO-MICROHABITATS DU HOUPPIER ET DES RHYTIDOMES CREVASSES

Le volume et la diversité du bois mort du houppier peuvent être évalués assez précisément depuis le sol par un observateur entraîné (Burnel *et al.* 2011). Le relevé des dendro-microhabitats depuis le sol et seulement sur le tronc et ses principales divisions verticales ne nécessite pas, dans la plupart des cas, d'aide optique et réduit le temps d'observation alloué à chaque arbre. Mais on sait qu'on sous-estime alors la population de dendro-microhabitats car certains d'entre eux sont localisés dans le houppier, principalement sur les charpentières (*e.g.* Tillon 2004), et participent activement à la biodiversité locale (Speight com. pers.) Néanmoins, leur observation n'est réalisée correctement que par grimpage (Tillon 2004) et leur observation depuis le sol est sujet à un fort effet observateur (Paillet sous presse).

Dans le but de mieux estimer l'offre en dendro-microhabitats des peuplements forestiers en prenant en compte les dendro-microhabitats du houppier, il serait judicieux sur un échantillon d'arbres *ad-hoc* de rechercher s'il existe des relations statistiques entre, d'une part, des variables observables ou mesurables depuis le sol comme l'essence, le diamètre du tronc et des variables de caractérisation de l'architecture et du volume du houppier, et, d'autre part, les dendro-microhabitats portés par les branches. Peut être que des relations de co-occurrence existent également entre les dendro-microhabitats du tronc et ceux du houppier. Un premier test a été mené dans une hêtraie-chênaie sessiliflore grâce au concours du groupe des grimpeurs EFPA et a montré (i) un effet de l'essence et (ii) une grande variabilité de ces relations.

Les structures développées par les écorces âgées constituent un ensemble original de dendro-microhabitats. On référence en France quelques champignons agaricales qui émettent des sporophores exclusivement dans des poches de substrat décomposé dans les fissures d'écorce, aussi bien sur feuillus (*Mycena pseudocorticola, M. alba, Phaeomarasmius rimulincola)* que sur certains résineux (*Mycena juniperina* sur *Juniperus* spp.) (Corriol com. pers.). Les écorces âgées ont été finement décrites sur le Douglas vert (*Pseudotsuga menziesii*) par Michel *et al.* (2011). Ces auteurs ont montré que plusieurs types de dendro-microhabitats s'y développent (particulièrement des cavités et des poches de substrat en décomposition) et que de nombreux taxons les utilisent : des insectes, des araignées et des plantes. Ce compartiment mériterait d'être mieux connu et nous projetons de réaliser une étude sur les écorces de Mélèze d'Europe, en profitant d'un bel ensemble de très gros arbres (jusqu'à plus de 6 m de circonférence) dans le parc national du Mercantour.

3.1.3 VALEURS ECOLOGIQUES COMPAREES DES DENDRO-MICROHABITATS « NATURELS » *VS* D'ORIGINE ANTHROPIQUE *VS* TOTALEMENT «ARTIFICIELS »

Une équipe italienne a entrepris en 1999 de créer artificiellement des dendro-microhabitats dans un bois ancien de 230 ha isolé dans une plaine agricole, le « Bosco della Fontana » (Masson *et al.* 2005). L'opération concernait essentiellement des creusements de cavités et des dendrothelmes à la tronçonneuse, mais aussi indirectement la formation de substrats favorables aux carpophores de champignons saproxyliques par annélation d'arbres vivants et création de chablis. Toutes ces opérations ont été quantifiées en temps et en coût. Mais quelle est la valeur écologique de ces dendro-microhabitats « anthropiques » pour les taxons ? Dans le cas du Bosco della Fontana, les oiseaux ont réagi très rapidement à la nouvelle ressource et dès 2002, plus de 33 % des cavités de chaque taille étaient utilisées pour la nidification (Masson *et al.* 2005). Les dendrothelmes ayant été creusés principalement dans le but de provoquer des pourritures favorisant l'apparition de cavités naturelles, ils n'ont pas fait l'objet de suivi des communautés spécifiques.

La mise en place d'un réseau de dispositifs analogue dans une gamme de milieux variés couplé à des suivis taxonomiques fournirait des éléments pour la mise en place éventuelle d'actions de restauration écologique, par exemple dans des peuplements dévolus à la conservation mais très altérés par leur exploitation récente, comme c'est le cas des jeunes réserves intégrales ou îlots de sénescence. Bien sûr, la reconstitution de dendro-microhabitats à longue évolution comme les cavités à terreau de stade 5 (Fig. 5) prendra dans le meilleur des cas quelques décennies. Il n'est pas certain non plus que les successions à partir de dendro-microhabitats anthropiques ne divergent pas significativement des successions naturelles, comme on peut l'observer pour les champignons saproxyliques. En effet, le polypore parasite de faiblesse *Fomes fomentarius* a une action stimulante sur la succession fongique qui débute (Heilmann-Clausen & Boddy 2005) et influence la composition des assemblages et sa diversité totale (Heilmann-Clausen & Christensen 2003). L'inoculation de spores de champignons sur des tissus volontairement blessés afin d'initier des cavités devrait tenir compte de l'importance de l'identité du champignon précurseur pour les trajectoires de succession.

3.2 POTENTIEL DES DENDRO-MICROHABITATS POUR TESTER DES THEORIES ECOLOGIQUES ?

La validation des théories écologiques par des études empiriques est laborieuse dans des écosystèmes complexes qui rendent difficiles la répétition ainsi que la traçabilité de l'opération car les facteurs qui interagissent sont très nombreux et mêlent les échelles spatiales. L'utilisation de microcosmes artificiels (« common gardens »), recréant *ex-situ* des mini systèmes écologiques bien délimités, permet un grand nombre de répétitions et facilite la traçabilité, mais leur réalisme est largement critiquable et cela altère la généricité des résultats (Carpenter 1996). Par contre, les microcosmes naturels ont prouvé qu'ils étaient parfaitement adaptés à la validation de théories, par exemple pour l'étude des effets de la perte de diversité sur le fonctionnement de l'écosystème ou des effets du fonctionnement en métacommunauté (*i.e.* un ensemble de communautés locales qui sont liées entre-elles par la dispersion de nombreuses espèces qui interagissent) sur la richesse spécifique (Srivastava *et al.* 2004).

L'ensemble des dendro-microhabitats cumule les propriétés suivantes : (i) les communautés associées sont spatialement bien délimitées, au moins pour les écophases strictement inféodées au dendro-microhabitat ; (ii) ils couvrent un large gradient d'hétérogénéité structurale interne ; (iii) malgré une dynamique conduisant irrémédiablement à leur disparition, ils couvrent un large gradient de « stabilité » d'habitat, en liaison avec la large gamme de vitesses d'évolution ; (iv) leur taille réduite permet un échantillonnage assez précis des communautés associées par le biais de dispositifs ciblés, d'émergence (*e.g.* Gouix 2011) ou de recherche active (*e.g.* Bussler & Müller 2009) ; (v) habitats isolés, ils sont séparés par une matrice, le peuplement forestier, dont on peut facilement faire varier la perméabilité ou la fonction de corridor écologique, *via* le contrôle du sous étage ou de la composition dendrologique et il est assez aisé, au moins pour les types de dendro-microhabitats fréquents, de faire varier leur densité dans le peuplement ; (vi) les espèces associées aux dendro-microhabitats couvrent une large gamme de capacités de dispersion ; (vii) pour faciliter l''expérimentation, des dispositifs artificiels peuvent être substitués aux dendro-microhabitats les moins évolués (*e.g.* des nichoirs pour des cavités de nidifications de pics (Jansson *et al.* 2009), des bâches pour les dendrothelmes à fond dur) ou utilisés pour compléter *in situ* un dispositif ; (ix) certains taxons inféodés aux dendro-microhabitats ont des cycles de vie courts permettant de multiplier les générations sur un temps d'étude économiquement raisonnable.

Ces nombreuses propriétés des dendro-microhabitats font des communautés associées de bons candidats pour servir de modèles de systèmes écologiques (Fig. 20). D'ailleurs, les communautés de deux dendro-microhabitats, les sporophores de champignons et les dendrothelmes, ont déjà été utilisées en tant que microcosmes naturels. Toda *et al.* (1999) et Wertheim *et al.* (2000) ont utilisé les insectes vivant dans les sporophores de champignons pour évaluer les effets relatifs des mécanismes de partition des ressources et d'agrégation spatiale sur la richesse spécifique. Starzomski *et al.* (2002) ont analysé les déplacements du Coléoptère mycétophage *Bolitotherus cornutus* dans le cadre théorique de populations structurées en métapopulation. Les phytotelmes ont été largement utilisés pour étudier les processus qui structurent les communautés (synthèse dans Kitching 2001). Kitching (2001) déclare même qu'ils sont des «instruments naturels proches de l'idéal pour des études plus approfondies des dynamiques des réseaux trophiques ». Sunahara et Mogi (1998) ont étudié les effets de l'isolement, de la surface et la sensibilité à la sécheresse de bosquets de bambous sur la dynamique d'une métapopulation du Diptère *Tripteroides bambusa*. Sous-groupe des phytotelmes, les dendrothelmes des forêts tempérées sont des écosystèmes moins diversifiés mais conservent une partie des qualités attribuées au groupe, en particulier le fait que les écophases des espèces associées soient pour la plupart strictement inféodées au dendro-microhabitat et quasiment indépendants de la matrice (au moins directement). D'ailleurs, Sota *et al.* (1994) ont utilisé les moustiques des dendrothelmes pour tester les effets des perturbations sur les communautés. Les cavités à terreau ont également été concernées par ces approches : Ranius (2000) et Ranius et Henin (2001) ont montré que les populations du Coléoptère saproxylique *Osmoderma eremita* sont structurées en métapopulation, ont quantifié la densité d'habitat favorable à la persistance d'une métapopulation et ont identifié les processus d'extinction et de colonisation.

On pourrait également imaginer d'étudier à l'aide des dendro-microhabitats la part des différents processus stochastiques qui provoquent l'extinction d'une population: (i) génétique, lié à des très faibles effectifs de taxons peu mobiles, (ii) démographique, lié aux variations du ratio natalité/mortalité, ou (iii) environnemental, lié au changement de conditions climatiques et aux relations prédation-parasitisme-compétition. Les conditions d'extrême fragmentation sont idéales pour définir les seuils d'extinction des espèces (Hanski 2005). Ils peuvent être abordés par la taille minimale du dendro-microhabitat ou par la densité minimale du type de dendro-microhabitat. La possibilité de manipuler à la fois les communautés et le gradient de continuité des dendro-microhabitats (par l'obturation ou la suppression des arbres supports ou, au contraire, par l'ajout de structures artificielles pour créer des corridors à l'aide de « pas japonais » (« stepping stones ») est un avantage certain pour l'étude des patrons de dispersion, ainsi que des processus de dettes d'extinction (« extinction debt », Tilman *et al.* 1994), de crédit d'espèce (« species credit », Hanski 2000), de crédit d'immigration ou du renouvellement des communautés (« immigration credit » et « species turnover », Jackson et Sax 2010) en liaison avec différents régimes de perturbation. Les dendro-microhabitats semblent également pertinents pour décrire simultanément les dynamiques écologiques et d'évolution adaptative (« eco-evolutionary dynamics », Hanski et Mononen 2011) en utilisant leur large gamme de patrons d'isolement, de dynamiques (fréquence d'apparition et durée de vie) et de stratégies de compromis de dispersion des espèces. Il est communément établi que les espèces vivant dans des milieux isolés et instables ont de fortes capacités de dispersion. Ce processus est également décrit au niveau inférieur à l'espèce, les phénotypes les plus dispersants dominant les habitats les moins stables alors que les phénotypes les moins dispersants sont plus communs dans les habitats les plus stables (Southwood 1962 *in* Hanski et Mononen 2011). Mais la fragmentation de l'habitat peut, en fait, influer soit positivement soit négativement sur les capacités de dispersion (Hanski 2005), probablement en liaison avec l'importance relative prise par de nombreux facteurs comme l'hétérogénéité de l'habitat, la compétition intra et inter-spécifique et le coût de la dispersion (Ronce 2007). Les résultats acquis pour démêler ces processus pourraient de surcroît nous éclairer sur les conséquences d'une réduction de densité des différents types de dendro-microhabitats, ainsi que sur l'adéquation des échelles d'échantillonnage des conditions environnementales et des espèces présumées en être dépendantes.

La vérification de la très ancienne règle d'augmentation de la richesse spécifique en fonction de la surface échantillonnée (courbes aire-espèces, Watson 1859 *in* Rosenzweig 1995) pourrait être conduite en augmentant progressivement le nombre de dendro-microhabitats du même type pris en compte dans l'échantillon. L'analyse des pentes des courbes révèlerait la variabilité intrinsèque du dendro-microhabitat, son degré d'isolement, et aiderait à fixer des valeurs d'abondance seuils pour la conservation de la biodiversité associée.

L'ensemble du complexe fonctionnel dendro-microhabitats saproxyliques-bois mort semble être un terrain d'étude pour la variabilité de la largeur de niche, en liaison avec le contexte local, en l'occurrence le type de macrohabitat ainsi que la naturalité et les caractéristiques structurales du peuplement. Définir, pour quelques espèces parapluies, la liste des habitats primaires, secondaires et de substitution et les fitness associées à la qualité intrinsèque de ces différentes catégories fournirait peut-être des solutions temporaires de reconstitution dans des écosystèmes dégradés ou alarmerait le biologiste de la conservation sur les risques de dette d'extinction.

Une meilleure connaissance des traits d'histoire de vie des espèces de dendro-microhabitats et de la distribution spatio-temporelle naturelle des dendro-microhabitats est néanmoins un préalable à ces études théoriques si l'on veut mettre en place des dispositifs d'étude pertinents et réalistes. D'autre part, une difficulté réside dans le contrôle de l'arbre support du dendro-microhabitat car son essence, sa grosseur, les conditions environnementales à une échelle très locale (éclairement, confinement) semblent influer à la fois sur la composition des assemblages et sur le comportement des espèces présentes.

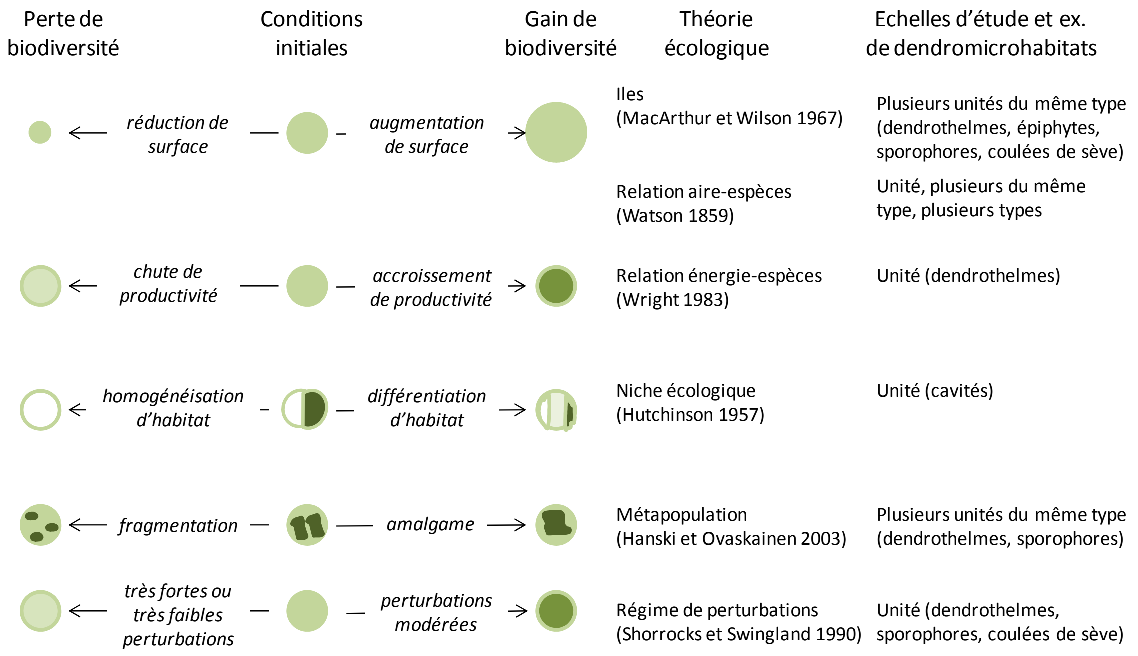

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Figure 20. Place potentielle des dendro-microhabitats dans l'examen de quelques théories écologiques (d'après Jackson & Sax 2010, modifié)

CONCLUSION : CHANGER LE REGARD DU FORESTIER POUR GERER DURABLEMENT DES ECOSYSTEMES

Ce travail de recherche appliquée avait pour ambition de fournir des éléments de réponse pratiques aux gestionnaires d'espaces forestiers soucieux d'intégrer la conservation d'une diversité d'espèces dans leur gestion courante. Nous croyons avoir répondu au moins partiellement à cet objectif : les dendro-microhabitats sont maintenant définis et classés dans une typologie, leurs liens avec les espèces ont été précisés et l'on connait mieux les effets à court et à moyen termes de l'exploitation forestière sur leur occurrence et leur diversité. Nous pensons que ce travail a également servi l'écologie forestière en mesurant le rôle écologique relatif des dendro-microhabitats et en cernant mieux leur intérêt en général. Ainsi, les dendro-microhabitats sont non seulement des outils pertinents en biologie de la conservation, mais ils ouvrent des perspectives de recherches en écologie plus fondamentale.

Les dendro-microhabitats ne sont que récemment perçus comme des objets écologiques clés pour la bio-complexité d'un habitat forestier et comme des outils utiles à une approche intégrée de la gestion forestière. Mais ils sont depuis longtemps observés par les forestiers, comme des objets sylvicoles, ce qui devrait faciliter leur requalification. Une sylviculture intégrant la conservation de la diversité des espèces devrait s'adapter à ce nouvel enjeu par un changement d'échelle spatiale de l'unité de gestion, en passant du peuplement forestier à la phase sylvigénétique et, simultanément, du peuplement à l'arbre et ses dendro-microhabitats, et par un changement d'échelle de temps, en consacrant une partie des peuplements gérés au déroulement complet des cycles sylvigénétiques, beaucoup plus longs que les cycles de production de bois. Au final, l'ambition sous tendue par nos travaux n'est donc pas d'apprendre au forestier à regarder un peuplement car c'est l'une de ses spécialités intrinsèques, mais seulement de changer son regard pour qu'il perçoive d'une façon plus globale l'écosystème qu'il gère.

BIBLIOGRAPHIE

BIBLIOGRAPHIE

Andren H., 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat - A Review. Oikos 71, 355-366.

ACEMAV coll., Duguet R., Melki F., (ed.), 2003. Les Amphibiens de France, Belgique et Luxembourg. Collection Parthénope, éditions Biotope. Mèze (France).

Andren,H., 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat - A Review. Oikos 71, 355-366.

Andren, H., 1997. Habitat fragmentation and changes in biodiversity. Ecol. Bull. 46, 171-181.

Angelstam P., Roberge J.M., Axelsson R., Elbakidze M., Bergman K.O., Dahlberg A., Degerman E., Eggers S., Esseen P.A., Hjalten J., Johansson T., Müller J., Paltto H., Snall T., Soloviy I., Tornblom J. 2013. Evidence-based knowledge versus negotiated indicators for assessment of ecological sustainability: the Swedish Forest Stewardship Council Standard as a case study. Ambio 42, 229–240.

Anonyme, 1977. *Vade-mecum du forestier*. IXème édition. Société forestière de Franche-Comté et des provinces de l'Est.

Anonyme, 1993. Présentation de Pro-sylva. Actes du 1er congrès européen Pro Sylva, Besançon, 21-24 juin.

Arthur L., Lemaire M., 2009. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope, Mèze (collection Parthénope). MNHN, Paris.

Barbalat S., 1995. Efficacité comparée de quelques méthodes de piégeage sur ceratins coléoptères et influence de l'anthophilie sur le résultat des captures. Bull. Soc. Neuchâteloise des Sciences Naturelles 118, 39-52.

Barbault A., 2000. Recherche fondamentale et pratiques de la conservation : un dialogue indispensable. In Barre V., Bigan M., Giral J. (coord.). Devenir des populations animales et végétales introduites ou réintroduites : déclin ou prolifération ? Revue d'Ecologie (la terre et la vie) supplément 7, 11-17.

Bardat J., Bioret F., Botineau M., Boullet V., Delpech R., Géhu J.M., Haury J., Lacoste A., Rameau J.C., Royer J.M., Roux G., and Touffet J., 2004. Prodrome des végétations de France. MNHN, Paris, France.

Barton P.S., Cunningham S.A., Macdonald B.C. *et al.* 2013. Species Traits Predict Assemblage Dynamics at Ephemeral Resource Patches Created by Carrion. PloS one 8.

Bassler C., Muller J., 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemela & Ryvarden. Fungal Biology 114, 129-133.

Bastien Y., Gauberville C. (coord.), 2011. Vocabulaire forestier. Écologie, gestion et conservation des espaces boisés. IDF/CNPF, AgroParisTech, ONF.

Baudry J., 1992. Introduction générale. *In* Auger P., Baudry J., Fournier F. : Hiérarchies en échelles en écologie. SCOPE, Naturalia Publications.

Bäuerle H., Nothdurft A., 2011. Spatial modeling of habitat trees based on line transect sampling and point pattern reconstruction. Revue canadienne de recherche forestière, 41(4), 715-727.

Bazzaz F.A., 1975. Plant Species Diversity in Old-Field Successionnal Ecosystems in Southern Illinois. Ecology (vol 56) n°2, 485-488.

Blandin P., 1986. L'étude de la structure spatio-temporelle des communautés d'araignées : une contribution à l'écologie évolutive. Actas X Congr. Int. Araenol., Jaca/España, 1: 143-167.

Begon M.E., Harper JL., Townsend CR., 1996. Ecology; individuals, populations and communities. Blackwell, Oxford.

Bensettiti F. (coord.), 2001. Cahiers d'habitats Natura 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire ; Tome 1 Habitats forestiers. La documentation Française.

Blondel J., 1995. Biogéographie. Approche écologique et évolutive. Collection d'Ecologie 27. Masson, Paris.

Bobiec A., Gutowski J.M., Audenslayer W.F., Awlaczyk P., and Ub K., 2005. The afterlife of the tree. WWF Poland, Warszawa.

Bollmann K., Braunisch V., 2013. To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. *In* Kraus D., Krumm F., (eds). Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp 18-31.

Bouget C., 2013. Déterminants des communautés saproxyliques en forêt tempérée : applications au suivi et à la conservation de la biodiversité. Mémoire d'HDR.

Bouget C., Brustel H., Nageleisen L.M., 2005. Nomenclature of wood-inhabiting groups in forest entomology: synthesis and semantic adjustments. Comptes Rendus Biologies 328, 936-948.

Bradshaw W. E., Holzapfel C.M., 1988. Drought and the organization of tree-hole mosquito communities. Oecologia 74, 507–514.

Bradshaw W. E., Holzapfel C.M., 1992. Resource limitation, habitat segregation, and species interaction of British tree-hole mosquitoes in nature. Oecologia 90, 227–237.

Brin A., Brustel, H., Jactel H., 2009. Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in Maritime pine plantations. Annals of Forest Science 66 (3): 306.

Brown J.H., Kodric-Brown A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449

Bruciamacchie M., 2005. Le marteloscope, un outil pour apprendre la gestion durable. Exemple d'évaluation de différents scénarios au marteloscope de Zittersheim (Vosges du Nord). *In* Vallauri *et al*. (coord.), Bois mort et à cavités ; une clé pour les forêts vivantes, Ed. Tec & Doc, Lavoisier.

Burel F., Baudry J., 1999. Ecologie du paysage. Concepts, méthodes et applications. Ed. Tec et Doc, Lavoisier, Paris.

Burgman M.A., Yemshanov D., 2013. Risks, decisions and biological conservation. Diversity and Distributions 19, 485-489.

Burnel L., Larrieu L., Cabanettes A., Willm J., 2011. Peut-on estimer rapidement depuis le sol le volume de bois mort des houppiers de chênes adultes avec une précision acceptable ? Cah. Tech. Inra n° 74.

Buse J., Ranius T., Assmann T., 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conservation Biology 22, 329-337.

Bussler H., Mueller J., 2009. Vacuum cleaning for conservationists: a new method for inventory of Osmoderma eremita (Scop., 1763) (Coleoptera: Scarabaeidae) and other inhabitants of hollow trees in Natura 2000 areas. Journal of Insect Conservation 13, 355-359.

Butler R., Angelstam P., Ekelund P., Schlaeffer R., 2004. Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biological Conservation 119, 305-318.

Bütler R., Lachat T., Larrieu L., Paillet Y., 2013. Habitat trees: key elements for forest biodiversity. *In* Kraus D., Krumm F., (eds). Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp 84-92.

Byers J.E., Cuddington K., Jones C.G., et al., 2006. Using ecosystem engineers to restore ecological systems. Trends in Ecology and Evolution 21, 493–500.

Cadenasso M.L., Pickett S.T.A., Grove J.M., 2006. Dimensions of ecosystem complexity: Heterogeneity, connectivity, and history. Ecological Complexity 3, 1-12.

Calow P., 1999. Blacwell's concise encyclopedia of ecology. Blackwell Sciences.

Carpenter S.R., 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77, 677-680.

Castella G., Chapuisat M., Moret Y. and Christe P., 2008. The presence of conifer resin decreases the use of the immune system in wood ants. Ecological Entomology 33, 408-412.

Castella E., Speight M.C.D., 1999. Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. Ecological Modelling, 85 (1), 13-25.

Cateau E.; Larrieu L.; Vallauri D.; Savoie J.M.; Touroult J.; Brustel H., (sous presse). Ancienneté et maturité : deux qualités complémentaires d'un écosystème forestier. Comptes Rendus Biologies.

Chapuisat M., Oppliger A., Magliano P., Christe P., 2007. Wood ants use resin to protect themselves against pathogens. Proceedings of the Royal Society B-Biological Sciences 274, 2013-2017.

Cooke H.A., Hannon S.J., 2012. Nest-site selection by old boreal forest cavity excavators as a basis for structural retention guidelines in spatially-aggregated harvests. Forest Ecology and Management 269, 37-51.

Courbaud B., Lafond V., Lagarrigues G., Vieilledent G., Cordonnier T., Jabot F., De Coligny F. (submitted to ecological modelling). Critical steps to build and evaluate a mechanistic ecological model: a worked example with the Samsara.2 forest dynamics model.

Cramp et al., (éd.). Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Wertern Paleartic. Vol. IV : Terns to woodpeckers. Oxford Univ. Press.

Dajoz R., 2007. Les insectes et la forêt. Rôle et diversité des insectes dans le milieu forestier. 2ème éd., Ed Tec & Doc, Lavoisier.

Dayton P.K., 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *In*: Parker BC (Ed). Proceedings of the colloquium on conservation problems in Antarctica. Lawrence, KS, Allen Press.

Diaz S., Cabido M., 2001. Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in* Ecology and Evolution 16, 646-655.

Diggle P. J., 1983. Statistical analysis of spatial point patterns. Academic Press, London, UK.

Dennis R.L.H., Shreeve T.G., Van Dyck H., 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102, 417-426.

Duchiron M.S., 1994. Gestion des futaies irrégulières et mélangées. Ed. par l'auteur.

Duelli P., 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agriculture Ecosystems & Environment 62, 81-91.

Dunning J.B., Danielson B.J., Pulliam H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos, vol. 65, Fasc 1 (oct 1992), 169-175.

Dupouey J.L., Grel A., Larrieu L., Heinz W., Leroy N., Montpied P., Corriol G., Hamdi E., Deconchat M., Vallauri D., (soumis). Cartographie de l'occupation des sols des Pyrénées vers 1850 et identification des espèces végétales de forêt ancienne. Actes du Xe colloque international de botanique pyrénéo-cantabrique ; Bagnères de Luchon, 8-10 juillet 2013. *Bulletin de la Société d'Histoire Naturelle de Toulouse.*

Edwards D.P., Gilroy J.J., Woodcock P., Edwards F.A., Larsen T.H., Andrews D.J., Derhe M.A., Docherty T.D., Hsu W.W., Mitchell S.L., Ota T., Williams L.J., Laurance W.F., Hamer K.C., Wilcove D.S., 2014. Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. Global Change Biology 20, 183-191.

Egan J., Mortensen D.A., 2012. A comparison of land-sharing and land-sparing strategies for plant richness conservation in agricultural landscapes. Ecological Applications 22, 459-471.

Ellison A.M., Bank M.S., Clinton B.D., Colburn E.A., Elliott K., Ford C.R., Foster D.R., Kloeppel B.D., Knoepp J.D., Lovett G.M., Mohan J., Orwig D.A., Rodenhouse N.L., Sobczak W.V., Stinson K.A., Stone J.K., Swan C.M., Thompson J., Von Holle B., Webster J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479-486.

Elton C.S., 1927. Animal ecology. New-York, Macmillan Co.

Emberger C., Larrieu L., Gonin P., 2013. Dix facteurs clés pour la diversité des espèces en forêt. Comprendre l'Indice de Biodiversité Potentielle (IBP). Document technique. Institut pour le développement forestier (IDF), Paris.

EUFORGEN, 2012. Distribution map of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*). http://www.euforgen.org

Fahrig L., 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling 105, 273-292.

Fahrig L., 2001. How much habitat is enough? Biological Conservation 100, 65-74.

Fahrig L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34, 487-515.

Fahrig L., Baudry J., Brotons L., Burel F.G., Crist T.O., Fuller R.J., Sirami C., Siriwardena G.M., Martin J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14, 101-112.

Fahrig L., Merriam G., 1994. Conservation of Fragmented Populations. Conservation Biology 8, 50-59.

FAO (Food and Agriculture Organization of the United Nations), 2000. Global forest resources assessment. FAO Forestry Paper 140, Rome.

Feio M.J., Doledec S., 2012. Integration of invertebrate traits into predictive models for indirect assessment of stream functional integrity: A case study in Portugal. Ecological Indicators 15, 236-247.

Finn J.A., 2001. Ephemeral resource patches as model systems for diversity-function experiments. Oikos 92, 363-366.

Fischer J., Abson D.J., Butsic V., Chappell M., Ekroos J., Hanspach J., Kuemmerle T., Smith H.G., von Wehrden H., 2014. Land Sparing Versus Land Sharing: Moving Forward. Conservation Letters 7, 149-157.

Fischer J., Batary P., Bawa K.S., Brussaard L., Chappell M., Clough Y., Daily G.C., Dorrough J., Hartel T., Jackson L.E., Klein A.M., Kremen C., Kuemmerle T., Lindenmayer D.B., Mooney H.A., Perfecto I., Philpott S.M., Tscharntke T., Vandermeer J., Wanger T.C., von Wehrden H., 2011. Conservation: Limits of Land Sparing. Science 334, 593.

Géroudet P., 1984. Les passereaux d'Europe. II : des mésanges aux fauvettes. Delachaux & Niestlé.

Gessner M.O., Chauvet E., 2002. A case for using litter breakdown to assess functional stream integrity. Ecological Applications 12, 498-510.

Gibbons P, McElhinny C, Lindenmayer D.B., 2010. What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south- eastern Australia. For. Ecol. Manag. 260: 975–982.

Gilg O., 2005. Old-Growth Forests; Characteristics, conservation and monitoring. GIP ATEN, technical report n°74 bis.

Gonin P., Larrieu L., 2013. Méthodes de relevé de l'Indice de Biodiversité Potentielle (IBP). IDF-CNPF, INRA Dynafor, v3.3, mars 2013, 13p.

Gonin P., Larrieu L., Emberger C., Deconchat M., (accepté), 2014. L'Indice de Biodiversité Potentielle (IBP) : 5 ans de développement à l'échelle nationale. In Vallauri D. (ed.) : Naturalité, vers une autre culture des eaux & des forêts. ed. Tec & Doc., Lavoisier.

Gorman G., 2011. The black woodpecker – a monograph on *Dryocopus martius*. Lynx Editions.

Gouix N., 2011. Gestion forestière et Biodiversité, les enjeux de conservation d'une espèce parapluie : *Limoniscus violaceus* (Coleoptera). Thèse de doctorat de l'Université P. & M. Curie.

Green R.E., Cornell S.J., Scharlemann J.P.W., Balmford A., 2005. Farming and the fate of wild nature. Science 307, 550-555.

Grime J.P., 1998. Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects. Journal of Ecology, vol. 86, n°6, 902-910.

Grinnell J., 1917. The Niche-Relationships of the California Thrasher. The Auk, Volume: 34, 427-433.

Grove S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33, 1-23.

Gu W.D., Heikkila R., Hanski I., 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17, 699-710.

Gustafsson L., Baker S.C., Bauhus J., Beese W.J., Brodie A., Kouki J., Lindenmayer D.B., Lõhmus A., Pastur G.M., Messier C., Neyland M., Palik B., Sverdrup-Thygeson A., Volney W.J.A., Wayne A., Franklin J.F., 2012. Retention forestry to maintain multifunctional forest : a world perspective. BioScience 62, 633–645.

Hall L.S., Krausman P.R., Morrison M.L., 1997. The habitta concept and a pea for standard terminology. Wildlife Socity Bulletin 25, 173-182.

Hanski I., 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37, 271-280.

Hanski I., 2005. The shrinking world: Ecological consequences of habitat loss. Excellence in Ecology 14. IEI, Germany.

Hanski I., Mononen T., 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. Ecology Letters 14, 1025-1034.

Hanski I.K., Stevens P.C., Ihalempia P., Selonen V., 2000. Home-range size, movements, and nest-site use in the Siberian flyng squirrel, *Pteromys volans*. Journal of Mammalogy 81, 798-809.

Harmon M.E., Franklin J.F., Swansson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkamper G.W., Cromack K.J., Cummins K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133-302.

Harris L.D., 1984. The fragmented forest ; Island biogeography theory and the preservation of biotic diversity. The University of Chicago Press.

Heilmann-Clausen J., Boddy L., 2005. Inhibition and stimulation effects in communities of wood decay fungi: Exudates from colonized wood influence growth by other species. Microbial Ecology 49, 399-406.

Heilmann-Clausen J., Christensen M., 2003. Fungal diversity on decaying beech logs - implications for sustainable forestry. Biodiversity and Conservation 12, 953-973.

Herpigny, Gosselin F., (submitted). Analyzing plant cover class data quantitatively: customized cumulative beta distributions show promising results. Ecological Informatics.

Hodge S.J., Peterken G.F., 1998. Deadwood in British forests: priorities and a strategy. Forestry 71, 99-112.

Hubert B., 2008. A shift in natural resources management paradigm: from resources sufficiency to functional integrity? Multifunctional grasslands in a changing world, Volume II: XXI International Grassland Congress and VIII International Rangeland Congress, Hohhot, China, 29 June-5 July 2008, 980.

Hubert M. (coord.), 1980. Le balivage. IDF, Paris.

Huston M.A., 1994. Biological diversity. The coexistence of species on changing landscape. Cambridge University Press. NY, USA.

Hutchinson G. E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415-427.

Ives A.R., Carpenter S.R., 2007. Stability and diversity of ecosystems. Science 317, 58-62.

Jackson S.T., Sax D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology & Evolution 25, 153-160.

Jakoby O., Rademacher C., Grimm V., 2010. Modelling dead wood islands in European beech forests: how much and how reliably would they provide dead wood? European Journal of Forest Research 129, 659-668.

Jansson N., Ranius T., Larsson A., Milberg P., 2009. Boxes mimicking tree hollows can help conservation of saproxylic beetles. – Biodiversity & Conservation 18, 3891-3908.

Johnson E.A., Miyanishi K., 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11, 419-431.

Jones C.G., Gutierrez J.L., Byers J.E., Crooks J.A., Lambrinos J.G., Talley T.S., 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119, 1862-1869.

Jones C.G., Lawton J.H., Shachak M., 1994. Organisms As Ecosystem Engineers. Oikos 69, 373-386.

Jones C.G., Lawton J.H., Shachak M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946-1957.

Jonsson N., Mendez M., Ranius T., 2004. Nutrient richness of wood mould in tree hollows with the Scarabaeid beetle Osmoderma eremita. Animal Biodiversity and Conservation 27, 79-82.

Junninen K., Kouki J., 2005. Woodland key habitats in Finland and their importance for polypores. 3rd Nordic Saproxylic Network meeting "Saproxylic species in Fennoscandian forests: gathering ecological knowledge for applied use", Lammi Biological Station, 7th-9th December.

Junninen K., Kouki J., 2006. Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? Scandinavian Journal of Forest Research 21, 32-40.

Kehler D., Bondrup-Nielsen S., 1999. Effects of isolation on the occurrence of a fungivorous forest beetle, Bolitotherus cornutus , at different spatial scales in fragmented and continuous forests. Oikos 84: 35–43.

Kitching R.L., 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. Journal of Animal Ecology 40, 281-302.

Kitching R.L., 1983. Community structure in water-filled treeholes in Europe and Australia: some comparisons and speculations. See Ref. 52a: 205–22

Kitching R.L., 2001. Food webs in phytotelmata: "Bottom-up" and "top-down" explanations for community structure. Annual Review of Entomology 46, 729-760.

Kolasa J., Allen C.R., Sendzimir J., Stow C.A., 2012. Predictions and retrodictions of the hierarchical representation of habitat in heterogeneous environments. Ecological Modelling 245, 199-207.

Labrid M., 1986. La Martre. Encyclopédie des carnivores de France, vol 9. SFEPM.

Lafond V., Lagarrigues G., Cordonnier T., Courbaud B., 2014. Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. *Annals of Forest Science* 71, 2, 173-186.

Lapeva-Gjonova A., 2013. Ant-associated beetle fauna in Bulgaria: A review and new data. Psyche, ID 242037, 14 p.

Larrieu L., 2007. Biodiversité des forêts de montagne et outils pour leur gestion durable ; exemple du « Groupement Forestier de Hèches » (vallée de la Neste, Hautes-Pyrénées). Mémoire IDPE, Ensat.

Larrieu L., (accepté), 2014. Vers une typologie pratique et écologiquement pertinente des dendro-microhabitats**.** In Vallauri D. (ed.) : Naturalité, vers une autre culture des eaux & des forêts. Lavoisier, ed. Tec & Doc.

Larrieu L., Brustel H., Sarthou J.P., 2005. Quelques propositions pour la prise en compte des insectes, en particulier saproxyliques, dans la gestion quotidienne des forêts. Plaquette couleur 4 pages. CRPF MP.

Larrieu L., Corriol G., 2008. Biodiversité et gestion durable des forêts. Quelques propositions pour la prise en compte des champignons. Plaquette couleur 4 pages. CRPF MP.

Larrieu L., Cabanettes A., Bouget C., (accepté), 2014. Les dendro-microhabitats: facteurs clés pour leur présence, impact de la gestion courante et biodiversité associée. *In* Vallauri D. (ed.) : Naturalité, vers une autre culture des eaux & des forêts. ed. Tec & Doc, Lavoisier.

Larrieu L., Gonin P., 2008. L'indice de Biodiversité Potentielle (IBP) : une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers ; Rev. For. Fr. 06-2008, 727-748.

Larrieu L., Gonin P., Deconchat M., 2012. Preliminary results of implementation at wide scale of a taxonomic biodiversity indicator: the Potential biodiversity index (PBI). IUFRO 2012. Second International Conference on Biodiversity in Forest Ecosystems and Landscapes; 28-31 August 2012. University College Cork, Ireland.

Larrieu L., Gonin P., Deconchat M., 2013. Le domaine d'application de l'Indice de biodiversité potentielle (IBP). *Rev. For. Fr* 5-2012*64* (5), 701-710.

Larsson, T. B.2001. Biodiversity evaluation tools for European forests. Ecol. Bull. 50.

Lassauce A., Lieutier F., Bouget C., 2012. Woodfuel harvesting and biodiversity conservation in temperate forests. Effects of logging residue characteristics on saaproxylic beetle assemblages. Biological Conservation 147, 1, 204-212.

Le Louarn H., Quéré P.J., 2003. Les rongeurs de France - Faunistique et biologie, 2ème édition. INRA ed.

Liggins G.W., Bradley M.J., Kennelly S.J., 1997. Detection of bias in observer-based estimates of retained and discarded catches from a multi species trawl fishery. Fisheries Research 32, 133-147.

Lindenmayer D.B., Franklin J.F., 2002. Conserving forest biodiversity: A comprehensive multiscaled approach. Island Press.

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J.P., Hector A., Hooper D.U., Huston M.A., Raffaelli D., Schmid B., Tilman D., Wardle D.A., 2001. Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294, 804-808.

MacArthur, R.H., Wilson E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton.

Magurran A.E., 2004. Measuring biological diversity. Blackwell publishing. Oxford UK.

Martin K., Eadie J.M., 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115, 243-257.

Maser C., Tarrant R.F., Trappe J.M., Franklin J.F., (ed.), 1988. From the forest to the sea: a story of fallen trees. Gen. Tech. Rep. PNW-GTR-229. Portland, OR: USDA Fores Service, Pacific Northwest Research Station.

Maser C., Trappe J., 1984. Seen and unseen world of the fallen tree. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW 164, 56 .

Mason N.W.H., Mouillot D., Lee W.G., Wilson J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112-118.

Mason F., Nardi G., Whitmore D., 2005. Recherches sur la restauration des habitats du bois mort : l'exemple du Life « Bosco della Fontana »(Italie). *In* Vallauri D. (ed.) : Bois mort et à cavités : Une clé pour des forêts vivantes. ed. Tec & Doc, Lavoisier.

MCPFE, 2007. State of Europe's forests. In: The MCPFE report on sustainable forest management in Europe. Ministerial conference on the protection of forests in Europe. Warsaw, Poland

Meschede A., Heller K.G., 2003. Ecologie et protection des chauvessouris en milieu forestier. MHN de Genève. Le Rhinolophe 16, 1–248.

Michel A.K., Winter S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. Forest Ecology and Management 257, 1453-1464.

Michel A.K., Winter S., Linde A., 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Canadian Journal of Forest Research 41, 300-308.

Millenium Ecosystem Assessment, 2005. Ecosystems and human well-being: synthesis. Washington, DC, Island Press.

Möller G., 2009. Struktur und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera - Käfer [Habitats and Substrates of Saproxylic Invertebrates, mainly beetles]. Dissertation Freien Universität Berlin, 284 p.

Mouchet M., Guilhaumon F., Villeger S., Mason N.W., Tomasini J.A., Mouillot D., 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. Oikos 117, 794-800.

Mouchet M.A., Villeger S., Mason N.W., Mouillot D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24, 867-876.

Müller J., Brunet J., Brin A. Bouget C. Brustel H., Bussler H., Förster B., Isacsson G., Köhler F., Lachat T., Gossner M.M., 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conservation and Diversity 6 (2): 162-169.

Müller J., Bussler H., Gossner M., Rettelbach T., Duelli P., 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. Biodiversity and Conservation 17, 2979-3001.

Müller J., Bütler R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129, 981-992.

Nageleisen L.M., Bouget C., 2009. L'étude des insectes en forêt : méthodes et techniques, eléments essentiels pour une standardisation. Synthèse des réflexions menées par le groupe de travail « Inventaires Entomologique en Forêt » (Inv.Ent.For.). Les dossiers forestiers n° 19, Office national des Forêts.

Nikitsky N.B., Schigel D.S. 2004. Beetles in polypores of the Moscow region: checklist and ecological notes. Entomologica Fennica 15, 6-22.

Nilsson S.G., Hedin J., Niklasson M., 2001. Biodiversity and its assessment in boreal and nemoral forests. Scand. J. For. Res. (Suppl. 3), 10-26.

Ockinger E., 2008. Distribution of burnet moths (*Zygaena* spp.) in relation to larval and adults resources on two spatial scales. Insect conservation and Biodiversity 1, 48-54.

Okland B., Hagvar S., 1994. The insect fauna associated with carpophores of the fungus *Fomitopsis pinicola* (Fr.) Karts. In a southern Norwegian spruce forest. Fauna Norvegica Serie B, 41, 29-42.

ONF, 2009. Conservation de la biodiversité dans la gestion courante des forêts publiques. INS-09-T-71, Paris.

Orians G.H., Soulé M.E., 2001. Whither conservation biology research? Conservation Biology 15, 1187-1188.

Ovaskainen O., Hanski I., 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? Theoretical Population Biology 64, 481-495.

Padoa-Schioppa E., Baietto M., Massa R., Bottoni L., 2006. Bird communities as bioindicators: The focal species concept in agricultural landscapes. Ecological Indicators 6, 83-93.

Paillet Y., Coutadeur P., Vuidot A., Archaux F., Gosselin F., (accepted). Strong observer effect on tree microhabitats inventories: a case study in a French lowland forest. Ecological Indicators.

Paradise C., Blue J., Burkhart J., *et al.*, 2008. Local and regional factors influence the structure of treehole metacommunities. BMC Ecology 8.

Paradise C. J., 1999. Interactive effects of resources and a processing chain interaction in tree-hole habitats. Oikos 85, 529–535.

Pascal M., Clergeau P., Lorvelec O., 2000. Invasions biologiques et biologie de la conservation. Courrier de l'environement de l'INRA 40, 23-32.

PEFC France, 2011. Cahier des charges relatif à la gestion durable de la forêt. http://www.pefc-france.org.

Pénicaud P., 2000. Chauves-souris arboricoles en Bretagne: typologie de 60 arbres-gîtes et éléments de l'écologie des espèces observées. Le Rhinolophe 14, 37-68.

Perfecto I., Vandermeer J., 2012. Separation or integration of biodiversity conservation: the ideology behind the "land-sharing" versus "land-sparing" debate. Ecosistemas 21, 180-191.

Petchey O.L., Gaston K.J., 2002. Functional diversity (FD), species richness and community composition. Ecology Letters 5, 402-411.

Petchey O.L., Gaston K.J., 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9, 741-758.

Petchey O.L., Hector A., Gaston K.J., 2004. How do different measures of functional diversity perform? Ecology 85, 847-857.

Petchey O.L., Gaston K.J., 2007. Dendrograms and measuring functional diversity. Oikos 116, 1422-1426.

Peterson A.T., Soberón J., Pearson R.G., Anderson R.P., Meyer E.M., Nakamura M., Araújo M.B., 2011. Ecological Niches and Geographic Distributions (MPB-49) Princeton University Press**.**

Phalan B., Onial M., Balmford A., Green R.E., 2011. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science 333, 1289-1291.

Power M.E., Tilman D., Estes J.A., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J., Paine R.T., 1996. Challenges in the quest for keystones. Bioscience 46, 609-620.

Pupin C., Courbaud B., Larrieu L., Cabanettes A., (in prep.). Dynamics of tree-microhabitats: inferring tree level processes from stand level data.

Rameau J.C., Gauberville C., Drapier N., 2000. Gestion forestière et diversité biologique ; Identification et gestion intégrée des habitats et espèces d'intérêt communautaire. IDF.

Ranius T., 2000. Minimum viable metapopulation size of a beetle, Osmoderma eremita, living in tree hollows. Anim Conserv 3, 37-43.

Ranius T., 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodiversity and Conservation 11, 931-941.

Ranius T., Fahrig L., 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scandinavian Journal of Forest Research 21, 201-208.

Ranius T., Hedin J., 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126, 363-370.

Ricarte A., Jover T., Marcos-García M. A., Micó E., Brustel H., 2009. Saproxylic beetles (Coleoptera) and hoverflies (Diptera: Syrphidae) from a Mediterranean forest: towards a better understanding of their biology for species conservation. Journal of Natural History 43, 9, 583-607.

Ricklefs R.E., 1987. Community Diversity - Relative Roles of Local and Regional Processes. Science 235, 167-171.

Rohlfs M., Hoffmeister T.S., 2004. Spatial aggregation across ephemeral resource patches in insect communities: an adaptive response to natural enemies? Oecologia 140, 654-661.

Ronce O., 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst. 2007. 38: 231–53.

Rosenzweig M.L., 1995. Species diversity in space and time. Cambridge University Press.

Rossi M., Vallauri D., 2013. Évaluer la naturalité. Guide pratique version 1.2, WWF, Marseille.

Roume A., Deconchat M., Raison L., Balent G., Ouin A., 2011a. Edge effects on ground beetles at the woodlot-field interface are short-range and asymmetrical. Agricultural and Forest Entomology 13, 395-403.

Roume A., Ouin A., Raison L., Deconchat M., 2011b. Abundance and species richness of overwintering ground beetles (Coleoptera: Carabidae) are higher in the edge than in the centre of a woodlot. European Journal of Entomology 108, 615-622.

Salek L., Zahradnik D., et al., 2014. "Forest edges in managed riparian forests in the eastern part of the Czech Republic." Forest Ecology and Management 305, 1-10.

Schmidl J., Sulzer P., Kitching R.L., 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia 598, 285-303.

Schmidl J., Sulzer P., Kitching R.L., 2008. The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. Hydrobiologia 598, 285-303.

Schroeder L., Ranius T., Ekbom B., Larsson S., 2007. Spatial occurrence of a habitat-tracking saproxylic beetle inhabiting a managed forest landscape. Ecological Applications 17, 900-909.

Siitonen J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11-41.

Sippola A.L., Halonen P., 2005. Retention trees and key habitats in preserving liche diversity in managed boreal forests. 3rd Nordic Saproxylic Network meeting “Saproxylic species in Fennoscandian forests: gathering ecological knowledge for applied use”, Lammi Biological Station, 7th-9th December.

Sommaggio D., 1999. Syrphidae: can they be used as environmental bioindicators? Agriculture Ecosystems & Environment 74, 343-356.

Sota T., 1998. Microhabitat size distribution affects local difference in community structure: Metazoan communities in treeholes. Researches on Population Ecology 40, 249-255.

Sota T., Mogi M., Hayamizu E., 1994. Habitat Stability and the Larval Mosquito Community in Treeholes and Other Containers on A Temperate Island. Researches on Population Ecology 36, 93-104.

Speight M.C.D., 1986. Criteria for the selection of insects to be used as bioindicators in nature conservation research. In: Velthuis, H.H.W. (Ed.), Proc. 3rd European Congress of Entomolog. Amsterdam, pp. 485–488.

Speight M.C.D., 1989. *Saproxylic invertrebrates and their conservation.* Concil of Europe. Nature and Environment Series 42, 1-79.

Speight M.C.D., Castella E., Sarthou J.P., 2013. StN 2013. *In*: Speight M.C.D., Castella E., Sarthou J.-P., Vanappelghem C., (eds). Syrph the Net on CD, Issue 9. The database of European Syrphidae. ISSN 1649-1917. Syrph the Net Publications, Dublin.

Speight M.C.D., Castella E., Sarthou J.-P., Monteil C., 2013. Species accounts of European Syrphidae (Diptera). Syrph the Net, the database of European Syrphidae. Syrph the Net Publications.

Srivastava D.S., Kolasa J., Bengtsson J., Gonzalez A., Lawler S.P., Miller T.E., Munguia P., Romanuk T., Schneider D.C., Trzcinski M.K., 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology & Evolution 19, 379-384.

Srivastava D.S., Lawton J.H., 1998. Why more productive sites have more species: An experimental test of theory using tree-hole communities. American Naturalist 152, 510-529.

Starzomski B.M., Bondrup-Nielsen S., 2002. Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae). Ecoscience 9, 20-27.

Stokland J. N., Siitonen J., Jonsson B. G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Stokland J.N., Tomter S.M., So¨derberg U., 2004. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti M (ed) Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality, EFI workshop, November 12th–15th 2003, Firenze, Italy, vol 51.

Sunahara T., Mogi M., 1998. Distribution and turnover of a mosquito (*Tripteroides bambusa*) metapopulation among bamboo groves. Ecological Research 13, 291-299.

Tews J., Brose U., Grimm V., Tielbörger K., Wichmann M.C., Schwager M., Jeltsch F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Thomas D.W., West S.D., 1989. Sampling methods for bats. Gen. Tech. Rep. PNW-GTR-243. USDA Forest service, Pacific Northwest Research Station, Portland, 20 p.

Tillon L., 2004. Gîtes sylvestre à chiroptères en forêt domaniale de Rambouillet (78) : Caractérisation dans un objectif de gestion conservatoire. Mémoire EPHE.

Tilman D., 1982. Resource competition and community structure. Monogr. Pop. Biol. 17. Princeton Univ. Press, Princeton, NJ.

Tilman D., 2001. Functional diversity. In: Levin, S. A. (ed.), Encyclopedia of biodiversity. Academic Press, pp. 109-120.

Tilman D., May R.M., Lehman C.L., Nowak M.A., 1994. Habitat Destruction and the Extinction Debt. Nature 371, 65-66.

Thompson I., Mackey B., McNulty S., Mosseler A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series n° 43, 67 pages.

Toda M.J., Kimura M.T., Tuno N., 1999. Coexistence mechanisms of mycophagous drosophilids on multispecies fungal hosts: aggregation and resource partitioning. Journal of Animal Ecology 68, 794-803.

Torossian C., Gion J.S., 1983. Les fourmis du groupe “*Formica rufa* » et leurs relations avec les milieux forestiers d’altitude. Acta Biologica Montana 2-3, 383-404.

Trudeau C., Imbeau L., Drapeau P., Mazerolle M.J., 2011. Site Occupancy and Cavity Use by the Northern Flying Squirrel in the Boreal Forest. Journal of Wildlife Management 75, 1646-1656.

Turckheim de B., 2005 – Conserver de très vieux arbres et du bois mort ; avantages et contraintes pour le propriétaire privé ? *In* Vallauri *et al.* (coordonateurs) : Bois mort et à cavités, une clé pour des forêts vivantes. Ed. Tec et Doc, Lavoisier.

Vaillant F., 1978. Les *Systenus* et leur habitat dendrotelme (Dipt. Dolichopodidae). Buletin de la Société entomologique de France Tome 83, 73-85.

Van der Wijen B., Verkem S., Lust N., Verhagen R., 2002 – L'importance du type de cavité et de la structure forestière pour la sélection de gîtes par des chauves-souris arboricoles ; Symbioses, 2002, nouvelle série, n° 6, pp.11-16.

Van Halder I., Barbaro L., Corcket E., Jactel H., 2008. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodiversity and Conservation 17, 1149-1169.

Vasseur C., Joannon A., Burel F., Goffi C., Meynard JM., Baudry J., 2008. The mosaic of cropping systems : a hidden part of agricultural landscape heterogeneity. *In*: The 15 th Annual IALE conference/ Lanscape Ecology and Conservation (ed. Carey, P.). IALE UK, Cambridge, pp. 33-41.

Villeger S., Mason N.W., Mouillot D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290-2301.

Vodka S., Konvicka M., Cizek L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. Journal of Insect Conservation 13, 553-562.

Vuidot A., Paillet Y., Archaux F., Gosselin F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144, 441-450.

Walker L.R., Wardle D.A., Bardgett R.D., Clarkson B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98, 725-736.

Weber R.W.S., 2006. On the ecology of fungal consortia of spring sap-flows. Mycologist 20, 140-143.

Weddell BJ., 2002. Conserving living natural resources. Cambridge University Press.

Wegge P., Rolstad J., 1986. The spacing of capercaillie leaks in relation to habitat and social organization. Behav. Ecol. Sociobiol. 19, 401-408.

Wertheim B., Sevenster J.G., Eijs I.E.M., Van Alphen J.J.M., 2000. Species diversity in a mycophagous insect community: the case of spatial aggregation vs. resource partitioning. Journal of Animal Ecology 69, 335-351.

Wiktander U., Olsson O., Nilsson S., 2001. Seasonal variation in home range size, and habitat area requirement of the lesser spotted wood pecker *Dendrocopos minor*. Biol. Conserv. 100, 387-395.

Whittaker R.H., Levin S.A., Root R.B., 1973. Niche, habitat and ecotope. American Naturalist 107, 321-328.

Wilhere G.F., 2002. Adaptive management in habitat conservation plans. Conservation Biology 16, 20-29.

Winter S., Möller G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251-1261.

Woodwell G.M., 2002a. On purpose in science, conservation and government - The functional integrity of the earth is at issue not biodiversity. Ambio 31, 432-436.

Woodwell G.M., 2002b. The functional integrity of normally forested landscapes: A proposal for an index of environmental capital. Proceedings of the National Academy of Sciences of the United States of America 99, 13600-13605.

Wright J.P., Gurney W.S.C., Jones C.G., 2004. Patch dynamics in a landscape modified by ecosystem engineers. Oikos 105, 336-348.

Wright J.P., Jones C.G., 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. BioScience. 56, 203-209

Yachi S., Loreau M., 1999. Proc. Natl. Acad. Sci. U.S.A. 96, 1463-1468.

Yoshimoto J., Kakutani T., Nishida T., 2005. Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecological Research 20, 405-414.

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