



Colonisation, par les coléoptères phloéophages et xylophages, de sapins baumiers défoliés par l'arpenteuse de la pruche

Mémoire

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Résumé

L'objectif de cette étude était de caractériser l'impact d'une épidémie d'arpenteuse de la pruche dans la sapinière à bouleau blanc, sur la communauté de coléoptères saproxyliques primaires. Pour ce faire, nous avons dans un premier temps comparé différentes approches afin de déterminer laquelle d'entre-elles pouvait facilement et efficacement estimer l'état de défoliation des arbres affectés par l'arpenteuse de la pruche. Par la suite, la réponse hâtive des coléoptères phloéo- et xylophages a été évaluée à l'aide de pièges à impacts multidirectionnels, de pièges à impact fixés aux troncs et de cages d'émergence. Les résultats montrent qu'une méthode d'estimation globale de la cime supérieure est optimale pour déterminer l'état de défoliation du sapin baumier suite au passage de l'arpenteuse de la pruche. Ils montrent aussi qu'un changement dans l'assemblage des coléoptères est survenu seulement en 2014 et dans les peuplements les plus défoliés. Un assemblage caractérisé par des espèces polyphages souvent associées aux forêts non-perturbées s'est remanié en une prédominance d'un xylomycétophage consommateur de conifère mourant: le scolyte birayé. Seul ce scolyte a été positivement associé avec la hausse de défoliation et de mortalité du sapin baumier mais aussi de la présence de coupes de récupération à proximité des parcelles étudiées. Les résultats ont également montré une réponse dichotomique du scolyte montrant une colonisation massive seulement au moment où les sapins atteignaient 95% de défoliation. Enfin, les pièges à impact se sont avérés utiles pour détecter les variations de fréquence de visite de peuplements et d'arbres le long du gradient de défoliation. Le scolyte birayé est donc le premier et presque le seul saproxylique à engager le processus de décomposition des arbres post-arpenteuse de la pruche deux années après la détection de l'épidémie. Par ailleurs, cette colonisation risque d'entraîner des désagréments car son symbionte fongique noircit les galeries creusées partout dans l'aubier des arbres infestés.

Abstract

The aim of this study was to characterise the impact of a hemlock looper outbreak, in the balsam fir-white birch forest, on the community of primary saproxylic beetles. To this end, we first compared different approaches in order to determine which of them could profile easily and efficiently the defoliation status of the trees affected by the hemlock looper. Then, the early response of the phloeo- and xylophagous beetles was assessed with flight-interception multidirectional and trunk-window traps along with emergence cages. Results show that an upper crown overall estimation method is optimal to determine the defoliation status of the balsam fir following hemlock looper. They as well show that a change in the beetle assemblage occurred only in 2014 and in the most defoliated stands. An assemblage characterised by polyphagous species often associated to undisturbed forests shifted to the predominance of a xylomycetophagous and dying conifer feeder: the striped ambrosia beetle. This scolytid alone was positively associated with the increase of defoliation and death of balsam firs but also with the presence of salvage logging nearby the study plots. Results have then showed a dichotomic response of the beetle, thus exhibiting massive colonization only when fir trees reached 95% of defoliation. At last, the flight-interception traps were found to be useful to detect variations in beetle visit frequencies of stands and trees along the defoliation gradient. The striped ambrosia beetle is therefore the first and almost the only saproxylic to initiate the decomposition process of post-hemlock looper fir trees two years after the detection of the outbreak. However, this colonization may raise concerns because its fungal symbiont stains the galleries throughout the sapwood of infested trees.

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code. The species codes are the following: *Crruf* (*Cryphalus r. ruficollis*), *Cusp* (Curculionidae sp.), *Draut* (*Dryocoetes autographus*), *Drcar* (*Dryocoetes caryi*), *Deruf* (*Dendroctonus rufipennis*), *Evmon* (*Evodinus monticola*), *Pispa* (*Pityokteines sparsus*), *Pidub* (*Pissodes dubius (striatulus)*), *Pisim* (*Pissodes similis*), *Poruf* (*Polygraphus rufipennis*), *Rhmac* (*Rhyncolus macrops*), *Scann* (*Scierus annectans*), *Trbet* (*Trypodendron betulae*), *Trlin* (*Trypodendron lineatum*). The dotted vectors represent the continuous explanatory variables: DDWV (down dead wood volume), Dead *A. balsamea* (dead balsam fir basal area), Defoliation (upper crown defoliation percentage), Hardwood (hardwood basal area), Logging (logged area in a 500 m buffer zone of the plot) and Softwood (softwood basal area).76

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Avant-Propos

Ce mémoire de maîtrise est constitué de trois chapitres, « Comparison of several methods for estimating defoliation from the hemlock looper (*Lambdina fuscellaria* (Guenée)) (Lepidoptera: Geometridae) on balsam fir », « Early succession of bark and wood boring beetles during an outbreak of the hemlock in boreal balsam fir forest » et « Numerical response of the striped ambrosia beetle (Coleoptera: Curculionidae) to hemlock looper (Lepidoptera: Geometridae) defoliation in boreal balsam fir forest ». Ces trois chapitres rédigés en anglais et sous la forme d'articles scientifiques sont destinés à être publiés dans des journaux scientifiques au cours de l'année 2017. Ces chapitres sont précédés d'une introduction et suivis d'une conclusion rédigées en français. Le candidat à la maîtrise a effectué l'installation du dispositif d'échantillonnage, l'estimation de la défoliation des arbres du dispositif, l'échantillonnage des insectes saproxyliques, la description des attributs de l'habitat dans les sites d'étude, le tri, l'identification et le montage de la collection d'insectes étudiés et a fait les différentes analyses statistiques. Les trois chapitres ont été écrits entièrement par le candidat à la maîtrise, encadré et soutenu par les commentaires et conseils des coauteurs Christian Hébert, Conrad Cloutier, Richard Berthiaume et Éric Bauce. L'étudiant a donc le statut d'auteur principal pour les trois articles paraissant dans ce mémoire et les coauteurs, énumérés à la phrase précédente, ont été également impliqués dans la conception des trois projets et articles. Cette étude a été financée par le consortium de recherche sur les insectes forestiers (iFor) sous des contributions du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), le Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP), le Conseil de l'industrie forestière du Québec (CIFQ), le Service Canadien des Forêts (SCF-RNCan) et de la Société de Protection des Forêts contre les Insectes et Maladies (SOPFIM).

Introduction générale

La zone bioclimatique boréale s'étend dans tout l'hémisphère nord de la planète. Au Canada, la forêt boréale (270 millions d'hectares) constitue 28% de la zone boréale mondiale et elle joue un rôle écologique important pour le stockage du carbone, la purification de l'air et la régularisation du climat (RNCan 2017). De plus, l'exploitation des forêts boréales génère environ 60% de l'activité économique de l'industrie forestière canadienne (Burton *et al.* 2003). Le bois d'œuvre, les produits forestiers non ligneux et le potentiel hydroélectrique des rivières constituent des sources de matières premières renouvelables (RNCan 2015). L'aménagement forestier est une perturbation humaine omniprésente dont les effets ont été documentés dans la forêt boréale Canadienne. Des superficies appréciables de la forêt boréale sont coupées chaque année mais elles ne représentent que 0,2% du territoire forestier du Canada (RNCan 2017). Les pratiques d'aménagement changent continuellement en réponse aux changements de politiques, aux conditions du marché, aux avancées technologiques en équipement pour la récolte, aux changements de régimes forestiers et à l'acquisition de nouvelles connaissances (Venier 2014). L'aménagement écosystémique et l'aménagement durable des forêts sont deux concepts récents qui se sont développés en réponse aux débats concernant la gestion environnementale des forêts (Grenon *et al.* 2010). L'aménagement écosystémique est une approche qui oriente les pratiques forestières pour que les critères environnementaux, économiques et sociaux de l'aménagement durable soient respectés (Grenon *et al.* 2010). Sa mise en œuvre vise à assurer le maintien de la biodiversité et la viabilité des écosystèmes en réduisant les écarts entre la forêt aménagée et la forêt jugée naturelle, dans le respect des valeurs sociales liées au milieu forestier et donc en répondant aux besoins socio-économiques de la population (Grenon *et al.* 2010).

Maintenir les processus écologiques en s'inspirant des perturbations naturelles fait partie des nouvelles approches d'aménagement dans l'écosystème boréal ayant comme objectif de conserver la biodiversité (Fischer *et al.* 2006, Mori 2011). Cette dernière est indéniablement affectée par les perturbations, naturelles ou anthropiques, et ce à de multiples échelles temporelles et spatiales (Pickett et White 1985, Levin 2000, Loreau 2010, Turner 2010). Les feux de forêt sont considérés comme la perturbation la plus importante pour renouveler la forêt boréale dans les zones biogéoclimatiques centrales et de l'ouest (Rowe et Scotter 1973, Bergeron *et al.* 2006). Dans les régions plus humides de

l'Est du Canada, où le cycle de feux est plus long, les insectes ravageurs sont les agents prédominants du régime de perturbations naturelles (Venier 2014). Au Québec, la dynamique de la pessière est principalement régie par le feu (Payette 1992, Bergeron *et al.* 2001, Bond-Lamberty *et al.* 2007), alors que celle de la sapinière l'est surtout par les épidémies de tordeuse des bourgeons de l'épinette (TBE; *Choristoneura fumiferana* Clemens) (Lepidoptera: Tortricidae) (Blais 1983). Connaître l'impact de ces perturbations naturelles sur la biodiversité des écosystèmes forestiers est primordial dans le contexte où on veut s'en inspirer à des fins d'aménagement. Indépendamment de la perturbation, elle provoque généralement une quantité considérable d'arbres stressés et morts qui deviennent une ressource privilégiée pour la faune saproxylique (Speight 1989). Les différentes perturbations forestières affectent alors négativement ou positivement les multiples espèces végétales et animales présentes dans l'écosystème.

Successions végétales et animales après perturbations naturelles

D'un point de vue socio-économique, les feux en forêt boréale sont perçus comme des désastres naturels (Drapeau *et al.* 2010). Pourtant, au plan écologique, ils engendrent des habitats prospères pour certaines communautés végétales et animales (Drapeau *et al.* 2010, Nappi *et al.* 2011). Le nouvel écosystème produit suite au passage du feu possède plusieurs attributs uniques qui sont favorables à des espèces opportunistes (Wikars 1997, Boulanger et Sirois 2007) mais également à plusieurs espèces «associées aux feux» (Boucher *et al.* 2012). Les essences ligneuses retrouvées dans les régions à haute fréquence de feux ont évolué et se sont adaptées pour devenir plus résistantes et/ou résilientes à cette perturbation (Pausas et Keeley 2009). Des traits acquis tels qu'une écorce épaisse, une discontinuité verticale protégeant les cônes ou la présence de cônes sérotineux peuvent avantager certaines espèces dans le processus de succession végétale après le passage du feu (Deslaurier *et al.* 1996, Mauri Ortuno *et al.* 2009). Par ailleurs, aux suites de sévères épidémies de TBE, l'ouverture des peuplements défoliés peut entraîner un renouvellement complet du peuplement grâce à une régénération préétablie (Bouchard *et al.* 2005). Par exemple, l'abondance du sapin baumier (*Abies balsamea* (L.) Mill.) dans le sous-bois sous forme de graines, de semis et de régénération avancée lui permet un retour rapide suite à ce type de perturbation. D'autres espèces de lumière, dites pionnières, comme le bouleau blanc (*Betula papyrifera* Marshall), ont besoin d'une ouverture de la voûte forestière pour se régénérer efficacement. Des épidémies

sévères et répétées de TBE leur procurent des conditions optimales en peuplements mixtes et dominés par les conifères (Bouchard *et al.* 2007). Les espèces végétales montrent des patrons de succession adaptés aux différentes perturbations forestières et on peut anticiper qu'il en soit de même pour les insectes, dont les espèces saproxyliques sont les premières à profiter de l'une des principales caractéristiques de ces perturbations naturelles, soit la production de bois mort en abondance.

Les organismes saproxyliques sont définis comme ceux qui utilisent, pendant au moins une partie de leur cycle vital, du bois moribond ou mort, ou d'autres organismes saproxyliques présents dans le bois comme les champignons et les bactéries (Speight 1989). Les coléoptères jouent un rôle considérable dans la colonisation du bois, contribuant à la décomposition et au recyclage des nutriments (Speight 1989, Kim 1993, Boulanger et Sirois 2007), en plus de faire partie de l'alimentation de base de plusieurs vertébrés (Morissette *et al.* 2002, Kennedy et Fontaine 2009, Nappi *et al.* 2010). Ainsi, dans le processus d'utilisation du bois mort issu d'une perturbation forestière, la première phase est celle de la colonisation primaire des tissus sous-corticaux et ligneux. Cette colonisation est généralement effectuée par les coléoptères. De plus, la communauté qui amorce la décomposition est directement associée au type de bois mort car le niveau de spécialisation de ces colonisateurs primaires est souvent très prononcé (Vindstad *et al.* 2014). Par conséquent, un coléoptère saproxylique peut normalement exploiter du bois mort à un stade spécifique de décomposition (Vindstad *et al.* 2014), et la spécialisation peut aller jusqu' au niveau de l'espèce ou même au diamètre de l'hôte (Lachat *et al.* 2013). De plus, les caractéristiques du bois mort varient selon le type et l'intensité de la perturbation (Pedlar *et al.* 2002). Alors que les feux de surface n'affectent que le sous-bois forestier, les feux de couronnes tuent la majorité des arbres et peuvent brûler l'humus jusqu'au sol minéral (Gauthier *et al.* 2001). En plus de brûler les arbres, les feux exposent davantage les tiges au soleil (Jonsell *et al.* 1998), résultant en des tissus sous-corticaux plus secs (Boulanger et Sirois 2006). D'un autre côté, en contexte d'épidémie sévère de TBE, la mortalité des arbres commence après quatre à cinq années de défoliation grave, mais cette mortalité s'échelonne sur plusieurs années (Taylor et MacLean 2009). Au Canada, plusieurs études ont porté sur l'impact des différentes perturbations naturelles sur les communautés végétales, ce qui n'est pas le cas pour les coléoptères saproxyliques. Seul l'impact des feux de forêt sur les coléoptères saproxyliques, en pessière noire à sphaignes (Saint-Germain *et al.* 2004a et b, Boulanger et Sirois 2007, Boulanger *et al.*

2010, Boucher *et al.* 2012), a retenu l'attention, mais très peu d'études ont porté sur l'impact des épidémies d'insectes comme la TBE sur ces mêmes coléoptères (Belyea 1952a et b). En 2012, une épidémie d'arpenteuse de la pruche (*Lambdina fuscellaria* (Guenée)) (Lepidoptera: Geometridae), le 2^e défoliateur en importance dans l'Est de l'Amérique du Nord (Hébert et Brodeur 2013) a été observée pour la première fois dans la Région de la Capitale-Nationale du Québec. Cette nouvelle perturbation naturelle majeure offre une occasion unique d'étudier son impact sur la communauté des coléoptères saproxyliques.

Une première épidémie d'arpenteuse de la pruche dans la Région de la Capitale-Nationale

Native de l'Amérique du Nord, l'arpenteuse de la pruche cause des pertes de croissance mais surtout une importante mortalité des arbres attaqués sévèrement dans les peuplements de sapins baumiers du domaine bioclimatique de la sapinière à bouleau blanc (Otvos *et al.* 1971). À Terre-Neuve, de nombreuses infestations d'arpenteuse de la pruche ont été observées au cours du 20^e siècle (Carroll 1956, Iqbal *et al.* 2011). Au Québec, plusieurs épidémies ont sévi à l'Île d'Anticosti (Jobin et Desaulniers 1981) pendant la même période, mais plus récemment, l'arpenteuse a défolié 924 971 ha de forêt sur la Côte-Nord en 2000 (Bordeleau 2000). Des dommages ont encore été recensés en 2015 sur Anticosti (MFFP 2015). En 2012, une première année de dommages causés par l'arpenteuse de la pruche a été signalée dans la région de la Capitale-Nationale, notamment à la forêt Montmorency, dans le Parc national de la Jacques-Cartier ainsi que dans la réserve faunique des Laurentides (3379 ha; MRNF 2012). L'étendue des premiers dommages causés par cette perturbation a alors été évaluée par survol aérien de la région dans le secteur de la Capitale-Nationale à l'aide d'un logiciel de «Relevé Aérien à Référence Spatiale» ou RARS (MRNF 2012).

L'arpenteuse de la pruche est une espèce univoltine qui passe l'hiver sous forme d'œuf (Carroll 1956). L'éclosion se produit entre la fin de mai et le début de juin, après le débourrement des bourgeons du sapin baumier (Hébert et Jobin 2001, Hébert *et al.* 2001; 2004). Les larves des deux premiers stades consomment les aiguilles des pousses annuelles des conifères puis, au milieu de leur développement, les larves se déplacent sur le vieux feuillage (Hébert et Jobin 2001, Iqbal et Maclean 2010). Elles se développent

en passant par quatre ou cinq stades larvaires durant l'été (Berthiaume *et al.* 2007). Indépendamment de l'âge larvaire, l'arpenreuse consomme partiellement les aiguilles des conifères (Carroll 1956). Ce comportement alimentaire particulier est très dommageable car toutes les aiguilles ayant été partiellement consommées sèchent et finissent par tomber à l'automne (Hébert et Jobin 2001). Cela peut entraîner une mortalité rapide des arbres défoliés, et ce, dès la première année où les dommages sont observés (Hudak *et al.* 1978, Jobin et Desaulniers 1981). Son hôte de prédilection est le sapin baumier mais elle peut aussi entraîner la mort d'autres Pinaceae comme la pruche du Canada (*Tsuga canadensis* (L.) Carrière) (Trial 1993) et les épinettes blanche et noire (MacLean and Ebert 1999). Vers la fin de juillet, les larves âgées montrent une phototaxie négative (Carroll 1956) et cherchent un endroit (lichen, mousse ou crevasse dans l'écorce) pour s'accrocher et former leur chrysalide. Après environ 20 jours de développement, les adultes émergent des chrysalides, s'accouplent et pondent leurs œufs (Carroll 1956, Dobesberger 1989). Les infestations débutent habituellement sur de petites surfaces, isolées et bien définies, puis elles forment des îlots rapprochés ou une grande infestation irrégulière. Les épidémies d'arpenreuse demeurent essentiellement localisées (Carroll 1956) comparativement à celles de la TBE. Conséquemment, une fois que tous les arbres d'un peuplement sont morts, les larves n'ont presque plus de ressources alimentaires car les capacités de déplacement de l'espèce se limitent au « ballooning » des premiers stades larvaires et au vol des papillons femelles, qui s'exprime seulement après avoir déposé au moins 50% de ses oeufs (Delisle *et al.* 1998). Les épidémies apparaissent et disparaissent donc soudainement, en persistant rarement plus que trois ans dans un même peuplement (Maclean et Ebert 1999, Hébert *et al.* 2001, Bordeleau 2002).

Les mortalités causées par l'arpenreuse de la pruche se situent temporellement entre celles causées par les feux de forêt, qui tuent instantanément la majorité des arbres affectés, et la TBE, qui nécessite plusieurs années de défoliation pour entraîner la mortalité des arbres. La défoliation grave de sapins baumiers par l'arpenreuse de la pruche cause un stress violent qui peut parfois entraîner la mort des arbres en aussi peu que trois mois. En conséquence, cette ouverture de la voûte forestière augmente l'entrée de lumière, entraîne une hausse de la température et facilite l'entrée du vent rendant les tiges mortes susceptibles aux chablis (Ostaff et MacLean 1989). De plus, la décomposition et le recyclage des nutriments contenus dans la biomasse végétale morte devraient alors être déclenchés par les coléoptères phloéophages et xylophages. Ces espèces

consomment respectivement les tissus sous-corticaux et les tissus de l'aubier et du duramen d'arbres stressés ou récemment morts (Langor *et al.* 2008). Plusieurs espèces de coléoptères appartenant à la famille des Buprestidae, Cerambycidae et Curculionidae sont parmi les premiers colonisateurs des arbres (Langor *et al.* 2008) et sont donc les portes d'entrée pour d'autres espèces saproxyliques de succession et de décomposition plus avancées. Le rôle écologique de ces colonisateurs primaires est donc important pour l'ensemble des organismes saproxyliques mais également pour assurer la décomposition des tiges et la remise en circulation d'éléments nutritifs dans l'écosystème qui pourraient rester séquestrés dans les chicots pour une longue période.

La coévolution des coléoptères phloéophages et xylophages avec leurs hôtes

Les coléoptères phloéophages et xylophages utilisent souvent des stratégies alimentaires de colonisation non-agressives car ils s'attaquent majoritairement aux arbres récemment morts, mais ils peuvent aussi utiliser des stratégies agressives s'ils s'attaquent à des arbres vivants. Les espèces très agressives tuent les arbres parfois sains en les colonisant massivement; ils appartiennent à la classe des parasites obligatoires (Raffa *et al.* 1993). Les espèces qualifiées de parasites facultatifs sont plus ou moins agressives et colonisent normalement des arbres tombés, stressés, blessés ou sous attaque d'autres insectes ou pathogènes. Ils s'attaquent seulement aux arbres sains lorsque leurs populations ont suffisamment augmenté grâce à une grande disponibilité d'arbres affaiblis (Raffa *et al.* 1993). Enfin, les espèces non-agressives qui colonisent des arbres récemment morts sont dites herbivores saprophytes (Raffa *et al.* 1993). Les différentes stratégies fournissent des avantages ou désavantages pour la reproduction selon la qualité nutritionnelle des tissus consommés ainsi qu'en fonction des mécanismes de défense naturelle des arbres. Il a été suggéré que les colonisateurs primaires sont surtout spécialistes dans la sélection de l'espèce d'arbre colonisée, tandis que les colonisateurs secondaires (fongivores, détritivores et prédateurs) sont plus généralistes (Langor 2008).

Les conifères et les scolytes (Curculionidae: Scolytinae) coexistent depuis le Mésozoïque précoce. Une relation étroite s'est développée entre ces insectes et les membres de la famille des Pinaceae qui produisent de la résine de manière constitutive (Seybold *et al.* 2000). La coévolution entre ces espèces implique une course aux armements entre les

colonisateurs et les colonisés (Franceschi *et al.* 2005). Certaines espèces de conifères, comme le sapin baumier, possèdent un système de défenses naturelles contre les pathogènes et les colonisateurs de tige qui se divise en une partie constitutive et une partie induite (Franceschi *et al.* 2005). Le système constitutif inclut des cellules et canaux qui accumulent de la résine dans les tissus vasculaires, des cellules dans le phloème qui contiennent des composés chimiques toxiques (e.g. phénols et terpénoïdes), et des propriétés mécaniques de l'écorce comme des couches de cellules subérisées et lignifiées, des sclérides et des cristaux d'oxalate de calcium (Franceschi *et al.* 2005). Le système induit implique une synthèse *de novo* ou une activation d'une grande gamme de composés chimiques de défense comme des protéines liées à la pathogenèse et des enzymes en plus d'autres phénols et terpénoïdes. Ce système induit agit parfois contre une infection en cours (réponse hypersensible et résistance locale) ou contre des infections/agressions futures de xylophages (résistance acquise) (Franceschi *et al.* 2005). Plusieurs études ont montré, par exemple, que la production de phénols et la régulation d'enzymes impliquées dans la défense sont rapidement induites dans des arbres précédemment colonisés et que les composés phénoliques sont plus toxiques et plus spécifiques à l'organisme invasif que ceux qui sont constitutifs (Franceschi *et al.* 2005). Grâce à ce système complexe de défenses naturelles, les conifères sont protégés contre une grande quantité d'organismes tentant de les attaquer, mais certains colonisateurs primaires ont aussi évolué en acquérant des stratégies permettant de les outrepasser ou de les vaincre (Franceschi *et al.* 2005). Le processus de colonisation des arbres par les coléoptères xylophages est spécifique à l'organisme, mais certaines espèces partagent des stratégies dans leur cycle vital. Afin d'en faire ressortir les traits avantageux, il est convenable de le diviser en trois phases: la dispersion, la colonisation et la reproduction (Stark 1982).

Généralement, une fois le développement des larves complété, l'adulte émerge de l'arbre et entre en phase de dispersion afin de sélectionner un hôte potentiel pour la colonisation. La décision d'accepter ou non un hôte dépend de signaux olfactifs, visuels, mécaniques et gustatifs, inhibiteurs et stimulants, balancés avec des signaux excitatifs et inhibiteurs internes (Miller et Strickler 1984). Il a été suggéré que certaines espèces ont développé de fortes réponses comportementales lors de la détection de composés volatils émis par l'espèce hôte indiquant un substrat potentiel pour se reproduire (Byers 1995). Les coléoptères non-agressifs seraient fortement attirés par des monoterpènes, qui sont

ironiquement des composés chimiques impliqués dans le système de défense des conifères, et par l'éthanol produit par le métabolisme anaérobique d'organismes présents dans les plantes stressées et en décomposition (Byers 1995). Cette attraction primaire, résultant de la détection de produits émis par l'hôte, démontre que les défenses naturelles des arbres peuvent devenir une faiblesse (Franceschi *et al.* 2005). Par ailleurs, les espèces agressives possèdent majoritairement des phéromones d'agrégation qui jouent le rôle d'attraction secondaire. La plupart des phéromones de scolytes sont synthétisés à partir des monoterpènes (Vanderwel et Oehlschlager 1987) ou par biosynthèse *de novo* (Ivarsson *et al.* 1993, Seybold *et al.* 1995, Seybold et Tittiger 2003), mais certaines espèces non-agressives ont aussi développé ce système qui entre en synergie avec les kairomones issues de l'arbre. Les défenses naturelles des arbres peuvent alors devenir un avantage pour les saproxyliques primaires qui ont développé cette stratégie durant cette course aux armements.

Une fois l'hôte choisi, les colonisateurs font face aux défenses naturelles de l'arbre. Ils doivent forer l'écorce puis passer à travers les défenses constitutives et ceux qui s'attaquent aux arbres vivants doivent aussi contrer les défenses induites. Deux issues sont possibles lors de la colonisation d'arbres vivants : soit l'arbre se défend efficacement et les coléoptères sont expulsés ou tués, soit l'arbre est colonisé et meurt (tué par annelage ou par infection) (Berryman *et al.* 1989). Les scolytes sont les plus grands ravageurs des forêts tempérées de conifères (Franceschi *et al.* 2005). Trois facteurs plus ou moins complémentaires et impliqués dans la colonisation sont souvent mentionnés comme les plus importants pour expliquer ce phénomène (Franceschi *et al.* 2005). Premièrement, les comportements d'agrégation sont utiles pour trouver des hôtes potentiels et des partenaires sexuels mais ils sont aussi décisifs dans le contexte de colonisation. La colonisation massive coordonnée par les phéromones d'agrégation serait essentielle pour épuiser le système de défense de l'arbre (Franceschi *et al.* 2005), car les scolytes ne semblent pas être généralement capables d'inhiber les défenses induites (Berryman *et al.* 1989). Deuxièmement, l'évolution d'une tolérance envers les mécanismes de défenses de l'hôte est importante, par exemple pour les pionniers émettant les phéromones d'agrégation ou lorsque les populations sont basses et qu'une attaque massive est impossible. Troisièmement, une des stratégies qui n'a pas été encore discutée et qui semble être décisive pour la colonisation est l'association de certaines espèces de coléoptères xylophages, notamment les scolytes, avec des symbiontes

fongiques. Cette association commune peut être mutualiste, donc avec de clairs bénéfices pour les deux partenaires comme pour les scolytes «à ambrosia» et leur symbionte. Cependant, l'association peut aussi être antagoniste (c.-à-d. compétiteurs pour la ressource ou pathogène du coléoptère), commensale ou occasionnelle, ou à effets inconnus (Francke-Grosmann 1967, Beaver *et al.* 1989, Franceschi 2005). L'intensité de la relation entre les scolytes et leurs symbiontes varie de facultative à obligatoire, mais elle peut être responsable de spectaculaires épidémies, lorsque favorisée par des conditions climatiques spécifiques, la pathogénicité du symbionte ou le comportement d'agrégation du scolyte (You *et al.* 2015). L'association entre les scolytes et les symbiontes infestant les conifères est complexe. Ainsi, distinguer l'espèce du symbionte et la manière dont ce dernier est transporté est pertinent dans la détermination de la nature de leur relation (Paine *et al.* 1997). Généralement, le symbionte est composé de champignons basidiomycètes et d'ascomycètes transportés sous forme de spores ou de mycélium à l'intérieur d'invaginations cuticulaires, les mycanges (Paine *et al.* 1997). Des espèces pathogènes de champignon de bleuissement, généralement des ascomycètes, sont responsables ou requises pour entraîner la mortalité des arbres attaqués lorsque les espèces de scolytes agressives en transportent (Paine *et al.* 1997). Une fois à l'intérieur des tissus sous-corticaux, le champignon transporté progresse dans les trachéides à travers les ponctuations aréolées ou en pénétrant directement les parois cellulaires (Gibbs 1993, Wallin et Raffa 2001). Ensemble, certaines espèces de coléoptères et de champignons interrompent le système vasculaire de l'arbre rendant le xylème non-conducteur, empêchant donc la circulation d'eau et de substances nutritives dans l'aubier, causant ultimement la mort de l'arbre (Wallin et Raffa 2001).

Enfin, une fois la colonisation effectuée, la phase de reproduction débute. Chez plusieurs Curculionidae, cette phase inclut l'accouplement, la construction de galeries, l'oviposition et le développement de la progéniture. Les adultes creusent une galerie principale où la femelle déposera ses œufs. Les galeries ont souvent des formes uniques à l'espèce à un point tel qu'elles sont parfois utilisées pour identifier les espèces ayant colonisé les arbres (Stark 1982). Lorsque les œufs éclosent, les larves creusent majoritairement des galeries individuelles qui s'allongent et croissent en volume tout le long du développement. Lorsque la phase d'alimentation se termine, la pupaison se produit dans une cellule nymphale. Les autres Curculionidae, les Cerambycidae et les Buprestidae pondent majoritairement leurs œufs dans de petites crevasses ou cavités. Les larves effectuent

donc la colonisation dans ce dernier cas et une seule galerie, souvent plus grosse, est observée dans les tissus sous-corticaux et parfois dans l'aubier. Le développement des larves et des pupes à l'intérieur des arbres constitue la plus grande partie du cycle vital des coléoptères phloéophages et xylophages. Cela peut durer de quelques semaines à quelques années.

Les comportements de détection d'hôtes potentiels et d'agrégation, ainsi que les mécanismes de tolérance aux défenses de l'arbre sont évolutivement avantageux et expliquent pourquoi les scolytes agressifs sont les agents les plus destructeurs de la forêt boréale tempérée (Franceschi *et al.* 2005). Cependant, le comportement alimentaire et l'association avec des symbiotes sont d'importants facteurs dans l'évaluation des conséquences économiques liées à la colonisation. Les phloéophages primaires sont des pionniers de la colonisation et se spécialisent dans la consommation du contenu des cellules du cambium, du phloème primaire et du xylème primaire, donc des tissus sous-corticaux en général situés juste sous l'écorce (Speigth 1989). Plusieurs espèces de xylophages foreurs primaires possèdent l'habileté de digérer la cellulose, grâce à des symbiotes ou des (hémi)-cellulases ainsi que des mandibules assez fortes pour forer des tunnels à travers l'écorce et le bois (Speigth 1989). La mortalité de grandes quantités d'arbres dans un peuplement cause des pertes importantes de profit liées à une réduction de rentabilité par rapport à sa productivité potentielle. Des pertes économiques sont aussi entraînées car le bois colonisé est souvent coloré et certaines espèces comme le longicorne noir (*Monochamus scutellatus* (Say)) (Coleoptera: Cerambycidae) peuvent coloniser des arbres brûlés avec une densité excédant 300 larves par m² de surface de tige creusant chacune des galeries pouvant atteindre 20 cm de long et pénétrant le bois de 7.5 cm en moyenne (Safranyik and Raske 1970, Cerezke 1977). Ces tiges sont toujours déclassées pour des causes d'esthétisme (Lowell *et al.* 1992). De plus, l'exportation de ce bois peut être l'objet de restrictions pour éviter le transfert potentiel de vecteurs de maladies comme le nématode du pin (Saint-Germain et Greene 2009). Les coléoptères phloéo- et xylophages sont pris au sérieux et peuvent être considérés comme nuisibles par les organismes de réglementation associés aux opérations forestières. Les enjeux économiques liés à la colonisation des arbres par ces coléoptères sont réels. Ainsi, dans une optique de bonification de l'aménagement écosystémique et de l'optimisation de la ressource forestière, l'étude du processus de colonisation des arbres

par les coléoptères xylophages suite à une nouvelle perturbation naturelle, au Québec, est pertinente afin d'en caractériser les impacts écologiques et économiques.

La colonisation par les coléoptères phloéophages et xylophages en contexte d'épidémie d'arpenreuse de la pruche

Les défenses induites par l'arbre dans les tissus sous-corticaux sont influencées non seulement par les nutriments emmagasinés localement mais aussi par la translocation de nouveaux photosynthétats issus des aiguilles (Fransceschi *et al.* 2005). Les assimilats sont alors utilisés par les structures de défense ainsi que pour synthétiser les composés chimiques et ne sont alors pas utilisés pour supporter la croissance et la reproduction, impliquant donc l'importance pour l'arbre de bien équilibrer l'allocation de ses ressources (Fransceschi *et al.* 2005). Des facteurs abiotiques variables, tels que le stress hydrique, la pollution de l'air, la température en plus de l'attaque par des agents biotiques, comme l'arpenreuse de la pruche, peut altérer la ressource en assimilats (Fransceschi *et al.* 2005). Wallin et Raffa (1999) ont montré que la défoliation du pin gris (*Pinus banksiana* Lamb.), par la tordeuse du pin gris (*Choristoneura pinus pinus* Freeman) (Lepidoptera: Tortricidae), affecte le contenu et la composition de monoterpènes constitutifs et induits en plus d'affecter des réponses physiologiques comme la réduction de croissance, la probabilité de mortalité, le taux de confinement fongique (du symbionte de scolytes) et le volume de résine. Ils ont montré que la défoliation entraînait plus de changements dans les tissus du phloème que dans le feuillage directement affecté par l'insecte ravageur. Ils ont aussi déterminé que la durée du stress (défoliation) était importante et entraînait en interaction avec son intensité ainsi qu'avec le profil de défenses naturelles. Dans un contexte semblable, Iqbal *et al.* (2011) ont montré que l'intensité de la défoliation par l'arpenreuse de la pruche était déterminante dans la diminution des taux de croissance et de mortalité des sapins baumiers et des épinettes noires affectés. De plus, Caron *et al.* (2013) ont rapporté l'augmentation de monoterpènes dans les tissus foliaires de sapins baumiers défoliés par la TBE. Il est donc probable que les profils de défense naturelle et de qualité nutritive des sapins baumiers, affectés par l'épidémie d'arpenreuse de la pruche de 2012, aient été modifiés. Des espèces de coléoptères xylophages primaires pourraient alors détecter les arbres défoliés et vulnérables, par signal olfactif majoritairement, comme une opportunité à la colonisation.

Les travaux de Bowers *et al.* (1996) ont porté sur la défoliation causée par la TBE et la présence du polygraphe de l'épinette (*Polygraphus rufipennis* (Kirby)) (Coleoptera: Curculionidae) dans des peuplements d'épinette noire (*Picea mariana* (Mill.) B.S.P.) à Terre-Neuve. Ils ont rapporté l'augmentation de l'incidence du coléoptère dans les peuplements sévèrement défoliés, particulièrement dans les arbres morts, mais ils n'ont pas pu préciser le niveau de défoliation requis pour déclencher la colonisation, car ils ont écorcé les arbres deux ans après la fin de l'épidémie de TBE. Wallin et Raffa (2001) ont étudié l'impact de la défoliation de la tordeuse du pin gris sur la densité de trous d'entrée du scolyte à grand corselet (*Ips grandicollis* Eichoff) (Coleoptera: Curculionidae), ainsi que du longicorne de la Caroline (*Monochamus carolinensis* (Olivier)) (Coleoptera: Cerambycidae) au Wisconsin. Ils ont montré que la colonisation par ces coléoptères augmentait exponentiellement en relation avec le niveau de défoliation des pins gris. Bien que les résultats soient très intéressants, les auteurs ont utilisé des classes de défoliation comme variable explicative et des décomptes de trous d'entrée comme variable réponse de la même manière que Bowers *et al.* (1996). Afin de déterminer un impact plus précis de la défoliation sur la communauté de coléoptères phloéo- et xylophages, et subséquemment, sur le processus de colonisation des arbres post-épidémie d'arpenteuse de la pruche, il serait pertinent d'étudier l'effet d'un niveau plus précis de défoliation des arbres en temps réel sur les assemblages d'espèces et les populations de ces coléoptères. La présence, l'abondance et la succession de ces coléoptères témoigne de leur sensibilité élevée aux changements dans l'écosystème forestier et pourraient faire office de bioindicateurs comme objectif à atteindre en contexte de simulation de perturbation naturelle. La conservation de telles espèces et donc des rôles qu'elles jouent suite à l'épidémie s'inscrit dans l'optique de respect et de la préservation des valeurs écologiques véhiculées par l'aménagement écosystémique. D'un autre point de vue, la caractérisation et la prédiction d'une trajectoire successionale d'espèces économiquement importantes en fonction de la défoliation pourrait s'avérer utile à des fins de détection et de prévention de dommages entraînant des pertes économiques. Les informations issues des résultats de la présente étude serviront à produire des recommandations afin de bonifier l'aménagement écosystémique. L'objectif principal est, par conséquent, de caractériser l'impact de la défoliation par l'arpenteuse de la pruche sur la communauté de coléoptères phloéo- et xylophages. Plus spécifiquement, les objectifs sont les suivants:

Objectif 1: Évaluer la justesse de différentes méthodes d'estimation de la défoliation annuelle et cumulative afin d'évaluer l'impact de l'arpenteuse de la pruche sur les sapins baumiers et sur les coléoptères phloéo- et xylophages.

Objectif 2: Déterminer si une succession à court terme survient chez les coléoptères phloéo- et xylophages en présence de défoliation et déterminer quelles sont les principales variables environnementales expliquant la ou les possibles trajectoires successioneelles.

Objectif 3: Déterminer un taux de défoliation seuil au-delà duquel survient la colonisation massive des coléoptères phloéo- et xylophages et déterminer si les pièges utilisés pourraient servir d'outil de détection dans la prédiction des attaques de coléoptères.

Chapitre 1

Comparison of several methods for estimating defoliation from the hemlock looper (*Lambdina fiscellaria* (Guenée)) (Lepidoptera: Geometridae) on balsam fir

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Résumé

Une épidémie d'arpenteuse de la pruche a été observée, pour la première fois, dans la région de Québec en 2012. Cette épidémie a fourni l'opportunité d'évaluer la précision d'une méthode d'inventaire aérien de la défoliation, récemment développée par le Ministère des Forêts, de la Faune et des Parcs du Québec. De plus, afin de développer une méthode d'estimation de la défoliation au niveau de l'arbre, nous avons comparé deux méthodes basées sur des estimations visuelles faites à partir du sol, avec la méthode classique de Fettes (1950). L'inventaire aérien a fourni des estimés justes de la défoliation après la première année d'épidémie mais s'est avéré inexact lors de la deuxième année alors que seuls les peuplements gravement défoliés ont été correctement classés. La défoliation cumulée sur toutes les classes d'âge de feuillage amène un nouveau défi aux équipes affectées aux programmes d'évaluation de la défoliation par voie aérienne. La défoliation de la pousse annuelle était fortement corrélée avec l'estimé de Fettes. Néanmoins, la défoliation estimée dans la couronne supérieure des arbres s'est avérée le substitut le mieux corrélé avec la défoliation totale estimée par la méthode de Fettes.

Mots-clés: Arpenteuse de la pruche; Défoliation; Inventaire aérien; Méthode d'estimation; Couronne supérieure

Abstract

An outbreak of the hemlock looper was observed in the Québec region for the first time in 2012. This outbreak provided the opportunity to test the efficacy of a new aerial defoliation survey method, developed by the Ministère des Forêts, de la Faune et des Parcs du Québec. In order to estimate defoliation at the tree level, we tested two proxies, which were easy and rapid to use from the ground level, and compared them with the classical Fettes method. First, we observed that aerial survey provided accurate estimates of defoliation severity during the first year of the outbreak but it was far less efficient after a second year of defoliation when only heavily defoliated stands were correctly classified. Cumulative defoliation on all age classes of foliage brings a new challenge to crews affected to aerial survey programs. Defoliation on current year shoots was strongly correlated with Fettes estimates combining all age classes. However, the overall defoliation estimated in the upper crown was more strongly correlated with Fettes estimates than defoliation on current year shoots.

Keywords: Hemlock Looper; Defoliation; Aerial survey; Estimation method; Current-year shoot; Upper crown

1 Introduction

The hemlock looper, *Lambdina fiscellaria* (Guenée) (Lepidoptera: Geometridae), is considered as the second most important insect defoliator of balsam fir (*Abies balsamea* (L.) Mill.) in eastern North America after the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Hébert and Brodeur 2013). Except when populations are extremely high, which may induce larval back-feeding on the old foliage, the spruce budworm usually feeds only on current-year shoots and thus kills balsam firs only after 4 to 5 years of severe defoliation (Blais 1958, MacLean 1980). In comparison, hemlock looper larvae chew on fir needles of all age classes without consuming them completely (Hébert and Jobin 2001, Iqbal and MacLean 2010). This wasteful feeding behaviour results in damaged needles eventually drying and falling in late summer and thus, the hemlock looper can kill trees within just one or two years of severe defoliation (Dobesberger 1989, Iqbal and MacLean 2010), which is much faster than for the spruce budworm.

Annual defoliation estimates are useful tools in forest pest management . They are usually obtained through aerial defoliation surveys used for assisting forest managers in their operational decisions (MacLean and MacKinnon 1996) but they are also useful for research purposes (MacLean and Lidstone 1982, Gray *et al.* 2000, Candau and Fleming 2005). These estimates are based upon the characteristic reddish-brown coloration of tree foliage resulting from insect feeding (Iqbal and MacLean 2010). For the spruce budworm, over a 10-year period, MacLean and MacKinnon (1996) concluded that aerial sketch-mapping of defoliation was appropriate for management purposes. Globally, misclassifications resulted mostly from the difficulty in detecting and correctly estimating light defoliation with aerial survey. On the other hand, the heavy defoliation class of aerial survey slightly overestimated defoliation according to ground estimates (MacLean and MacKinnon 1996).

Estimating the annual defoliation by the hemlock looper is more challenging than for the spruce budworm as it affects all age classes of foliage but also because successive years of defoliation include previous years of defoliation (Iqbal and MacLean 2010). Moreover, methods used to produce defoliation estimates vary between jurisdictions and their accuracy also depends upon observers (Dorais and Kettela 1982). Data from Iqbal and MacLean (2010), using a shoot-count defoliation chart, applied in the laboratory on shoots from field-collected branches (e.g. Fettes 1950), showed that aerial surveys, carried out in

Newfoundland with helicopters, overestimated defoliation in both moderate and heavy defoliation areas (no data was available for lightly defoliated stands). In Quebec, aerial defoliation surveys are carried out using aircrafts by the Ministère des Forêts, de la Faune et des Parcs (MFFP; named Ministère des Ressources naturelles et de la Faune or MRNF in 2012). The MFFP has developed a spatially explicit mapping tool, which has been used since 2003, but its accuracy for assessing hemlock looper defoliation has not yet been appraised. Moreover, at ground level, it is often impractical to use a shoot-count method, like the Fettes method, due to time and resource limitations. Easier and faster field estimation methods are thus needed for research purposes. For instance, we may hypothesize that, even if the hemlock looper feeds on multiple age classes of foliage, current-year shoot defoliation could be a good proxy of the overall tree defoliation. For a conifer-feeding insect such as the hemlock looper, current-year shoots are the only ones on which defoliation can be categorized with certainty as annual. Also, an estimation of defoliation in the upper crown could be a good proxy of the overall tree defoliation for research purposes that need defoliation estimates at the tree level.

In this paper, our objectives were 1) to verify the accuracy of aerial surveys carried out in Quebec for assessing hemlock looper annual defoliation at the stand level, over the first two years of an outbreak, and 2) to compare two ground-level methods for assessing defoliation at the tree level.

2 Methods

2.1 Study area

The study was realized in the Parc national de la Jacques-Cartier (47°06' N, 71°20' W) and in the Forêt Montmorency (47°19' N, 71°09' W), both located approximately 70 km north of Quebec City. Both areas belong to the balsam fir-white birch bioclimatic domain, within the continuous boreal forest sub-zone (Saucier *et al.* 2011). Balsam fir stands largely dominate the landscape and black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss.), white birch (*Betula papyrifera* Marsh.), American mountain-ash (*Sorbus americana* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are the most common companion species in these stands.

2.2 Stand selection and defoliation estimation

Aerial surveys were conducted in August 2012 and 2013 by the MFFP to assess hemlock looper annual defoliation. Aircraft flew at 160 km/h and 240 m altitude along flight lines spaced by 4.5 km (MRNF 2012). Their spatially explicit mapping tool was used to collect and digitize images by delineating defoliated patches with a stylus on a touchscreen computer. To make it easier, a topographic map rolled out as a background on the screen, linked with the aircraft route. Images were directly digitized and georeferenced with a GIS software. Defoliated patches were classified according to three severity classes: light (1–34%), moderate (35–69%) and heavy (70–100%). Light defoliation is defined as a loss of foliage in the upper crown for some trees in a stand, moderate defoliation as a loss of foliage in the upper crown of most trees and on the full crown length of several trees, and heavy defoliation as a loss of foliage along the full crown length of most trees (MRNF 2012).

During spring 2013, 12 balsam fir stands were selected among four defoliation classes (trace, light, moderate and heavy) according to the 2012 MFFP aerial survey. Three 400 m² circular plots, spaced at least by 50 m, were established within each selected stand for estimating defoliation from ground-level. Four co-dominant balsam firs, labeled as «sample trees», were selected in each plot for estimating defoliation during this hemlock looper outbreak. Defoliation was visually estimated on sample trees using the chart developed for the spruce budworm by Fettes (1950). This method is usually applied in the laboratory on

all shoots of field collected branches but here, to avoid disturbing and stressing the experimental trees under study, we used binoculars to apply the Fettes method based on direct observations in the field. The 2012 defoliation (1st year of the outbreak) was estimated before the 2013 bud break by two observers, who randomly selected 3 branches of the upper crown of each sample tree, and visually assessed defoliation on the shoots of the past five years (shoots numbered backward as n to $n-4$, corresponding to 2012 down to 2008 foliage). This method is hereafter called the Field Fettes Method (FFM) in this study. Mean defoliation estimates based on the Field Fettes Method were obtained by averaging defoliation of all recorded shoots from each of the three selected branches on a tree. Current-Year Shoot (CYS) defoliation estimates were derived from this method by averaging values of the « n » annual shoots across each sample tree. In addition, an overall visual defoliation estimate of the upper crown of each tree was also obtained. Sample trees were individually classified as defoliated from 0 to 100%, based on ten 10% classes of defoliation by two observers using binoculars. This method is hereafter called the Upper Crown Estimation Method (UCEM). Defoliation was re-estimated again for each tree before the 2014 bud break, in order to estimate the 2nd year (2013) defoliation and therefore the cumulative defoliation due to the persisting hemlock looper outbreak. These estimates were from the same four sample trees in each stand. Table 1.1 summarizes the relevant information about the different methods used to assess defoliation.

2.3 Statistical analysis

In order to appraise the accuracy of the aerial survey, we averaged ground-level defoliation estimates obtained with Current-Year Shoots, Field Fettes and Upper Crown Estimation Methods in each plot, and compared them between aerial survey defoliation classes using ANOVAs followed by Tukey all pair-wise comparison tests (post hoc analysis) for 2012 and 2013 separately. Then, to determine if Current-Year Shoot estimates could be used as a proxy of the overall tree defoliation, we carried out linear and non-linear regressions between those estimates and estimates on each of the $n-1$ to $n-4$ shoots, as well as with the combined defoliation on $n-1$ to $n-4$ shoots, also called Previous-Year (PY) defoliation estimate, for 2012 and 2013 separately. Finally, to identify the best proxy for estimating overall tree defoliation, we used linear regressions between Current-Year Shoot estimates or Upper Crown Estimation Method estimates with Field Fettes estimates for 2012 and 2013 separately. The *lm* function from the *stats* package (R

Core Team 2014) was used for ANOVAs and for linear regressions and the *glht* function from the *multcomp* package (Hothorn *et al.* 2008) was used for the post hoc tests. When linear regressions did not provide a good fit, mostly because of a strong effect of the 100% maximum defoliation (asymptote), we used the *nls* function from the *stats* package (R Core Team 2014) to fit asymptotic regressions with weighted least-squares estimations of parameters.

3 Results

The ANOVAs comparing ground-level defoliation estimates according to the aerial survey classes were highly significant for both 2012 (FFM: $F = 30.98$; $df = 3, 32$; $P < 0.001$, UCEM: $F = 37.75$; $df = 3, 32$; $P < 0.001$, CYS: $F = 32.60$; $df = 3, 32$; $P < 0.001$) and 2013 (FFM: $F = 19.09$; $df = 2, 33$; $P < 0.001$, UCEM: $F = 24.04$; $df = 2, 33$; $P < 0.001$, CYS: $F = 19.01$; $df = 2, 29$; $P < 0.001$). For 2012, the Tukey pairwise comparisons showed that defoliation was significantly different for all pairs of classes except between the “none” (control plots) and the light defoliation classes (Figure 1.1). All plots of the none defoliation class were clearly misclassified as light to moderate defoliation was noticed in all plots while estimating defoliation from each ground-level method (Table 1.2; Figure 1.1). Nevertheless, plots of the light, moderate and heavy defoliation were generally well assessed in 2012 (Table 1.2; Figure 1.1). This was not the case in 2013, the 2nd year of the outbreak (Table 1.2), even if ANOVAs showed significant differences in defoliation according to the aerial survey classes (Figure 1.1). Nevertheless, according to the three methods, plots that belong to the heavy defoliation aerial survey class were well assessed. However, four of these plots were in fact misclassified as no annual defoliation could have been observed because all trees died in early fall 2012. All none defoliation classified plots were clearly misclassified as light to heavy defoliation was noticed in all plots (Table 1.2; Figure 1.1). There was no significant difference of Field Fettes or Upper Crown estimates, which cumulate two years (2012 and 2013) of defoliation, between moderate and heavy defoliation aerial survey classes in 2013 but there were significant differences when considering only current-years shoots, which represent only 2013 defoliation. Moreover, in 2013, the aerial survey entirely skipped the light defoliation class among our survey plots.

Relationships between Current-Year and Previous-Year shoots defoliation estimates were strongly significant but the strength of the relationships (R^2) decreased progressively from $n-1$ to $n-4$ shoots for both years (Table 1.3). Relationships were linear in 2012 but clearly non-linear in 2013 (Figure 1.2). A light defoliation on 2013 current-year shoots occurred on trees that were affected by all levels of defoliation on previous-year foliage (see the white area on Figure 1.2b). However, current-year shoots defoliated at moderate to heavy levels were always observed on trees on which previous-year foliage was heavily to completely defoliated (see the grey area on Figure 1.2b).

Linear and non-linear regressions between defoliation proxies (Current-Year Shoot or Upper Crown defoliation estimates) and the more detailed Field Fettes estimates were strongly significant ($P < 0.001$) for both years of study but always higher for the Upper Crown with $R^2 \geq 0.96$ (Table 1.4; Figure 1.3). Moreover, the relationship using Current-Year Shoot estimates during the 2nd year of the outbreak was clearly not linear, while that using Upper Crown estimates was nearly linear.

4 Discussion

Our results show that the aerial defoliation survey system implemented in 2003 in Quebec is reliable for delineating stand defoliation during the first year of a hemlock looper outbreak. The average defoliation estimates, at ground-level, fell within the limits of the light, moderate and heavy classes obtained with the 2012 aerial survey and most plots were well classified. The light defoliation class of the aerial survey was composed of plots that tended to be in the upper portion of this class, while all controls, which should have range between 0 and 5% defoliation, were in fact around the middle of the light class. This is in agreement with MacLean and MacKinnon (1996) who showed, for the spruce budworm, that most errors came from the inability to detect light defoliation (11-30% in their study) from the air. Nevertheless, the system implemented in Quebec provided better estimates than those made previously in Newfoundland where trees of the moderate level class were in fact defoliated at 25.8%. Similarly, in our study, the average plot defoliation for the heavy class was 79.3 to 97.5% compared with 43.4% in Newfoundland (Iqbal and MacLean 2010). On the other hand, in our study, only the heavy defoliation class of the aerial survey was found accurate according to all ground-level estimates in 2013. It indicates that the new system is not as accurate for a 2nd year of hemlock looper defoliation as it consistently underestimates cumulative defoliation. However, defoliation on current-year shoots provided a better fit with moderate and heavy defoliation classes of the 2013 aerial survey, suggesting that this survey provides reliable estimates of the annual defoliation but not of cumulative defoliation. In Newfoundland, Iqbal and MacLean (2010) still reported overestimation of defoliation by the aerial survey during the second year of an outbreak. However, defoliation in Newfoundland was much lower than in Quebec with an average of 54.6% after two years of defoliation (moderate and heavy) and of 36.7% on current year foliage, which was not strongly different than for the first year of heavy defoliation (43.4 and 26.8% for overall and current year foliage defoliation respectively).

The level of defoliation during the first year of an outbreak might influence the accuracy of the defoliation assessment during the second year of this outbreak. Aerial defoliation survey might be much more difficult to appraise during the second year of an outbreak as the green background coloration of trees during a first year outbreak is replaced by a characteristic grey coloration when trees lose their needles, which also vary with the

severity of defoliation. The severity of annual defoliation might be the same or even be higher than during the first year of an outbreak but the presence of smaller and discontinuous red patches due to the lower amount of needles to redden may lead to underestimation of defoliation. Because of the difficulty of correctly assessing light defoliation from aerial survey even during the first year of an outbreak, a much larger proportion of balsam fir was lightly defoliated than reported in 2012. This also suggests that population increases are more related to local build-ups than to moth immigration, thus requiring tools that can rapidly detect hemlock looper population increases in numerous stands distributed over large areas. This should be taken into account if the objective is to implement an early-intervention strategy against the hemlock looper. Such strategy is actually being tested for interrupting or delaying the spruce budworm outbreak in New Brunswick (Bécharde *et al.* 2014).

Defoliation estimated on current-year shoots may provide additional information at a finer level as it is closely linked with defoliation on previous year shoots during the first year of the outbreak, the relationship being stronger on the young foliage ($n-1$), which provides the highest contribution to photosynthesis, with current-year foliage (Clark 1961). The relationship was still strong during the second year of the outbreak but it was no longer linear. Nevertheless, it could be useful to predict tree survival. Indeed, if the first year of defoliation was not complete and the second year defoliation on current-year shoots was light (under 35% of defoliation), we noticed that most trees (98%) had survive and recover in 2014 (unpublished data). However, as all other shoots were almost completely defoliated, a second year of moderate to heavy defoliation on the current year shoots showed that most trees (80%) died by 2014. When populations remain stable or even increase in the second year of an outbreak, the back-feeding (up to $n-4$) can be very extensive. Carroll (1999) reported that, despite the unsuitability of old foliage to newly emerged hemlock looper larvae, later instars survived better and produced larger pupae when 1- and 2-year-old foliage was added to their diet. Developing models for predicting defoliation on current-year shoots, using egg density, would be useful for assisting forest pest managers in their decision making.

Finally, in order to provide a rapid estimate of balsam fir tree condition for research purposes, estimating the overall defoliation in the upper crown appears as a very good

proxy of the cumulative defoliation, for both the first and second year of an outbreak. Moreover, the relationships are mostly linear for both years. This fast method should be incorporated into experimental designs testing the impact of defoliation on specific trees, as the information is more detailed (10% classes) than a 3 classes system as provided by the aerial survey (light-moderate-heavy). Moreover, this approach is simpler and cheaper than other currently available methods. In fact, the use of finer defoliation classes increases the predictive power of models or the understanding of complex ecological processes resulting from defoliation, like the emission of volatile defensive chemical compounds that may initiate colonization by phloeophagous and xylophagous insects.

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Tables

Table 1.1 List of defoliation estimation methods compared in this study.

Method	Description	Time of data acquisition
Aerial Survey	Realised from aircraft with a spatially explicit mapping tool developed by the MFFP. Data are then linked to a Geographic Information System (GIS) software which analyses the georeferenced data. Observers classify the delimited defoliated patch severities as light, moderate and heavy.	August (2012–2013)
Field Fettes	Realised from the ground using binoculars by two observers. Three branches of the tree upper crown were randomly selected and shoots of each of the past 5 growth years (labelled n to n-4 shoots) were examined and classed on the basis of 10% defoliation classes.	June (2013–2014)
Current-Year Shoot	Defoliation estimates of the current-year shoot, as assessed by the Field Fettes Method.	June (2013–2014)
Upper Crown	Realised from the ground using binoculars by two observers. The overall defoliation of the upper crown was assessed on the basis of 10% defoliation classes.	June (2013–2014)

Table 1.2 Accuracy of defoliation classes determined through aerial survey of hemlock looper defoliation, according to three ground-level methods estimating defoliation (FF, UC and CYS) on balsam fir trees in 2012 and 2013 in the Laurentian Wildlife Reserve, Quebec, Canada.

Year	Defoliation class (from aerial survey)	Number of plots	Number of plots correctly classified		
			FF ¹	UC ¹	CYS ¹
2012	None	14	0	0	0
	Light	8	6	7	6
	Moderate	6	5	6	5
	Heavy	8	4	5	5
2013	None	21	0	0	0
	Light	0	–	–	–
	Moderate	5	1	1	3
	Heavy	10	10	10	4

¹ FF: Field Fettes estimates; UC: Upper Crown estimates; CYS: Current-Year Shoot estimates

Table 1.3 Regressions between defoliation on Current-Year Shoots and that on each of n-1 to n-4 shoots, as well as with the average defoliation on n-1 to n-4 shoots, also called Previous-Years defoliation (PY). *P*-values are shown for linear regressions and R² are shown for both linear and non-linear regressions.

Year	Compared estimates	<i>P</i>-value	R²
2012	PY	<0.001	0.81
	n-1	<0.001	0.92
	n-2	<0.001	0.80
	n-3	<0.001	0.73
	n-4	<0.001	0.71
2013	PY	-	0.82
	n-1	-	0.86
	n-2	-	0.81
	n-3	-	0.78
	n-4	-	0.76

Table 1.4 Regressions between defoliation estimated using the Field Fettes (FF) method and that estimated on current-year shoots (CYS) or by the upper crown (UC) method. Significance of Intercept (β_0) and slope, (β_1) coefficients with standard error (SE), t-statistics, and *P*-values are shown with the adjusted R² of each linear model.

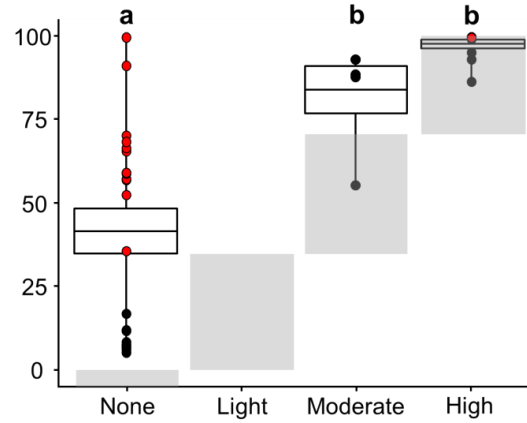
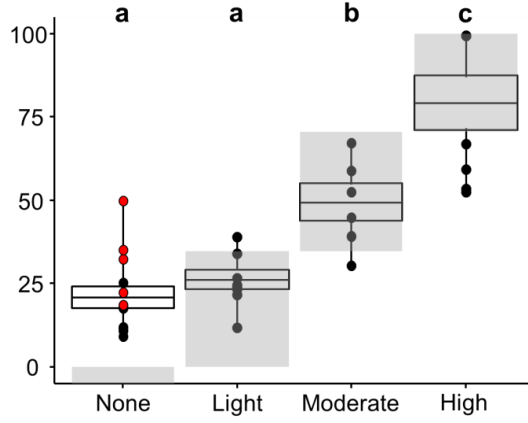
FF	Proxy	Coef.	Estimate	SE	t-statistics	<i>P</i> -value	R ²	Non-linear model R ²
2012	UC	β_0	2.45	0.72	3.39	<0.001		
		β_1	0.96	0.01	66.17	<0.001	0.97	–
	CYS	β_0	10.25	1.28	7.99	<0.001		
		β_1	0.92	0.03	31.92	<0.001	0.88	–
2013	UC	β_0	5.86	1.22	4.80	<0.001		
		β_1	0.96	0.02	55.02	<0.001	0.96	0.97
	CYS	β_0	26.33	2.56	10.30	<0.001		
		β_1	0.82	0.05	16.66	<0.001	0.70	0.85

Figures

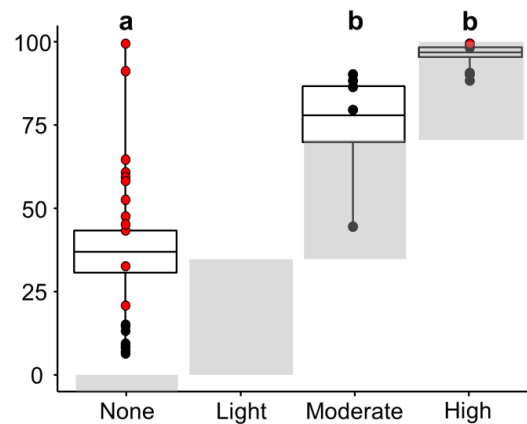
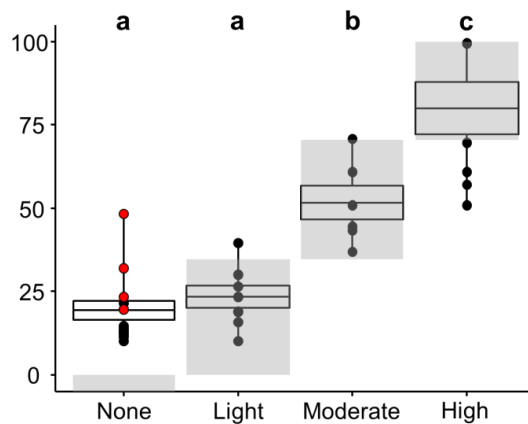
2012

2013

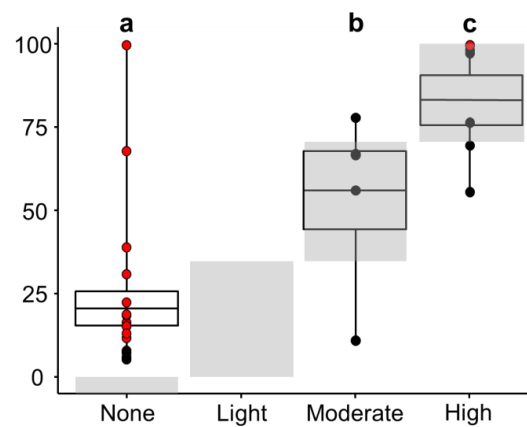
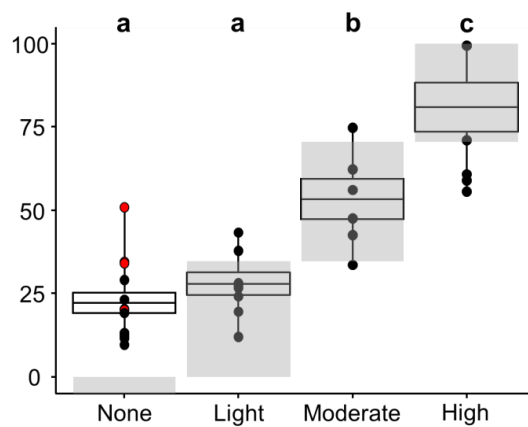
Field Fettes estimates



Upper Crown estimates



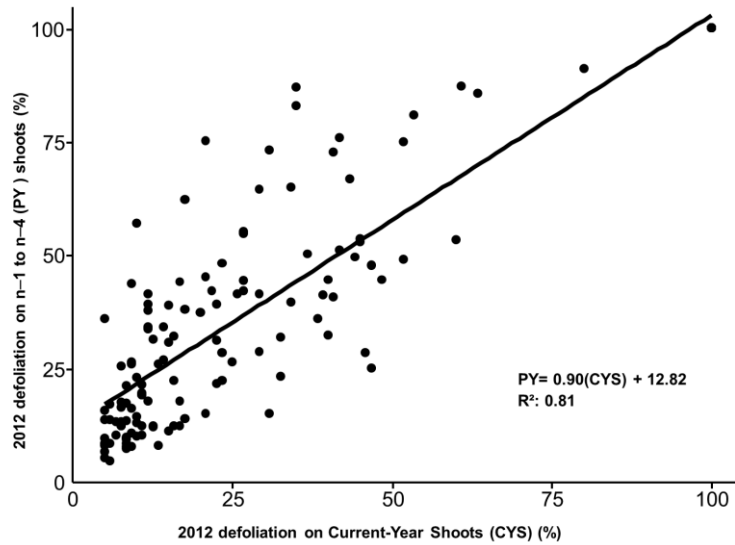
Current-Year Shoot estimates



Aerial Survey defoliation (MFFP classes)

Figure 1.1 Validation of aerial survey defoliation classes using defoliation estimated with three ground-level methods (Field Fettes, Upper Crown estimates and Current-Year Shoot estimates) in 2012 and 2013. Significantly different classes have different letters, after Tukey pair-wise comparison, based on significant ANOVAs. Dot symbols represent sample trees, Middle bar of the box represents mean defoliation per treatment (with letters indicating differences between means above each boxplot) and box outlines represent the standard error. Grey areas represent % defoliation interval of MFFP classes. For the None class, distinct plots from our controls were represented by red dots. Completely defoliated plots in 2012 were also represented by red dots in 2013 boxplots

a)



b)

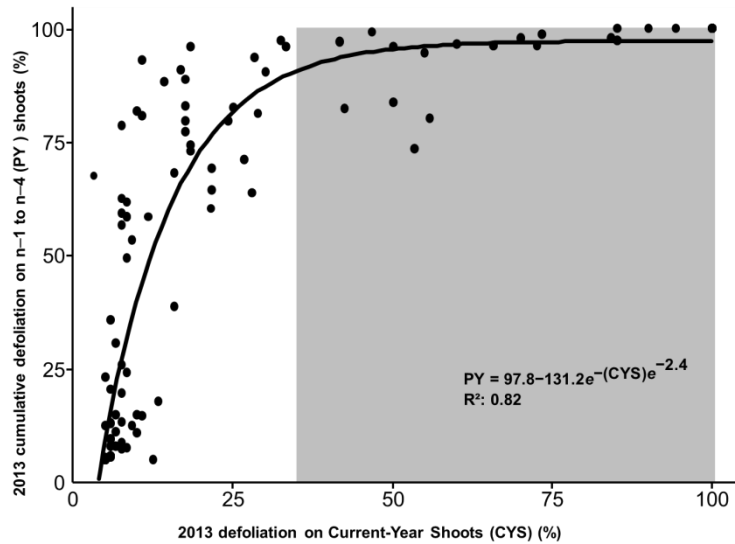
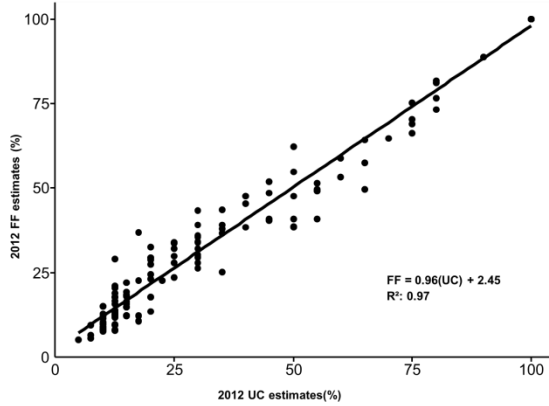


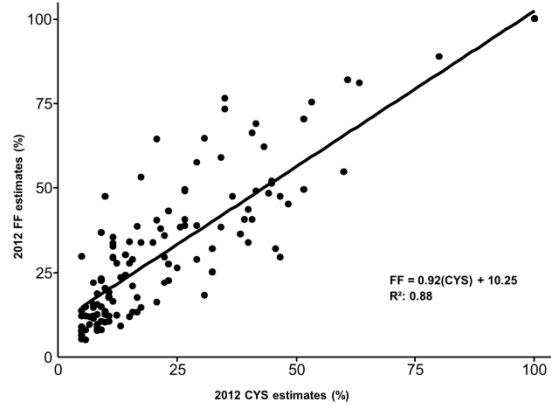
Figure 1.2 Relationships between annual defoliation estimated on Current-Year Shoots and cumulative defoliation estimated on previous year shoots (PY; n-1 to n-4 mean) in 2012 and 2013 as assessed by the Field Fettes method. The grey shading in 3b show trees on which current-year shoots were moderate- heavily defoliated, according to MFFP classification.

2012

a)

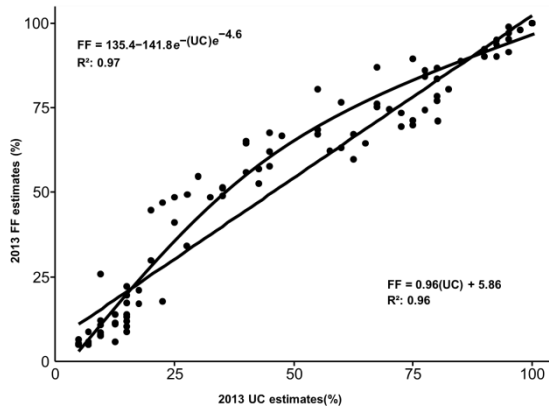


b)



2013

c)



d)

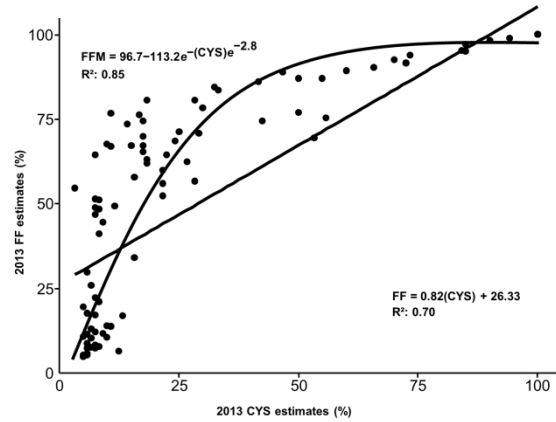


Figure 1.3 Relationships between two defoliation proxies on balsam fir trees and a complete estimation of defoliation using the Field Fettes method in 2012 and 2013 in the Laurentian Wildlife Reserve in Quebec, Canada. a) Defoliation estimated in the Upper Crown in 2012. b) Defoliation estimated on Current-Year Shoots in 2012. c) Defoliation estimated in the Upper Crown in 2013. d) Defoliation estimated on Current-Year Shoots in 2013.

Chapitre 2

Early succession of bark and wood boring beetles during an outbreak of the hemlock looper (*Lambdina fiscellaria* (Guenée)) (Lepidoptera: Geometridae) in boreal balsam fir forest

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Résumé

La récente épidémie d'arpenreuse de la pruche dans la région de Québec (2012) a donné l'opportunité d'étudier la réponse des coléoptères phloéo- et xylophages à un apport substantiel d'arbres stressés ou récemment morts. Nos objectifs étaient de vérifier 1) si une succession hâtive d'espèces saproxyliques survenait et 2) si des variables environnementales expliquaient les changements dans la communauté. Les résultats montrent qu'une succession est survenue essentiellement 2 ans après le début de l'épidémie et seulement dans les peuplements les plus défoliés. Un assemblage pré-épidémique caractérisé par des espèces associées aux forêts non perturbées s'est remanié en une prédominance du scolyte birayé. La défoliation, la surface terrière de conifères, celle de sapins baumiers morts ainsi que l'étendue des coupes de récupération adjacentes étaient des variables positivement corrélés avec sa présence. Les arbres vivants étaient faiblement colonisés par divers phloéophages alors que ceux défoliés mortellement étaient massivement attaqués par le scolyte birayé.

Mots clés: Arpenreuse de la pruche; Succession; Saproxylique; Défoliation; Prédominance; Scolyte birayé; Colonisation

Abstract

The latest outbreak of the hemlock looper in the Quebec region (2012) provided the opportunity to study the first response of phloeophagous and xylophagous beetles to an extensive supply of stressed or recently died trees. Our objectives were 1) to verify if an early succession of saproxylic species occurred and 2) to verify if environmental variables could explain changes in species assemblages. Results showed that saproxylic beetle early succession began mostly two years after the beginning of the outbreak and only in the most heavily defoliated stands. A “pre-outbreak” assemblage characterised by polyphagous beetles shifted to one predominated by the striped ambrosia beetle. The defoliation level, the conifer basal area, that of dead balsam firs along with the extent of the adjacent salvage logged area were positively correlated with its presence. Living trees were only scarcely colonized by several phloeophagous species while dead trees were massively colonized by the striped ambrosia beetle.

Keywords: Hemlock Looper; Succession; Saproxylic; Defoliation; Striped ambrosia beetle; Colonization; Predominance

1 Introduction

Ecosystem-based forest management is an approach aimed to maintain ecological processes by emulating natural disturbances (Gauthier *et al.* 2008, Mori 2011, Stockdale *et al.* 2016). Its implementation requires reducing the gap between managed and unmanaged forests, the latter remaining only under natural disturbance regimes (Grenon *et al.* 2010). Thus, ecosystem-based management aims to withhold similar forest composition and structure as in forests under natural disturbance regimes. This should maintain ecosystem resilience to a broad range of environmental stresses, through the presence of species assemblages that are well-adapted to disturbances. The objectives of biodiversity conservation and its associated ecological processes should thus be reached (Long 2009). While this approach is welcome from an ecological perspective, the success of ecosystem-based management relies on our ability to mimic natural disturbances through silviculture. This depends upon the level of understanding of how disturbances modify ecosystems (Stockdale *et al.* 2016).

In the eastern part of North America, boreal forest ecosystems are mostly regulated by fire and spruce budworm (*Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae)) outbreaks. Such disturbances generate large amounts of dead trees that are used by saproxylic insects, which depend, during at least part of their life cycle, upon the dead or dying wood of moribund or dead trees, or upon other saproxylic organisms (Speight 1989). In North American boreal forest, most studies carried on the early responses of saproxylic insect communities to large-scale forest disturbance have dealt with wildfire in black spruce (*Picea mariana* (Mill.) B.S.P.) dominated stands (Boulanger *et al.* 2010, Azeria *et al.* 2012, Boucher *et al.* 2012). The only studies to examine the effects of spruce budworm outbreaks on saproxylic insect communities were done 15 to 20 years after the outbreak in balsam fir (*Abies balsamea* (L.) Mill.) dominated stands (Barnouin 2005, Norvez *et al.* 2013). However, some studies have addressed the early responses of saproxylic insects to insect outbreaks (Bowers *et al.* 1996, Wallin and Raffa. 2001, Vindstad *et al.* 2014). In Newfoundland, the abundance of the four-eyed spruce bark beetle (*Polygraphus rufipennis* (Kirby)), was much higher in black spruce trees severely defoliated by the spruce budworm than in the light and moderate ones (Bowers *et al.* 1996). In Wisconsin, the eastern fivespined ips (*Ips grandicollis* Eichoff), a bark beetle, and the Carolina pine sawyer (*Monochamus carolinensis* (Olivier)), a wood boring beetle, showed exponential

colonization in jack pine (*Pinus banksiana* Lamb.) as a function of jack pine budworm (*Choristoneura pinus* Freeman) defoliation (Wallin and Raffa. 2001). These studies used beetle entry or exit holes as response variables and defoliation classes as independent variable. Studying the early succession of saproxylic insect communities requires other sampling approaches (interception traps and emergence cages in example) and this has rarely been done. However, recently, a study addressing the early response of saproxylic beetles to a massive outbreak of two geometrid moths has been done in a mountain birch forest of Norway (Vindstad *et al.* 2014). With flight-interception traps, they detected a weak response in the abundance of two early-successional saproxylic species which utilize dead birch in early stages of decay.

Saproxylic species such as bark and wood boring insects (phloeophagous and xylophagous species), play a key role in nutrient cycling of dead wood in forest ecosystems (Siitonen 2001, Spence 2001, Smith *et al.* 2009) as they are the first to physically penetrate dying and recently dead trees (Morin *et al.* 2015). They facilitate further colonization by fungal and microbial decomposers, thus promoting saproxylic diversity (Speight 1989, Spence 2001) and speed of decomposition. Besides, the colonization of recently dead trees by phloeo- and xylophagous insects raises economic concerns for the timber industry (Langor *et al.* 2008, Bélanger *et al.* 2013, Cadorette-Breton *et al.* 2016). For example, after forest fires, longhorned beetles (Cerambycidae) of the genus *Monochamus* attack burned trees and can rapidly downgrade logs and reduce wood value. Xylophagous insects may reduce wood value by as much as 30 to 35% in wood piled along forest roads (Safranyik and Raske 1970). Because of their rapid response to habitat disturbances (Raffa and Berryman 1980, Martikainen *et al.* 2000), their general sensitivity to forest management (Similä *et al.* 2002), and good knowledge of their taxonomy and ecology (Langor *et al.* 2008), early responding phloeo- and xylophagous beetles are of high interest in studying short-term ecological response and early succession after disturbances (Morin *et al.* 2015).

The hemlock looper (*Lambdina fiscellaria* (Guenée)) (Lepidoptera: Geometridae) is considered as the second most important insect defoliator of coniferous trees in eastern North America after the spruce budworm (Hébert and Brodeur 2013). Historically, the hemlock looper has defoliated large areas of balsam fir forests in eastern coastal Canada.

During summer 2012, an outbreak of the hemlock looper was detected for the first time in the Laurentian Wildlife Reserve, which is located 70 km north of Québec City, far away from usual outbreak areas (Arsenault *et al.* 2014). The hemlock looper feeds on balsam fir foliage of all age classes, chewing on needles without eating them completely (Hébert and Jobin 2001, Iqbal and MacLean 2010). The needles dry out and fall at the end of the summer. Because of this wasteful feeding behaviour, the hemlock looper can kill fir trees within only one or two years (Dobesberger 1989, Iqbal and MacLean 2010), which is much faster than the spruce budworm. The spruce budworm feeds almost only on current-year foliage and begins to induce balsam fir tree mortality after four to five years of heavy defoliation (MacLean 1980). The recent hemlock looper outbreak offers a great opportunity for studying the early succession of phloe- and xylophagous beetles during an insect outbreak and for understanding which successional trajectories might be induced by various patterns of defoliation. Insect defoliation stresses trees, which may reduce their defense mechanisms as Wallin and Raffa (2001) noted that the constitutive mechanism, resin volume, and subsequent induced defenses, histological responses to infection and allelochemical accumulation, were influenced by defoliation level. Therefore, we may expect a quick numerical response of the beetles when heavy defoliation is reached. However, while defoliation levels of every severity (light, moderate and heavy) were recorded, some areas were defoliated at an extremely high level as trees were being killed massively as soon as in late July 2012, the first year in which defoliation was detected. We may hypothesize that, oppositely to trees stressed over several years, those trees should be less convenient for beetles because subcortical tissues should have dried by the next spring. While fire rapidly kills trees and produces snags that also desiccate rapidly in open stands, insect outbreaks usually kill trees progressively, over several years, and these dead trees gradually desiccate (Vindstad *et al.* 2014). We may hypothesize that trees killed by various disturbances should provide subcortical tissues with variable nutritional quality that could lead to contrasting successional trajectories in saproxylic insect communities (Stokland and Siitonen 2012, Vindstad *et al.* 2014). Yet, subcortical and woody tissues attractiveness to beetles during their spring peak activity and food suitability for brood rearing may strongly steer the successional trajectories of early responding phloe- and xylophagous beetles.

In 2013, we started to study the early colonization, by saproxylic insects, of balsam fir trees/plots defoliated by the hemlock looper along a defoliation gradient. Our objectives

were 1) to determine if an early succession in the phloeo- and xylophagous beetle community occurs during a hemlock looper outbreak and 2) to determine how defoliation and other environmental variables are linked with species composition changes in the phloeo- and xylophagous beetle assemblages.

2 Methods

2.1 Study area

The study was conducted in the Parc national de la Jacques-Cartier (47°06' N, 71°20' W) and in the Forêt Montmorency (47°19' N, 71°09' W). Both sectors are located in the Laurentian Wildlife Reserve at about 70 km north of Québec City. The national park is a protected area which covers 670 km². Forest logging and extensive management has not been authorized since the park's creation in 1981 and thus its forest ecosystems have a high level of ecological integrity (Sépaq 2014). The Forêt Montmorency is an experimental forest owned and managed by l'Université Laval, in which scientific research and integrated forest management are carried out. The studied area belongs to the balsam fir-white birch bioclimatic domain, within the continuous boreal forest sub-zone (Saucier *et al.* 2011). Forest dynamics is mostly driven by insect outbreaks and windfalls (Leblanc and Bélanger 2000). Balsam fir stands dominate notably the forest matrix and black spruce, white spruce (*Picea glauca* (Moench) Voss.), white birch (*Betula papyrifera* Marsh.), American mountain-ash (*Sorbus americana* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are the most commonly found companion species.

2.2 Stand description

Aerial surveys were carried out by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP; named Ministère des Ressources naturelles et Faune or MRNF in 2012) to assess hemlock looper defoliation (MRNF 2012) in August 2012 and 2013. Evaluators delineated defoliated patches and, with a GIS software, the collected images were directly digitized and georeferenced. The delimited patches were classified as light (1–34%), moderate (35–69%) or heavy (70–100%) defoliation severity (MRNF 2012). Light defoliation represents a loss of foliage in the crown upper third of some trees in a stand. Moderate defoliation represents a loss of foliage in the crown upper third of most trees and on the full length of the crown of several trees. Heavy defoliation represents complete loss of foliage along the full crown length of most trees (MRNF 2012). During spring 2013, we selected 9 experimental balsam fir stands, splitted among these three hemlock looper defoliation classes (light, moderate and heavy) as well as three non-defoliated control stands for a total of 12 experimental stands.

Three 400 m² circular plots, spaced by at least 50 m, were established within each stand (total of 36 plots) for sampling insects and describe forest attributes. Four co-dominant balsam firs labeled as «sample trees» were selected in each plot for installing insect traps in spring 2013. The overall defoliation of the upper crown of each sample tree was estimated before the 2013 bud break (defoliation of 2012), from 0 to 100% by 10% classes, by two evaluators using binoculars. Defoliation was re-estimated on the same four sample trees before the 2014 bud break. In each plot, tree species and diameter at breast height (DBH; 1.3 m high) were recorded for every live or dead tree > 9 cm DBH. Four 11.28 m transects were drawn from the plot center toward each cardinal point to estimate the volume (m³/ha) of down dead wood (DDWV). Each woody debris larger than 5 cm, which intercepted transects, was identified whenever possible and its diameter was measured perpendicularly to the log at the intersection point (Warren and Olsen 1964). The DDWV was estimated according to Van Wagner (1968). Salvaged logging areas (ha), done in 2012 and 2013, were determined using ArcGIS in 500 m buffer zones around each plot.

2.3 Beetle sampling

Beetles flying in the selected balsam fir stands were sampled with a multidirectional flight-interception trap hanged on a rope tightly stretched between two trees near the center of each plot. The trap consisted of a 10 cm diameter black ABS cylinder positioned vertically to simulate a tree bole. Two rectangular Plexiglas[®] panes (15 x 40 cm) and two mosquito nets of the same size were assembled alternatively in cross shape around the cylinder. A 35 cm diameter plastic funnel, under which a 500 mL plastic collecting jar was attached, allowed collecting falling beetles. The collecting jar was equipped with an overflow netted hole on its upper half. A reverse plastic funnel was also placed on the top of the cylinder in order to collect beetles that could land on the mosquito net and then move upward. Another collecting jar (250 mL) was attached to a bottle on the top of the reverse funnel. Traps were installed so that the bottom base jar was at one meter above ground, thus intercepting beetles flying at DBH. Collecting jars contained 150 mL of 80% propylene glycol, which is unattractive to insects because of its low volatility (Skvarla *et al.* 2014), as killing and preserving liquid.

Beetles visiting trees were sampled using trunk-window traps (Kaila 1993, Boulanger and Sirois 2007). A trunk window-trap was installed at DBH on two randomly selected sample trees in each plot. The trap was made of a rectangular Plexiglas® panel (15 x 40 cm) screwed to the bole with two 90° angle brackets. A 15 cm plastic funnel was screwed to the bole underneath the pane under which a plastic collecting jar (500 mL) was attached. The collecting jar was equipped with an overflow netted hole on its upper half, and contained 250 mL of 80% propylene glycol.

Beetles emerging from previously colonized trees were sampled using emergence cages placed around the two other sample trees in each plot. A stainless steel net (40 mesh gauge, 0.381 mm openings) was vertically wrapped around tree bole centered on DBH and covering 60 cm of bole length. The upper part of the cage was sealed with a band of rubber foam, screwed with the net to the bole, and secured with foam sealant. Two large bendable polypropylene funnels were tacked to the bole and stapled to the net so that all insects emerging from the tree would fall in the funnels. Plastic collecting jars (500 mL) containing 250 mL of 80% propylene glycol, were attached to the funnels. In each of the 2013 and 2014 summer season, 36 multidirectional flight-interception traps, 72 trunk-window traps and 72 emergence cages were installed during the first week of June and operated until the last week of August. In 2014, the 72 emergence cages were installed on new sample-trees in each plot but the interception traps were not moved. Defoliation was re-estimated on the four “active” sample trees before the 2014 bud break. Samples were collected biweekly and insects were stored in a cold room (4°C) at the Laurentian Forestry Centre. All beetles were preserved but only Cerambycidae and Curculionidae were identified at the species level. Up to ten voucher individuals of each species were pinned, labelled and incorporated to the laboratory reference collection.

2.4 Statistical analysis

In order to determine if a succession of saproxylic beetles began rapidly during or after a hemlock looper outbreak, we first used principal component analyses (PCA) to compare the species assemblages in 2013 (2nd year of defoliation) and 2014 (3rd year after the beginning of the outbreak; no significant defoliation) without being constrained by environmental variables (Legendre and Gallagher 2001). Because each type of trap provides a different level of information about beetle succession in stands or trees

defoliated at various levels (multidirectional flight-interception traps for measuring adult flight activity of beetle within stands; trunk-window traps for measuring visit rates on trees; emergence cages for measuring tree colonization), we ran separate analyses for each type of trap. Beetles collected were pooled by trap for each sampling year and their abundances were Hellinger transformed to minimize the importance of double-zeros and thus reduce the weight of rare species (Legendre and Gallagher 2001). In addition, this transformation decreases the importance of the most abundant species, which may grow exponentially under favourable conditions (Legendre and Birks 2012) and may hide less abundant species in the ordinations. For each type of trap, a data table transformed in this way produces a matrix of Hellinger distances among sites (Legendre and Birks 2012) resulting in a correlation matrix used as a measure of association between all pairs of variables. Correlation biplots (scaling = 2), were used to express variation in saproxylic assemblages, as we wanted to emphasise the correlation between species and stand/tree. Beetle assemblages in traps placed in control plots approximate the pre-outbreak assemblage because defoliation had not manifestly altered trees and ecosystem. In order to facilitate interpretation about early succession, we averaged and showed the 2013 and 2014 trap score centroids to illustrate how beetle assemblage differed between years. We highlighted defoliation associated with each trap/stand using shapes and colors (control, light, moderate, heavy and dead for 100% defoliated trees and plots). Furthermore, only the predominating and the highly correlated species were identified on the biplots to facilitate interpretation.

Canonical redundancy analyses (RDA), the constrained form of PCA, were then used to express how annual variations in beetle assemblages were related to explanatory environmental variables (Legendre and Birks 2012). Six quantitative variables were used, two of them being a direct consequence of the hemlock looper outbreak: overall upper crown defoliation (mean plot defoliation for the multidirectional flight-interception traps and sample tree defoliation for the trunk-window traps and emergence cages) and basal area of dead balsam firs (m^2/ha). The four other variables were more generally related to the type and the amount of wood resource in each stand or in its immediate vicinity: basal area of hardwood (m^2/ha), basal area of softwood (m^2/ha), DDW volume (m^3/ha) and logged area (ha), in a 500 m buffer zone around the plot, as salvage logging was conducted to prevent extensive economic losses. Unlike PCAs, RDAs were computed separately for 2013 and 2014 because the environmental variables values varied among

years. Beetles collected were again pooled by trap and sampling year and submitted to Hellinger transformation before running the RDAs. To highlight the causes of changes in beetle assemblages, correlation triplots (scaling=2) were used again to express saproxylics variation but also to display relationships between them. Defoliation and predominant species were again highlighted as in PCAs.

In all ordinations, the length of each eigenvector is proportional to its specific variance and they cannot be compared directly (Zuur *et al.* 2007). The angles between eigenvectors (species or environmental variables) reflect their correlations: no correlation (90°), maximum positive correlation (0°) and maximum negative correlation (180°). PCAs and RDAs were computed with the R software using the *rda* function of the *vegan* package (Oksanen *et al.* 2015). From the same package, the *decostand* function was used to transform species abundances and the *vif.cca* function was used to test if the collinearity between variables could be problematic. An overall test of significance was done for each RDA by permutation (up to 999) of residuals under a full model for the joint effect of constraints (Legendre and Legendre 2012). The *anova.cca* function of the *vegan* package was used. The *ggplot* function from the *ggplot2* package (Wickham 2009) was used to plot the ordinations.

3 Results

Over the two years of the study, a total of 6445 adult Cerambycidae and Curculionidae were collected and identified to the species level whenever possible: 570 (30 species) were collected with multidirectional flight-interception traps, 755 (37 species) with trunk-window traps and 5120 beetles (19 species) with emergence cages (Table 1). Over 85% of beetles were collected in 2014. By far, the most abundant species was the striped ambrosia beetle (*Trypodendron lineatum* (Olivier)), with 5546 specimens (86.0%). Two other species of weevils, *Pissodes similis* Hopkins, *Rhyncolus macrops* Buchanan, and a scolytid, *Pityokteines sparsus* (LeConte), followed with respectively 232 (3.6%), 133 (2.1%) and 102 (1.6%) specimens.

3.1 Early succession of saproxylic beetles in defoliated balsam fir stands

Only beetle species with scores greater than 0.1, on at least one of the first two PCA axes, were highlighted on correlation biplots (Figure 2.1) and triplots (Figure 2.2) as the most influential species. Centroids of the two sampling years were in opposite directions for both multidirectional flight-interception trap and trunk-window trap PCA ordinations (Figure 2.1a-b), indicating that the beetle assemblage changed markedly between the two years. For both trap ordinations, the first axis (PC1) explained 29% and 27% of variation respectively, and was strongly influenced by *T. lineatum*, which was located on the right hand side of the axis. Along with *T. lineatum*, most of the heavily defoliated and dead trees/plots were located on the right side of both PC1 axes. In addition, both 2014 centroids were strongly and positively correlated with *T. lineatum*, with an opposite relationship with the 2013 centroids. Still for both trap ordinations, a more diverse beetle assemblage was observed on the left sides of the PC1s, along with most control and lightly to moderately defoliated trees/plots. The second PCA axis (PC2) accounted for 14% and 15% of variation respectively for each trap, and was moderately influenced by *R. macrops*, which was located on the upper side of the axes, and with no clear relation to defoliation. A cluster of several species was located in opposite directions to *T. lineatum* and *R. macrops* (on the lower left quadrant), and tended to be associated with control trees/plots and with the 2013 centroid. The pattern differed for the ordination based on emergence cages (Figure 2.1c) as PCA1 (38% variation) was less influenced by *T. lineatum* on its right hand side than by two *Pissodes* species (*P. dubius* (*striatulus*) and *P. similis*) on the left hand side. Most cages placed on dead trees clearly showed lower

scores for the two emerging *Pissodes* species in comparison with living trees, but showed high scores for *T. lineatum*. The PCA2 (21% variation) was strongly influenced by *T. lineatum* and *R. macrops* in opposite directions, with higher scores for *T. lineatum* in the cages of heavily defoliated and dead trees and an absence of relation with defoliation again for *R. macrops*. Centroids for the two years showed that in general, emergence cages had higher scores for *T. lineatum* and *Pissodes* in 2014 and higher scores for *R. macrops* in 2013. Emergence cages placed on control trees were near the center of the ordination, indicating very low variation caused presumably by very low rates of colonization during both years.

3.2 The variation in saproxylic beetle assemblages explained by environmental variables

Multicollinearity was tested (see Statistical analysis in Methods) and no variance inflation factors (VIF) was higher than 5. Multicollinearity was therefore present, but not problematic, resulting in valid ordinations for interpretation. Hair *et al.* (1995) showed that values less than 10 are indicative of inconsequential collinearity. No RDA carried out on 2013 data was significant. However in 2014, all RDAs were statistically significant (Multidirectional flight-interception trap: $F = 1.708$, $df = 6$ and 29 , $P = 0.015$; Trunk-window traps: $F = 3.083$, $df = 6$ and 65 , $P = 0.001$; Emergence cages: $F = 3.239$, $df = 6$ and 65 , $P = 0.001$). Overall, environmental variables accounted for 26, 22 and 23% of the variation in beetle assemblages in the three trap ordinations respectively. The first two RDA axes explained respectively 56% and 19% for multidirectional flight-interception trap, 75% and 10% for trunk-window traps and 78% and 11% for emergence cages (Figure 2.2). As in PCAs, the two flight interception traps showed similar patterns. In both triplots, *T. lineatum* was almost completely explained by the first axis along which it showed strong positive correlations with defoliation, dead balsam fir basal area, softwood basal area, and logged area around plots. Most traps placed in heavily defoliated plots or on dead trees were on the right hand side of both RDA1. With few exceptions, traps on the left hand side were associated with less defoliated (control to moderate) plots/trees and tended to be associated with hardwood basal area and weakly associated with several phloeophagous species. Those beetle species had generally low scores and were close to the origin but spread along both triplots second axes (RDA2), mostly linked with DDW volume and slightly with amount of hardwood in plots. In both triplots, except for *Polygraphus*

rufipennis, few species were strongly and positively correlated with DDW volume. In the emergence cages triplot, only *T. lineatum* was strongly linked to the right hand side of RDA1, and thus its score was strongly linked with defoliation but also with DDW volume and dead balsam fir basal area. The weevils *P. dubius* (*striatulus*) and *P. similis* and the scolytid *P. sparsus* were found on the left hand side of RDA1, being positively correlated with living softwood and hardwood basal areas, while being strongly and negatively correlated with *T. lineatum* and its associated environmental variables. Trees of almost all defoliation levels were spread along RDA2 to which no species was strongly linked, showing the particularity of emergence cage trapping, which was mainly composed of very low (near 0) colonization rates in living trees.

4 Discussion

Our results clearly show that a rapid succession of saproxylic beetles began after a hemlock looper outbreak. Centroids summarizing beetle community scores in PCAs, an ordination approach not constrained by environmental variables, were in opposite directions for the first two years after the beginning of the outbreak, attesting for rapid shifts in beetle community. This early succession was consistently characterized by a close association of the striped ambrosia beetle with heavily defoliated plots, with dead balsam firs and conifers. In multidirectional flight-interception and trunk-window trap ordinations, the 2013 related vectors were formed by saproxylic beetles associated with control and lightly defoliated plots/trees. Beetles such as *Evodinus monticola* and *Dryocoetes autographus*, which have been shown to be associated with closed canopy (undisturbed) balsam fir forests (Morin *et al.* 2015), were notably represented in the associations. On the other hand, the weevil *R. macrops* was notably present throughout the study but far away from the 2013 and 2014 centroids. It was not related to defoliation like all other beetle species and thus, it cannot be identified as an early succession species. In fact, *R. macrops* is thought to be associated with post-disturbance forest, as it was only collected in unsalvaged balsam fir stands previously affected by a spruce budworm outbreak (Norvez *et al.* 2013). Given that the forest matrix of the study area is somewhat composed of post-SBW stands (Leblanc and Bélanger 2000, Bélanger 2001), the omnipresence of *R. macrops* is thus not surprising. It was also caught in emergence cages, but in low numbers, closely linked with the 2013 centroid. Again, no clear link with defoliation could be seen and so far, the ecological niche of *R. macrops* remains to be determined. In 2014, we also observed increased tree colonization by *P. similis* and *P. dubius (striatulus)* in heavily defoliated trees but not in dead trees. Defoliation might have stimulated colonization by these two *Pissodes* species as their abundances increased more than twice in 2014. This pattern was not observed in flight-interception or trunk-window traps, indicating that these tools might not allow detecting less pronounced responses by such species. It is interesting to note that there was no discernable pre-outbreak beetle assemblage in trees, suggesting very poor tree colonization levels.

Environmental variables were significantly linked with beetle assemblages only in 2014 RDAs. For beetles flying in stands and visiting trees, a pre-outbreak assemblage characterized by several species with low abundances was still present in most control

and lightly or moderately defoliated stands. It contrasts with the predominance of *T. lineatum* in heavily defoliated stands in which tree mortality was observed. Logging around study plots was also associated with the presence of *T. lineatum*. Using multidirectional flight-interception traps inside the same study area, Morin *et al.* (2015) also noted increased flight activity of the striped ambrosia beetle in thinned stands where slashes and injured trees may have provided suitable habitat for this beetle, conditions that are also found after an insect outbreak. This striped ambrosia beetle is known to colonize slashes, stumps and woodpiles in salvaged areas, and fly to the nearest forest stands to overwinter (Kingham and Chapman 1959, Dyer and Kinghorn 1961). Alternately, the presence of *P. sparsus* on the emergence cages RDA triplot was opposite to *T. lineatum* on the first axis. A total of 76 beetles (among which 64 were *P. sparsus*) emerged from a single tree in a control plot. The tree was apparently healthy and undefoliated when the emergence cage was installed but it died during summer. No *T. lineatum* emerged from this tree, suggesting that it might not colonize trees potentially killed by other saproxylics. However, further investigations are needed to better understand saproxylic colonization in trees dying from senescence in green forest in order to determine if succession trajectories may differ from those observed in hemlock looper killed trees.

Dyer and Chapman (1965) noted that *T. lineatum* clearly preferred logs felled from August to January but did not attack those cut from February to May when exposed to both. Females are generally attracted by tree volatiles and they emit lineatin to attract both sexes to complete a massive attack. Several studies have shown that needle removal stresses trees and cause changes in monoterpene (e.g. α -pinene and β -phellandrene) qualitative and quantitative profiles which affect volatile emissions in foliar and subcortical tissues (Wallin and Raffa 1999, Caron *et al.* 2013). Wallin and Raffa (1999) suggested that these changes interact with tree attractiveness and susceptibility to saproxylic beetle colonization. In our study, balsam fir trees that died in late July 2012 were not colonized by any saproxylic. This suggests that there is a temporal window of opportunity for tree colonization by *T. lineatum*. Trees that were killed in late July 2012 could have dried to such an extent that they became unsuitable for *T. lineatum* colonization the following spring. Trees in these plots were not attractive to *T. lineatum* as shown by the presence of some “dead” plots/trees in opposite direction to the *T. lineatum* vector in ordinations for the two types of flight-interception traps. Some dead trees, being orthogonal to the *T. lineatum*

vector in the emergence cage triplot, also show unattractiveness and/or unsuitability for the beetle.

From an ecological perspective, tree colonization by *T. lineatum* is the first step in tree decomposition and it might have a very important role as it was essentially the only species to colonize massively balsam fir trees killed by the hemlock looper. Thus, it may act as a gateway species for other saproxylics (whether they are insects or fungi) that may need entry points in order to penetrate the woody material and further contribute to decaying dead wood. Tree colonization by this ambrosia beetle-fungus complex may weaken the snag structure, thus leading to faster tree felling and also certainly contributes to efficient nutrient recycling in wood biomass (Chen and Forschler 2016). Nutrient recycling and canopy opening may afterward lead to faster stand regeneration in comparison with heavily defoliated stands composed of un-colonized standing snags, which could decompose slowly.

Adversely, from an economical perspective, colonization by *T. lineatum* results in degraded lumber, hidden costs in extra processing of infested material, and rejection of export-bound products in commercial timber-producing areas (Nijholt 1979). This species is considered as an economic pest in many countries (Nijholt 1979). The degradation of sawlogs by ambrosia beetles, mainly *T. lineatum*, processed through the Vancouver log market in 1980/81 was estimated at \$63.7 million CAN (McLean 1985). In 2004, *T. lineatum* was still estimated to reduce log market values in United States by as much as 50% (Livingston 2004).

The multidirectional flight-interception traps and trunk-window traps are efficient tools to quickly detect early succession in the saproxylic beetle assemblage within disturbed stands and around disturbed trees, respectively. However, further studies should be conducted by collecting dead wood samples in order to understand the ecology of ubiquitous species, such as *R. macrops* and *P. rufipennis*, with emphasis on decay classes. Further studies should also be carried out on the impact of hemlock looper defoliation on tree physiology and chemistry in order to understand how the constitutive and induced defenses of balsam fir can prevent saproxylic colonization. It would also help

understanding why trees killed during early summer are unattractive for all species the following spring.

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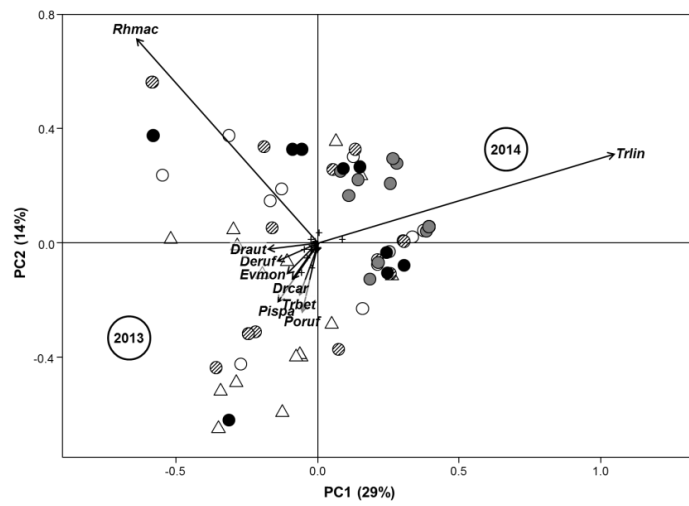
Tables

Table 2.1 Abundance of Cerambycidae and Curculionidae, captured in 2013 and 2014, with multidirectional flight-interception (MFIT), trunk-window (TWT) and emergence cage (EC) traps. Species marked in bold account for more than 1% of total capture.

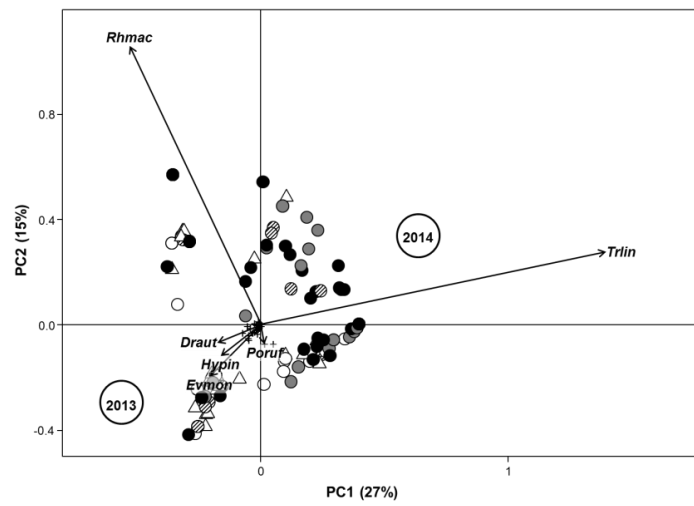
Family	Genus	Species	Authority	MFIT		TWT		EC		Total	% of total capture	
				2013	2014	2013	2014	2013	2014			
Cerambycidae	<i>Acræops</i>	<i>proteus</i>	(Kirby)	-	-	1	1	-	-	2	0.03	
	<i>Asemum</i>	<i>striatum</i>	(Linné)	-	-	-	1	-	-	1	0.02	
	<i>Evodinus</i>	<i>monticola</i>	(Randall)	5	5	10	7	-	1	28	0.43	
	<i>Microclytus</i>	<i>compressicollis</i>	(Laporte & Gory)	1	-	1	-	-	-	2	0.03	
	<i>Monochamus</i>	<i>s. scutellatus</i>	(Say)	1	1	-	1	1	-	4	0.06	
	<i>Phymatodes</i>	<i>dimidiatus</i>	(Kirby)	-	-	1	-	-	-	1	0.02	
	<i>Rhagium</i>	<i>inquisitor</i>	(Linné)	-	2	-	2	-	-	4	0.06	
	<i>Stictoleptura</i>	<i>c. canadensis</i>	(Olivier)	-	-	-	1	-	-	1	0.02	
	<i>Trachysida</i>	<i>mutabilis</i>	(Newman)	1	-	1	-	-	-	2	0.03	
	<i>Xestoleptura</i>	<i>tibialis</i>	(LeConte)	-	1	-	-	-	-	1	0.02	
	<i>Xylotrechus</i>	<i>undulatus</i>	(Say)	-	-	-	1	-	-	1	0.02	
	Curculionidae	<i>Anthonomus</i>	<i>rubricus</i>	Schenkling & Marshall	2	2	1	1	-	-	6	0.09
		<i>Barypeithes</i>	<i>pellucidus</i>	(Boheman)	1	-	-	-	-	-	1	0.02
<i>Cossonus</i>		<i>platalea</i>	Say	-	-	-	1	-	-	1	0.02	
<i>Hylobius</i>		<i>congener</i>	Dalla Torre <i>et al.</i>	-	-	-	1	-	2	3	0.05	
<i>Hylobius</i>		<i>pinicola</i>	(Couper)	1	-	11	12	6	5	35	0.54	
<i>Hylobius</i>		<i>warreni</i>	Wood	1	-	1	-	-	-	2	0.03	
<i>Pissodes</i>		<i>dubius (striatulus)</i>	Randall ((Fabricius))	-	4	4	5	7	32	52	0.81	
<i>Pissodes</i>		<i>rotundatus</i>	LeConte	-	-	-	-	-	2	2	0.03	
<i>Pissodes</i>		<i>similis</i>	Hopkins	5	6	23	12	54	132	232	3.60	
<i>Pseudanthonomus</i>		<i>validus</i>	Dietz	2	-	-	-	-	-	2	0.03	
<i>Rhyncolus</i>		<i>macrops</i>	Buchanan	23	22	29	35	17	7	133	2.06	
-		<i>sp.</i>	-	-	5	4	-	2	3	14	0.22	
(Scolitynae)		<i>Cryphalus</i>	<i>r. ruficollis</i>	Hopkins	2	2	2	8	-	1	15	0.23
		<i>Crypturgus</i>	<i>borealis</i>	Swaine	-	-	-	1	-	-	1	0.02
		<i>Dendroctonus</i>	<i>punctatus</i>	LeConte	-	-	1	-	-	-	1	0.02
	<i>Dendroctonus</i>	<i>rufipennis</i>	(Kirby)	2	4	1	-	-	-	7	0.12	
	<i>Dryocoetes</i>	<i>affaber</i>	(Mannerheim)	-	4	1	3	1	-	9	0.14	
	<i>Dryocoetes</i>	<i>autographus</i>	(Ratzeburg)	11	9	20	16	1	2	59	0.92	
	<i>Dryocoetes</i>	<i>betulae</i>	Hopkins	4	8	10	8	2	-	32	0.50	
	<i>Dryocoetes</i>	<i>caryi</i>	Hopkins	4	13	-	6	1	-	24	0.37	
	<i>Gnathotrichus</i>	<i>materiaris</i>	(Fitch)	2	-	-	2	-	-	4	0.06	
	<i>Ips</i>	<i>pini</i>	(Say)	-	1	-	-	-	-	1	0.02	
	<i>Orthotomicus</i>	<i>caelatus</i>	(Eichhoff)	-	-	-	1	1	2	4	0.06	
	<i>Phloeotribus</i>	<i>piceae</i>	Swaine	-	-	-	1	-	-	1	0.02	
	<i>Pityokteines</i>	<i>sparsus</i>	(LeConte)	2	12	-	19	-	69	102	1.58	
	<i>Pityophthorus</i>	<i>sp.</i>	-	-	-	1	-	1	2	0.03		
	<i>Polygraphus</i>	<i>rufipennis</i>	(Kirby)	11	16	9	21	1	4	62	0.96	
	<i>Scierus</i>	<i>annectans</i>	LeConte	7	3	2	-	-	-	12	0.19	
	<i>Trypodendron</i>	<i>betulae</i>	Swaine	9	6	-	2	-	-	17	0.26	
	<i>Trypodendron</i>	<i>lineatum</i>	(Olivier)	70	274	116	323	445	4318	5546	86.05	
	<i>Xylechinus</i>	<i>americanus</i>	Blackman	2	-	6	7	-	-	15	0.23	
	<i>Xyloterinus</i>	<i>politus</i>	(Say)	1	-	-	-	-	-	1	0.02	
Total				170	400	255	500	539	4581	6445	100.00	

Figures

a)



b)



c)

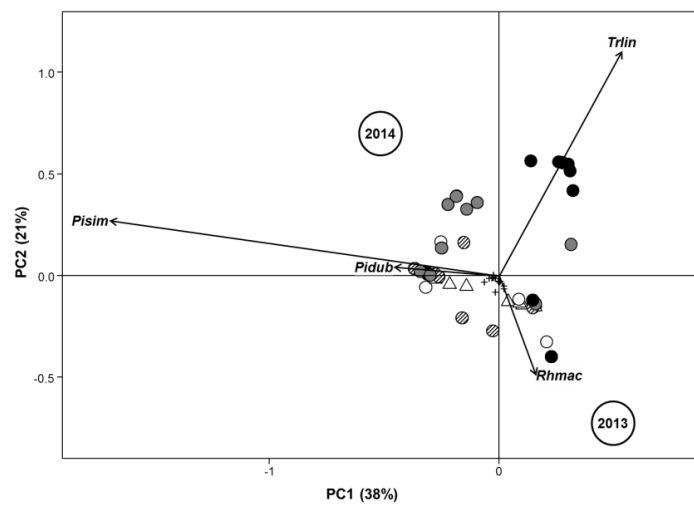
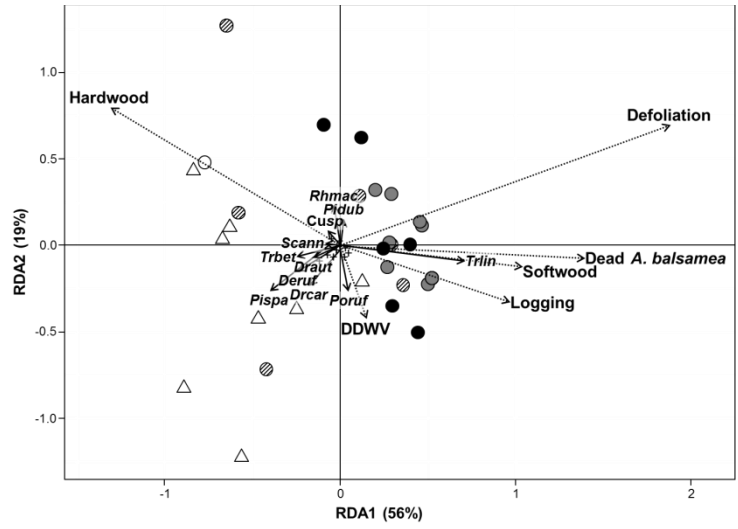
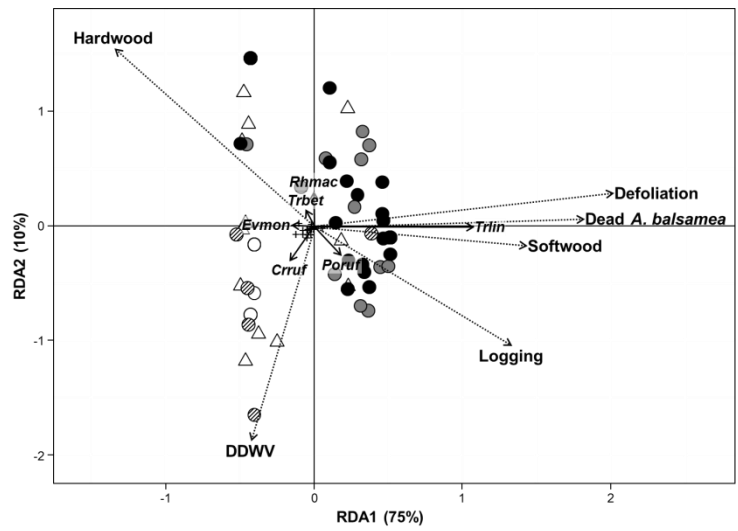


Figure 2.1 Principal components analyses (PCA) correlation biplots (scaling = 2) of the saproxylic beetle assemblages in balsam fir stands shortly (1–2 years) after a hemlock looper) outbreak in the Laurentian Wildlife Reserve. Biplots show ordinations of beetle assemblages in (a) multidirectional flight-interception traps, (b) trunk-window traps and (c) emergence cages. Dots show the position of each trap (or plot for multidirectional flight-interception traps), and dot filling represent the defoliation level: white for light, hatched for moderate, grey for high and black for dead. The white filled triangles represent the control plots or trees. Beetle species with a score < 0.1 are marked with a + symbol and species with a score > 0.1 are identified on their score coordinates by a species code. The species codes are the following: *Draut* (*Dryocoetes autographus*), *Drcar* (*Dryocoetes caryi*), *Deruf* (*Dendroctonus rufipennis*), *Evmon* (*Evodinus monticola*), *Hypin* (*Hylobius pinicola*), *Pispa* (*Pityokteines sparsus*), *Pidub* (*Pissodes dubius (striatulus)*), *Pisim* (*Pissodes similis*), *Poruf* (*Polygraphus rufipennis*), *Rhmac* (*Rhyncolus macrops*), *Trbet* (*Trypodendron betulae*), *Trlin* (*Trypodendron lineatum*). The 2013 and 2014 mean plot or tree scores are shown.

a)



b)



c)

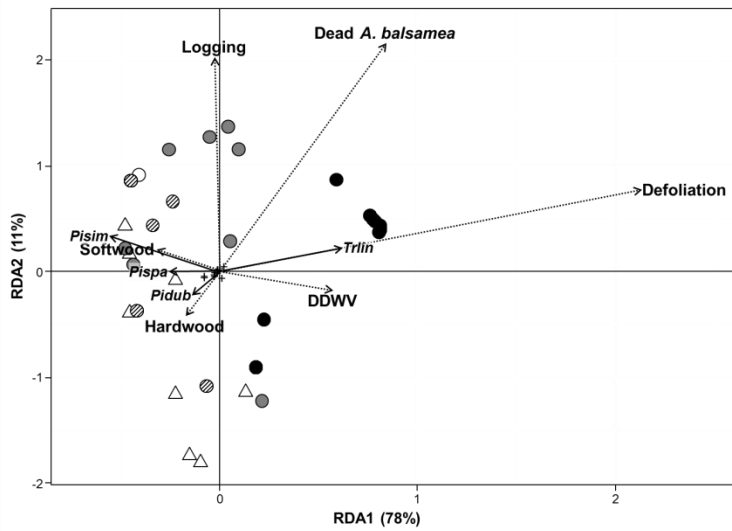


Figure 2.2 Canonical redundancy analyses (RDA) correlation triplots (scaling = 2) of the saproxylic beetle assemblages in balsam fir stands shortly two years after a hemlock looper outbreak in the Laurentian Wildlife Reserve and the variables explaining the species succession. Triplots show ordinations of beetle assemblages in (a) multidirectional flight-interception traps, (b) trunk-window traps and (c) emergence cages. Dots show the position of each trap (or plot for multidirectional flight-interception traps), and dot filling represent the defoliation level: white for light, hatched for moderate, grey for heavy and black for dead. The white filled triangles represent the control plots or trees. Beetle species with a score < 0.1 are marked with a + symbol and species with a score > 0.1 are identified on their score coordinates by a species code. The species codes are the following: *Crruf* (*Cryphalus r. ruficollis*), *Cusp* (*Curculionidae sp.*), *Draut* (*Dryocoetes autographus*), *Drcar* (*Dryocoetes caryi*), *Deruf* (*Dendroctonus rufipennis*), *Evmon* (*Evodinus monticola*), *Pispa* (*Pityokteines sparsus*), *Pidub* (*Pissodes dubius (striatulus)*), *Pisim* (*Pissodes similis*), *Poruf* (*Polygraphus rufipennis*), *Rhmac* (*Rhyncolus macrops*), *Scann* (*Scierus annectans*), *Trbet* (*Trypodendron betulae*), *Trlin* (*Trypodendron lineatum*). The dotted vectors represent the continuous explanatory variables: DDWV (down dead wood volume), Dead *A. balsamea* (dead balsam fir basal area), Defoliation (upper crown defoliation percentage), Hardwood (hardwood basal area), Logging (logged area in a 500 m buffer zone of the plot) and Softwood (softwood basal area).

Chapitre 3

Numerical response of the striped ambrosia beetle (Coleoptera: Curculionidae) to hemlock looper (Lepidoptera: Geometridae) defoliation in boreal balsam fir forests

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Résumé

Une récente étude sur la succession à court terme de coléoptères saproxyliques, après épidémie d'arpenteuse de la pruche, a montré la prédominance du scolyte birayé en peuplement gravement défoliés. Dans la présente étude, nous avons examiné la réponse numérique du scolyte le long d'un gradient de défoliation. Nos objectifs étaient de déterminer 1) un niveau de défoliation seuil initiant une colonisation massive du scolyte dans les sapins baumiers à l'aide de cages d'émergences fixées aux troncs et 2) la capacité des pièges à interceptions (multidirectionnels et fixés aux troncs) à prédire l'activité du scolyte. Les résultats montrent que la colonisation suit une réponse dichotomique et positive seulement lorsque l'arbre atteint un seuil de 95% de défoliation deux ans après le début de l'épidémie. Tôt au printemps 2014, de tels sapins possédaient 55% de chances d'être colonisés massivement par le scolyte et jusqu'à 91% lorsque entièrement défoliés. Ensuite, nous recommandons l'utilisation de pièges à impacts fixés aux troncs pour prédire la colonisation des arbres par le scolyte birayé afin d'aider les gestionnaires forestiers responsables des opérations de récupération.

Mots clés: Arpenteuse de la pruche; Scolyte birayé; Seuil de défoliation; Colonisation massive; Pièges à impact fixé au tronc.

Abstract

A recent study on the short-term succession of saproxylic beetles, after a hemlock looper outbreak, has pointed towards the predominance of the striped ambrosia beetle in severely defoliated stands. In this present study, we investigated the numerical response of this beetle along a defoliation gradient. Our objectives were to determine 1) a defoliation threshold that initiates massive beetle colonization of balsam fir with emergence cages placed on trees and 2) if we could forecast the beetle activity with flight-interception traps (multidirectional and trunk-window traps). Results show that the colonization follows a dichotomous and positive response only when a tree reaches a defoliation threshold of 95% two years after the beginning of the outbreak. In early spring 2014, the probability that balsam firs defoliated at this threshold experience a massive colonization was of 55% and it could reach 91% when total defoliation was attained. Then, we recommend using trunk-window traps for predicting tree colonization by the striped ambrosia beetle to assist forest managers responsible of salvage logging plans.

Keywords: Hemlock looper; Striped ambrosia beetle; Defoliation threshold; Massive colonization; Trunk-window trap.

1 Introduction

Trees killed by natural disturbances are usually colonized by bark and wood boring insects (Langor *et al.* 2008). In eastern North American boreal forests, most studies have addressed insect succession after wildfire (Saint-Germain *et al.* 2004c, Boulanger and Sirois 2007, Azeria *et al.* 2012) but few have dealt with insect defoliator outbreaks and none specifically with the hemlock looper, *Lambdina fiscellaria* (Guenée) (Lepidoptera: Geometridae). The hemlock looper is known as the second most important insect defoliating conifers in eastern North America, after the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Hébert and Brodeur 2013). Both defoliators feed on balsam fir, *Abies balsamea* (L.) Mill., on which the most important damage are also recorded. The spruce budworm mainly feeds on current-year needles while the hemlock looper chews on needles of all age classes without eating them completely (Hébert and Jobin 2001, Iqbal and MacLean 2010). Because of this wasteful feeding behaviour, the hemlock looper can kill trees within one or two years (Otvos *et al.* 1971, 1979), which is much faster than for the spruce budworm, fir mortality beginning only after 4-5 years of severe budworm defoliation (Blais 1958, MacLean 1980). Hence, distinct post-disturbance succession of saproxylic insects may occur in killed balsam fir trees after budworm or looper outbreaks.

Hemlock looper outbreaks are usually observed in remote areas but in 2012, a first outbreak was detected in the Laurentian Wildlife Reserve, a highly accessible area near Quebec City, in eastern Canada. This provided an opportunity to study early succession of saproxylic insects in defoliated or recently killed balsam fir trees by the hemlock looper (Chap. 2). A succession began during the 2nd year after the beginning of the outbreak and this succession was dominated by the striped ambrosia beetle (*Trypodendron lineatum* (Olivier)), in the most severely defoliated stands. This ambrosia beetle is a Holarctic species known to overwinter as adults in forest duff or in the bark of the lower part of tree boles (Dyer and Kinghorn 1961). In fact, adults emerge in late-summer or early-fall and rapidly seek overwintering sites (Bright 1976). After a winter reproductive diapause, the new brood matures and emerges in early spring (Borden 1988). They fly and swarm only when temperature exceeds 15.5°C (Chapman and Kinghorn 1958, Shore *et al.* 1987). The heaviest attack period occurs in early spring (Bright 1976) and especially when the temperature exceeds the 15.5°C threshold for several successive days (Chapman and

Nijholt 1980). When a breeding pair has selected a suitable tree for colonization, adults inoculate wood with blue stain fungi (symbiotic ambrosia fungi; Bakshi 1950, Beaver 1989), when they bore into bark and reach sapwood. They cultivate fungi as it is their main food source for both adults and larvae development (Beaver 1989). The striped ambrosia beetle is known to respond to semiochemicals (Salom and McLean 1990). Alpha-pinene, a common monoterpene of conifer oleoresin, and ethanol, which is produced by micro-organism anaerobic activity in stressed, dying and decaying plants, were found to be highly attractive to striped ambrosia beetle field populations (Graham 1968, Borden 1988).

To our knowledge, no study has addressed the colonisation by the striped ambrosia beetle of trees killed by insect defoliators in the boreal forest. This is important as the beetle is considered as an economic pest in many countries (Nijholt 1979). The conspicuous black stained pinholes and galleries excavated by the striped ambrosia beetle have degraded timber value by \$63.7 million CAN (McLean 1985) in British Columbia, Canada, in 1980-1981. In 1994, the timber value downgrading ranged from \$3.27 to \$77.40 CAN/m³, depending on tree species and grade (Orbay *et al.* 1994). In 2004, losses caused by this species were estimated at least at 50% of wood value in United States (Livingston 2004). Consequently, quantifying the numerical response of the striped ambrosia beetle to hemlock looper defoliation and developing tools to detect potential massive colonization is clearly needed as such colonization could downgrade large stocks of standing defoliated trees.

In this paper, we studied the numerical response of the striped ambrosia beetle to hemlock looper defoliation, one and two years after the beginning of the outbreak. We hypothesized that a temporal window exists for colonization by the beetle, defined by defoliation threshold and by the time since tree death. Our first objective was to determine the defoliation threshold that initiates massive beetle colonization in balsam fir trees. Our second objective was to determine if we could forecast massive colonization by simply sampling beetles visiting trees or flying in a stand with flight interception traps.

2 Methods

2.1 Study area

The study was carried out in two sectors of the Laurentian Wildlife Reserve both located at about 70 km north of Québec City. The Parc national de la Jacques-Cartier (47°06' N, 71°20' W) is a 670 km² protected area where forest ecosystems have a high level of ecological integrity as forest logging is forbidden since its creation in 1981 (Sépaq 2014). The Forêt Montmorency (47°19' N, 71°09' W) is an experimental forest owned and managed by l'Université Laval where integrated forest management and scientific research are conducted. Within the continuous boreal forest sub-zone, the Laurentian Wildlife Reserve belongs to the balsam fir-white birch bioclimatic domain (Saucier *et al.* 2011). At a landscape scale, stands are dominated by balsam fir but black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss.), white birch (*Betula papyrifera* Marsh.), American mountain-ash (*Sorbus americana* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are frequently found as companion species in the reserve.

2.2 Stand description

In August 2012 and 2013, the Ministère des Forêts, de la Faune et des Parcs (MFFP; named Ministère des Ressources naturelles et de la Faune or MRNF in 2012) carried out aerial surveys to assess hemlock looper defoliation (MRNF 2012). Evaluators overlaid the collected data on ecoforest maps using a Geographic Information System and classified the delimited defoliated patches as light (1–34%), moderate (35–69%) and heavy (70–100%) severities (MRNF 2012).

During early spring 2013, we selected 9 balsam fir stands, splitted among these three hemlock looper defoliation classes as well as three non-defoliated control stands for a total of 12 stands. Within each selected stand, three 400 m² circular plots spaced by at least 50 m were established for sampling saproxylic beetles. Four co-dominant balsam firs were selected in each plot for installing insect traps. The overall defoliation of the upper crown of each selected tree was estimated, from 0 to 100% by 10% classes, by two observers using binoculars before 2013 bud break. Defoliation was re-estimated on the same four sample trees before 2014 bud break.

2.3 Beetle sampling

Striped ambrosia beetles which have colonized trees were sampled using emergence cages placed around the boles of two co-dominant balsam fir trees in each plot. Cages were made with a stainless steel net (40 mesh gauge, 0.381 mm openings) covering 60 cm in length and centered on the tree DBH. The upper part of the cage was sealed with a band of rubber foam. The net and the band were then vertically wrapped, screwed to the bole and isolated with foam sealant. Two custom bendable funnels made of polypropylene were tacked to the bole and stapled to the net. Emerging beetles from the encaged part of the bole could not escape from the cage and eventually fell into collecting jars (500 mL) containing 250 mL of 80% propylene glycol, attached and tightened at the base of the large funnels. Propylene glycol is unattractive to insects mainly because of its low volatility (Skvarla *et al.* 2014). An overflow netted hole was supplied on the upper half of each jar.

Striped ambrosia beetles which visited trees were sampled using trunk-window traps (Kaila 1993, Boulanger and Sirois 2007). Traps were made with a rectangular Plexiglas[®] pane (15 x 40 cm) over a 15 cm funnel, both screwed with metal brackets to tree bole. A collecting jar (500 mL), supplied with a netted overflow, was attached under the funnel and filled with 250 mL of 80% propylene glycol. Traps were installed at DBH on two co-dominant balsam fir trees in each plot.

Striped ambrosia beetles that flew within a stand were sampled using multidirectional flight-interception traps. One flight-interception trap was hanged on a rope tightened between two trees at the center of each plot. Traps were made of a 10 cm diameter black ABS cylinder which was vertically positioned in order to simulate a tree bole. In a cross shape, two mosquito nets and two rectangular Plexiglas[®] panels (15 x 40 cm) radiated from the cylinder. Intercepted flying beetles then fell into a 35 cm diameter funnel, under which a 500 mL collecting jar, again supplied with a netted overflow, was attached. Another reverse funnel was attached above the cylinder and the pane cross in order to collect beetles which moved upward after interception. A bottle and a second collecting jar (250 mL) were attached to the top of the reverse funnel. Traps were installed at DBH height. Collecting jars contained 150 mL of 80% propylene glycol.

Overall, 72 emergence cages, 72 trunk-window traps and 36 multidirectional flight-interception traps were installed during the first week of June and operated until the last week of August of both 2013 and 2014. In 2014, before bud break, new emergence cages were installed on two other co-dominant balsam fir trees, on which defoliation was estimated. Defoliation was also re-estimated on balsam fir trees supplied with trunk-window traps. Beetle samples were collected biweekly and stored in a cold room (4°C) at the Laurentian Forestry Centre until processed for sorting, identifying and counting.

2.4 Statistical analysis

In order to assess the numerical response of the striped ambrosia beetle to hemlock looper defoliation, we used generalized linear mixed models (GLMM) for emergence cages as well as for both types of interception traps. Seasonal collections of beetles were pooled by trap for each year (total of six data sets) and a series of GLMMs were produced for each data set. Poisson Generalized linear models (GLM) were first used to check assumptions concerning data independence, distribution of residuals, variance structure and the presence of outliers. We used the *c_hat* function of the *AICcmodavg* package (Mazerolle 2015) to check if overdispersion occurred in the models, in which case we used the negative binomial distribution. Binomial GLMs (logistic regression) were used simultaneously to determine beetle colonization probabilities as a function of defoliation. The nested or random effects (between plots and between sites) based on the two levels of data nestedness were specified in the models. Fixed and random intercepts and slopes were estimated using the Laplace approximation (Bolker *et al.* 2009). Mixed-effect models best generalize when they include the maximal random effect structure (Barr *et al.* 2013). Overfitting the data with a maximal model, in case of negligible variation, has only minimal consequences for Type I error and power whereas underfitting the design can incur levels of anticonservativity with little real benefit to power (Barr *et al.* 2013). The regressions were produced with the R software using the *confint* and *glm* functions from the *stats* package (R Core Team 2014), the *glm.nb* function from the *MASS* package (Venables and Ripley 2002), the *glmer* and *glmer.nb* function from the *lme4* package (Bates *et al.* 2015) and the *ggplot* function from the *ggplot2* package (Wickham 2009) was used to plot the regressions.

3 Results

3.1 Colonization rates vs tree defoliation

Over the two years, 4763 specimens were collected in emergence cages, 445 in 2013 and 4318 in 2014. Abundance data structure prevented the use of GLMMs and even GLMs. Figure 3.1 shows the numerical response of the striped ambrosia beetle as a function of defoliation. The figure shows that very few beetles (1 to 5 but most often 0) emerged from trees except for those that were very heavily defoliated (95%–100%) in which massive colonization (over 100 beetles/cage) occurred, mainly in 2014 (Figure 3.1b). Logistic regression was better suited to provide estimates of the probability of colonisation along the defoliation gradient. In 2013, the relationship was not significant but in 2014, the probability of colonisation significantly increased as a function of defoliation ($P = 0.036$) (Figure 3.2). There was a $7.621 \cdot 10^{-5}$ odd that an undefoliated balsam fir could be colonized by striped ambrosia beetles. There is an 11% (SE: 5.127, Wald 95% CI: 0.713–22.654) increase in the odds for a 1% increase of defoliation. The random effects (random intercept and defoliation SDs) caused by variation between sites (3.182 and 0.046) and between plots within site (3.914 and 0.039) were both of the same magnitude as their corresponding fixed effect in log odds (-9.482 and 0.106). Figure 3.2 shows that these major variations occurred generally when defoliation increased. Colonisation probabilities of striped ambrosia beetles showed a funnel shaped scatter plot, explained by strong variability in heavily defoliated sites and plots but the exponential response was largely explained by the increasing defoliation. By looking at the abundance data (Figure 3.1b), we noted that balsam firs were nearly not colonized along the defoliation gradient until massive colonization started to occur when firs reached 95% of cumulative defoliation in spring 2014. At this threshold, firs had 55% (ranging up to 77%) as predicted with the random effects chances to be massively colonized by the striped ambrosia beetle two years after the beginning of the hemlock looper outbreak. Furthermore, when trees were totally defoliated by spring 2014, they reached the maximum modeled colonisation probabilities of 62% (also ranging from 32%–91%) chance to be massively colonized by the striped ambrosia beetle. We can note that the smoother in the Figure 3.2, as modelled without random effects (GLM), show generally higher colonization probabilities for trees under 75% of defoliation while it is better fitted in the funnel for balsam fir trees over 75%. The predicted colonisation probabilities with the both fixed and random effects show that both defoliation and plot/site effect actually start to induce variation at 75% of defoliation.

However, except for one cage in 2013 and another one in 2014, all balsam fir trees that were totally defoliated in late July 2012 were not or only very slightly colonized as shown in Figure 3.1 by the red dots. In Figure 3.2, their low probability of being colonized was displayed by the large red dot at 100% defoliation, thus notably contrasting with all other completely defoliated trees that were massively colonized (as displayed by the large black dot at the highest probability). In fact, all trees of the three plots of a single site (6 cages per year) were completely defoliated and killed in late July 2012. Among these 12 trees on which emergence cages were installed, only one tree was colonized (89 emerged beetles) by the striped ambrosia beetle in 2014.

3.2 Visit rates vs tree defoliation

Over the two years, 439 specimens were collected with trunk-window traps, 116 in 2013 and 323 in 2014. In 2013, the relationship was not significant but in 2014 striped ambrosia beetle abundance increased significantly as a function of defoliation ($P < 0.001$) (Figure 3.3b). The model predicts that only 0.092 striped ambrosia beetle visit undefoliated balsam firs and that there is an expected numerical response of beetle of 1.043 (SE: 1.011, Wald 95% CI: 1.021–1.065) for a 1% increase in defoliation which is a positive exponential response with a slow growth rate (Figure 3.3b). The random effects caused by variation between plots within site (1.226 and 0.012) were both of the same magnitude as their corresponding fixed effect in log counts (-2.383 and 0.042). The Figure 3.3b shows that these variations occurred generally when defoliation increased. Predicted visit responses of striped ambrosia beetles show a funnel shaped scatter plot, caused by strong plot variability but the exponential response was largely explained by increasing defoliation. The highest visit responses were clearly on completely defoliated balsam firs. Traps set on balsam firs that were completely defoliated in late July 2012 (red dots; 6/10 being the completely defoliated site in late July 2012) caught very few striped ambrosia beetles (in some cases with no capture at all), thus restraining the exponential response of the model, as for the emergence cages. However, few other traps set on tree dying and dead in 2013, which were supposed to be attractive, also restrained the response of the model with low captures.

3.3 Flight activity vs stand defoliation

Over the two years, 344 striped ambrosia beetles were collected with the multidirectional flight-interception traps, 70 in 2013 and 274 in 2014. In both 2013 and 2014, no significant relationship was obtained between beetle abundance and defoliation. However, because of the presence of an outlier in 2014 (Figure 3.4b) which brought enormous variance into the model (very high beetle abundance in one heavily defoliated plot), we produced another model without this outlier and the relationship then became significant ($P = 0.011$) (Figure 3.4b). The model predicts that only 0.719 striped ambrosia beetle fly in undefoliated balsam fir stands and that there is an expected numerical response of beetle of 1.026 (SE: 1.010, Wald 95% CI: 1.006–1.047) for a 1% increase in defoliation which is a positive exponential response with a growth rate that is even slower than for the tree visit rates (Figure 3.4b). The random effects caused by variation between sites were both approximately of 0 ($8.222 \cdot 10^{-5}$ and $9.930 \cdot 10^{-7}$), thus implying undetectable variation between sites. Figure 3.4b shows weak variability between sites unlike the two other traps numerical responses as predicted flying responses follow the smoother. The numerical response of striped ambrosia beetles is largely explained by the almost flat but exponential curve of increasing defoliation. The highest responses were recorded in completely defoliated stands. It also shows that very few striped ambrosia beetles flew in stands that were completely defoliated in late July 2012 (red dots; 3/4 of them being in the completely defoliated site in late July 2012), thus restraining again the exponential response of the model. Again, few other traps set in heavily defoliated stands in 2013, which were supposed to be attractive, also restrained the response of the model with low captures.

4 Discussion

Our study demonstrates that the striped ambrosia beetle massively colonized heavily defoliated ($\geq 95\%$) or recently killed balsam fir trees following hemlock looper defoliation. We also showed that flight-interception traps can be useful tools to detect beetles visiting trees and flight activity in stands as similar numerical response patterns to defoliation was observed. Stands and trees defoliated over 70% showed greater flight activity and higher visit frequency respectively than less defoliated ones. Moreover, the same pattern was observed with respect to the hypothesized asynchrony between the time of tree death and *T. lineatum* attack period. This asynchrony has kept colonization and visit rates much lower on balsam firs killed in late July 2012. Lower flight activity was also recorded in such conditions. These results are unique because, as far as we know, it is the first study to address the numerical response of the striped ambrosia beetle to tree defoliation in northeastern North America. Except for Belyea (1952; part 1), which exclusively observed attacks and counted *T. lineatum* pinholes on balsam fir defoliated by the spruce budworm in Ontario, no study has aimed to understand the colonization by *T. lineatum* of insect killed trees.

4.1 Host selection and colonization processes

By looking at the three numerical responses, we can note that the flight interception trapping data provide continuous and exponential responses along the defoliation gradient while the colonization pattern is more a dichotomous type response. Hence, this species can detect and find suitable stands at landscape level but the host selection of dying/recently dead balsam fir trees apparently fits in a small window of time and tree physiological status.

Defoliation induced physiological changes in composition and emission of various coniferous tree defensive compounds, mostly terpenoids, have been shown for both the Jack pine budworm, *Choristoneura pinus pinus* Freeman (Wallin and Raffa 1999) and the spruce budworm (Caron *et al.* 2013). However, emission of volatile compounds is bounded by the tree production capacity. Monoterpenes require carbon and its production is influenced by local nutrients stored and needle new photosynthate formation (Deslauriers *et al.* 2015). Insect defoliation also affects the production of defensive compounds that are attractive to beetles, stopping metabolic activity and thus stopping production and

transport of these compounds through vascular system. For balsam firs that died from extremely heavy defoliation in late July 2012, after only six weeks of defoliation, the production of defensive compounds may have occurred over a very short period. Moreover, drying of subcortical tissues from late summer to the following spring may have slowed or stopped microorganism decaying activity and reduced ethanol emission, thus leading to a low spring emission of an important olfactory cue for the striped ambrosia beetle. On the other hand, balsam firs that experienced defoliation stress over a longer period (e.g. fir trees which died during winter 2013 or 2014) were more likely to emit attractive volatile compounds over a longer period. Such volatiles might not be released (or below a threshold to which beetles respond) in undisturbed forest and from lightly defoliated trees.

As Wallin and Raffa (1999) suggested, total monoterpene production tend to be linked with carbon allocation and therefore defoliation. Some of their results showed a strong and consistent inverse relationship between defoliation level and induced monoterpene concentration in foliage but also in phloem. They also reported that injury to foliage resulting from defoliation causes chemical changes in other tissues, like phloem. These changes can be even greater in the uninjured tissue than in the foliage. It may seem contradictory that the most severely defoliated trees may contain lower amounts of defensive compounds in subcortical and woody tissues but also emit greater amounts of primary attractants like distinct defensive compounds. However, several mechanisms have been proposed to explain this contradiction. For instance, the stress duration, how the stress impact on the regulation of constitutive and induced defensive mechanisms, and the difference in composition and concentration of defensive compounds that are volatiles emitted into the environment versus those confined in tree tissues (Wallin and Raffa 1999) may all be involved.

Furthermore, when populations of the striped ambrosia beetle colonize trees, slashes, stumps or woodpiles in salvaged area, a large brood is produced and adults can fly to the nearest stand by the end of summer to overwinter (Kinghorn and Chapman 1959; Dyer and Kinghorn 1961). By the following spring, greater amount of beetles fly in stands where massive overwintering occurred and this positive feedback loop may be repeated until the supply of suitable hosts ceases. As reported in Chap. 2, the striped ambrosia beetle is mostly important in severely defoliated stands located in the direct vicinity of recently

logged areas. In fact, several stands close to our study sites in the Forêt Montmorency were salvaged after hemlock looper defoliation in 2012 and 2013. The striped ambrosia beetle may have used the residual debris to produce large broods and overwinter in stands just apart our sampling plots. Hence, in early spring 2014, such increasing populations may have emerged from overwintering sites, selected and massively colonized vulnerable fir trees ($\geq 95\%$ defoliation or died after summer 2013).

4.2 Forecasting massive colonization to improve salvage logging

Okland (1996) and Kaila *et al.* (1997) reported that trunk-window traps were efficient for comparing different substrates within the same forest environment even if numerical responses were not necessarily high. Here, we corroborate those conclusions and we propose that high abundances obtained through the use of attractants are not required to obtain significant results. Moreover, trunk-window traps are useful and efficient in studies involving a link with continuous variables at the tree level such as defoliation. From a practical point of view, trunk-window traps provide a closer link between beetles and defoliation as the experimental unit is single trees compared with the multidirectional flight interception trap which provide a relationship at the stand level. For this reason, we recommend the use of trunk-window traps to forecast massive colonization by the striped ambrosia beetle.

Once conspicuous hemlock looper defoliation is recorded in a forest stand, trunk-window traps should be installed on several co-dominant balsam firs and their defoliation level should be followed throughout the outbreak. In order to improve forest management during an outbreak, salvage logging should be planned by taking into account that recently harvested stands or any available conifer woody material could fasten beetle population build-ups. Heavily defoliated stands left apart salvaged areas should be targeted first in new salvage logging plans. If stands could be harvested in early summer and timber processed rapidly, it would reduce economic losses and beetle population. In fact, such practice would act as “trap stand”. Post-hemlock looper salvage logging could then be confined and prescribed quickly when required and prevented when irrelevant, thus optimizing forest management.

Further studies must deal with the effect of defoliation severity on tree defensive mechanisms, particularly volatile emission, and how it stimulates or repels saproxylic insects. In addition, studies on the impact of the striped ambrosia beetle on timber value should be updated for the eastern North American context, particularly for balsam fir as it is affected by two major insect defoliators, the spruce budworm and the hemlock looper.

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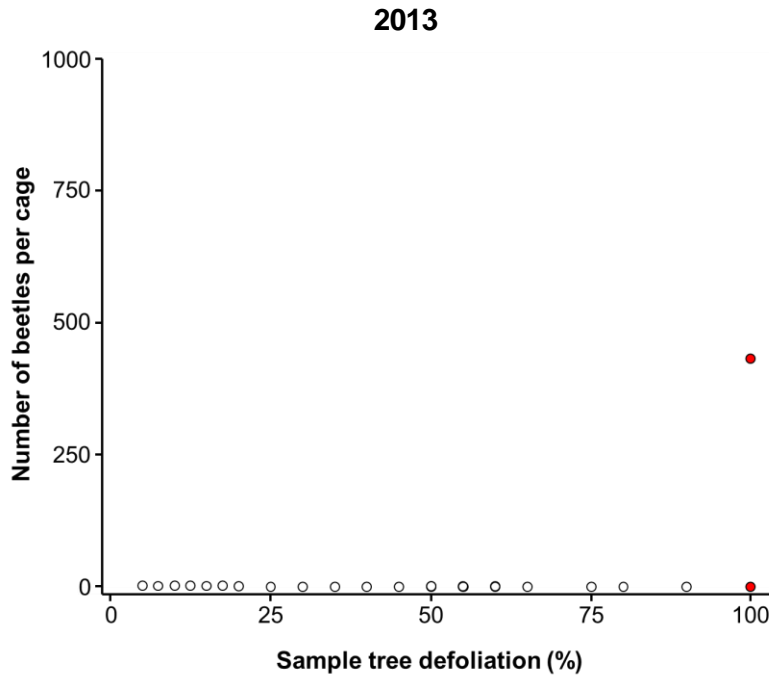
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Figures

a)



b)

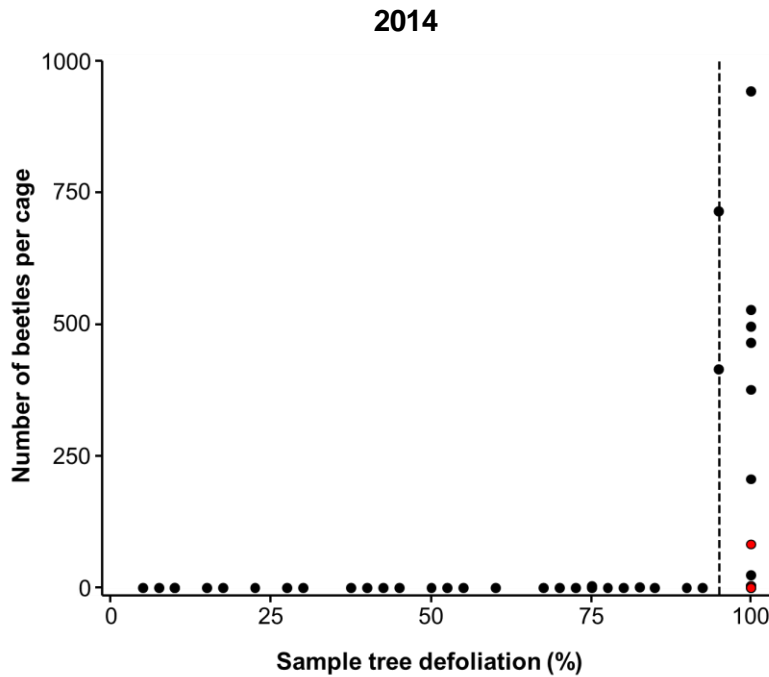


Figure 3.1 Abundance scatter plot of striped ambrosia beetles (*Trypodendron lineatum*) as sampled by emergence cages in relation with upper crown overall defoliation. Cages placed on fir trees totally defoliated in 2012 are in red. Dashed vertical line represents the defoliation threshold at which massive emergences occurred. a) 2013 collect. b) 2014 collect.

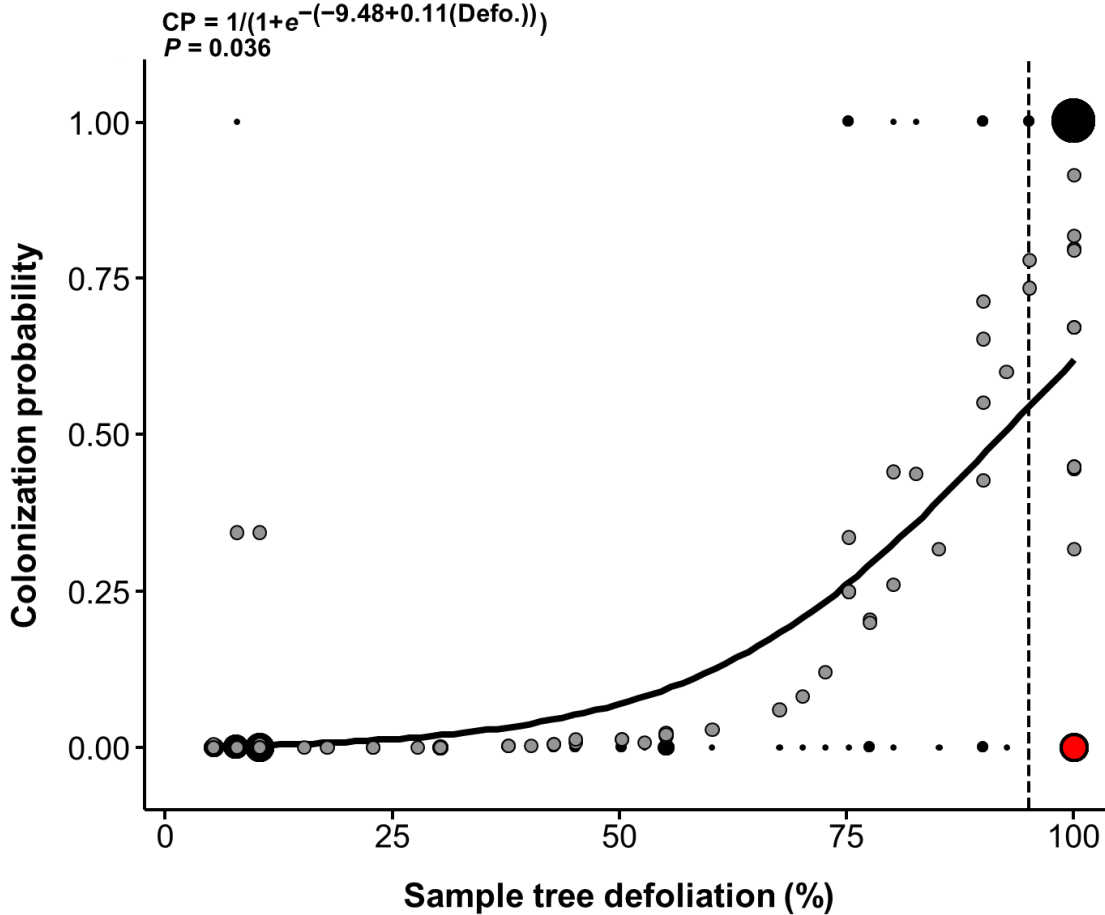
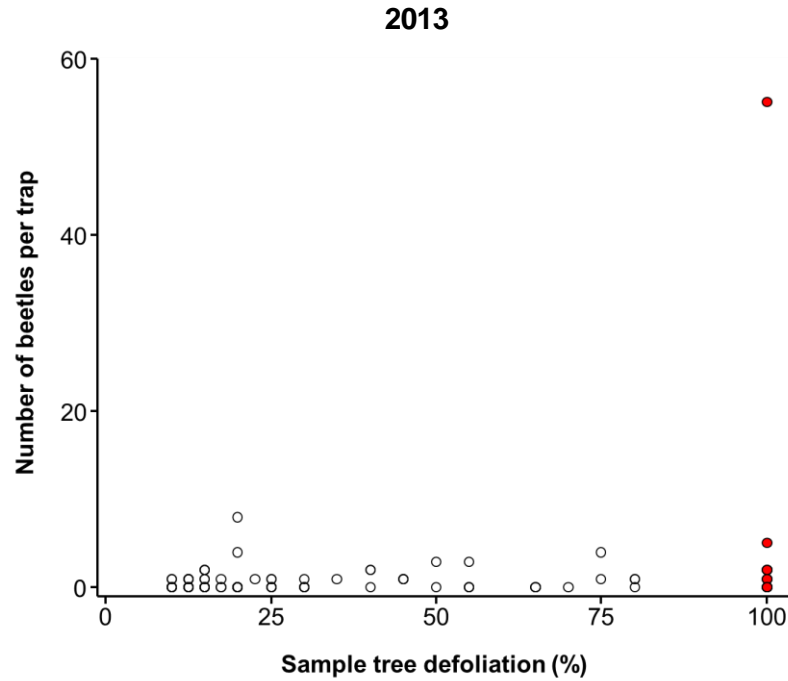


Figure 3.2 Results of binomial (GLMM) regressions between upper crown overall defoliation and the 2014 presence/absence of striped ambrosia beetles (*Trypodendron lineatum*) as sampled by emergence cages. Black points represent occurred events and their size represents the event frequencies at a defoliation status. Points at 0.00 represent absences while points at 1.00 represent presences. Cages placed on fir trees totally defoliated in 2012 are in red. Dashed vertical line represents the defoliation threshold at which massive emergences occurred. Predicted colonisation probabilities with fixed and nested effects are represented by grey points.

a)



b)

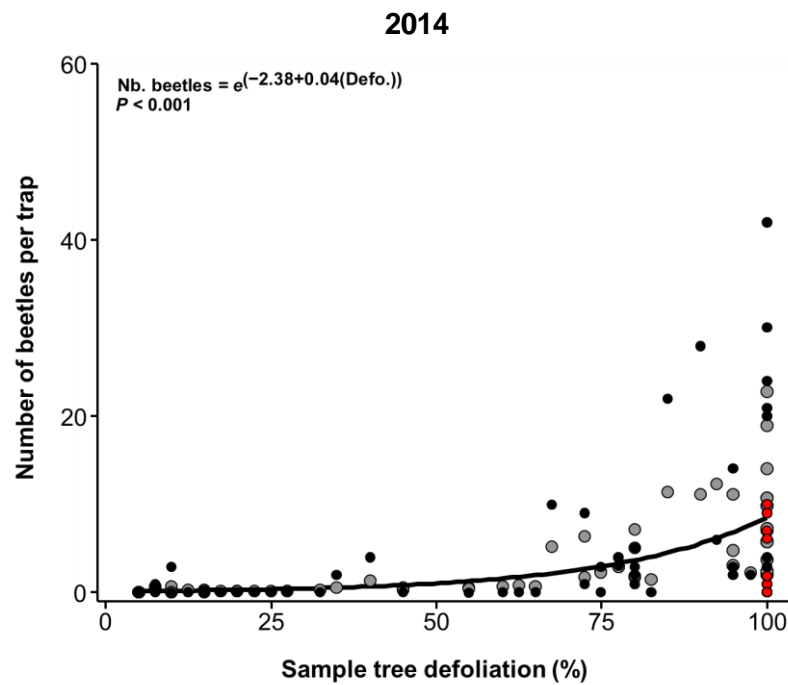
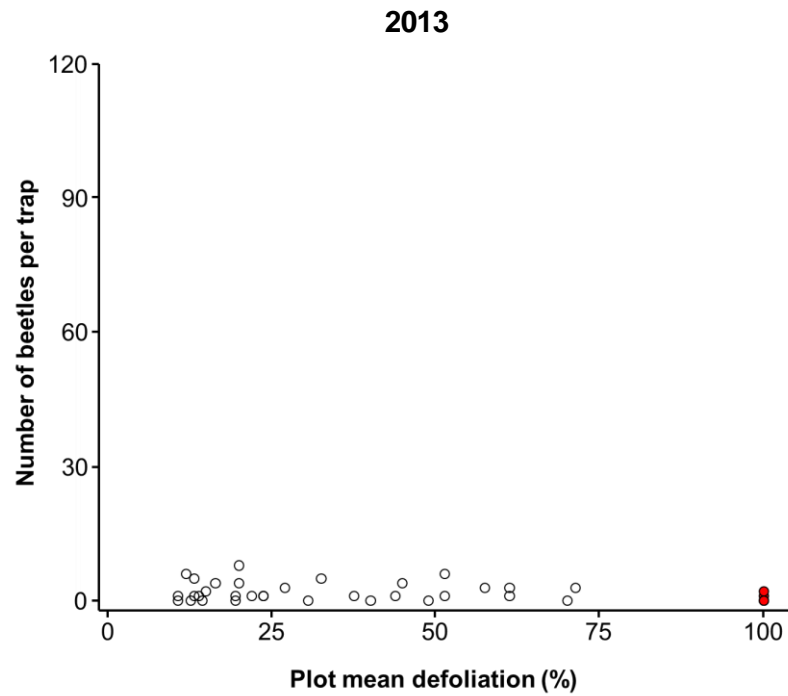


Figure 3.3 Results of negative binomial (GLMM) regressions between upper crown overall defoliation and the abundance of striped ambrosia beetles (*Trypodendron lineatum*) as sampled by trunk-window traps. Traps placed on fir trees totally defoliated in 2012 are in red. Predicted abundances with fixed and nested effects are represented by grey points. a) 2013 collect. b) 2014 collect.

a)



b)

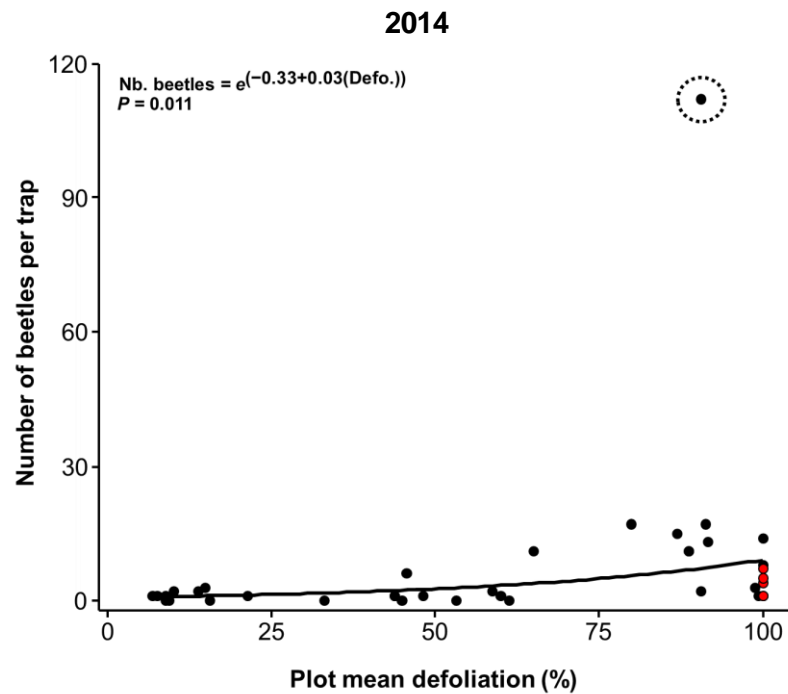


Figure 3.4 Results of negative binomial (GLMM) regressions between the mean upper crown overall defoliation and the abundance of striped ambrosia beetles (*Trypodendron lineatum*) as sampled by multidirectional flight-interception traps. Traps placed in stands totally defoliated in 2012 are in red. a) 2013 collect. b) 2014 collect without the circled outlier trap.

Conclusion générale

L'épidémie d'arpenteuse de la pruche, qui est survenue dans la Réserve faunique des Laurentides en 2012, a permis d'étudier l'impact de l'insecte ravageur sur les coléoptères phloéophages et xylophages. Pour une première fois, une étude a démontré que le stress et la mortalité engendrés par la défoliation, causée l'arpenteuse de la pruche, initiait une succession, en moins de deux ans, dans cette communauté de coléoptères. En peuplements dominés par le sapin baumier, on a noté que la défoliation grave a entraîné la diminution de diverses espèces phloéophages associées aux forêts non perturbées, et l'augmentation importante du scolyte birayé (*Trypodendron lineatum* (Olivier)) (Coleoptera: Curculionidae) dans les forêts gravement affectés par l'épidémie. Le scolyte birayé est considéré comme xylomycétophage (Beaver 1989) car il se nourrit exclusivement d'un symbiote fongique (champignon « ambrosia ») qu'il inocule et cultive dans les galeries creusées jusque dans l'aubier de conifères moribonds ou récemment morts (Bakshi 1950, Beaver 1989). De plus, nous avons développé et testé l'efficacité d'une méthode d'évaluation de la défoliation, causée par l'arpenteuse de la pruche, impliquant une estimation globale de la cime supérieure. Cette méthode impliquant deux observateurs utilisant des binoculaires s'est avérée rapide, peu coûteuse et précise (10 classes de 10% allant de 0 à 100% de défoliation). Nous avons alors testé la capacité de pièges à impacts multidirectionnels et fixés au tronc ainsi que de cages d'émergence fixées au tronc dans la détection des changements au sein de la communauté des phloéophages et des xylophages. Le long d'un gradient de défoliation, tel qu'évalué avec la méthode d'estimation globale, nous avons noté une réponse exponentielle du scolyte birayé allant de faible (lorsqu'on utilise des pièges à impact multidirectionnels) à extrêmement forte (lorsqu'on utilise des cages d'émergence placées autour des troncs), voire à réponse dichotomique. La force de la réponse augmente ainsi en fonction du niveau d'association des pièges aux sapins défoliés. À l'aide des cages d'émergence, nous avons déterminé un taux seuil de 95% de défoliation pour la colonisation. À ce seuil, l'arbre possédait 55% de chance d'être colonisé massivement et cette probabilité montait à 91% s'il atteignait 100% de défoliation. Ainsi, l'activité du scolyte birayé atteint un maximum dans l'entourage immédiat des arbres les plus défoliés mais la colonisation réelle des arbres suit un patron plus complexe. Ce patron semble impliquer des variables qui devront être explorées dans des études futures, impliquant les défenses chimiques et les taux d'humidité dans les tissus sous-corticaux et ligneux des arbres défoliés. Malgré la performance des cages,

l'utilisation de pièges à impact fixés au tronc s'avère un outil plus simple à installer, moins coûteux et très sensible pour détecter les visites du scolyte birayé aux arbres gravement défoliés. Ce piège à impact est pratique d'utilisation et peut être mis en relation avec des variables continues comme la défoliation. Nous suggérons fortement son utilisation comme outil de surveillance et de prévision de la colonisation par le scolyte birayé dans un contexte d'épidémie d'arpenteuse de la pruche.

Comment expliquer la prédominance du scolyte birayé

Pour comprendre la prédominance de ce coléoptère, les relations écologiques entre le sapin baumier, le scolyte birayé et le symbiote fongique du scolyte doivent être approfondies. En plus d'une détection efficace des sapins baumiers fortement défoliés grâce aux attractants primaires (monoterpènes et éthanol), un attractant secondaire, impliquant une phéromone d'agrégation produite par les femelles colonisatrices, est connue chez cette espèce (Borden *et al.* 1979). La phéromone, la linéatine, attire des adultes des deux sexes et entre en synergie avec l'éthanol (Hoover *et al.* 2000). La phase de colonisation débute alors avec un couple géniteur qui pénètre l'écorce saine et qui creuse jusqu'à l'aubier de l'arbre. Le symbiote profite ainsi de la situation car les dommages créés aux tissus internes permettent une pénétration rapide des hyphes (Batra 1963). L'urée ainsi que l'acide urique présente dans les déjections des scolytes servent alors de source d'azote pour le symbiote (Batra 1963). Par ce comportement xylomycétophage, le scolyte birayé n'a pas besoin d'extraire l'eau et les nutriments nécessaires à sa survie dans les tissus sous-corticaux vivants ou récemment morts et n'a donc pas à combattre les mécanismes de défenses chimiques constitutives et induits déployés par l'arbre (Franceschi *et al.* 2005). Ainsi, les changements suggérés dans le profil de défenses chimiques dans les tissus sous-corticaux d'arbres défoliés risquent d'avoir moins affecté la colonisation par le scolyte birayé contrairement à d'autres colonisateurs phloéophages potentiels. Les processus de détection et de sélection d'hôtes par le biais des composés volatils ainsi que les mécanismes de défenses naturelles d'arbres défoliés, blessés et morts sont des pistes qui se doivent d'être explorées. De cette façon, il serait possible d'approfondir les connaissances sur les trajectoires successionales après perturbation naturelle et sur les caractéristiques biochimiques expliquant la colonisation et menant à la dégradation des produits forestiers convoités.

Implications pour l'industrie forestière et perspectives de recherche

Le scolyte birayé est un des insectes colonisateur du bois qui est responsable des plus grandes pertes économiques en foresterie autant en Europe (Dubbel 1992) que dans l'ouest de l'Amérique du Nord (Borden et McLean 1981, McLean 1985). L'utilisation de composés sémiocchimiques dans la lutte contre ce scolyte a beaucoup été réalisé par l'utilisation de répulsifs et par la capture massive des adultes colonisateurs en utilisant la linéatine comme attractif (Borden et McLean 1981, Dubbel 1992). En Colombie-Britannique, le piégeage de masse à l'aide de linéatine pendant quelques années a résulté en une réduction de la quantité d'adultes hivernant en forêts adjacentes à des zones de transformation du bois au Canada ainsi qu'en une considérable réduction des dommages causés aux billes de bois empilées (Borden et McLean 1981). Malgré le développement de techniques sophistiquées, des empilements de bois subissent encore des colonisations importantes réduisant jusqu'à 50% la valeur du bois dans l'Ouest des États-Unis (Livingston 2004). Pour l'instant, dans l'Est de l'Amérique du Nord, il n'y a par contre pas d'études qui ont porté sur l'impact du scolyte birayé sur la réduction de la valeur économique des billes de conifères.

En Ontario, Belyea (1952a) avait remarqué la présence du scolyte birayé après une épidémie de tordeuse des bourgeons de l'épinette mais seulement 10% des sapins baumiers semblaient avoir été colonisés par cette espèce avec une densité maximale de 10 trous d'émergence/ π^2 d'écorce. Dans notre étude, toutes les colonisations massives dépassaient 10 trous d'émergence/ π^2 et ont atteint un maximum de 64.1 trous d'émergence/ π^2 (résultats non présentés). Toujours après la même épidémie, Basham et Belyea (1960) ont finalement indiqué que le scolyte birayé pénètre seulement de manière limitée dans le bois, cause des dommages à un volume faible de bois et est insignifiant d'un point de vue économique. Ils ont par contre indiqué que le scolyte pourrait être relié avec l'introduction de champignons détériorant l'aubier, mais sans aller plus loin. En 2015, des sections de 50 cm ont été prélevées des tiges de sapins baumiers encagés lors de notre étude et seront disséquées et/ou soumises à un CT-scan afin d'évaluer la relation entre la densité des galeries et la dévaluation des billes. Un suivi de la colonisation des espèces saproxyliques attaquant les stades de décomposition plus avancés et de la qualité de la fibre du bois en contexte d'inoculation fongique du symbionte est aussi en cours.

Tout récemment, le scolyte birayé a été noté comme l'espèce la plus récoltée dans un projet visant à tester l'impact des coupes partielles sur la succession hâtive des coléoptères phloéophages et xylophages à la Forêt Montmorency, Québec. À l'aide de pièges à impacts multidirectionnels, Morin *et al.* (2015) ont échantillonné de grandes quantités de scolytes birayés et ont noté son association avec de hautes températures ainsi qu'avec l'augmentation du nombre de blessures causées aux arbres. Il est donc possible que l'arrivée d'une épidémie dans la sapinière à bouleau blanc de la réserve faunique des Laurentides ait procuré des conditions favorables ainsi qu'un climat propice pour un développement des populations du scolyte birayé.

Grâce aux connaissances acquises via les études discutées dans les trois chapitres de ce mémoire, nous proposons une méthode simple de détection du scolyte birayé pour anticiper ses dommages potentiels. Une fois qu'une épidémie d'arpenteuse de la pruche est détectée, des pièges à impact fixés aux troncs devraient être installés sur des arbres sentinelles. D'un point de vue écologique, une trajectoire successionale caractérisée par la prédominance du scolyte birayé pourrait être suggérée comme naturelle et recherchée en contexte d'aménagement écosystémique. Alternativement, les aménagistes forestiers pourraient vouloir mettre en oeuvre rapidement des plans de récupération en cas d'augmentation des populations. Ces coupes de récupérations pourraient être prescrites tard à l'automne, à l'hiver ou tôt au printemps afin d'éviter toute colonisation par le scolyte.

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Annexes

Annexe A. Piège à impact multidirectionnel



Annexe B. Piège à impact fixé au tronc



Annexe C. Cage d'émergence

