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Hétérogénéité des paysages et des pratiques agricoles: effets sur la diversité des abeilles sauvages et la pollinisation

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« Un jour, dit la légende, il y eut un immense incendie de forêt. Tous les animaux terrifiés et atterrés observaient, impuissants, le désastre. Seul le petit colibri s'active, allant chercher quelques gouttes d'eau dans son bec pour les jeter sur le feu. Au bout d'un moment, le tatou, agacé par ses agissements dérisoires, lui dit : « Colibri ! Tu n'es pas fou ? Tu crois que c'est avec ces gouttes d'eau que tu vas éteindre le feu ? » « Je le sais, répond le colibri, mais je fais ma part »

Un conte améridien.

"Si un plus grand nombre d'entre nous préférait la nourriture, la gaieté et les chansons aux entassements d'or, le monde serait plus rempli de joie."

J.R.R. Tolkien, Bilbo le Hobbit

« La loutre et le héron sont mes amiiiiiiiis ! »

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Sommaire

Introduction générale

Les écosystèmes cultivés occupent une large part des territoires en Europe (40% de la surface totale dédiée à la production agricole dans l'UE, Agreste 2008) et abritent une importante biodiversité animale et végétale (Lüscher et al., 2016). En Europe et en Amérique du Nord, les politiques agricoles mises en place après la seconde guerre mondiale ont mis l'accent sur l'augmentation de la productivité agricole des territoires ruraux afin de maximiser la production de denrées alimentaires (Tilman, 1999). Cette intensification de la production agricole s'est traduite par : i) la simplification des paysages (disparition des zones de végétation permanente comme les haies et jachères ainsi que l'augmentation de la taille des parcelles) permettant l'utilisation de machines agricoles et l'augmentation des surfaces cultivées, ii) la sélection de variétés annuelles productives et iii) l'augmentation du recours aux intrants chimiques en vue d'augmenter les rendements (Benton et al., 2003; Burel and Baudry, 1990; Robinson and Sutherland, 2002). Ces changements massifs ont participé à la perte de biodiversité dans les agroécosystèmes (Benton et al., 2003; Krebs et al., 1999; Robinson and Sutherland, 2002), aussi bien en termes de biodiversité planifiée (réduction de la diversité génétique des plantes cultivées et du nombre de cultures différentes au sein des assolements) que de biodiversité associée (espèces colonisant les agroécosystèmes telles que la faune du sol, les adventices). Ils ont agit sur la biodiversité par la destruction des habitats, leur fragmentation, la réduction de leur qualité mais aussi via des effets létaux (utilisation de pesticides, labour, etc.) (Robinson and Sutherland, 2002; Tilman, 1999)

Cette perte de biodiversité peut mettre en danger le fonctionnement des agroécosystèmes. En effet, plusieurs fonctions écologiques au sein des agroécosystèmes dépendent de la biodiversité, telles que la production de biomasse, les flux de matière et de nutriments, la prédation ou la pollinisation (Hooper et al., 2005). Certaines de ces fonctions écologiques peuvent, dans certains cas, bénéficier à l'Homme et sont appelées services écosystémiques. Cette notion, apparue dans les années 90, désigne les bienfaits que l'Homme tire, directement ou indirectement, du fonctionnement des écosystèmes et des espèces au sein de ces écosystèmes (Costanza et al., 1997; Millenium Ecosystem Assessment, 2005). La notion de service écosystémique est donc étroitement liée à la biodiversité. Le Millenium Ecosystem Assessment (MEA) a ainsi été développé par l'ONU entre 2000 et 2005 pour permettre la prise de conscience de la dépendance de l'Homme vis-à-vis de la biodiversité. La classification du MEA distingue 4 types de services : les services de support, d'approvisionnement, de régulation et les services culturels (Figure 1).

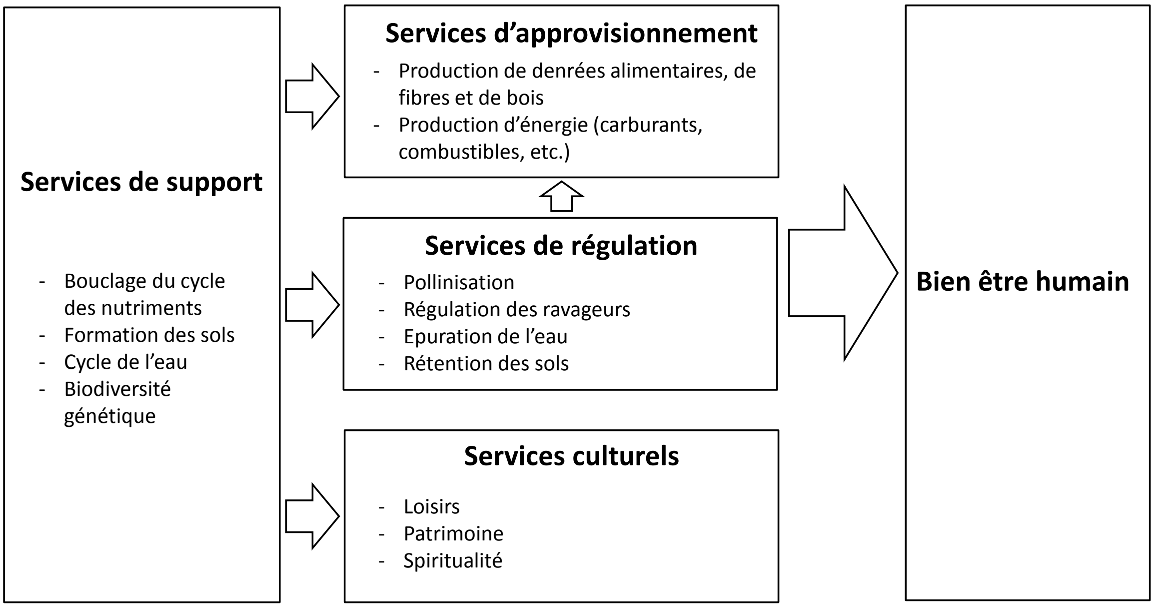


Figure 1 Classification des services écosystémiques suivant le Millenium Ecosystem Assessment (adapté de Zhang et al., 2007). La gestion des agroécosystèmes est typiquement orientée vers la maximisation des services d'approvisionnement, mais nécessite un panel important de services de support et de régulation.

Au sein de ces services écosystémiques, la pollinisation entomophile tient une place centrale. En effet, en concernant plus de 90 % des espèces végétales (Kearns et al., 1998), elle est le mode privilégié de transfert du pollen et participe au maintien de la diversité végétale dans les écosystèmes (Memmott et al., 2004; Potts et al., 2010a). De plus, la pollinisation entomophile contribue à 35% de la production agricole mondiale (en volume de production), assurant le rendement de 70% des plantes cultivées dans le monde (Klein et al., 2007). Elle est donc en soi un service (service de régulation), mais a aussi des conséquences sur d'autres services tels que la production de denrées, de fibres et de bois (service d'approvisionnement), les services dépendant de la diversité végétale des plantes sauvages (stockage du carbone, cycle des nutriments) et la provision de services culturels (pollinisation d'espèces de plantes patrimoniales).

Du fait de leurs caractéristiques morphologiques et comportementales, les abeilles (Hyménoptères apiformes) sont considérées comme les principaux insectes pollinisateurs au niveau mondial (Danforth, 2007). Les abeilles sauvages, c'est-à-dire l'ensemble des espèces d'abeilles excluant les abeilles domestiques comme *Apis mellifera*, contribuent significativement aux rendements des cultures au seins de divers agroécosystèmes (Garibaldi et al., 2013) et sont d'autant plus importantes quand l'apiculture est absente des territoires.

La relation entre l'intensification agricole et les abeilles sauvages est complexe. En effet, la plupart des conséquences de l'intensification (perte d'habitats à l'échelle des paysages, utilisation de pesticides, etc.) a un impact négatif sur la diversité et l'abondance des abeilles sauvages (Le Féon et al., 2010;

Williams et al., 2010; Winfree et al., 2009; Woodcock et al., 2016). La diversité et l'abondance des abeilles sauvages étant un facteur important de l'élaboration du rendement des plantes cultivées entomophiles (Garibaldi et al., 2013), l'intensification agricole aurait tendance à diminuer l'effet bénéfique des abeilles sauvages sur les rendements. Or, l'objectif majeur de l'intensification agricole est l'augmentation des rendements, et cet objectif ne peut être atteint que si la pollinisation des cultures entomophile est réalisée efficacement. De plus, les surfaces de cultures entomophiles tendent à augmenter au sein des territoires ruraux en Europe (Breeze et al., 2014) et la densité de ruches d'abeilles domestiques est en nette diminution (Breeze et al., 2014; Ellis et al., 2010; Potts et al., 2010b), rendant indispensable la pollinisation fournie par les abeilles sauvages pour maintenir les rendements de ces cultures. Afin de conserver des agroécosystèmes productifs tout en augmentant leur durabilité, une des pistes privilégiée est d'adopter une démarche d'agroécologie en profitant de possibles synergies entre certains processus écologiques et la production agricole (Wezel et al., 2009). Plusieurs études ont identifié que les paysages agricoles avec de fortes proportions de milieux semi-naturels (forêts, haies, prairies permanentes), avec de faibles usages d'intrants chimiques dans les parcelles agricoles, accueillent un diversité en abeilles sauvages plus forte (Garibaldi et al., 2011; Le Féon et al., 2010; Winfree et al., 2009). Le maintien ou la restauration de milieux semi-naturels dans les paysages mais aussi le recours à des pratiques extensives pourraient donc être des pistes pour conserver les abeilles sauvages dans les paysages agricoles.

L'objectif de cette thèse est d'approfondir les connaissances sur de possibles leviers paysagers et agronomiques visant à favoriser le maintien de la diversité des pollinisateurs et à accroître la provision de pollinisation dans les paysages agricoles. Elle s'intéresse plus particulièrement aux effets des milieux semi-naturels et des pratiques agricoles, considérées à l'échelle locale et paysagère, sur la structure des communautés d'abeilles sauvages et des conséquences de ces effets sur la pollinisation.

I- Contexte scientifique et cadre théorique

1 - Pollinisateurs et paysages agricoles : la composition, la structure des paysages et les pratiques des agriculteurs structurent les communautés d'abeilles sauvages

a- Les habitats des abeilles sauvages

Les abeilles sauvages (Hyménoptère, Apoidae) sont des insectes thermophiles vivant préférentiellement dans les milieux ouverts, riches en fleurs et en végétation permanente (Danforth, 2007; Plateaux-Quénu, 1972). Il existe environ 10 000 espèces d'abeilles dans le monde, et la France en compte environ 1000 (Rasmont et al., 1995). Elles se subdivisent en 7 familles (Andrenidae, Colletidae, Halictidae, Apidae, Megachilidae, Melittidae et Stenotritidae) dont seulement 6 sont présentes en France (Stenotritidae exlcue)(Hedtke et al., 2013). Une grande majorité des espèces sont solitaires (une seule femelle par nid qui assure les activités de butinage, de ponte et de fabrication des cellules de pontes) et passent l'hiver sous forme de larve, les adultes mâles et femelles mourant avant l'hiver (Danforth, 2007). Les abeilles sociales ne représentent que 6% des espèces au niveau mondial. Il y a une diversité de comportement sociaux chez ces abeilles, allant du partage du nid accompagné de coopération dans les activités de butinage jusqu'à l'eusocialité, définie par une répartition stricte des tâches (des femelles pondeuses et des femelles assurant la défense du nid, butinage, entretien du couvain) (Danforth, 2007; Michener, 2000). La plupart des espèces sociales passent l'hiver sous forme d'adultes (seulement les femelles pondeuses).

Deux types de ressources sont indispensables aux abeilles sauvages pour qu'elles complètent leur cycle de vie :

- **Les ressources florales** : les abeilles récoltent le nectar et le pollen des fleurs et s'en servent comme ressources trophiques. Le nectar leur apporte principalement des glucides et le pollen des protéines (Michener, 2000). Ces deux types de ressources sont à la fois consommés par les adultes mais aussi par les larves, sous formes de « pain ». En effet, au sein de chaque cellule de ponte, un pain de nectar et de pollen est formé et sur lequel la femelle pond un œuf. Ce pain servira de ressource alimentaire pour la larve après l'éclosion (Michener, 2000; Plateaux-Quénu, 1972). Les abeilles dites polylectiques (régime généraliste) récoltent du pollen sur une large diversité de familles d'espèces florales, tandis que les abeilles oligolectiques (régime spécialisé) n'en récoltent que sur une seule famille de plantes.
- **Les sites de nidification** : tous les nids sont composés de plusieurs cellules de pontes, reliées ou non par un tunnel principal (Fig. 2). Même si la plupart des espèces sont terricoles, il existe

une diversité de stratégie de nidification chez les abeilles sauvages. Certaines abeilles cavicoles utilisent des cavités préexistantes afin d'y construire des cellules de ponte. Elles peuvent utiliser des tiges creuses (Fig. 2), des anfractuosités dans la roche ou dans des murs, des cavités dans du bois (mort ou vivant) ou dans le sol comme des galeries de rongeurs (pour certaines espèces de bourdons) (Michener, 2000). Pour fermer les cellules, elles utilisent plusieurs types de matériaux comme de la terre, des feuilles, des pétales de fleurs, des sécrétions ou des cailloux. D'autres espèces d'abeilles cavicoles creusent des cavités dans du bois tendre comme les Xylocopes. Quant aux abeilles terricoles, elles creusent leurs nids dans le sol et préfèrent les zones de végétation éparses, en pente et exposées au soleil (Potts et al., 2005). Les exigences en termes de structure du sol sont variables suivant les espèces (Michener, 2000; Potts et al., 2005). D'autres espèces dites parasites ou « coucous » ne construisent pas de nid mais pondent dans les cellules d'autres espèces d'abeilles afin que la larve coucou consomme la larve parasitée ainsi que le pain de nectar et de pollen.

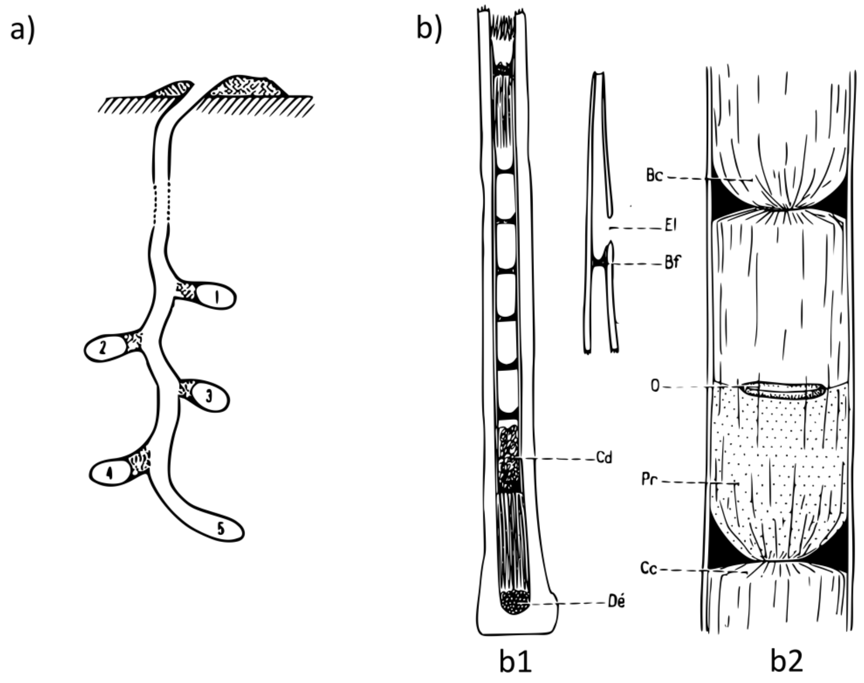


Figure 2 Les deux stratégies de nidification majeures chez les abeilles sauvages en contexte agricole, pour les abeilles terricoles (a) et les abeilles cavicoles (b) ; a : Nid de *Colletes cunicularius*, avec un conduit principal, menant à des cellules de ponte construites dans l'ordre de la numérotation, bouchées par la femelle après la ponte; b : Nid de *Chilicola ashmeadi*, typique d'un nid construit dans une tige creuse, avec le rameau comportant les cellules alignées fermées par une membrane sécrétée par la femelle (b1), et le détail d'une cellule de ponte (b2) contenant le pain de nectar et de pollen (Pr), l'œuf (O) et le couvercle de la cellule (Cc). Autres légendes : Dé= débris, Cd=cellule à détritus, Bf=bouchon de fermeture, El=entrée latérale, Bc=base de la cellule (d'après Plateaux-Quénu, 1972).

Les abeilles sauvages ont donc besoin de zones de végétation peu perturbées pour nidifier mais aussi de ressources florales disponibles pendant une longue période, du fait des phénologies contrastées entres espèces (Blüthgen and Klein, 2011).

b- Influence de la structure et de la composition des paysages sur les communautés d'abeilles sauvages

Les abeilles sauvages sont des « central place foragers », c'est-à-dire que les femelles reviennent toujours au même endroit (au nid) pour l'approvisionner en pollen et en nectar. Le plus souvent, les ressources alimentaires dans les paysages agricoles ne se trouvent pas dans les mêmes taches de milieu que les sites de nidification et les femelles doivent rechercher ces ressources dans des taches distantes (Westrich, 1996). Dans les paysages agricoles, les ressources florales nécessaires aux abeilles sauvages sont principalement trouvées dans les milieux dits semi-naturels (haies, prairies, lisières forestières)(Westrich, 1996). En effet, une grande partie des agroécosystèmes Européens et Nord-Américains sont occupés par des céréales à paille, n'apportant peu ou pas de ressources aux abeilles à part sous la forme de plantes adventices des cultures. Ces ressources en adventices disparaissent quand leur contrôle est important, par le labour ou l'utilisation d'herbicides (Aubertot et al., 2006; Bretagnolle and Gaba, 2015). Cependant au sein de la mosaïque cultivée, les cultures entomophiles (colza, tournesol, légumineuses, etc.) peuvent représenter une ressource alimentaires importante pour les abeilles (Holzschuh et al., 2012; Westphal et al., 2003).

Deux effets majeurs du contexte paysager sur les communautés d'abeilles sauvages ont été mis en évidence :

- Un effet de la composition des paysages en milieux semi-naturels : le pourcentage de milieux semi-naturels dans un paysage va conditionner la **disponibilité** des ressources pour les abeilles sauvages. En effet, il a été montré que plus un paysage a une forte proportion de milieux semi-naturels et plus les communautés d'abeilles sauvages des parcelles agricoles étaient riches en espèces (Garibaldi et al., 2011; Tscharntke et al., 2005; Winfree et al., 2009). Différents milieux semi-naturels peuvent apporter différents types de ressources : dans les agroécosystèmes tempérés, les lisières forestières et les haies peuvent apporter des ressources florales et des sites de nidification pour les abeilles cavicoles (Bailey et al., 2014; Morandin and Kremen, 2013) tandis que les prairies permanentes fournissent des ressources florales et des zones de sols nus utilisées par les abeilles terricoles (Hopfenmüller et al., 2014; Jauker et al., 2013; Potts et al., 2005). La composition des paysages en milieux semi-naturels va ainsi agir sur les abeilles sauvages via un changement dans la proportion totale en milieux semi-naturels, mais aussi via un changement dans la proportion relative de différents types de milieux (Fahrig et al., 2011).
- Un effet de la configuration des paysages : des variations dans la configuration des paysages impliquent des changements dans la distance entre les taches de milieux, dans la taille moyenne des taches mais aussi dans la quantité d'interfaces entre taches, pour des surfaces de taches de milieux constantes (Fahrig, 2003). La configuration des paysages agricoles a donc le

potentiel de faire varier l'**accessibilité** aux ressources pour les abeilles sauvages. Il y a peu d'études empiriques ayant exploré l'effet des changements de configuration des paysages sur les abeilles sauvages (Holzschuh et al., 2010; Hopfenmüller et al., 2014). De façon théorique, la configuration des paysages peut influencer les communautés d'abeilles sauvages par :

a) La **distance** entre sites de nidification et ressources florales, ou entre plusieurs taches de milieux contenant des ressources florales (Westrich, 1996)

b) La **quantité d'interfaces** entre plusieurs taches d'habitats, pouvant potentiellement avoir un effet positif ou négatif sur les communautés. En effet, une forte quantité d'interfaces entre différents types de milieux peut augmenter les opportunités d'échanges entre milieux semi-naturels et zones cultivées (spillover) (Holzschuh et al., 2010; Tscharntke et al., 2012) mais peut aussi favoriser la dispersion de certaines espèces via l'accroissement de la connectivité. Par exemple, certaines espèces de bourdons se servent des bordures de taches comme corridors de déplacement ou comme habitats (Öckinger and Smith, 2007; Osborne et al., 2008; Svensson et al., 2000). Cependant, une forte quantité d'interfaces peut aussi exposer les pollinisateurs des milieux semi-naturels aux perturbations des zones cultivées (« negative edge-effect ») (Fahrig, 2003; Kleijn and Snoeijing, 1997).

c) La **surface moyenne des taches de milieux**, pouvant affecter les espèces qui se déplacent peu et qui ont besoin localement d'une certaine surface d'habitat pour maintenir des populations viables (Bommarco et al., 2010).

Même si les abeilles répondent via des processus différents aux changements de composition et de configurations des paysages agricoles, ces changements paysagers sont souvent corrélés (Fahrig, 2003, 2013). En effet, des paysages avec de fortes proportions de milieux semi-naturels vont apporter une quantité et une diversité importante de milieux permettant de soutenir une forte diversité d'abeilles sauvages dans les parcelles agricoles (Garibaldi et al., 2011; Winfree et al., 2009). Et dans ces mêmes paysages, la distance entre la parcelle agricole échantillonnée et les milieux semi-naturels va aussi être faible (faible isolement), permettant des échanges plus importants entre parcelles agricoles et milieux semi-naturels (Garibaldi et al., 2011; Ricketts et al., 2008). Du fait de cette corrélation naturelle entre composition et configuration des paysages, peu d'études ont pu statistiquement séparer ces deux effets paysagers sur les communautés d'abeilles sauvages. Pour les études ayant cherché à les décorréler, il s'est avéré que la configuration avait des effet faibles ou inexistants sur la structure des communautés d'abeilles sauvages, comparés à la composition des paysages (Holzschuh et al., 2010; Hopfenmüller et al., 2014; Kennedy et al., 2013).

Les effets de la structure et de la composition des paysages sur la diversité des abeilles sauvages sont fortement liés aux capacités de dispersion des espèces (Greenleaf et al., 2007; Steffan-Dewenter et al., 2002). En effet, il a été montré que seulement les abeilles à forte capacité de dispersion peuvent coloniser des taches d'habitats isolées alors que les abeilles à faible capacité de dispersion ne se retrouvent que dans les taches d'habitats étant à proximité d'autres taches (Bommarco et al., 2010). Dans les paysages agricoles, les abeilles à faible capacité de dispersion vont donc être beaucoup plus sensibles à des changements dans la composition et la configuration des paysages que les abeilles à forte capacité de dispersion, pouvant aisément se déplacer à longue distance pour trouver leurs ressources (Steffan-Dewenter et al., 2002; Williams et al., 2010).

c- *Effet de l'intensité des pratiques agricoles sur les communautés d'abeilles sauvages*

L'intensité des pratiques agricoles est le niveau de production par unité de surface pour une année donnée ou par type de production (Shriar, 2000). Augmenter l'intensité d'une pratique vise à augmenter la production d'une parcelle agricole, via l'augmentation des intrants (matériel, équipement, produits phytosanitaires, quantité de travail) par unité de surface. Dans notre cas, on considérera qu'une pratique agricole donnée est comparativement plus intensive qu'une autre si sa fréquence de réalisation est plus importante (fréquence de labour, fréquence de pulvérisation d'insecticide) et/ou si son intensité l'est aussi (effet « dose-dépendant ») (Herzog et al., 2006).

L'effet de l'intensité des pratiques agricoles sur les abeilles sauvages a souvent été étudié à l'échelle locale (échelle de la parcelle cultivée). On distingue deux possibles effets sur les populations d'abeilles suivant les pratiques considérées :

- **Via la modification de la disponibilité des ressources florales et sites de nidification**. La quantité et la diversité des ressources florales peuvent être négativement influencées par l'utilisation intensive d'herbicides et de fertilisants provoquant l'homogénéisation des communautés végétales, en parcelles annuelles et dans les prairies permanentes (Gámez-Virués et al., 2015; Kleijn et al., 2009) et par le labour. De plus, les fauches précoces et le surpâturage peuvent aussi entrainer une diminution de la diversité végétale en prairie permanente (Le Féon et al., 2010; Sjödin, 2007; Sjödin et al., 2008) et peuvent engendrer un tassement des sols, défavorisant la nidification (Potts and Willmer, 1997).
- **Via des effets directs sur la survie et le comportement des individus**. La majorité des études sur l'effet des insecticides sur les abeilles se sont portées sur l'abeille domestique (*Apis mellifera*) (Desneux et al., 2007) mais de récentes études ont montré que les abeilles sauvages étaient aussi exposées (C. A. Brittain et al., 2010; Whitehorn et al., 2012; Woodcock et al.,

2016). L'effet des insecticides peut se faire via contact direct avec le produit pendant la pulvérisation, par contact avec du feuillage/des fleurs contaminés ou par ingestion de pollen ou nectar contaminés (Brittain and Potts, 2011; Le Féon, 2010). Les insecticides peuvent affecter la survie des individus (effets létaux directs) mais peuvent aussi avoir des effets sub-létaux, en entrainant des troubles physiologiques (baisse de la fécondité, modification du sex-ratio, troubles du développement larvaires, etc.) ou des troubles du comportement (désorientation, baisse de l'activité de butinage, perturbation de la mémoire) (Brittain and Potts, 2011; Desneux et al., 2007). Certaines études montrent des effets sub-létaux importants des insecticides néonicotinoïdes sur les abeilles sauvages : réduction de la fertilité des reines de *Bombus terrestris* (Whitehorn et al., 2012) et des femelles d'*Osmia bicornis* (Sandrock et al., 2014) et réduction de la persistance à long terme de plusieurs espèces à l'échelle d'un pays (Woodcock et al., 2016). D'autres études détectent des effets négatifs sans distinguer leur caractère létal ou sub-létal (C. A. Brittain et al., 2010). Aussi, les pratiques agricoles peuvent affecter directement les abeilles en détruisant les nids, par le travail du sol profond dans les parcelles agricoles (Kim et al., 2006; Shuler et al., 2005) ou le tassement par le bétail dans les prairies.

Un important corpus d'études a aussi exploré les effets des pratiques agricoles sur la biodiversité en comparant des parcelles gérées en agriculture conventionnelle avec d'autres gérées en agriculture biologique. Elles montrent que la diversité en abeilles sauvages est plus importante dans les parcelles biologiques que conventionnelles (Batáry et al., 2011; Bengtsson et al., 2005; Holzschuh et al., 2010; Rundlöf et al., 2008b), et prouvent que des parcelles agricoles gérées globalement de façon moins intensives peuvent accueillir plus d'espèces d'abeilles sauvages. En effet, une des conséquences positives de l'agriculture biologique est le maintien d'une diversité florale intra-parcelle plus importante que dans les exploitations conventionnelles, permettant d'attirer localement une plus grande diversité de pollinisateurs (Batáry et al., 2011; Holzschuh et al., 2007; Roschewitz et al., 2005a).

Cependant, il y a peu de connaissances sur l'effet de l'intensité des pratiques agricoles à l'échelle des paysages sur les abeilles sauvages. En effet, les pratiques agricoles sont susceptibles de modifier la quantité et la répartition spatiale des ressources mobilisées par les pollinisateurs (Herzog et al., 2006; Le Féon et al., 2010), au même titre que des changements dans la composition et la configuration des paysages. Par conséquent, l'étude de l'effet des pratiques agricoles à une échelle supra-parcellaire s'avère indispensable pour mieux appréhender les effets de l'intensification de l'agriculture sur les abeilles sauvages. Les études explorant cette dimension paysagère des pratiques agricoles ont utilisé des indices intégrateurs de plusieurs pratiques, tels que des indices normalisés d'intensité des pratiques (agrégeant plusieurs types de pratiques entre elles) (Le Féon et al., 2010) ou une proportion de parcelles gérées en agriculture biologique *vs* conventionnelle (Holzschuh et al., 2008). Leurs résultats montrent que la diversité des abeilles sauvages dans les parcelles agricoles est plus élevée dans les paysages ayant une forte proportion de parcelles gérées de manière extensive (en agriculture biologique ou avec de faibles indices d'intensité). Cependant ces études n'ont pas considéré la diversité de pratiques que recouvrent les systèmes de production conventionnels et biologiques et elles n'apportent pas d'informations sur les effets relatifs de différents types de pratiques sur la diversité des abeilles sauvages (Puech et al., 2014; Vasseur et al., 2012).

La proportion et la configuration des milieux semi-naturels ainsi que les pratiques des agriculteurs au sein des paysages agricoles apparaissent comme deux leviers importants pour la conservation des abeilles sauvages (Fig. 3). L'extrême majorité des études ont utilisé des méthodes corrélatives pour identifier l'effet de ces deux facteurs sur les abeilles sauvages le long de gradient environnementaux. Cependant, plusieurs études ont relevé que la perte d'habitats ainsi que l'accroissement de l'utilisation d'intrants au cours du temps étaient des facteurs explicatifs importants du déclin des abeilles sauvages (Biesmeijer et al., 2006; Woodcock et al., 2016). Pour rendre les études corrélatives plus mécanistes (c'est-à-dire essayer d'inférer sur des processus en jeu au lieu de seulement décrire des corrélations), des concepts et des outils de l'écologie du paysage et de l'écologie fonctionnelle sont à mobiliser pour mieux prédire l'effet des variables paysagères sur les communautés de pollinisateurs et la pollinisation.

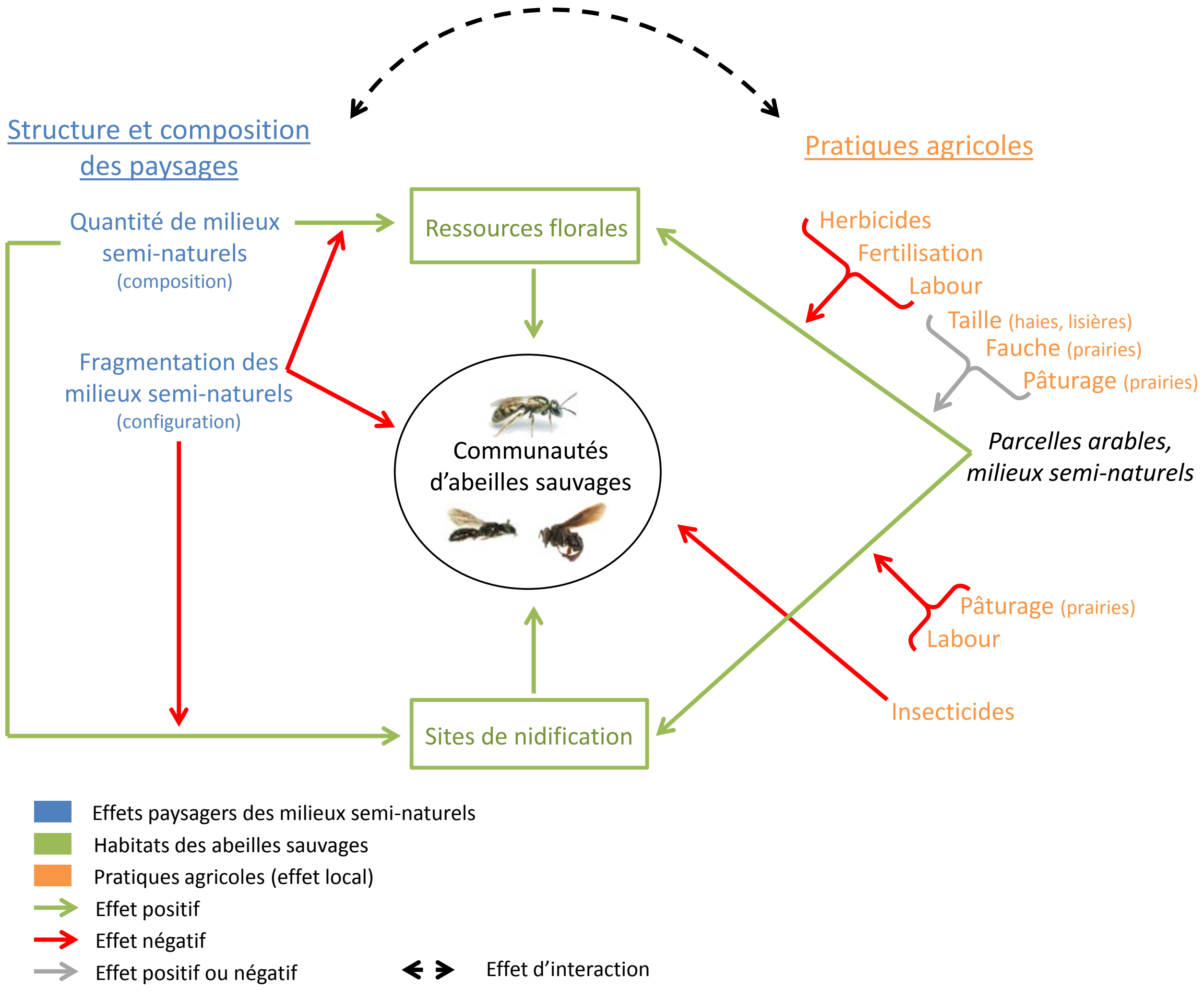


Figure 3 Représentation des différents facteurs relatifs au contexte paysager et aux pratiques agricoles affectant la structure des communautés d'abeilles sauvages. Il est à noter que les effets connus de l'intensité des pratiques agricoles sont déduits d'études menées à une échelle locale (parcelles agricoles, prairies). Les pratiques influencent les abeilles sauvages, au sein des parcelles agricoles ou dans les milieux semi-naturels, soit par modification des ressources (quantité et qualité des ressources florales, sites de nidification), soit par des effets directs (insecticides). Certaines pratiques, comme la fauche, ont un effet positif ou négatif sur certaines ressources utilisées suivant leur intensité ou leur fréquence d'application. La structure et la composition des paysages influent sur la quantité de ressources disponibles, mais aussi conditionnent l'accès des abeilles sauvages aux ressources (la fragmentation diminue l'accessibilité aux ressources) mais peuvent aussi directement influencer la dynamique des populations (en limitant la dispersion inter-patchs et diminuant les chances de recolonisation de patchs isolés par exemple). Les facteurs de structure/composition du paysage et l'intensité locale des pratiques ont un effet interactif sur les abeilles sauvages (Batáry et al., 2011). Les facteurs comme les changements climatiques, les pathogènes ou l'effet de la structure de la mosaïque cultivée ne sont pas représentés sur ce schéma.

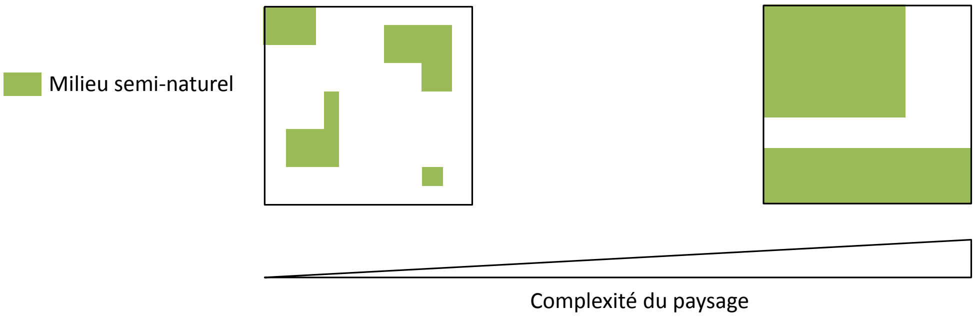
2 – Caractériser l'hétérogénéité des paysages agricoles

a – D'une vision binaire habitat-matrice à celle de l'hétérogénéité de la mosaïque paysagère

La caractérisation de l'hétérogénéité des paysages et l'étude de son influence sur les patrons et processus écologiques est un des objectifs principaux de l'écologie du paysage. En effet, le paysage est « un niveau d'organisation des systèmes écologiques, supérieur à l'écosystème ; il se caractérise essentiellement par son hétérogénéité et par sa dynamique gouvernée en partie par les activités humaines » (Baudry and Burel, 1999). Un corpus important d'études empiriques ont caractérisé les paysages suivant leur niveau de complexité. Cette approche subdivise les paysages en « habitats », dans lesquels toutes les ressources peuvent être trouvées et en « matrice agricole hostile », qui n'apportent pas de ressources et peuvent être le lieu de perturbations. Plus un paysage contient des habitats (milieux semi-naturels), plus il est complexe, et les paysages dominés par des champs cultivés sont considérés comme simples (Batáry et al., 2011; Holzschuh et al., 2010; Roschewitz et al., 2005a; Tscharntke et al., 2005). Cette vision des paysages comme des îlots d'habitats dans une mer hostile prend ses racines dans la théorie biogéographique des îles, qui a été appliquée aux paysages agricoles. Cependant, il y a maintenant un consensus selon lequel les espèces ont une perception beaucoup moins binaire du paysage, car elles sont susceptibles d'utiliser plusieurs types d'habitats au cours de leur cycle de vie (Duflot et al., 2016; Sarthou et al., 2005; Westrich, 1996). De même, il a été montré que les parcelles cultivées ne sont pas qu'hostiles et peuvent aussi apporter des ressources (Batáry et al., 2011; Duflot et al., 2016; Fahrig et al., 2015; Holzschuh et al., 2007) et influencer les mouvements des individus entres taches d'habitats (Burel and Baudry, 2005). Une représentation plus précise des paysages, basée sur l'hétérogénéité des taches d'habitats que les paysages peuvent fournir, est donc nécessaire (Fahrig et al., 2011). Deux aspects de l'hétérogénéité des paysages sont à considérer, du fait de leur potentiel à influencer la biodiversité: l'hétérogénéité de composition et de configuration. L'hétérogénéité de composition varie avec le nombre et la proportion relative de différentes taches d'habitats. L'hétérogénéité de configuration varie en fonction de l'arrangement spatial des taches.

En confrontant les deux types de représentation des paysages, on se rend compte que des paysages dits complexes peuvent être considérés comme homogènes, et inversement des paysages dits simples peuvent êtres hétérogènes (Fig. 4). Ces deux représentations peuvent donc s'opposer de façon contre intuitive et il est donc important de considérer leurs apports respectifs en écologie du paysage. D'une part, la représentation binaire habitat-matrice peut expliquer une part importante de la biodiversité observée le long de gradients paysagers (Holzschuh et al., 2007, 2010; Roschewitz et al., 2005a) et cette catégorisation dichotomique peut permettre d'apporter de l'information quand il est statistiquement impossible de séparer des effets de composition et de configuration des paysages. Cependant, afin d'affiner notre compréhension de l'effet des patrons spatiaux sur les processus écologiques, et de tester de nouveaux leviers dans la gestion de la biodiversité dans les paysages agricoles, il est nécessaire de dépasser cette vision binaire (Fahrig et al., 2011). En effet, en explorant les effets de l'hétérogénéité des paysages agricoles sur la biodiversité, on peut tester des processus tels que la complémentation paysagère (Dunning et al., 1992), qui représente le bénéfice pour des populations de pouvoir utiliser plusieurs taches de milieux apportant des ressources non substituables au cours de leur cycle de vie.

a) Approche binaire habitat-matrice



b) Approche d'hétérogénéité du paysage

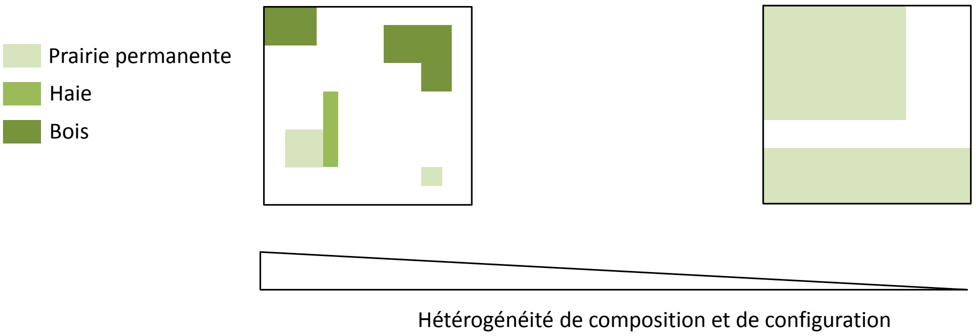


Figure 4 Illustration des conséquences de l'approche binaire habitat-matrice (a) ou d'hétérogénéité du paysage (b) sur la représentation des paysages. Seulement les milieux semi-naturels ont été considérés dans le schéma. Dans l'approche binaire habitat-matrice, la complexité du paysage augmente avec le pourcentage de milieux semi-naturels. Cependant, avec une approche prenant en compte les deux dimensions de l'hétérogénéité du paysage, dans ce cas de figure les paysages complexes sont considérés homogènes car ils n'ont qu'un seul type de milieu semi-naturel (prairie) et les taches d'habitats n'ont pas un arrangement complexe (taille moyenne élevée et faible longueur d'interface par exemple).

b – Caractériser l'hétérogénéité cachée des paysages agricoles

La prise en compte de l'hétérogénéité des paysages agricoles permet d'approfondir les connaissances sur leurs relations avec la biodiversité (Fahrig et al., 2015), mais cette approche est limitée par le fait qu'elle ne considère que l'hétérogénéité « visible » de la mosaïque cultivée ou des milieux semi-naturels (on considère qu'un type de tache apporte des ressources identiques, Vasseur et al., 2012). La diversité des pratiques des agriculteurs (gestion des parcelles annuelles mais aussi des milieux semi-naturels) et leur arrangement spatial dans les paysages induit une hétérogénéité « cachée », non visible à l'œil humain, qui est peu étudiée (Vasseur et al., 2012). Au sein de la mosaïque agricole, cette hétérogénéité peut naître de la diversité des assolements au sein des exploitations agricoles, mais aussi de l'entremêlement de plusieurs exploitations agricoles au sein des paysages. En effet, il existe une diversité de systèmes de culture pour des agriculteurs d'un même territoire (Puech et al., 2014; Thenail et al., 2009; Vasseur et al., 2012; Vuillot et al., 2016). Les pratiques de gestion des milieux semi-naturels (prairies permanentes, bordures enherbées, lisières forestières, haies) peuvent aussi varier fortement suivant les agriculteurs en raison d'objectifs de production différents mais aussi de contextes pédoclimatiques variés (Doré et al., 2006; Ryschawy, 2012; Vuillot et al., 2016). Il est aussi intéressant de considérer les différences micro-climatiques entre plusieurs taches du même type d'habitat, qui peuvent influencer la capacité de ces taches à fournir des ressources à certaines espèces. Par exemple, il a été montré que les lisières forestières orientées sud étaient préférées en hiver par les femelles du syrphe auxiliaire *Episyrphus balteatus* pour leur fournir un abri et des ressources trophiques, alors que les lisères nord sont préférées en été pour leur richesse en fleurs (Sarthou et al., 2005).

Deux grands types de méthodes peuvent être déployés pour considérer cette hétérogénéité cachée. La première est l'utilisation d'enquêtes standardisées et spatialisées réalisées chez un maximum d'agriculteurs au sein des paysages étudiés (Herzog et al., 2006; Le Féon et al., 2010; Puech et al., 2015; Vasseur et al., 2012). Pour ne pas à avoir à relever toutes les composantes des itinéraires techniques (« combinaison logique et ordonnée de techniques qui permettent de contrôler le milieu et d'en tirer une production donnée », Sebillotte, 1974), il est nécessaire de cibler les pratiques ayant un potentiel effet direct ou indirect sur les espèces considérées (Herzog et al., 2006). L'intensité des pratiques est mesurée suivant la fréquence d'application, l'intensité d'application (Herzog et al., 2006; Vasseur et al., 2012) ou la présence/absence d'une pratique (Holzschuh et al., 2008; Puech et al., 2015). Ensuite, il est nécessaire d'intégrer ces indices d'intensité à l'échelle du paysage. La majorité des études utilisent des moyennes d'intensité à l'échelle du paysage (Hendrickx et al., 2007; Le Féon et al., 2010) ou l'étendue spatiale de certaines pratiques (surface de parcelles en bio *vs* conventionnel) (Holzschuh et al., 2008). Ces études montrent que plus une parcelle donnée est entourée d'une forte proportion de parcelles gérées de manière intensive, plus la biodiversité y est faible. Les études dichotomiques biologique vs conventionnelle ont des résultats très contrastés, reportant des effets positifs de la couverture en parcelles biologiques (Holzschuh et al., 2008), une absence d'effet ou un effet négatif (Gabriel et al., 2010; Puech et al., 2015). D'autres études ont exploré, en plus de l'effet de l'entendue spatiale de certaines pratiques (composition), l'effet de l'arrangement spatial des pratiques agricoles (configuration) (Puech et al., 2015). Elles ont montré qu'il n'y a pas de preuves d'un tel effet de l'arrangement spatial des pratiques sur la biodiversité (Puech et al., 2015).

Une deuxième méthode pour décrire l'hétérogénéité cachée des paysages est l'utilisation des outils de la télédétection. L'utilisation d'images satellites permet en effet de décrire la structure des paysages agricoles et de prédire la distribution d'espèces ou d'assemblages d'espèces sur de grandes étendues, là où il serait impossible de mener autant de relevés de terrain (Kerr and Ostrovsky, 2003). La représentation d'un paysage peut se faire de manière discrète (utilisation d'images satellites classées en différent type d'utilisation des sols, Bertrand et al., 2016; Kerr et al., 2001; Sheeren et al., 2011) ou en adoptant une représentation continue (chaque point du paysage ou « pixel » possède une valeur d'un indicateur donné, Sheeren et al., 2014). Le NDVI (Normalized Difference Vegetation Index) est un indice souvent utilisé pour représenter l'hétérogénéité des paysages de façon continue (Kerr and Ostrovsky, 2003; Pettorelli et al., 2005), car il est fortement corrélé à la biomasse végétale aérienne et à la productivité primaire des couverts végétaux (Pettorelli et al., 2005). Ces mesures de l'hétérogénéité des paysages par télédétection permettent par exemple de prédire avec une grande précision les variations de la richesse spécifique d'oiseaux (Sheeren et al., 2014) ou de papillons (Kerr et al., 2001) sur de grandes étendues spatiales. Les outils de la télédétection permettent aussi de caractériser la qualité des habitats et leur hétérogénéité structurale interne au sein des paysages (Goetz et al., 2007; Kerr et al., 2001). Ainsi, des taches d'habitats que l'on considèrerait équivalentes avec une approche d'écologie du paysage classique (par exemple des taches de prairies permanentes) deviennent de taches d'habitats de qualités différentes avec la télédétection (taches de prairies ayant différentes valeurs de productivité en herbe par exemple).

3 - Etudier les relations paysage – pollinisateurs – pollinisation : une approche fonctionnelle de l'écologie des communautés et du paysage

a- Réponse fonctionnelle des communautés d'abeilles sauvages aux variables paysagères

L'écologie des communautés cherche à comprendre les lois qui définissent la distribution des espèces, et leur agrégation en assemblages. Ces règles d'assemblage ont été définies comme l'ensemble des lois qui définissent la coexistence des espèces (Cody and Diamond, 1975). Pour comprendre ce qui détermine la distribution des espèces, la notion de niche écologique a été formalisée au début du 19$^{\text{ième}}$ siècle comme l'ensemble des conditions environnementales qui permettent la survie de l'espèce. L'étude des ces conditions environnementales a mis l'accent sur le rôle des contraintes abiotiques pour définir les contours des niches. C'est en 1957 qu'Hutchinson définit le concept de niche multidimensionnelle, qui considère à la fois la dimension abiotique ainsi que les interactions biotiques dans la définition de la niche d'une espèce donnée. Dans sa définition, la niche fondamentale est l'ensemble des conditions abiotiques sous lesquelles l'espèce peut potentiellement survivre. La niche réalisée désigne la distribution réellement observée de l'espèce, qui a été influencée par son interaction avec d'autres espèces, pouvant potentiellement modifier son accès aux ressources (Hutchinson, 1957). Définir des règles d'assemblage des communautés revient donc à connaître la distribution des niches des espèces pour comprendre les conditions de coexistence ou non des espèces dans un habitat donné.

Une façon analogue de définir la niche multidimensionnelle est de caractériser la niche fonctionnelle des espèces. La niche fonctionnelle est un espace multidimensionnel défini par l'ensemble des propriétés fonctionnelles de l'espèce (ex : taux de prédation, production de biomasse, etc.). Elle représente donc à la fois son utilisation des ressources, sa tolérance aux contraintes abiotiques mais aussi les conséquences écologiques qu'aura l'espèce dans un habitat donné (réponse des assemblages à l'environnement ou effet sur une fonction donnée) (Blüthgen and Klein, 2011; Rosenfeld, 2002). Une description fine de la niche fonctionnelle passe par la mesure de caractères décrivant les propriétés fonctionnelles des espèces, ou traits fonctionnels.

Un trait fonctionnel est défini comme toute caractéristique morphologique, physiologique ou phénologique mesurable à l'échelle de l'individu, sans référence à l'environnement, et qui peut influencer sa performance dans un habitat donné (Violle et al., 2007). Chez les abeilles sauvages, un ensemble de traits écologiques a été décrit, traduisant leur capacité de dispersion (taille du corps, mesurée par distance inter-tégulaire ou DIT), leur spécialisation alimentaire, leur site de nidification ou la longueur de leur pièces buccales. Caractériser la structure fonctionnelle des communautés en fonction de variations environnementales revient à explorer les traits qui conditionnent la coexistence des espèces au sein des communautés (Lavorel and Garnier, 2002; Suding et al., 2008). L'utilisation de traits permet donc d'établir des règles d'assemblage des communautés plus mécanistes et plus prédictives (Keddy, 1992; Lavorel and Garnier, 2002).

L'assemblage des communautés a été conceptualisé via le modèle des filtres (Fig. 5), qui décrit l'occurrence des espèces en présence dans un habitat donné comme étant le résultat d'une succession de filtres agissant à différentes échelles spatio-temporelles, excluant successivement certaines espèces à partir d'un pool d'espèces global (Belyea and Lancaster, 1999; Keddy, 1992). Depuis un pool total d'espèce (résultat de l'histoire biogéographique, de la spéciation, etc., Bernard-Verdier, 2012), un premier filtre exclut les espèces n'ayant pas les capacités de dispersion adéquates pour coloniser l'habitat, formant ainsi le pool géographique. Ensuite, le pool écologique est façonné par les contraintes de l'environnement, excluant les espèces incapables de tolérer les conditions abiotiques de l'habitat. Et enfin le pool réel est le résultat de l'exclusion d'espèces du fait d'interactions biotiques (compétition par exemple) (Belyea and Lancaster, 1999).

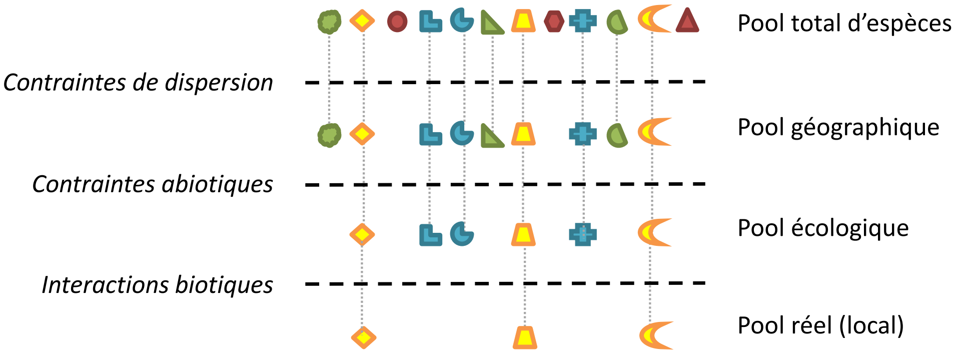


Figure 5 Représentation du modèle de filtres écologiques (tirets horizontaux) sélectionnant les espèces (formes des polygones) en fonction de leurs traits de réponse (couleurs des polygones). Le pool total d'espèces est déterminé par des processus à larges échelle spatio-temporelles (histoire biogéographique, spéciation). Un premier filtre exclut les espèces qui ne peuvent effectivement pas disperser jusqu'à l'habitat donné et détermine le filtre géographique. Un deuxième type de filtre exclut les espèces ne pouvant pas survive dans les conditions abiotiques (T°C, humidité) imposées par le milieu. Un troisième type de filtre, correspondant aux contraintes imposées par les interactions biotiques (exclusion compétitive par exemple) détermine le pool d'espèces effectivement présentes (adapté de Belyea and Lancaster, 1999).

Ainsi, les filtres successifs sélectionnent les espèces suivant leurs caractéristiques fonctionnelles (dispersion, compétitivité, spécialisation alimentaire) et l'étude de la distribution des traits fonctionnels permet donc d'élucider une partie de ces filtres. Les filtres vont exercer une restriction dans la gamme de valeurs de traits des espèces (exclusion des espèces avec des valeurs de trait données) et sont donc considérés comme une réponse extrême aux variations de l'environnement (« hard edge », Kraft et al., 2015). D'autres processus vont faire varier les fréquences de valeurs de traits dans les communautés comme les interactions biotiques (Bernard-Verdier et al., 2012) ou de réponse à des facteurs abiotiques n'entraînant que des variations d'abondance relative des espèces, sans exclusion (Kraft et al., 2015). L'ensemble des traits, conditionnant le filtrage des espèces ainsi que la variation des abondances des espèces, sont appelés **traits de réponse** (Suding et al., 2008).

La plupart des études explorant le lien entre l'hétérogénéité du paysage et la structure fonctionnelle des communautés d'abeilles sauvages ont étudié les changements d'abondance relative de valeur de traits le long de gradients paysagers (De Palma et al., 2015; Hopfenmüller et al., 2014; Williams et al., 2010). Seulement une étude a explicitement testé l'existence de filtres due à des variables paysagères contraignant l'assemblage des espèces observées, mais n'a pas trouvé de résultats significatifs (Sydenham et al., 2015). Cependant, l'absence d'effet de filtre dû au contexte paysager dans cette étude pourrait être provoquée par l'absence d'un gradient paysager prononcé. Une autre étude a explicitement testé l'existence de filtres d'espèces d'abeilles le long d'un gradient altitudinal (Hoiss et al., 2012), pouvant influencer la disponibilité en ressources florales mais aussi les conditions abiotiques (température, humidité, différence de saisonnalité, etc.). Les auteurs ont trouvé que les espèces cavicoles, solitaires et de petites tailles étaient exclues des sites situés à une haute altitude, du fait de leur exigences écologiques strictes et de leur faible capacité de dispersion (Hoiss et al., 2012). Ces résultats suggèrent que dans des conditions où les ressources sont rares, les filtres environnementaux peuvent influencer les assemblages d'espèces d'abeilles sauvages. Cependant il y a très peu de connaissances sur les potentiels effets de filtres exercés par l'hétérogénéité des paysages sur les communautés d'abeilles sauvages.

De la même manière qu'au sein d'un gradient altitudinal, on s'attend à ce que des paysages simples et fragmentés, offrant une disponibilité et une accessibilité faibles aux ressources florales et en sites de nidification filtrent les espèces dépendantes des milieux semi-naturels et ayant de faibles capacité de dispersion (Tscharntke et al., 2012). Au contraire, une hétérogénéité forte des paysages, favorisant la co-existence d'une diversité d'espèces (multitude d'habitats limitant la compétition, fonctionnement en méta-communauté, connectivité forte, etc.) aurait le potentiel de favoriser une importante diversité fonctionnelle (Tscharntke et al., 2012). Elle favoriserait une diversité de stratégies fonctionnelles différentes (richesse fonctionnelle : gamme de valeurs de traits dans une communauté) mais aussi limiterait la compétition entre espèces aux stratégies différentes (équitabilité fonctionnelle : distribution de la fréquence relative des valeurs de traits) (Fig. 6).

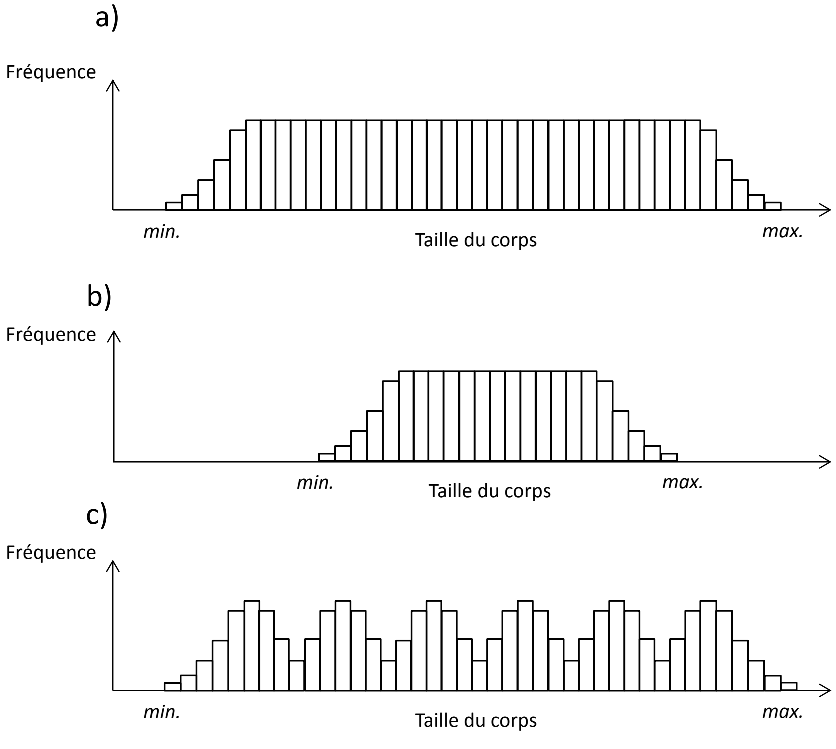


Figure 6 Effets de la variation de la richesse et de l'équitabilité fonctionnelle sur la diversité fonctionnelle. Dans ces exemples, l'abscisse représente les différentes valeurs de taille du corps des espèces en présence dans une communauté, et l'ordonnée mesure la fréquence des différentes tailles du corps. L'équitabilité représente la régularité de la distribution des valeurs de traits, tandis que la richesse fonctionnelle représente la largeur de la gamme de valeur de traits au sein de la communauté. Cas A : forte diversité fonctionnelle car équitabilité et richesse fonctionnelle élevée. Cas B : plus faible diversité fonctionnelle que le cas A due à la baisse de richesse fonctionnelle par rapport au cas A. Cas C : Plus faible diversité fonctionnelle que le cas A due à la baisse d'équitabilité fonctionnelle (adapté de Mason et al., 2005)

b- Approche fonctionnelle du lien biodiversité-fonction écologique

L'étude du lien entre biodiversité et fonction écologique (pollinisation, prédation, production de biomasse, etc.) est un champ de recherche fécond (BEF research : biodiversity-ecosystem functioning). Plusieurs décennies d'expérimentations ont abouti à un consensus sur le fait que la perte de biodiversité était généralement associée à une réduction du niveau de fonctionnement des écosystèmes (Cardinale et al., 2012; Hooper et al., 2005). La diminution de la richesse spécifique, mais aussi la perte de certaines espèces en particulier ont d'importants effets sur les fonctions écologiques (Hooper et al., 2005). Ces résultats soulignent deux possibles mécanismes qui lient perte d'espèces et fonctionnement écosystémique :

- **Un effet positif de la diversité spécifique ou fonctionnelle sur une fonction** : cet effet positif s'explique par les mécanismes de complémentarité et de facilitation. La complémentarité des espèces résulte de la réduction de la compétition par la partition des ressources qui provoque une meilleure utilisation globale de la ressource (Blüthgen and Klein, 2011; Hooper et al., 2005) : les espèces se concentrent sur différentes dimensions spatiales ou temporelles de la ressource. La facilitation est une interaction positive entre espèces, et provient de l'effet positif d'une espèce sur une autre en modifiant les conditions de l'environnement ou d'accès aux ressources (Hooper et al., 2005).
- **Un effet d'une espèce ou d'un groupe d'espèces sur une fonction**: ce mécanisme stipule que seule une fraction réduite d'espèces présentes dans une communauté est fonctionnellement importante et que l'effet positif de l'augmentation de la biodiversité sur une fonction vient d'un effet d'échantillonnage. Cet effet d'échantillonnage décrit le fait que plus il y a d'espèces en présence et plus il y a de chance d'avoir des espèces efficaces pour extraire une ressource. Des preuves théoriques et empiriques démontrent que, dans certains cas, les espèces contribuent à une fonction proportionnellement à leur abondance (hypothèse « mass-ratio », Grime, 1998), et par conséquent les espèces les plus fonctionnellement importantes seraient des espèces dominantes au sein des communautés (Hooper et al., 2005; Winfree et al., 2015).

Un ensemble important d'études a montré que la diversité spécifique et/ou fonctionnelle était fortement corrélée à l'intensité de pollinisation, que l'on estime généralement par le nombre de graines par fruit ou par le poids moyen des fruits (Garibaldi et al., 2013; Hoehn et al., 2008; Klein et al., 2008; Martins et al., 2015). Ces études suggèrent un lien entre diversité fonctionnelle des abeilles et pollinisation par la présence de mécanismes de complémentarité entre espèces d'abeilles sauvages, liés l'utilisation contrastée des ressources (Blüthgen and Klein, 2011). Cependant, d'autres études ont montré que c'était la variation d'abondance d'espèces dominantes d'abeilles sauvages qui déterminait le niveau de pollinisation, car seulement certaines espèces dominantes, aux valeurs de traits similaires, étaient fonctionnellement importantes (Kleijn et al., 2015; Winfree et al., 2015).

Il est important de noter que ces deux mécanismes ne s'excluent pas forcément, et il y aurait un continuum d'effets de la diversité sur les fonctions écologiques (Hooper et al., 2005). En effet, des communautés plus diverses ont plus de chance d'inclure une espèce dominante ou une combinaison d'espèces qui sont complémentaires. La compréhension de ces deux types de mécanismes, et des conditions qui favorisent leur émergence, permettrait de mieux piloter la diversité des pollinisateurs pour maximiser les services de pollinisation (Kleijn et al., 2015).

Ces deux hypothèses reposent sur le fait que la distribution de traits écologiques peut influencer le niveau de pollinisation. On les nomme des **trais d'effets** (Suding et al., 2008). Le lien fonctionnel entre réponse des espèces à l'environnement et l'implication de cette réponse sur les fonctions écologiques a été conceptualisé dans le cadre du « response-and-effect trait framework » (Suding et al., 2008). Ce cadre conceptuel stipule qu'un changement dans la distribution de traits d'effets le long d'un gradient environnemental est dû à une relation entre traits de réponse et traits d'effet. Cette relation pourrait être le résultat d'une corrélation entre traits de réponse et traits d'effet ou le fait que certains traits d'effets sont aussi impliqués dans la réponse des communautés aux changements environnementaux.

II- Objectifs de la thèse et questions de recherche

Grâce aux études mobilisant des gradients environnementaux (études synchroniques) mais aussi à celles utilisant le suivi de populations au court du temps (études diachroniques), la littérature s'accorde sur l'effet majeur de la perte d'habitats et de l'intensification des pratiques agricoles sur le déclin des abeilles sauvages (Biesmeijer et al., 2006; Potts et al., 2010a; Woodcock et al., 2016). L'ambition de cette thèse est d'améliorer les connaissances sur quatre facteurs susceptibles d'influencer les communautés d'abeilles sauvages et la pollinisation :

- **L'effet paysager de l'intensification des pratiques agricoles**. Comme nous l'avons vu précédemment, la littérature abonde sur l'effet local de l'intensité des pratiques agricoles sur les abeilles sauvages, mais nous avons peu de connaissances sur un potentiel levier agronomique au niveau des paysages (Batáry et al., 2011; Bengtsson et al., 2005; Holzschuh et al., 2007; Woodcock et al., 2016). En effet, puisque les abeilles sauvages utilisent des ressources à une échelle plus large que la parcelle agricole (Westrich, 1996; Zurbuchen et al., 2010), et que l'intensification agricole se produit aussi à une l'échelle paysagère (Burel and

Baudry, 1990; Herzog et al., 2006; Robinson and Sutherland, 2002), l'exploration d'un levier agronomique à l'échelle paysagère pour conserver les abeilles est pertinente.

- **L'effet de l'hétérogénéité des paysages sur les abeilles sauvages**. En effet la plupart des études rassemblent différents milieux semi-naturels présents en étudiant l'effet de la complexité du paysage (pourcentage total en milieu semi-naturels) (Garibaldi et al., 2011; Winfree et al., 2009). D'autres études se placent dans des gradients paysagers faisant varier la proportion d'un seul type de milieu semi-naturels (Holzschuh et al., 2007; Hopfenmüller et al., 2014; Jauker et al., 2013). L'effet de complémentation entre plusieurs types de milieux semi-naturels mais aussi l'effet relatif de ces différents milieux sur les communautés ou sur des groupes fonctionnels n'est donc pas encore bien connu.
- **L'effet d'interaction entre intensité paysagère des pratiques et hétérogénéité du paysage** (Potts et al., 2010a). Il a été montré que l'effet local de l'intensité des pratiques agricole sur la diversité des abeilles sauvages dépend de la proportion de milieux semi-naturels environnants (Batáry et al., 2011; Holzschuh et al., 2007). Ces études ont montré que dans les parcelles gérées de manière intensive, la diversité locale en abeilles sauvages est fortement expliquée par les variations de la proportion de milieux semi-naturels environnants (Fig. 7). Au contraire, dans des parcelles gérées de manière extensive, la diversité des abeilles sauvages semble moins dépendre des milieux semi-naturels. Ces résultats suggèrent que les pratiques extensives permettent de maintenir une richesse locale en ressources favorisant la visite d'abeilles sauvages, alors que le pool local observé en parcelles intensives dépendrait de l'immigration d'individus depuis les milieux semi-naturels environnants, du fait de la pauvreté en ressources dans la parcelle (Holzschuh et al., 2007). L'étude de ces interactions, en considérant l'intensité des pratiques à l'échelle paysagère, permettrait de tester si cette interaction est aussi vérifiée à l'échelle du paysage. De plus, l'exploration du type de milieu semi-naturel ou du type de pratique qui influence le plus la diversité des abeilles sauvages permettraient de mieux connaître les ressources influencées par les pratiques et de tester l'existence de phénomènes de complémentation/supplémentation entre milieux semi-naturels et mosaïque cultivée.

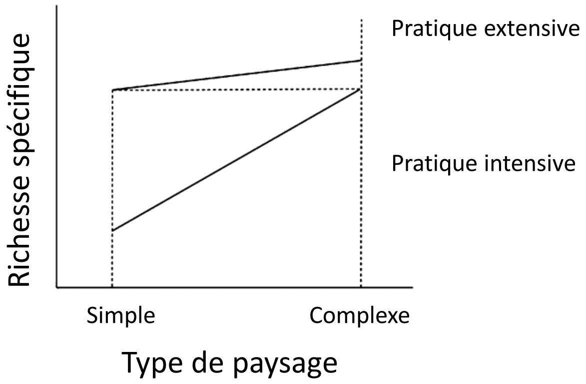


Figure 7 Diversité des abeilles sauvages des parcelles agricoles en fonction de la gestion agronomique locale (intensive vs. extensive) et de la complexité du paysage. La diversité des abeilles sauvages est plus forte en en parcelles gérées de manière extensive mais la complexité du paysage peut compenser l'intensité locale des pratiques (adapté de Tscharntke et al., 2005)

- **La relation entre la structure des communautés d'abeilles sauvages et le niveau de pollinisation le long de gradients paysagers.** Comme précédemment évoqué, deux hypothèses sur le lien entre diversité des abeilles et pollinisation, vérifiées par des données empiriques, sont proposées dans la littérature : (1) l'hypothèse de la complémentarité des espèces, stipulant qu'une augmentation de la diversité fonctionnelle dans les communautés provoque une augmentation de la pollinisation (Blüthgen and Klein, 2011 ; Hoehn et al., 2008), (2) l'hypothèse du « mass-ratio », stipulant que puisque les espèces contribuent à une fonction proportionnellement à leurs abondance, les variations de niveau de pollinisation sont expliquées par les variations d'abondance des espèces dominantes (Garibaldi et al., 2015; Kleijn et al., 2015 ; Winfree et al., 2015). Le long de gradients paysagers, la diversité fonctionnelle au sein des communautés d'abeilles mais aussi l'abondance de certaines abeilles dominantes sont susceptibles de varier (Larsen et al., 2005; Martins et al., 2015). Il est donc important de connaître les situations dans lesquelles ces deux hypothèses se vérifient ou non (car possiblement, ces hypothèses peuvent mutuellement s'exclure ou se vérifier ensemble).

Les objectifs principaux de la thèse sont donc de :

1. Comprendre la réponse des communautés abeilles sauvages aux variations d'hétérogénéité des paysages et d'intensité paysagère des pratiques, par la caractérisation de leur structure fonctionnelle.
2. Caractériser finement les causes de changements dans la structure fonctionnelle des communautés, en essayant de différentier les traits répondant à l'environnement (traits de réponses) d'autres traits n'ayant pas d'importance dans la structuration des communautés en fonction de changements environnementaux (corrélation entre traits).

3. Identifier les patrons de variation dans la structure des communautés d'abeilles sauvages qui sont le plus corrélés aux variations de pollinisation.

Dans les différents chapitres de cette thèse, nous avons testés les hypothèses suivantes (Fig. 8) :

1. Les abeilles sauvages capturées en parcelles agricoles répondent différemment à la composition et à la configuration des milieux semi-naturels des paysages suivant leurs traits : les espèces potentiellement dépendantes des milieux semi-naturels (niche alimentaire étroite, faible capacité de dispersion, nid dans des cavités préexistantes) sont plus affectées par la composition et la configuration des milieux semi-naturels que d'autres espèces moins inféodées à ces milieux. Nous faisons aussi l'hypothèse que l'hétérogénéité des paysages peut filtrer les espèces suivant leurs traits, les espèces dépendantes des milieux semi-naturels étant exclues dans les paysages homogènes (**chapitre 1**).
2. Les traits écologiques dont la distribution varie le long des gradients paysagers ne sont pas tous des traits de réponse. En effet, nous faisons l'hypothèse que la distribution de certains traits écologiques dépend de celle d'autres traits déterminant effectivement la réponse des espèces à l'environnement (traits de réponse « réels »). Cette co-variation entre traits écologiques et traits de réponse serait due à une corrélation de ces traits à l'échelle des espèces ou à une structuration phylogénétique des communautés le long des gradients environnementaux (un groupe d'espèces phylogénétiquement proches, ayant des valeurs de traits similaires, répond aux gradients paysagers, contrairement à d'autres espèces). Nous faisons aussi l'hypothèse que les changements dans la distribution des traits écologiques peuvent affecter l'efficacité de pollinisation (**chapitre 2**).
3. L'hétérogénéité des paysages et l'intensité paysagère des pratiques agricoles ont un effet interactif sur la diversité des abeilles sauvages. Nous nous attendons à ce que les variations de diversité d'abeilles sauvages dépendent fortement de la composition des paysages en milieux semi-naturels dans les paysages intensifs. L'effet des milieux semi-naturels sur les abeilles sauvages des parcelles agricoles serait donc modulé par l'intensité des pratiques au sein de la mosaïque cultivée (**chapitre 3**).
4. La détermination de la disponibilité en sites de nidification dans les prairies permanentes permet de prédire la diversité des abeilles sauvages des parcelles cultivées, car elles peuvent offrir des zones de sols nus peu perturbés (sans travail du sol), idéales pour les abeilles terricoles (**chapitre 4**).
5. L'hétérogénéité des paysages et l'intensité locale des pratiques agricoles influencent la diversité des pollinisateurs et le niveau de pollinisation. Nous nous attendons à ce que des paysages hétérogènes et aux pratiques localement extensives aient un effet positif sur la diversité des abeilles sauvages (**chapitre 5**).

6. Le niveau de pollinisation est déterminé par l'abondance des espèces dominantes d'abeilles sauvages et/ou par la diversité fonctionnelle des communautés (**chapitre 5 et 6**).

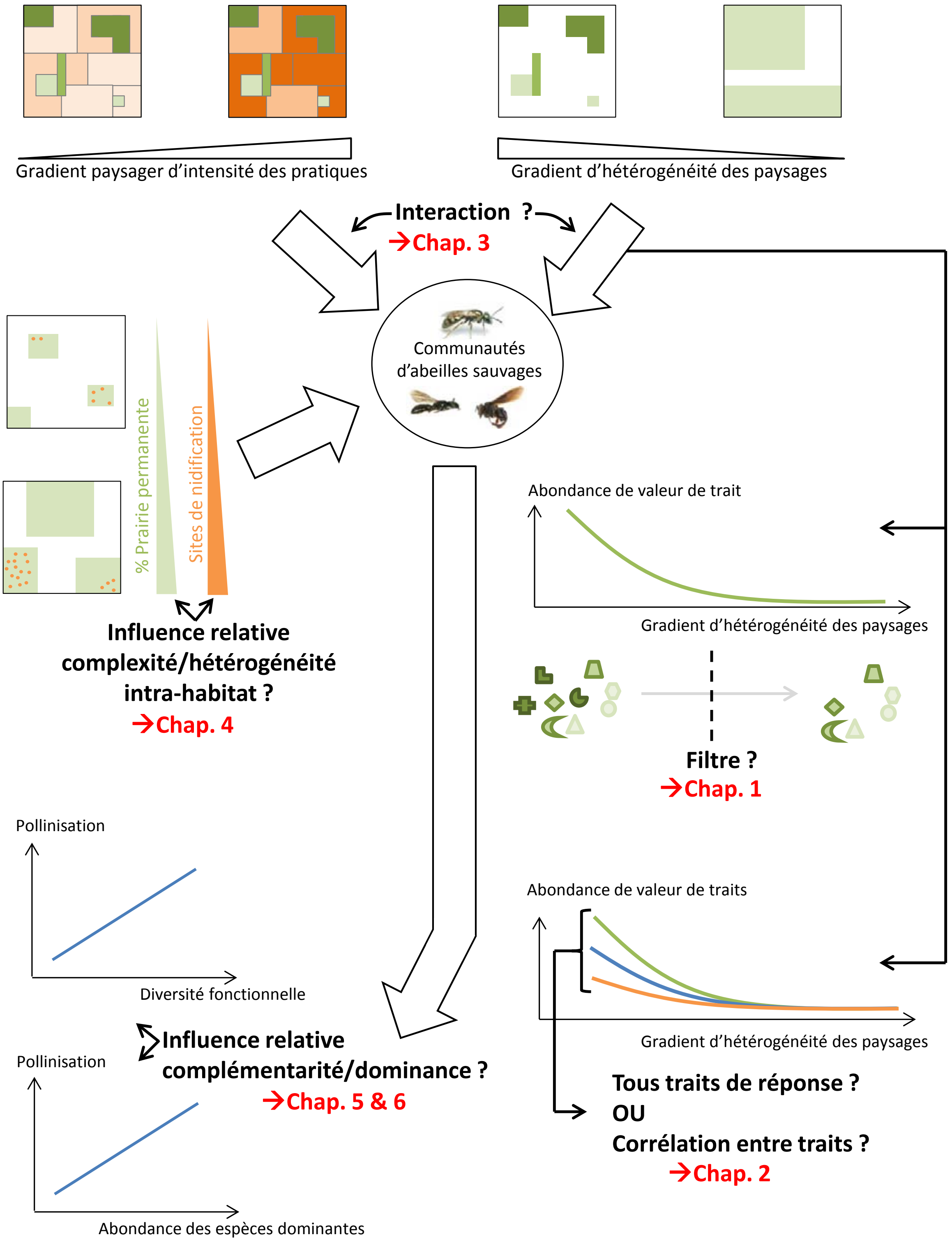


Figure 8 Organisation de la thèse en fonction des hypothèses testées dans les différents chapitres. Les chapitres 1 et 2 s'attachent à caractériser la réponse fonctionnelle des communautés d'abeilles sauvages à l'hétérogénéité des paysages. Les chapitres 3 et 4 explorent l'effet de l'hétérogénéité cachée des paysages agricoles (pratiques agricoles dans la mosaïque cultivée, hétérogénéité intra-prairie) sur la diversité des abeilles sauvages. Les chapitres 5 et 6 explorent l'influence relative de la diversité fonctionnelle et de l'abondance des espèces d'abeilles dominantes sur la fourniture en pollinisation.

III- Matériels et méthodes

1- Site d'étude

La récolte des données de terrains s'est déroulée dans les Vallées et Coteaux de Gascogne, une région suivie par le laboratoire DYNAFOR depuis environ 30 ans. Ce site d'étude est labellisé LTER (Long Term Socio-Ecosystem Research). Cette région, située à environ 60 km au sud-ouest de Toulouse dans le Comminges, est caractérisée par la présence de coteaux parallèles, dont les fond de vallons sont orientés NNO-SSE. Les sécheresses fréquentes en été, alliées à des sols en forte pente, ont privilégié l'implantation de cultures annuelles en fond de vallons, sur les sols les plus productifs, et la présence de prairies permanentes et de forêts sur les coteaux (Choisis et al., 2010; Ryschawy, 2012). Du fait de ces pentes, et des systèmes en polyculture-élevages qui dominent la région (environ 48% des exploitations, Ryschawy, 2012), le site d'étude a une part importante de ses assolements occupés par des prairies permanentes (21% en moyenne dans les paysages étudiés). De plus, le système traditionnel « à maison » (logique d'autosubsistance familiale), dominant dans la région, a permis le maintien d'une mosaïque diverse d'occupations des sols et plus particulièrement de zones boisées tels que des petits bois, bosquets et haies (Sourdril and Ladet, 2008).

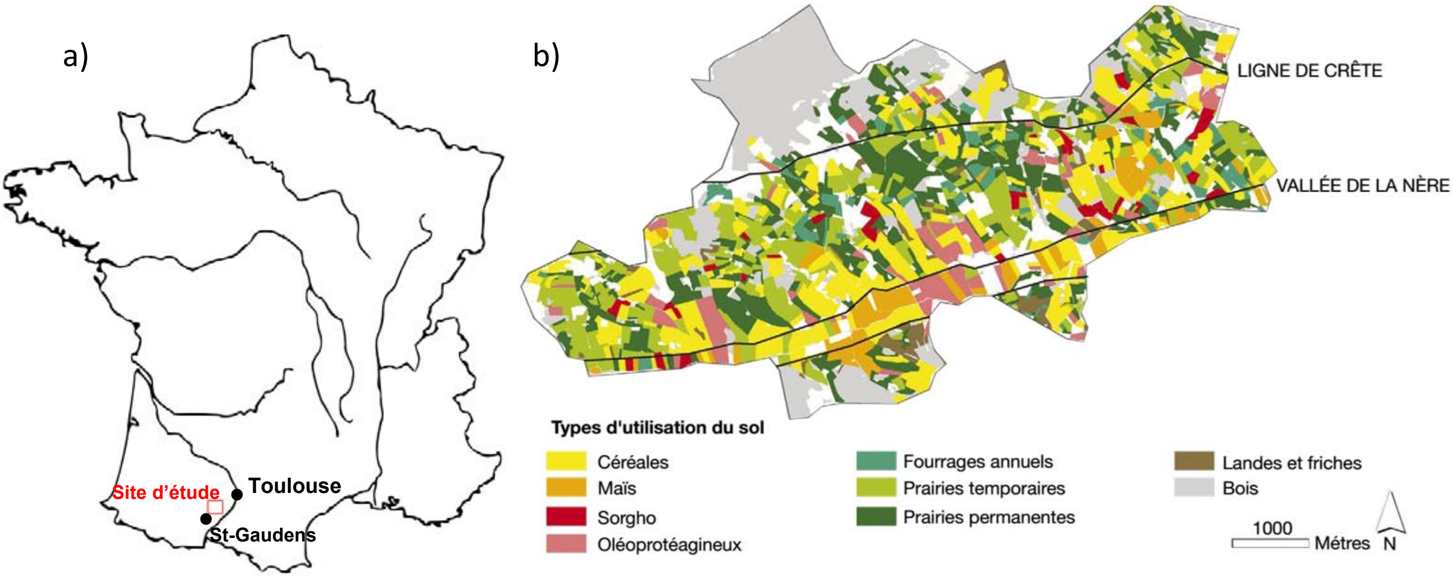


Figure 9 Localisation du site d'étude (a) et principaux types d'utilisation des sols en 2006 autour d'une vallée et d'une ligne de crête dans la zone d'étude (b) (d'après Choisis et al., 2010).

Le milieu forestier y est très fragmenté (forêt paysanne), avec la présence de nombreux petits ilots boisés allant de 0,5 à 20 ha (Roume, 2011).

Le climat du site est de type océanique dégradé avec des influences montagnardes et méditerranéennes (température et précipitations annuelles moyennes: 12,5°C et 750 mm).

2- Sélection des paysages

Les conclusions de cette thèse sont basées sur l'étude de gradients paysagers. Les gradients de paysages permettent de faire varier continument et de façon indépendante plusieurs descripteurs des paysages décrivant par exemple leur structure ou leur composition. L'objectif des procédures de sélection des paysages est de minimiser la corrélation entre plusieurs descripteurs des paysages et de maximiser la gamme de variation de chaque descripteur, afin de détecter avec plus de précision statistique la corrélation entre ces facteurs paysagers et des variables écologiques (Pasher et al., 2013; Smith et al., 2009).

Ce type de sélection de paysage suit une approche nommée « pseudo-expérimentale » : « expérimentale » puisqu'on cherche à faire varier indépendamment des facteurs environnementaux pour mieux détecter leurs effets relatifs, et « pseudo » car il n'y a pas de réellement manipulations de l'environnement (Pasher et al., 2013).

Pour la construction du gradient d'**intensité paysagère des pratiques agricoles**, nous avons utilisé la procédure de sélection des paysages du projet FarmLand, projet qui a permis de financer la récolte des données en 2013 et 2014. Cette procédure recherche à maximiser l'hétérogénéité de la mosaïque cultivée, qui est fortement corrélée à l'intensité paysagère moyenne des pratiques (Herzog et al., 2006; Roschewitz et al., 2005b). Sur la base d'une carte d'occupation des sols réalisée à partir d'images satellites SPOT 5, un tirage aléatoire de 20 000 carrés de 1x1 km a été réalisé (procédure des fenêtres glissantes). Dans chacun des carrés, deux métriques paysagères ont été calculées : l'indice de Shannon des cultures (SHDI, hétérogénéité de composition) et la taille moyenne des parcelles (TMP, hétérogénéité de configuration). Un nuage de point comportant les 20 000 tirages aléatoires a alors été réalisé, et la sélection de 4 zones comportant les valeurs extrêmes des deux indices a permis de décorréler ces deux facteurs tout en maximisant leur amplitude de variation (Fig. 10) (Pasher et al., 2013). Des paysages candidats ont ensuite été retenus dans chacune des 4 catégories. Ils devaient contenir entre 60 et 90% de surface agricole et être distants d'au moins 1,5 km.

Ensuite, des campagnes de relevés d'occupation des sols sur le terrain ont été effectuées pour confirmer et préciser les types de cultures et le contour des parcelles, prairies et bois. Parmi chacun des carrés de 1 km², deux parcelles de céréales d'hiver et une culture de printemps (tournesol ou maïs) ont été sélectionnées. Ces types de culture ont été choisis du fait de leur dominance dans les paysages des Coteaux de Gascogne. Ces parcelles devaient contenir une bordure enherbée et les trois parcelles au sein des carrés devaient être distantes d'au moins 200 m. Parmi tous les paysages carrés candidats, 32 paysages ont été retenu (20 en 2013, 12 en 2014).

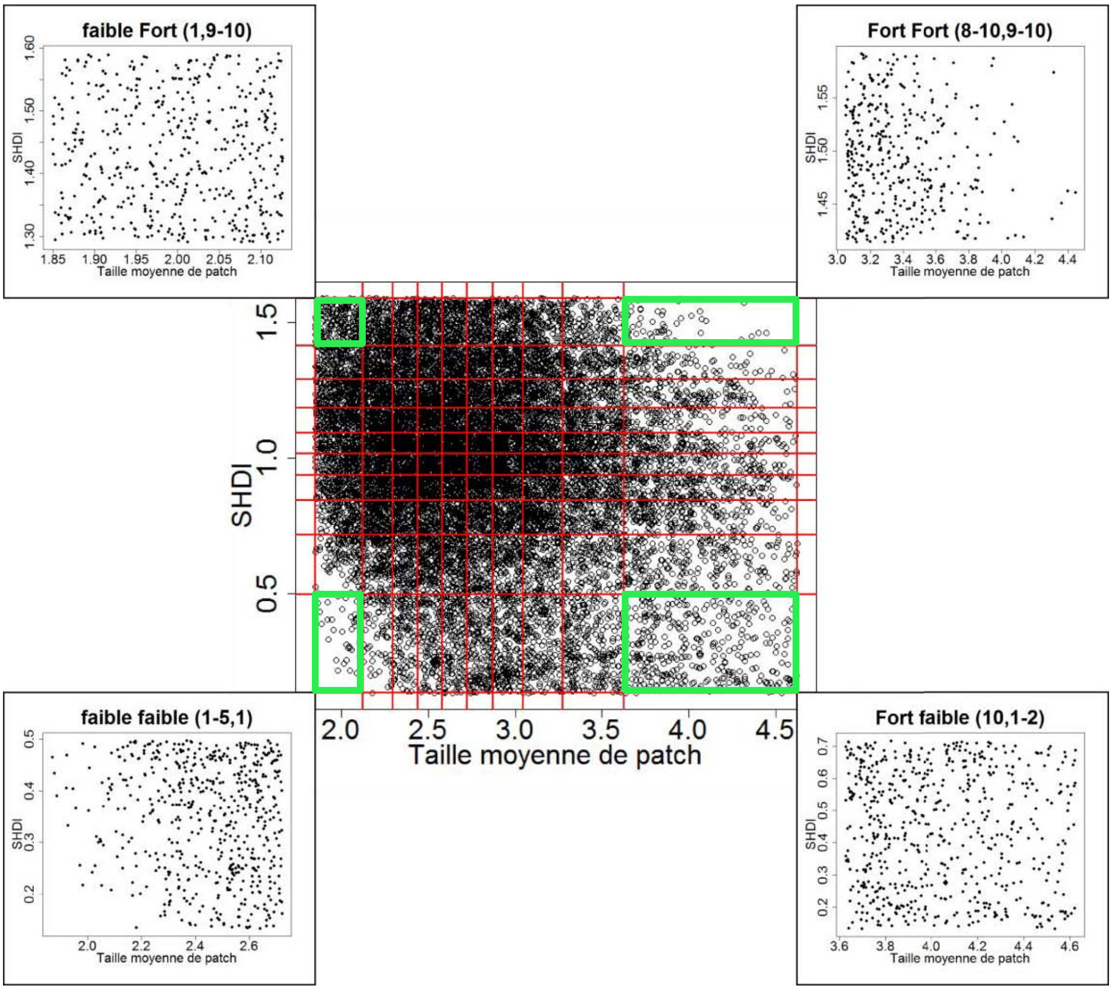


Figure 10 Nuage de points de l'indice de Shannon des cultures (SHDI) et de la taille moyenne des parcelles (TMP) pour les 20 000 tirages aléatoires de paysages de 1x1 km. Les 4 coins représentent les 4 déciles des valeurs extrêmes de SHDI et de TMP. La sélections de ces 4 coins permettent de décorréler les variations de SHDI et de TMP mais aussi de maximiser l'amplitude de variation de ces deux variables.

Pour la construction du **gradient d'hétérogénéité des milieux semi-naturels**, nous avons utilisé des buffers circulaires (zones tampons) de 500 m de rayon, centrés sur le milieu des bordures enherbées des 96 parcelles de céréales d'hiver sélectionnées en 2013 et 2014 (au sein des carrés de 1km²). Comme la plupart des buffers circulaires dépassait des carrés de 1km² dont l'occupation des sols était connue, la présélection des paysages circulaires a été réalisée à partir du RPG (Registre Parcellaire Graphique) pour les prairies permanentes et de la BD TOPO (IGN) pour les éléments boisés (haies, bois). En utilisant ces deux sources de données, nous avons sélectionné 16 parcelles en céréales supplémentaires (de celles sélectionnées pour le projet FarmLand) pour décorréler au maximum les proportions de prairies permanentes et d'éléments boisés au sein des paysages circulaires. Une campagne de relevés d'occupation des sols a été réalisée pour vérifier les contours des prairies et zones boisées. Parmi tous les paysages circulaires candidats, 80 paysages ont été retenus (40 en 2013 et 40 en 2014).

Pour la construction du **gradient de complexité du paysage** (terrain effectué en 2015), nous nous sommes reposés sur les 112 parcelles échantillonnées en 2013 et 2014. Grâce aux données du RPG et de la BD TOPO, nous avons calculé la proportion en milieux semi-naturels (prairies + éléments boisés) dans des buffers circulaires de 500 m de rayon centrés sur le milieu des bordures enherbées des parcelles. Des paysages circulaires candidats ont été sélectionnés afin de maximiser l'amplitude de variation en pourcentage de milieux semi-naturels. Une campagne de relevés d'occupation des sols a ensuite été réalisée pour vérifier les contours des prairies et zones boisées, et aussi pour sélectionner les parcelles qui étaient semées en céréales d'hiver. Parmi les 112 paysages candidats, 20 paysages circulaires ont été retenus.

Nous avons donc utilisé deux types de paysages dans cette thèse : des paysages carrés de 1 km² et des paysages circulaires de 500 m de rayon. En plus de la différence de forme, l'effort d'échantillonnage était différent dans les deux types de paysages, avec un point d'échantillonnage par paysage circulaire, et trois pour les paysages carrés. L'utilisation de paysages circulaires avec un point d'échantillonnage au centre est une approche classique en écologie du paysage. Elle vise à identifier les facteurs paysagers qui influencent la biodiversité observée localement. D'autres études en écologie du paysage échantillonnent plus de taches d'habitats par paysage (Fig. 11) afin de mieux rendre compte de la réponse de la biodiversité à l'échelle paysagère (Bennett et al., 2006; Duflot et al., 2014; Fahrig et al., 2015). Ces approches permettent de décomposer la biodiversité à l'échelle paysagère (diversité gamma), en sa composante locale (diversité alpha, à échelle de la tache d'habitat) et inter-habitats (diversité béta). Cependant dans cette thèse, nous n'avons pas calculé de diversité en abeilles sauvages à l'échelle gamma (échelle paysagère) et nous avons considéré seulement la diversité à l'échelle locale des parcelles agricoles. Cette approche par triplet nous a permis de faire des conclusions sur l'effet paysager des pratiques agricoles (parcelles incluses dans une « ambiance » paysagère équivalente) tout en tenant compte de la variation de l'intensité locale des pratiques. Cet échantillonnage en multiplet est souvent utilisé pour comparer des effets locaux avec des effets paysagers (parcelles bio vs. conventionnelles appariées au sein d'un gradient de complexité paysagère par exemple, Batáry et al., 2011; Holzschuh et al., 2010, 2007).

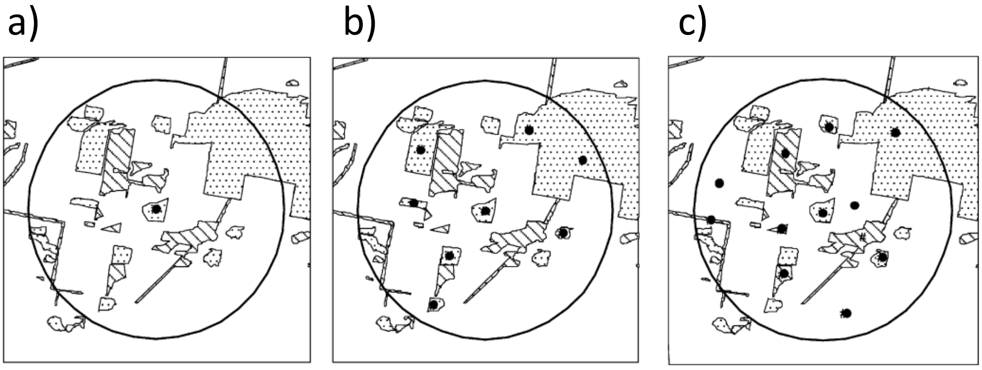


Figure 11 Comparaison des différentes procédures d'échantillonnage de la biodiversité dans les paysages agricoles. (a) Diversité alpha, mesurée sur une seule tache d'habitat par paysage ; (b) Diversité gamma, mesurée sur plusieurs taches d'un même type d'habitat ; (c) Diversité gamma, mesurée sur plusieurs taches de plusieurs types d'habitats (d'après Bennett et al., 2006)

3- Echantillonnage des abeilles sauvages, indentification à l'espèce et rassemblement des données sur les traits

a- Capture des abeilles sauvages

La technique de capture par piège à noyade (« pan traps », coupelles colorées contenant de l'eau savonneuse) a été utilisée pour chaque site d'échantillonnage de la thèse. Cette méthode permet de rendre compte de la diversité des communautés d'abeilles sauvage dans divers habitats de manière très satisfaisante tout en limitant le temps passé à la capture (par rapport à l'utilisation de filets sur des transects par exemple) (Westphal et al., 2008).

Pour les parcelles échantillonnées en 2013 et 2014, six points d'échantillonnage ont été établis par parcelle (Fig. 12) : trois points à 50 cm de la bande enherbée, séparés de 25 m chacun et trois points à 25 m de la bordure à l'intérieur des parcelles, disposés de manière parallèle aux points de bordure. Sur chaque point d'échantillonnage était planté un poteau en bois portant deux coupelles colorées de couleurs différentes (coupelle de plastique de 15 cm de diamètre et 7 cm de profondeur, Fig. 13). L'ordre des couleurs de pièges était identique pour chaque parcelle. Trois couleurs ont été utilisées : bleu, blanc et jaune (peinture réfléchissant les UV, SparVar® Allemagne). Les coupelles ont été remplies au 2/3 avec de l'eau et une petite quantité de savon pour diminuer les tensions de surface (Teepol ® multipurpose detergent). La hauteur des coupelles était adaptée à la hauteur du couvert des cultures. Les pièges étaient placés pendant deux périodes de 3 à 4 jours par parcelle. Du fait de la forte abondance des abeilles sauvages récoltées en 2013 et 2014, seulement la moitié des pièges (6 pièges par parcelle) a été utilisée pour l'identification au rang de l'espèce.

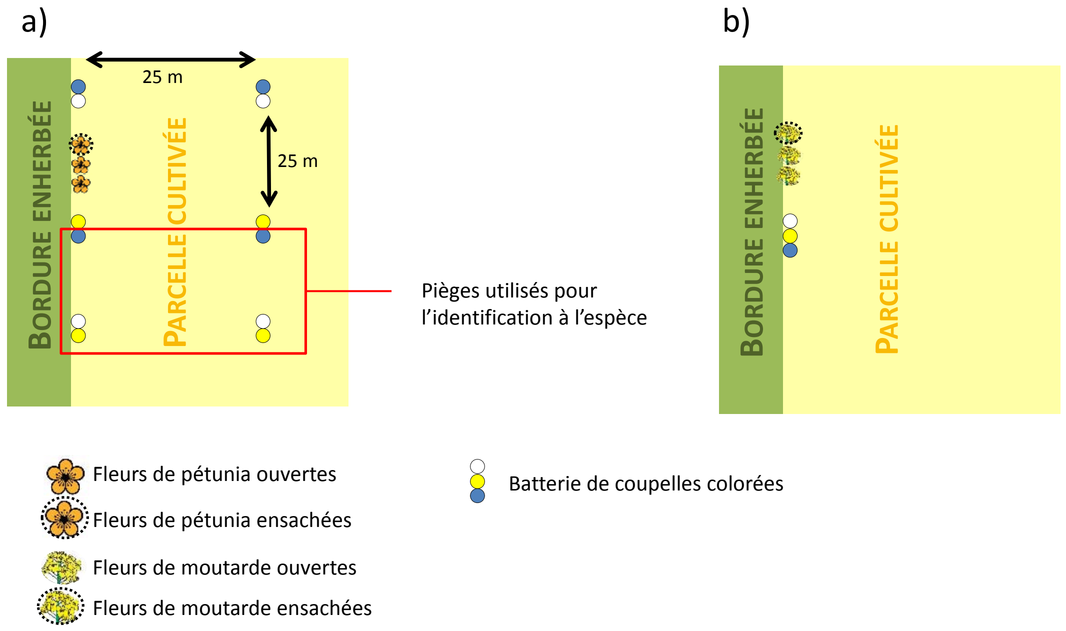


Figure 12 Représentation du plan d'échantillonnage des campagnes de 2013 et 2014 (a), et de 2015 (b).

Pour les parcelles échantillonnées en 2015, trois pièges ont été disposés par parcelle, et seulement en bordure de parcelle. L'unique point d'échantillonnage dans les parcelles correspondait à la position du poteau central pour les parcelles échantillonnées en 2013 ou 2014. Les pièges ont été disposés pendant une session de 4 jours par parcelle.

Figure 13 Photographie d'un site d'échantillonnage, constitué d'un poteau portant deux coupelles colorées, dont la hauteur était ajustée à la hauteur du couvert de la culture (photo : Léa Frontero).

J'ai personnellement contribué aux campagnes de terrain de 2014 et 2015, et j'ai utilisé les données acquise lors d'une campagne de terrain qui a été réalisée au printemps 2013 avant le début de la thèse.

Cette thèse repose donc sur l'échantillonnage de 132 parcelles de cultures annuelles, échantillonnées en 2013, 2014 et 2015.

b- Identification des spécimens à l'espèce

Après les 3 ou 4 jours de piégeage, les insectes capturés dans les coupelles ont été stockés dans des piluliers. Un premier tri a été réalisé pour séparer les abeilles sauvages du reste des insectes. Ensuite, chaque spécimen d'abeille a été séché, épinglé, étalé et étiqueté. L'étape de séchage et d'étalage est important, puisqu'elle permet de rendre visible la pilosité, la structure de la cuticule et de bien rendre visibles certains détails clés de l'anatomie des abeilles pour l'identification des espèces (Fig. 14).

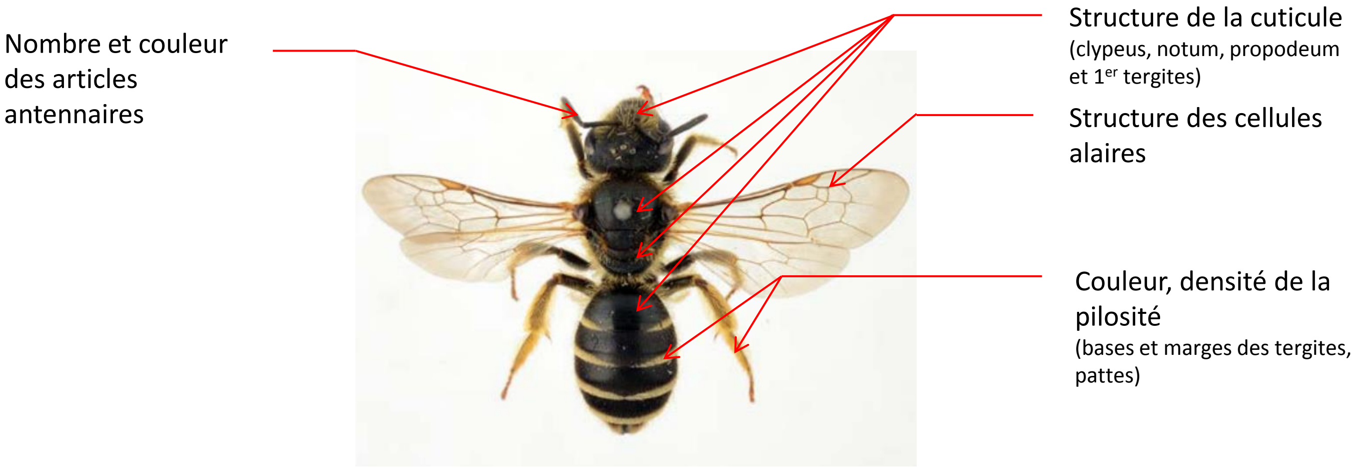


Figure 14 Localisation des principaux critères observés pour l'identification à l'espèce des abeilles sauvages.

Grâce à la formation suivie auprès de David Genoud (entomologiste spécialiste des abeilles sauvages) l'identification de 20 espèces a été possible au laboratoire (majoritairement de la famille des Halictidae, représentant environ 70 % des spécimens capturés). Les autres spécimens ont été identifiés par David Genoud. Pour certains spécimens rares, la confirmation de l'identification a été faite par Alain Pauly (Institut Royal des Sciences naturelles de Belgique, Bruxelles). Les spécimens mâles étaient systématiquement identifiés par David Genoud, après l'extraction et l'étalage des pièces génitales. En effet, les critères classiques d'identification des espèces d'abeilles sauvages ne sont valables que pour les individus femelles mais la structure des pièces génitales permet d'identifier les individus mâles à l'échelle de l'espèce.

c- Traits écologiques des espèces

Une base de données de traits a été construite grâce aux données issues de la littérature et à l'expertise de David Genoud pour la phénologie de butinage (sources des données: Bommarco et al., 2010; Forrest et al., 2015, 2015; Fortel et al., 2014; Gathmann and Tscharntke, 2002; Michener, 2000; Settele et al., 2005; Tscharntke et al., 2002; Williams et al., 2001). En utilisant les résultats d'études précédentes, des traits impliqués dans la réponse à des changements environnementaux locaux ou paysagers, mais aussi pouvant influencer l'efficacité de pollinisation ont été sélectionnés : taille du corps, socialité, spécialisation alimentaire, localisation du nid, type de construction du nid, début et longueur de la période de butinage (Tableau 1).

Pour certaines espèces, la taille du corps (mesurée par la distance inter-tégulaire, Tableau 1) n'était pas disponible dans la littérature. Cinq spécimens femelles par espèce ont donc été sélectionnés aléatoirement afin de mesurer la distance inter-tegulaire moyenne pour les espèces non informées.

Nous avons fait l'hypothèse implicite, dans toute cette thèse, que la variation inter-spécifique dans les valeurs de traits était plus importante que la variation intra-spécifique (plasticité phénotypique). En donnant une valeur moyenne de trait pour chaque espèce, nous nous plaçons dans une situation où la distribution des valeurs de traits dans les communautés ne peut changer qu'en fonction de variations de composition spécifique ou d'abondance relative des espèces (Violle et al., 2012).

Tableau 1 Traits utilisés dans les analyses et rôles écologiques correspondants.

Trait	Unité	Description and implications écologiques
Distance inter-tégulaire (DIT)	mm.	Distance entre les points d'insertion des ailes sur le thorax, qui mesure la taille du corps. Cette mesure est fortement corrélée aux capacité de vol des abeilles sauvages (Greenleaf et al., 2007) et est susceptible d'affecter l'utilisation des ressources dans les paysages et la réponse à la quantité d'habitats (Bommarco et al., 2010; Williams et al., 2010).
Localisation du nid	Catégoriel. Terricole (62 sp.); Cavicole (11 sp.)	Peut affecter la réponse des espèces d'abeilles sauvages à la quantité d'habitats et aux perturbations (travail du sol, déforestation, fréquence de fauche, surpâturage, Kremen and M'Gonigle, 2015; Shuler et al., 2005; Williams et al., 2010).
Type de construction du nid	Catégoriel. Cavité préexistante (13 sp.); Cavité creusée (60 sp.)	
Spécialisation alimentaire	Catégoriel Oligolectique (14 sp.); Polylectique (59 sp.)	La spécialisation alimentaire est définie par le nombre de familles de plantes visitées par les femelles d'abeilles sauvages. Les espèces polylectiques (généraliste, collectant du pollen sur plusieurs familles de plantes) ont plus de chance de survivre en utilisant des ressources florales alternatives que les espèces oligolectiques (spécialiste, collectant le pollen sur une famille de plantes). Les abeilles oligolectiques ont plus de chance de disparaitre en cas de perte d'habitats dans les paysages (Steffan-Dewenter et al., 2006; Williams et al., 2010)
Socialité	Catégoriel. Sociale (27 sp.); Solitaire (40 sp.)	L'intensification des pratiques agricoles et la perte d'habitats affectent différemment les espèces sociales et solitaires mais les mécanismes en jeu sont encore inconnus (Forrest et al., 2015; Kremen and M'Gonigle, 2015a; Williams et al., 2010).
Début de la saison de butinage; Durée de la saison de butinage	Numéro du mois (1-12) ; Nombre de mois (1-12)	Un décalage dans le début de la saison de butinage à l'échelle des communautés d'abeilles sauvages pourrait être le résultat d'un changement de la disponibilité des ressources florales dans les paysages (plantes sauvages ou cultivées). Une grande quantité de milieux semi-naturels est susceptible de favoriser les espèces émergeant avant ou après la période de floraison des cultures entomophiles (Bretagnolle and Gaba, 2015; Rollin et al., 2013).

4- Estimation du niveau de pollinisation dans les parcelles

Pendant les campagnes de terrain de 2014 et 2015, nous avons estimé expérimentalement le niveau de pollinisation entomophile via la technique des phytomètres (Steffan-Dewenter et al., 2001; Steffan-Dewenter and Tscharntke, 1999). Les phytomètres sont des plantes sentinelles produites en conditions contrôlées apportées sur le terrain, permettant ici de mesurer le niveau de pollinisation.

En 2014, une variété de colza entomophile (variété Visby) a été mise en culture sous serre pour mesurer la pollinisation dans le cadre du projet FarmLand. Les plants de colza n'ayant pas fleuri, nous avons choisis d'utiliser des plants de pétunia issus du commerce en raison de leur facilité de culture et de leur dépendance à la pollinisation entomophile. En 2015, une espèce proche du colza, la moutarde blanche (*Sinapis alba* L.), a été mise en culture sous serre pour mesurer la pollinisation en bordure de parcelle.

Que ce soit en 2014 ou en 2015, même si les espèces des phytomètres étaient différentes, les protocoles étaient identiques. Les plantes en pot étaient maintenues sous une enceinte imperméable aux insectes (moustiquaire en 2014 et tentes « insect-proof » en 2015) jusqu'à leur floraison (Fig. 15). Ensuite, la dernière fleur ouverte sur chaque plant était repérée à l'aide d'un scotch imperméable bleu. Trois plantes ont été déposés par parcelles (Fig. 12): deux plantes ouvertes à la pollinisation et une plante ensachée dans de la gaze et donc non accessibles aux pollinisateurs. Les plantes ensachées dans la gaze ont donc servi à mesurer la dépendance des phytomètres à la pollinisation entomophile mais aussi à mesurer la pollinisation réellement fournie par les insectes sur chaque site de mesure (car on soustrait l'autopollinisation et la pollinisation anémophile de la pollinisation totale). Les plantes étaient disposées dans des plateaux contenant un fond d'eau pour leur irrigation. En 2014, 180 plantes de pétunia en pots ont été amenées sur le terrain, et 60 plants de moutarde en 2015.

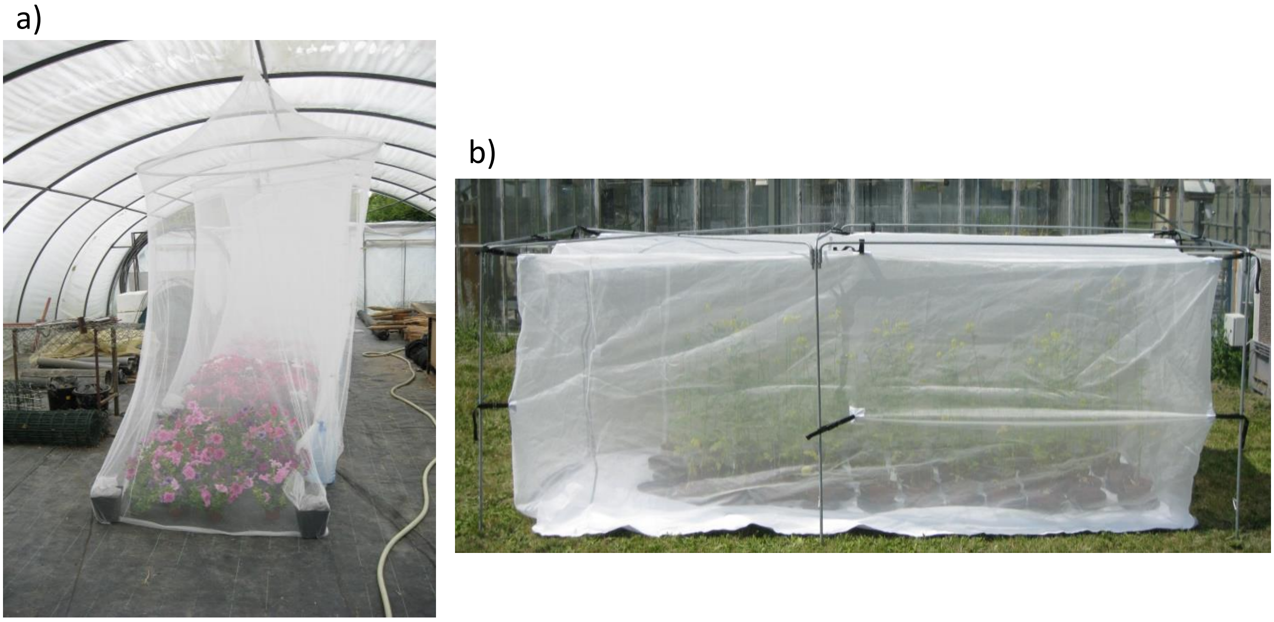


Figure 15 Photographie des phytomètres au sein des enceintes imperméables aux insectes. (a) Plants de pétunia dans les moustiquaires en 2014 ; (b) Plants de moutarde blanche dans une des tentes « insect-proof » en 2015.

Après 4 jours d'exposition, les plants ont été ramenés au laboratoire, après avoir marqué les dernières fleurs ouvertes sur les parcelles d'un scotch rouge. Le marquage au scotch rouge et bleu a donc permis de distinguer les fleurs ayant été pollinisées sur les parcelles étudiées des autres fleurs s'étant ouvertes après l'expérimentation.

Après une phase de maturation, les fruits issus des fleurs marquées ont été récoltés et séchés en étuve pendant 72 heures (9864 fruits en 2014, 1138 fruits en 2015). Chaque fruit a été décortiqué et le nombre de graines fertiles par fruit a été compté. Pour les graines de pétunia, nous n'avons pas pu avoir accès directement au nombre de graines par fruit en raison de leur petite taille et de leur trop grand nombre. Nous avons donc pesé 10 graines fertiles par fruit et pesé le total des graines, et obtenu le nombre de graine via un produit en croix. Les graines de moutarde étaient assez volumineuses pour les compter.

Nous avons utilisé le nombre moyen de graines par fruit à l'échelle des phytomètres pour mesurer le succès de pollinisation (« seed set », Fontaine et al., 2005; Steffan-Dewenter et al., 2001; Steffan-Dewenter and Tscharntke, 1999), qui est fortement corrélé à un dépôt de pollen efficace (Aizen and Harder, 2007), c'est-à-dire menant à la fécondation du maximum d'ovules contenus dans les ovaires de la plante.

5- Recueil des pratiques agricoles

Pour recueillir les informations sur les pratiques des agriculteurs au sein des paysages, nous avons utilisé des enquêtes standardisées. Dans chaque enquête étaient demandées des informations sur diverses pratiques agricoles pouvant influencer les abeilles sauvages : fréquence et dose de pulvérisation de pesticides (insecticides, herbicides), fréquence et quantité de fertilisation organique et minérale, fréquence et type de travail du sol (labour, travail superficiel). D'autres types de pratiques, dont l'impact n'a pas été étudié durant la thèse, ont aussi été relevées : gestion des bordures (haies, bandes enherbées, lisières), gestion des prairies permanentes (fauches, dates de pâturage, fertilisation), et dates de semis. Pendant le mois de septembre 2013 et février-mars 2015, un total de 80 exploitations ont été enquêtés, dont 73 ont été finalement intégrées dans l'étude.

Les enquêtes ont été spatialisées : une carte du ou des paysages contenant toutes les parcelles de l'agriculteur enquêté lui était montrée, et les pratiques étaient relevées pour chaque type de culture. L'objectif était de maximiser le nombre de parcelles dont on connaissait les pratiques au sein de la mosaïque cultivée (2 à 5 agriculteurs par paysages, représentant 34.2% à 85.2% de la surface totale des paysages).

Pour chaque type de pratique, l'intensité moyenne à l'échelle des paysages a été calculée grâce à une moyenne pondérée par la surface des parcelles (I= indicateur d'intensité) :

$$I_{moyen} = \frac{Surface_{parcelle\ 1} \times I_{parcelle\ 1} + \cdots + Surface_{parcelle\ n} \times I_{parcelle\ n}}{Surface_{totale\ connue\ dans\ le\ paysage}}$$

Le choix a donc été fait de considérer un indice traduisant l'intensité moyenne d'une pratique donnée dans le paysage et non la variabilité d'intensité au sein de différentes parcelles d'un même paysage. De plus, cet indice est à même de traduire un effet sur la quantité de ressources dans la mosaïque cultivée, puisque à même niveau d'intensité, une parcelle agricole de grande taille va plus faire varier l'indice d'intensité qu'une petite parcelle.

Partie A : Réponse des communautés d'abeilles sauvages à la composition et la configuration des milieux semi-naturels dans les paysages agricoles.

Chapter 1: Functional responses of wild bee communities to the heterogeneity of agricultural landscapes

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Abstract

Wild bee species are known to differ in their response to changes in landscape heterogeneity depending on their ecological traits, but the relative importance of different semi-natural habitats in determining the functional structure of wild bee communities has been little explored. In this study, we investigated two possible effects of landscape composition and configuration on the functional structure of wild bee communities (environmental filter and shift in community trait values) in 78 cereal fields in southwest France. We found that bee body size, beginning of foraging season and diet breadth shifted along the independent gradients of grassland and woodland proportions (landscape composition). Very small-bodied and early-emerging species were favored in landscapes with high proportion of grasslands, whereas oligolectic and summer-emerging species were more abundant in landscape with low woodland cover. Landscape configuration only affected shifts in bee body size, as the abundance of very small-bodied species was negatively correlated to the length of cropland/grassland interfaces. We also found that only one trait value was filtered out along the landscape gradient, with oligolectic species being excluded in landscapes with the highest woodland cover. These results suggest that environmental filtering was of minor importance in explaining shifts in community trait values along landscape gradients, and that other ecological processes might have influenced such shifts.

Key words: Landscape composition, landscape configuration, pollinators, semi-natural habitats, life-history traits.

Introduction

The role of landscape heterogeneity in shaping biodiversity in human-modified landscapes is a key issue in landscape ecology (Fahrig 2003; Tscharntke et al. 2005) but there is a need for more mechanistic approaches to better predict and understand how community structure responds to changes in landscape structure (Kremen et al. 2007; Williams et al. 2010; Tscharntke et al. 2012). Some studies have already shown promising results by identifying consistent responses of plant, bird and insect species with shared traits to landscape variables (Williams et al. 2010; Duflot et al. 2014; Hopfenmüller et al. 2014; De Palma et al. 2015; Gámez-Virués et al. 2015). Two types of functional responses of communities to environmental variables can be identified (Fig. 1): (i) environmental filtering, that predicts which assemblage of species with a particular set of traits is able to persist in a particular environment, the other species with unsuitable trait values being locally excluded (Keddy 1992; Cornwell and Ackerly 2009; Bernard-Verdier et al. 2012) and (ii) shift in community trait values, which takes into account the relative abundance of species and focuses on the sensitivity to environmental variables of species groups with shared traits (Bernard-Verdier et al. 2012; De Palma et al. 2015).

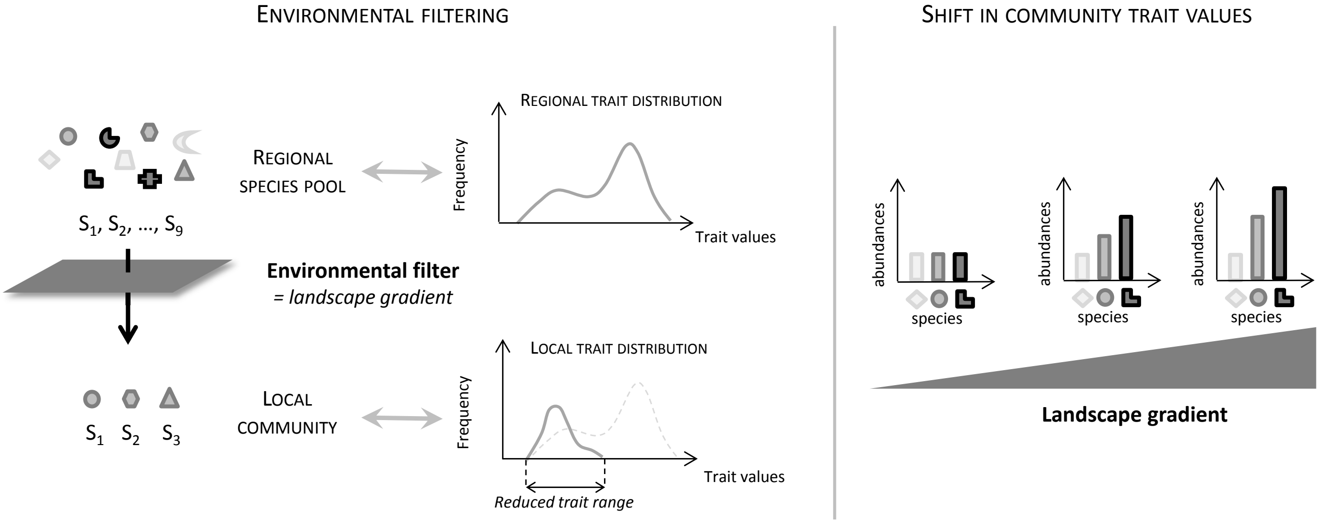

Figure 1 Framework of the trait-based analysis on the effect of landscape properties on wild bee communities. Environmental filtering (left-hand side) consists in the exclusion of species with inappropriate trait values in a given environmental context. Species are represented by different shapes, trait values by a grey gradient. The trait distribution is represented for the species pool and the local community. The exclusion of unfit trait values is indicated by the reduction in trait range compared to the regional trait distribution. Shift in community trait values (right-hand side) describes the shift in relative abundance of different trait values in response to a landscape gradient. A case with three species with contrasted trait values is illustrated, where the changes in relative abundance in response to the environment depend on the species trait value.

Most of the studies linking functional community structure to landscape variables used the second approach (shift in community trait values: Williams et al. (2010); Jauker et al. (2013); Hopfenmüller et al. (2014); De Palma et al. (2015)) but did not explicitly test whether landscape properties could act as filters of species traits. Studies that explored both types of functional responses found strong shifts in trait abundance distributions along environmental gradients, but detected environmental filtering only at the extreme ends of the gradients, due to harsh environmental conditions (Bernard-Verdier et al. 2012; Hoiss et al. 2012). Therefore, environmental filtering can be seen as the “hard edge” of any shift in community trait values (Kraft et al. 2015) as environmental conditions can lead to strong shifts in trait abundance distributions due to an exclusion of certain species in extreme conditions. However, shifts in community trait values can occur without environmental filtering, due to changes in the population size of different functional groups without species exclusion (Bernard-Verdier et al. 2012; Hoiss et al. 2012; Kraft et al. 2015). There is therefore a need to explicitly test in what landscape context shifts in community trait values can lead to local species exclusion (environmental filtering), or is only due to changes in species relative abundance.

Wild bees are ecologically and economically important in agroecosystems, contributing to crop production (Klein et al. 2007; Garibaldi et al. 2013) and to the maintenance of wild plant communities (Memmott et al. 2004; Kremen et al. 2007). At the landscape scale, the proportion of semi-natural habitats was found to positively affect wild bee diversity and abundance because of key resources they provide (Winfree et al. 2009; Garibaldi et al. 2013; Kennedy et al. 2013). However, while different types of semi-natural habitats such as woody or herbaceous permanent vegetation may have contrasting effects on wild bee species depending on the resources they provide and on bee ecological requirements (Morandin et al. 2007; Bailey et al. 2014; Hopfenmüller et al. 2014; Forrest et al. 2015), their relative effects on wild bee communities are still unclear. For example, the proportion of all semi-natural habitats combined was found to affect the abundance of social bee species compared to solitary ones (Williams et al. 2010), but the type of habitat responsible for this relationship was not addressed.

Landscape configuration – which can be measured as the edge density between habitat types – is also expected to influence trait distribution of farmland bee species. Indeed, bee species use multiple habitats during their life span (Westrich 1996) and an increase in edge density in the landscapes could improve the access to critical resources, by reducing habitat isolation and increasing the opportunity of spillover between patches (Kremen et al. 2007; Holzschuh et al. 2010; Tscharntke et al. 2012). Previous studies have found a weak or an absence of effect of landscape configuration on farmland bee communities (Holzschuh et al. 2010; Kennedy et al. 2013) but they have not separated the effects of the configuration of different habitat types, nor explored a possible differential response of bee species depending on their shared trait values.

To our knowledge, environmental filtering has never been explicitly tested in farmland wild bee communities along a gradient of landscape composition and configuration. A previous study along an altitudinal gradient revealed the occurrence of strong shifts in trait abundance distributions along the whole gradient but found that bees with specific trait values were filtered out only at high altitudes, due to extreme climatic conditions and scarce resources (Hoiss et al. 2012). As with an altitudinal gradient, changes in the proportion and spatial complexity of semi-natural habitats also influence the availability and accessibility of resources used by wild bees in agricultural landscapes. It is therefore important to test whether changes in and configuration of semi-natural habitats exert a filtering effect in extreme situations – low availability or access to critical resources – for bee species specialized on these habitats.

In the present study, we aimed to detect the presence of shifts in trait abundance distributions along gradients of landscape composition and configuration and the extent to which these shifts were due to environmental filtering. We first expected that farmland community trait values would shift along the gradient of landscape composition and configuration due to the decrease in abundance of species with traits linked to the dependence to semi-natural habitats (Table 2). More specifically, we expected that species with narrow diet breadth, building above-ground nests and with small body size (trait associated with low dispersal abilities) would be more affected by the availability and accessibility of semi-natural habitats than highly mobile, generalist below-ground nesters which can survive on alternative food resources, can nest in crop mosaic and can access isolated habitat patches (Steffan-Dewenter et al. 2002; Williams et al. 2010).

Second, we expected that changes in the proportions and configuration of semi-natural habitats would affect the distribution of different traits depending on the type of semi-natural habitat. For example, we expected that oligolectic species would be more affected than polylectic ones by changes in the proportion and configuration of grasslands, due to the critical flowering resources permanent grasslands can provide (Jauker et al. 2013; Hopfenmüller et al. 2014). Indeed, the number of flowering plant species usally increases with herbaceous habitat area (Steffan-Dewenter et al., 2006; I. Steffan-Dewenter and Tscharntke, 2000). Also, an increase in the proportion woodlands and length of cropland/woodland interfaces would favor above-ground over below-ground nesters due to the provision of critical nesting sites in woodland edges (Bailey et al. 2014). Third, we expected that shifts in community trait values would be due to the filtering (exclusion) of species depending on semi-natural habitats in landscapes with the lowest amounts of semi-natural habitats and of interfaces between semi-natural habitats and farmed area.

Materials and methods

Study site and sampling design

The study was conducted in southwestern France (Fig. 1a), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Socio-Ecological Research Network (LTSER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17’N, 0°54’E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al. 2010). The climate is sub-Atlantic with a slight Mediterranean influence (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

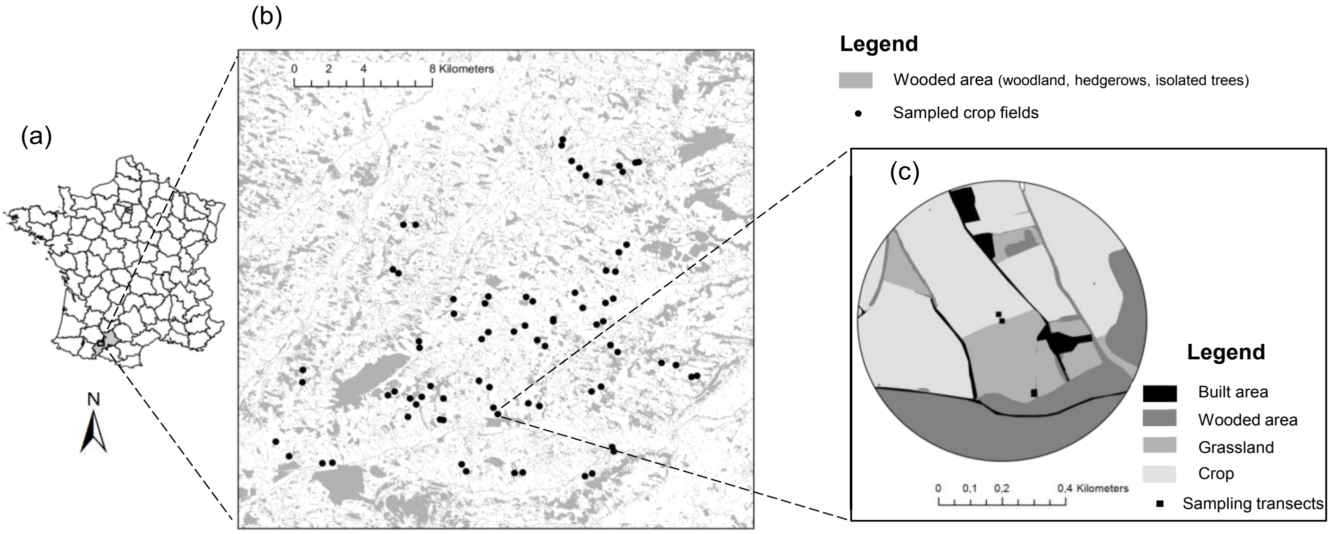

Fig. 2 Maps showing (a) the study area, (b) the 78 sampled crop fields and (c) the location of the sampling transects (3 traps per transect) within one sampled crop.

Within the studied region, we selected 80 cereal fields (hereafter sampling sites, 40 different sites for each year, in 2013 and 2014) differing in the surrounding proportion of semi-natural habitats within a 500-m buffer, to cover independent gradients of woodland and grassland proportions. Preselection of sampling sites was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). As some of the sampling sites were from another sampling procedure, sampling sites were paired and sites from a pair were at least 200 m apart. In each field, the sampling points were located next to a field border that consisted of a grassy margin, at least 100 m from a non-cropped area (woodland or built area). In each crop field, we established four sampling points: two 50 cm inside the field and 25 m apart from each other (field border transect), and two 25 m inside the field and parallel to the first two points (field interior transect). We sampled bees with six pan traps per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of four poles (one pole per sampling point), one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint, SparVar® Germany), and each pole had two different colors. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension. The poles were designed such that the height was adjustable to the crop canopy. The traps were left in place for two periods of 3 or 4 days per sampling site. The sampling periods were 22 April to 24 May and 27 May to 21 June in 2013, and

17 April to 12 May and 22 May to 16 June in 2014. All wild bee individuals (solitary and social species) were identified at the species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than the result of a direct effect of landscape structure. The number of individuals and the number of species determined for each field represented the sum of all traps from the two sampling periods conducted on that field.

Landscape variables

Landscape variables were calculated within a radius of 500 m centered on the field border transect in each site (Fig. 2c). The radius was chosen according to the results of previous studies on the functional scale of wild bees (Gathmann and Tscharntke 2002; Zurbuchen et al. 2010; Holzschuh et al. 2010). Using aerial photographs (IGN 2013) the different land covers (woodlands, hedgerows, permanent grasslands, crop fields and isolated trees) were mapped using ArcGIS 10.2 (ESRI). Crop field and grassland boundaries were validated by ground surveys in July 2013, May 2014 and April 2015.

In each 500-m buffer (hereafter landscape), we calculated 6 variables measuring landscape composition and configuration (Table 1) using ArcGIS 10.2 (ESRI). Composition was estimated using the proportions of grasslands, woodlands (grassland, woodland), and hedgerow length (hedgerow). Configuration was assessed using the length of interface between patch-like semi-natural habitats (*grasslands* and *woodlands*) and cultivated areas (*crop_woodland* and *crop_grassland*). Because of the sampling design (paired sampling sites) many buffers overlapped each other. As a consequence, spatial autocorrelation of the richness and abundance of wild bee species was checked in the data: after a random resampling process, two sampling sites were finally removed from the analysis to suppress the spatial autocorrelation (Moran index = 0.07, *P* = 0.19). Statistical analyses were then performed on 78 landscapes (Fig. 2b).

Table 1 Description of landscape variables assessing semi-natural composition and configuration (n=78).

	Code	Variable (units)	Mean (min–max)
Composition	*woodland*	Proportion of woodlands (%)	10.2 (0–38.7)
	grassland	Proportion of grasslands (%)	20.9 (0–60.1)
	hedgerow	Length of hedgerow (m)	3,448.1 (880.7–7,655.3)
Configuration	*crop_woodland*	Length of interface between cropland and woodland (m)	914.7 (0–2,995)
	crop_grassland	Length of interface between cropland and grassland (m)	1,064.7 (0–3,570.8)

Bee traits

Six ecological and life-history traits were chosen according to their implication in the response of wild bees to environmental changes and because of their availability in the literature (Table 2): body size (measured as inter-tegular distance or ITD), sociality, nest location, type of nest construction, diet breadth, and beginning of the foraging season (Williams et al. 2010; Forrest et al. 2015; Kremen and M'Gonigle 2015). Sources for trait information were the ALARM project database (Settele et al. 2005), Michener (2000), Gathmann and Tscharntke (2002), Bommarco et al. (2010), Fortel et al. (2014) and Forrest et al. (2015). For body size values, when no data were available on a particular taxon, ITD was measured on at least five female individuals per taxon, and queens were used for eusocial species. Social bees were defined as species that live in colonies characterized by cooperative brood care, therefore including eusocial and primitively social species. Solitary bees were defined as species that care only for their own offspring. The beginning of the foraging season was based on expert knowledge (David Genoud, pers. com.). We were able to obtain traits for 68 of 111 species in our data (representing 98% of the sampled individuals). The 43 species for which insufficient trait information was available were removed from the data set.

Table 2 Traits used in the analyses and corresponding ecological roles

Trait	Unit	Description and ecological implications
Inter-tegular distance (ITD)	mm. Nominal form: very small (<1 mm, 5 sp.), small (1-1.5 mm, 12 sp.); medium (1.6-2 mm, 17 sp.); large (2.1-3mm, 19 sp.); very large (>3mm, 15 sp.)	Distance between the nearest edges of the tegulae (plates covering the wing bases), which measures body size. This measure is strongly correlated with bee foraging ranges (Greenleaf et al. 2007) and is likely to affect resource utilization in landscapes and response to habitat loss (Bommarco et al. 2010; Williams et al. 2010).
Nest location	Nominal. Below-ground nesters (62 sp.); Above-ground nesters (11 sp.)	Can affect the response of bees to habitat loss and disturbances (tillage regimes, deforestation, mowing regimes, overgrazing; Kremen and M'Gonigle (2015), Shuler et al. (2005); Williams et al. (2010)).
Type of nest construction	Nominal. Rent (13 sp.); Excavate (60 sp.)	
Diet breadth	Nominal Oligolectic (14 sp.); Polylectic (59 sp.)	Diet specialization defined by the number of plant families bees collect pollen from. Polylectic species (pollen generalists = several plant families) are more likely to survive and persist on alternative flower resources than oligolectic species (pollen specialists = one plant family), which may be more prone to become extinct with habitat loss (Steffan-Dewenter et al. 2006; Williams et al. 2010).
Sociality	Nominal. Social (27 sp.); Solitary (40 sp.)	Sociality can affect bee response to habitat amount, but studies have found contradictory results regarding responses of solitary *vs.* social species. Social species seems to be more sensitive to the loss of herbaceous habitats (Hopfenmüller et al., 2014), whereas solitary species tend to be more affected by the proportion of woody habitats (Williams et al., 2010).
Beginning of foraging season	Number of the start month (1-12). Nominal form: winter (Jan-Feb, 5 sp.); early spring (Mar, 13 sp.); late spring (Apr-May, 38 sp.); summer (Jun-Jul, 10 sp.).	Shift in the beginning of foraging season could be the result of changes in the flower resources available in the landscapes (wild or cropped plants). A high amount of semi-natural habitats is likely to sustain species that emerge before or after the blooming periods of the main flowering crops (Rollin et al. 2013; Bretagnolle and Gaba 2015).

Statistical analyses

All analyses were performed using R 3.0.2 (R Development Core Team 2011). To test the level of collinearity in our models, we followed Smith et al. (2009) by calculating Spearman rank correlations, and the variance inflation factor (VIF) was computed for each variable (Table 3). Even though some variables were correlated (*woodland* and *crop_woodland*, r = 0.7, $P < 0.001$), the VIFs of all the variables were far below the threshold of 10 and all $|r| \leq 0.7$, indicating low collinearity in our models (Smith et al. 2009; Dormann et al. 2013). Thus, all the composition and configuration variables were included in the same statistical models and were standardized to better assess their relative effects on the response variables.

Table 3 Spearman rank correlations among composition and configuration variables (n=78). Numbers in parentheses are the variance inflation factors for each variable (P<0.05 *; P<0.01 **; P<0.001 ***).

	woodland	*grassland*	*hedgerow*	*crop_woodland*	*crop_grassland*
woodland	(2.39)	0.30*	-0.47***	0.7***	0.02
grassland		(1.87)	0.1	-0.04	0.53***
hedgerow			(1.37)	-0.28**	0.02
crop_woodland				(1.76)	-0.02
crop_grassland					(1.43)

We estimated statistical association between traits among species with Spearman rank correlations (Table 4), because the effect of one trait on response to environmental change may not be biologically or statistically independent of others (Williams et al. 2010; Ekroos et al. 2013; Forrest et al. 2015).

Table 4 Spearman rank correlations among species traits (n=68). For nominal traits, trait values were coded as 0 or 1 to allow for correlation calculation. Sociality: social=0, solitary=1; nesting location: below-ground=0, above-ground=1; diet breadth: oligolectic=0, polylectic=1; type of nest construction: excavate=0, rent=1 (P<0.05 *; P<0.01 **; P<0.001 ***).

	Sociality	Nesting location	Diet breadth	Beginning of foraging season	Nesting construction
Body size (ITD)	0.09	0.31*	-0.01	-0.25*	0.52***
Sociality		0.16	-0.35**	-0.17	-0.22
Nesting location			0.08	-0.18	0.54***
Diet breadth				0.01	0.11
Beginning of foraging season					-0.23

To test whether trait abundance distributions of wild bee communities shifted in response to landscape variables, we used generalized linear mixed models (GLMM) assuming Poisson error distribution (log-link function) with the R *lme4* package. We chose trait abundance over community weighted means (CWMs) to quantify these shifts as we had many categorical traits in our dataset and because CWMs are likely to overlook underrepresented trait values in the communities (such as cavity nesters, Hopfenmüller et al. (2014)). Even if there was no spatial autocorrelation for total species richness and abundance of bees among the 78 sampling sites, a landscape random factor was included in the models to account for a possible non-independency of paired sampling sites for species that forage over distances greater than 200 m (minimum distance between two sampling sites). We added a sampling site random factor nested into the landscape random factor to account for possible overdispersion in the data (Lee and Nelder 2000). Fixed factors were the composition (*grassland*, *woodland* and *hedgerow*) and configuration variables (*crop_woodland*, *crop_grassland*). Response variables were the abundance of bees within a given trait category (oligolectic/polylectic, social/solitary, etc.). As some traits were continuous (body size and beginning of foraging season), we created trait categories (Table 2) to fit models for each type of category.

Environmental filtering exerted by landscape variables on bee species was tested following the procedure of Bernard-Verdier et al. (2012). For continuous traits (body size and beginning of the foraging season), trait range was calculated in each sampling site (maximum–minimum) and was compared to the range expected given the species pool and the local species richness. For categorical traits (binary traits here), as the range could not be computed, we used the occurrence of each trait value per sampling site (presence=1, absence=0 of a given trait value at a given sampling site). This occurrence, calculated for each sampling site, was compared to the occurrence expected given the species pool and the local species richness. A smaller trait range than expected given the species pool or an absence of trait value compared to expectations was interpreted as an indicator of trait filtering (Keddy 1992). Expected trait ranges or occurrences of trait values were estimated from a null model of community assembly built to test the null hypothesis “species are randomly distributed among sampling sites, irrespective of traits or environment”. This null model consisted of a lottery model randomly drawing a given number of species (i.e. the observed species richness in a sampling site) from the regional species pool (Cornwell and Ackerly 2009; Bernard-Verdier et al. 2012), and was built with R *picante* package. As we considered that the ability to colonize a sampling site of a given species was proportional to its frequency in the species pool, the random draws were weighted by the relative abundance of each species in the species pool (Bernard-Verdier et al. 2012). For each trait, the observed value of the metric (trait range or occurrence of a given trait value) was compared with the distribution generated by 4999 runs of the null model. An effect size (ES) was calculated (1) based on the one-tailed probability P that the observed value was greater than predicted by the null model (2).

$$ES = 2 \times (P - 0.5) \qquad (1)$$

$$P = \frac{number(null<obs) + \frac{number(null=obs)}{2}}{5000} \qquad (2)$$

ES values range from -1 to 1. When ES is close to 0, observed values are not different from null expectation. Negative values of ES indicate narrower trait range than expected or an absence of a given trait value, whereas the null model predicts the occurrence of this value, suggesting environmental filtering. We tested significant trends between ES and landscape variables using linear mixed models (LMM), with composition and configuration variables as fixed factors and a landscape random factor to account for possible spatial autocorrelation. These tests were performed for the two continuous traits (body size and beginning of foraging season) and for trait categories that were not represented in the whole landscape gradient, i.e. oligolectic species, above-ground nesters and renters.

Results

Shift in community trait values in response to semi-natural habitat composition and configuration

A total of 4665 individuals belonging to 111 species were sampled across the 78 sampling sites, from which 4574 individuals belonging to 68 species with informed trait values were kept for the analyses (Table S1).

Community trait values shifted along the gradient of landscape composition and configuration, but the majority of trait shifts were linked to variations in landscape composition (Table 5, Fig. 3).

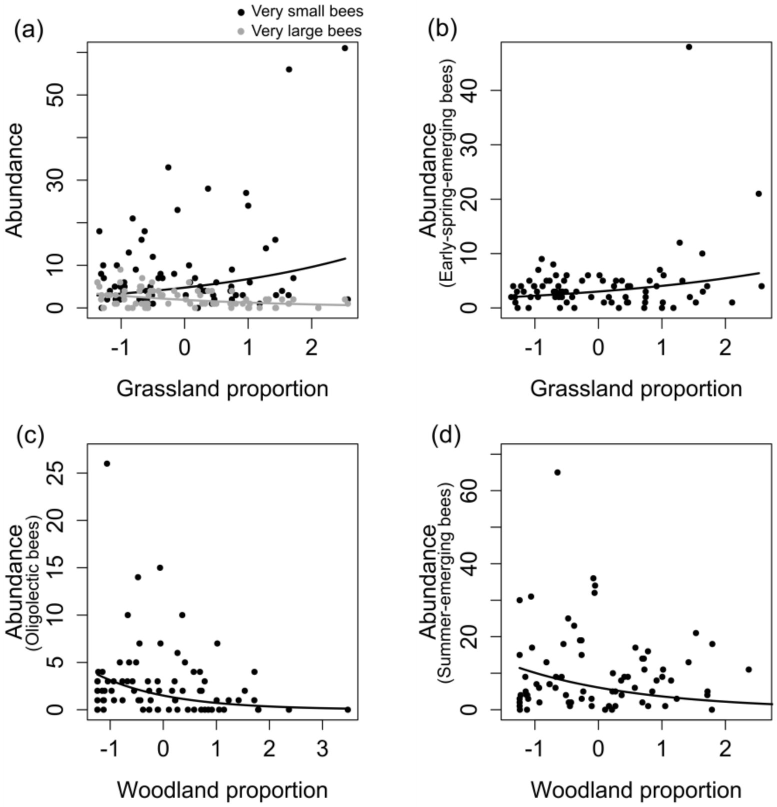

Figure 3 Response of the abundance of species differing in trait values to the proportions of grasslands (a, b) and woodlands (c, d). Response of the abundance of very small (ITD <1 mm) and very large (ITD>3 mm) bee species (a) and species emerging in spring (b) to the proportion of grasslands. Response of the abundance of oligolectic bee species (c) and species emerging in summer (d) to the proportion of woodlands. Only significant trends from Table 5 are displayed. All predictors are shown in a standardized form in the graphs.

Table 5 Results of the generalized linear mixed models testing the effects of SNH proportion and configuration on the abundance of wild bee communities depending on species traits. Only significant relationships are given. A model was run for each trait category, using abundance of bee species within the given trait category as a response variable and SNH proportion and configuration as explanatory variables.

Trait	Trait value (Response variable)	Explanatory variables	Estimate	SE	*P*-value
Body size	very small	*grassland*	0.35	0.17	0.0389
		crop_grassland	-0.37	0.14	0.0100
	small	-	-	-	-
	medium	*hedgerow*	-0.23	0.11	0.0317
	large	-	-	-	-
	very large	*grassland*	-0.41	0.15	0.0057
Beginning of foraging season	winter	*grassland*	-0.45	0.20	0.0264
	early spring	*grassland*	0.30	0.12	0.0134
		hedgerow	-0.23	0.11	0.0376
	late spring	-	-	-	-
	summer	*woodland*	-0.51	0.23	0.0265
Diet breadth	oligolectic	*woodland*	-0.73	0.26	0.0050
		hedgerow	-0.50	0.17	0.0040
	polylectic	-	-	-	-
Nest location	above-ground	*hedgerow*	-0.46	0.23	0.0493
	below-ground	-	-	-	-
Nest construction	rent	-	-	-	-
	excavate	-	-	-	-
Sociality	solitary	*hedgerow*	-0.31	0.10	0.0033
	social	-	-	-	-

The response of wild bee abundance to hedgerow length differed depending on bee traits. The abundances of medium-sized, solitary, above-ground nesters, oligolectic and early-spring emerging species were negatively correlated with hedgerow length, whereas the abundance of other trait values remained unaffected by this landscape variable (Table 5, Fig. 4).

The abundances of very small species and species emerging in early spring were positively affected by the proportion of permanent grasslands, whereas this landscape variable negatively influenced the abundances of very large bees and species that forage in winter (Table 5, Fig. 3a). The configuration of grasslands only affected small-bodied species, as their abundance was negatively correlated with the length of cropland/grassland interfaces (Table 5, Fig. 5).

The abundance of oligolectic species was negatively correlated with the proportion of woodlands (Table 5, Fig. 3c). The same trend was detected for the abundance of late-emerging species (Table 5, Fig. 3d).

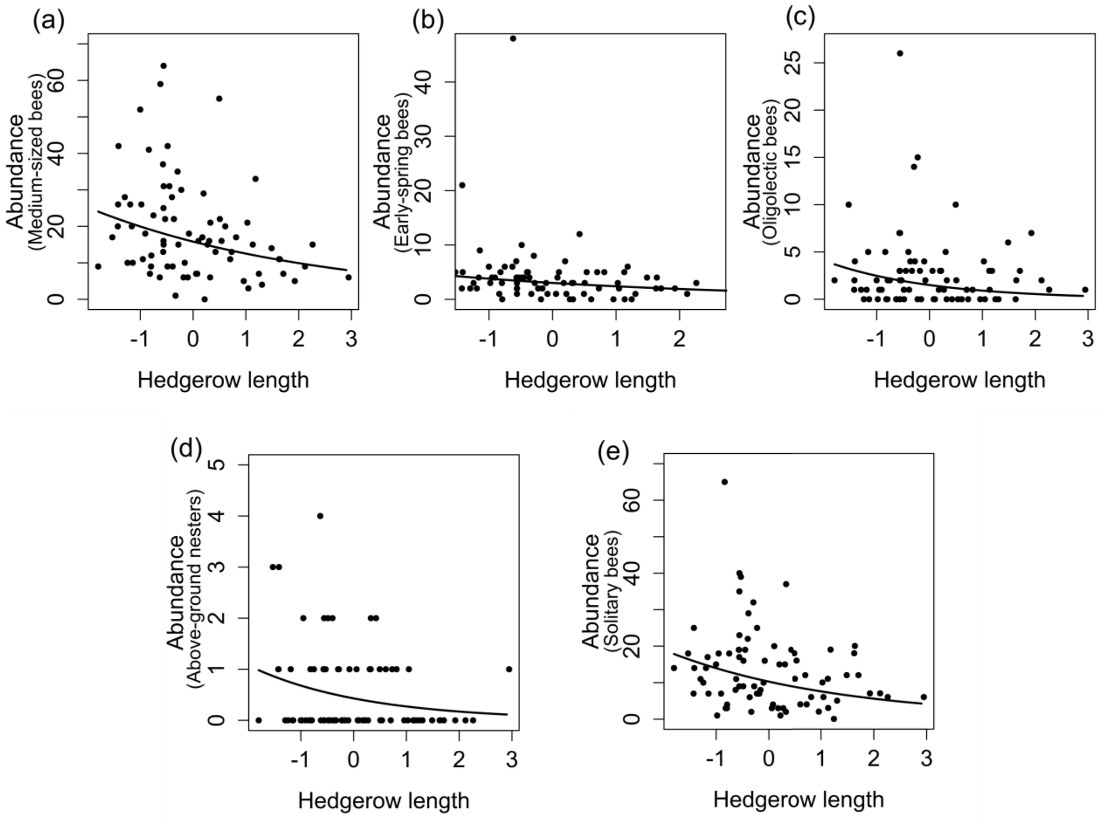

Figure 4 Response of the abundance of medium-sized (a), early-spring emerging (b), oligolectic bees (c), above-ground nesters (d) and solitary bees (e) along the gradient of hedgerow length. Only significant trends from Table 5 are displayed. All predictors are shown in a standardized form in the graphs.

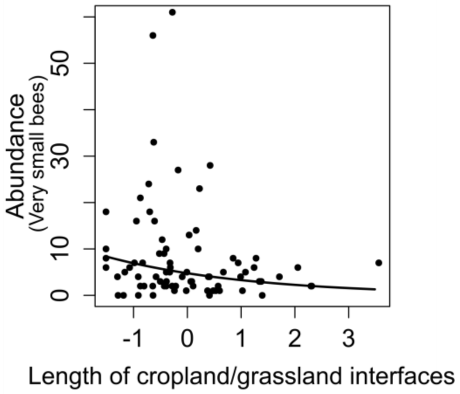

Figure 5 Response of the abundance of very small-bodied species (ITD<1 mm) to the length of cropland/grassland interface. Only significant trends from Table 5 are displayed. All predictors are shown in a standardized form in the graphs.

Trait filtering along the gradient of semi-natural habitat composition and configuration

Landscape filtering on bee traits was detected when the range or the occurrence of a trait value was lower than predicted by the null model. Only the effect size (ES) related to the presence/absence of oligolectic species was significantly affected by landscape variables (Table 6). The ES calculated for oligolectic species was negatively affected by the proportion of woodlands in the landscapes, suggesting that oligolectic species were filtered out in landscapes with the highest woodland cover (Fig. 6). No trends in ES were detected for the other traits, suggesting that none of the trait values (for ITD, sociality, nest location and construction, foraging phenology) was significantly excluded at any end of the landscape gradients.

Table 6 Results of the linear mixed models testing the effects of SNH proportion and configuration on the effect size (ES) of trait metrics. Trait metrics, indicated in parentheses, were trait range for continuous traits and trait occurrence for binary traits. Negative ES indicates a narrower trait metrics than expected, suggesting environmental filtering. Additionally, a significant negative trend indicates trait filtering for high values of the landscape variables, the opposite trend being an indication of filtering for low values of landscape variables. Significant coefficients are in bold (P<0.01**).

	ES body size (range)		ES foraging beginning (range)		ES oligolectic (occurrence)		ES above-ground (occurrence)		ES rent (occurrence)	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
woodland	0.01	0.13	-0.01	0.09	**-0.20****	**0.07**	-0.06	0.08	0.01	0.08
grassland	-0.10	0.12	-0.07	0.08	0.05	0.06	0.09	0.07	0.01	0.07
hedgerow	-0.05	0.10	-0.11	0.07	-0.08	0.05	-0.08	0.06	0.00	0.06
crop_woodland	-0.07	0.11	0.02	0.07	-0.01	0.06	-0.04	0.07	0.04	0.07
crop_grassland	0.00	0.10	-0.06	0.07	0.06	0.05	-0.09	0.06	0.00	0.06

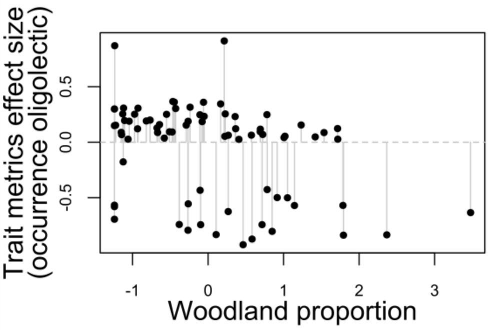

Figure 6 Variation in trait metrics effect size (ES) of oligolectic species along the gradient of woodland proportion. Only significant trends from Table 6 are displayed. All predictors are shown in a standardized form in the graphs.

Discussion

Our hypothesis concerning the increase in the abundance of species with specialized ecological requirements (above-ground nesting and oligolectic speces) and low dispersal abilities with increasing habitat amounts and amount of interfaces between cropland and semi-natural habitats (SNH) was partly validated. Indeed, we found that the proportion of permanent grasslands positively affected the abundance of small-bodied species. This result was consistent with our expectation that small-bodied species, which have limited dispersal abilities and therefore need to nest closer to floral resources (Greenleaf et al. 2007), would be more affected by the amount of SNH than large species. Due to the diversity and large amount of nesting and flowering resources permanent grasslands can provide to wild bees (Öckinger and Smith 2007; Jauker et al. 2013; Hopfenmüller et al. 2014), an increase in grassland proportion might increase the occurrence of low-dispersing wild bees in cereal fields by reducing the isolation between grasslands and crop fields (Steffan-Dewenter and Tscharntke 1999; Ricketts et al. 2008). However, contrary to our expectation, low-dispersing species were negatively affected by the length of cropland/grassland interface. An increase in the quantity of interfaces between cropland and SNH is usually associated with an increased arthropod diversity and abundance in crop fields, due to higher chances of spillover of individuals from SNH to cultivated areas (Kremen et al. 2007; Holzschuh et al. 2010; Tscharntke et al. 2012). Here, this negative trend suggests a negative edge effect exerted on grasslands by crop fields (Fahrig 2003), which might reduce the quality of grasslands as habitats for bees due to the increased risk of exposure to agricultural disturbances such as agro-chemical drift (Kleijn and Snoeijing 1997). We can therefore assume that permanent grasslands surrounded by non-crop habitats might be important habitats for low-dispersing species in farmlands. We also showed that permanent grasslands favored species emerging in early spring (March), when no mass-flowering crops such as oilseed rape can sustain their population (Holzschuh et al. 2012). As these early-emerging species had contrasted body sizes (no “very small” species), this suggests that this positive effect of permanent grasslands on the early-emerging species was independent of the dispersal capacities of bees. Our results therefore suggest that permanent grassland may have supported early-emerging species, presumably by the provision of flowering and/or nesting resources (Öckinger and Smith 2007; Jauker et al. 2013; Hopfenmüller et al. 2014).

We also found that the abundance of very large-bodied species was negatively correlated with the proportion of grasslands. These species were mostly bumblebees (Table S1), which are known to preferentially nest in linear features such as field margins or grassland boundaries in the crop mosaic rather than inside permanent grasslands (Svensson et al. 2000; Öckinger and Smith 2007; Osborne et al. 2008). As there was a high negative correlation between the proportion of annual crops and permanent grasslands in the studied landscapes ($r=-0.92$, $P<0.0001$), the increase in the proportion of grasslands might have decreased the opportunity to find suitable nesting sites for bumblebee queens in the annual crop mosaic. The availability of suitable nesting sites can be a stronger determinant of community structure than flowering resources (Potts et al. 2005), and may explain the reduced number of bumblebee individuals we found in grassland-dominated landscapes, even though these landscapes offered high availability of foraging resources. The same explanation might also hold for the negative association between the abundance of winter-foraging species and hedgerow length, as the very large-bodied species were also winter foragers in our dataset (Table S1).

Another result that contradicts our expectations was that the abundance of oligolectic bees was negatively correlated with the proportion of woodlands. Oligolectic species are usually more sensitive to habitat loss than polylectic ones due to their specific feeding resources requirements (Steffan-Dewenter et al. 2006; Williams et al. 2010; Kremen and M’Gonigle 2015). The oligolectic species we captured in our sites were dominated by species from the *Andrena* and *Eucera* genera, foraging principally on plants from the Brassicaceae and Fabaceae families respectively, which can be easily found in the crop mosaic, as mass-flowering crops (oilseed rapes) or weed species (clover or mustard) for example (Le Féon et al. 2013; Bretagnolle and Gaba 2015; Rollin et al. 2016). As woodland and annual crop proportions were negatively correlated in our landscapes (r=-0.55, $P<0.0001$), oligolectic species were less abundant in wooded landscapes, presumably because they found fewer suitable floral resources compared to less wooded landscapes.

We found a negative correlation between hedgerow length and the abundance of species with traits that make them more vulnerable to habitat loss (oligolectic, above-ground nesters and solitary) and with intermediate body size. In agricultural landscapes, the critical resources these specialized species depend on are likely to be found in separate habitat patches (Westrich 1996) and thus they need to fly between different patches to find them (Gathmann and Tscharntke 2002). The negative correlation we found between the length of hedgerows and the abundance of these bees suggests that hedgerows acted as barriers which impeded their movements within the landscapes.

Our last hypothesis about filtering of bees with specialized resources requirements (above-ground nesting and oligolectic species) and low dispersal capacities in landscapes with a low amount and accessibility of SNH was not supported by our results. Here we found that the oligolectic species captured inside and at the border of wheat fields were not specialized on resources provided by SNH and were filtered out in landscapes with the highest proportions of woodlands. The flowering crops these species can forage on, such as oilseed rape or legumes (soybean, alfalfa) were in a minority in the studied landscapes (2.3% and 7.4% on average for oilseed rape and legumes respectively). We can thus assume that these flowering crops were scarce in the crop rotations of farmers, which can induce a year to year discontinuity in the availability of these foraging resources (Schellhorn et al. 2015). This scarcity, temporal discontinuity and isolation of these flowering crops in landscapes with low crop cover might have prevented the oligolectic species from maintaining viable populations, and presumably caused their local extinction. This result is thus consistent with other studies that explored functional responses of communities along gradients of resources and disturbances, and that found evidence for environmental filtering in cases of reduced resource availability (Cornwell and Ackerly 2009; Bernard-Verdier et al. 2012; Hoiss et al. 2012). This result therefore suggests that the strong shift in the abundance of oligolectic species along the gradient of woodland proportion was explained by an exclusion of these species (filtering) in the landscapes with the highest woodland cover. Also, the absence of filtering of other trait values shows that the trait shifts we detected were not due to environmental filtering, and might involve other biotic and abiotic processes that influence trait relative abundances, such as variation of species tolerance to changes in resource availability (Kraft et al. 2015).

Our sampling approach allowed us to measure the relative effects of composition and configuration of different types of semi-natural habitats on the functional structure of bee communities. Our results support our hypothesis that the amount and configuration of different types of semi-natural habitats differentially influence bees with distinct trait values. Here, we found that body size and the date of the beginning of the foraging period were traits that determined the response of bees to grassland proportion or configuration and that diet breadth was a response trait to variations in woodland proportion. Contrary to other studies that assessed the effect of landscape complexity by considering solely non-crop elements in the landscapes (Winfree et al. 2009; Williams et al. 2010; Batáry et al. 2011; Kennedy et al. 2013), here we explored the independent effects of different semi-natural habitats on bee traits. Our approach therefore reveals that not all the semi-natural habitats are important for wild bee communities in the agricultural landscapes and that targeting particular habitats could be useful for the conservation of specific functional groups.

Our study also highlights the importance of determining the ecological determinants of shifts in trait values along landscape gradients. Even though our study shows that environmental filtering is of minor importance in explaining the occurrence of such shifts, further studies in contrasted agricultural contexts and with wider landscape gradients would allow better predictions of the occurrence of filtering effects of simplified landscapes on functionally important species.

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Compliance with ethical standards

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Supplementary information

Table S1 Bee abundance and trait assignment per species (females only). For details on trait ecological implications, see Table 2.

Species	ITD (mm)	Sociality	Nest location	Type of nest construction	Diet breadth	Beginning of foraging season (month nb.)	Abundance in 2013	Abundance in 2014
Andrena angustior	1.88	solitary	below-ground	excavate	polylectic	4	0	4
Andrena bucephala	2.15	solitary	below-ground	excavate	polylectic	4	0	2
Andrena distinguenda	1.68	solitary	below-ground	excavate	oligolectic	2	2	0
Andrena ferox	1.88	solitary	below-ground	excavate	oligolectic	4	0	1
Andrena flavipes	2.3	solitary	below-ground	excavate	polylectic	3	30	31
Andrena haemorrhoa	2.64	solitary	below-ground	excavate	polylectic	4	3	2
Andrena humilis	2.4	social	below-ground	excavate	oligolectic	4	18	4
Andrena lagopus	2.34	solitary	below-ground	excavate	oligolectic	3	1	4
Andrena nigroaenea	2.84	solitary	below-ground	excavate	polylectic	4	1	4
Andrena nigroolivacea	2.46	solitary	below-ground	excavate	oligolectic	3	8	2
Andrena nitida	2.97	solitary	below-ground	excavate	polylectic	3	3	3
Andrena nitidula	NA	solitary	below-ground	excavate	oligolectic	4	0	1
Andrena ranunculi	1.75	solitary	below-ground	excavate	oligolectic	3	0	1
Andrena ventricosa	1.63	solitary	below-ground	excavate	oligolectic	4	0	3
Anthophora plumipes	4.3	solitary	below-ground	excavate	polylectic	3	1	5
Bombus hortorum	5.7	social	below-ground	rent	polylectic	3	1	12
Bombus humilis	4.77	social	below-ground	rent	polylectic	6	0	1
Bombus lapidarius	4.9	social	below-ground	rent	polylectic	3	7	4
Bombus pratorum	4.6	social	below-ground	rent	polylectic	2	3	3
Bombus ruderarius	4.73	social	above-ground	rent	polylectic	4	1	4
Bombus sylvarum	4.44	social	above-ground	rent	polylectic	5	5	4
Bombus terrestris	5.7	social	below-ground	rent	polylectic	1	26	45
Ceratina cucurbitina	1.45	solitary	above-ground	excavate	polylectic	4	1	1
Chelostoma florisomne	1.79	solitary	above-ground	rent	oligolectic	4	2	0
Colletes cunicularius	3.5	solitary	below-ground	excavate	polylectic	2	2	0
Eucera clypeata	2.75	solitary	below-ground	excavate	oligolectic	5	16	7
Eucera interrupta	0.67	solitary	below-ground	excavate	oligolectic	5	1	0
Eucera nigrescens	3.5	solitary	below-ground	excavate	oligolectic	5	10	10
Eucera nigrifacies	2.8	solitary	below-ground	excavate	oligolectic	6	81	42
Halictus fulvipes	2.13	social	below-ground	excavate	polylectic	7	0	1
Halictus maculatus	1.55	social	below-ground	excavate	polylectic	4	5	4
Halictus patellatus	2.38	NA	below-ground	excavate	polylectic	7	2	0
Halictus quadricinctus	2.93	solitary	below-ground	excavate	polylectic	6	16	41
Halictus scabiosae	2.44	social	below-ground	excavate	polylectic	4	200	324
Halictus simplex	1.9	social	below-ground	excavate	polylectic	4	276	474
Halictus smaragdulus	1.03	social	below-ground	excavate	polylectic	6	0	1
Halictus tumulorum	1.49	social	below-ground	excavate	polylectic	4	2	1
Lasioglossum albipes	1.64	social	below-ground	excavate	polylectic	4	3	1
Lasioglossum corvinum	1.29	solitary	below-ground	excavate	polylectic	6	59	400

Lasioglossum discum	4.4	NA	below-ground	excavate	polylectic	6	1	2
Lasioglossum glabriusculum	0.73	social	below-ground	excavate	polylectic	5	70	64
Lasioglossum griseolum	0.93	NA	below-ground	excavate	polylectic	4	1	17
Lasioglossum interruptum	2.23	social	below-ground	excavate	polylectic	6	63	5
Lasioglossum laevigatum	1.84	solitary	below-ground	excavate	polylectic	4	8	1
Lasioglossum lativentre	1.55	solitary	below-ground	excavate	polylectic	4	8	5
Lasioglossum leucozonium	1.91	solitary	below-ground	excavate	polylectic	4	29	8
Lasioglossum malachurum	1.79	social	below-ground	excavate	polylectic	4	227	132
Lasioglossum marginatum	1.59	social	below-ground	excavate	polylectic	3	88	94
Lasioglossum mesosclerum	1.31	NA	below-ground	excavate	polylectic	NA	1	0
Lasioglossum minutissimum	0.86	solitary	below-ground	excavate	polylectic	4	3	18
Lasioglossum morio	1.1	social	below-ground	excavate	polylectic	3	9	5
Lasioglossum nigripes	1.97	social	below-ground	excavate	polylectic	6	204	12
Lasioglossum pallens	1.59	solitary	below-ground	excavate	polylectic	4	45	3
Lasioglossum pauxillum	1.24	social	below-ground	excavate	polylectic	4	59	85
Lasioglossum politum	0.82	social	below-ground	excavate	polylectic	4	233	222
Lasioglossum punctatissimum	1.23	solitary	below-ground	excavate	polylectic	4	8	18
Lasioglossum puncticolle	1.49	social	below-ground	excavate	polylectic	5	100	241
Lasioglossum subhirtum	1.2	NA	below-ground	excavate	polylectic	4	2	0
Lasioglossum tricinctum	1.25	solitary	below-ground	excavate	polylectic	NA	5	1
Lasioglossum truncaticolle	NA	NA	below-ground	excavate	polylectic	5	0	1
Lasioglossum villosulum	1.33	social	below-ground	excavate	polylectic	4	91	42
Lasioglossum xanthopus	2.37	solitary	below-ground	excavate	polylectic	4	2	1
Lasioglossum zonulum	1.95	solitary	below-ground	excavate	polylectic	4	28	54
Osmia bicornis	3.1	solitary	above-ground	rent	polylectic	3	7	2
Osmia cornuta	3.36	solitary	above-ground	rent	polylectic	3	1	1
Osmia rufohirta	2.53	solitary	above-ground	rent	polylectic	4	4	1
Xylocopa iris	4.33	solitary	above-ground	excavate	polylectic	3	0	2
Xylocopa violacea	6.5	solitary	above-ground	excavate	polylectic	2	2	5

Chapter 2: Relationship among ecological traits of wild bee communities along gradients of habitat amount and fragmentation

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Abstract

Amount of habitat and its level of fragmentation are among the main determinants of wild bee diversity in agricultural landscapes. However, the impact of habitat amount and fragmentation on the functional structure of bee communities and the consequences for pollination services have received little attention. In this study, we aimed to explore whether changes in the distribution of bee ecological traits along gradients of habitat amount and fragmentation were due to a direct effect of landscape context on multiple traits ('response traits') or to a correlation of ecological traits with true response traits. In two study regions in south-west France and south-east Australia, we used a three-table analysis to link bee traits with habitat amount and patch isolation measured at the landscape scale. We found that ecological traits shifted at the community-level in association with landscape gradients, whereas species-level associations among traits and phylogenetic clustering in bee communities were of only minor importance in determining such shifts. We found that traits such as body size and nest location were closely linked to habitat amount and fragmentation. We also observed regionally-specific relationships among ecological traits, suggesting that the regional species pool can play an important role in determining the pattern of linkages. Our findings suggest that improved knowledge about how trait-based responses mediate the impact of landscapes on functional community structure will allow better prediction and understanding of subsequent effects on pollination services.

Introduction

Human activities shape biodiversity at all scales, affecting ecosystem processes via changes in climate and alteration of habitat availability and quality (Parry, 2007; Pimm et al., 1995). Agricultural intensification has led to simplification of landscapes and changes in farming practices, and has been identified as the main cause of biodiversity decline in temperate agricultural landscapes (Krebs et al., 1999; Potts et al., 2010a; Robinson and Sutherland, 2002; Tilman, 1999). These environmental changes can lead to biotic homogenization (Chapin et al., 1997; Gámez-Virués et al., 2015) and alteration of ecosystem processes through changes in functional community structure (Lavorel and Garnier, 2002; Loreau et al., 2001; Suding et al., 2008). The relationship between the response of a community to environmental factors and subsequent impacts on ecosystem processes has been formalized in the response-and-effect framework (Lavorel and Garnier, 2002; Suding et al., 2008). In this trait-based framework, response traits are associated with the response of species to environmental factors and effect traits determine their contribution to ecosystem function (Lavorel and Garnier, 2002; Suding et al., 2008).

In agricultural landscapes, wild bees are ecologically and economically important, contributing to crop production (Garibaldi et al., 2013; Klein et al., 2007) and ecosystem functions that rely on wild plant communities (Kremen et al., 2007b; Memmott et al., 2004). Both wild bee species richness and pollination are affected by the loss and fragmentation of natural or semi-natural habitats (Garibaldi et al., 2011; Kremen et al., 2007b; Winfree et al., 2009), but the functional mechanisms that link wild bee community structure and pollination provision at the community level are poorly understood (Kremen et al., 2007b; Wood et al., 2015). Farmland bee species differ in their responses to habitat amount and fragmentation depending on their traits: for example, the proportion of semi-natural habitats in the landscapes increases the abundance of social bee species compared to solitary ones (Hopfenmüller et al., 2014; Williams et al., 2010). Other traits such as body size and diet breadth have been found to influence the pollination efficiency of bee species (Garibaldi et al., 2015; Larsen et al., 2005).

Wild bee communities may vary in the combinations of response and effect traits present, thus shaping the effect of landscape structure on ecosystem function. For example, if functionally important species respond negatively to an environmental change, this would drive an overall decrease in function. This was observed in wild bee communities, where large bodied species were the most efficient crop pollinators but also the most sensitive to habitat amount (Larsen et al., 2005). Response and effect traits could be related in communities because i) some response traits also act as effect traits, reinforcing the effect of environmental change on ecosystem functions (Larsen et al., 2005; Suding et al., 2008); ii) many traits are correlated among species, such that effect trait distributions may not be biologically or statistically independent of response traits (Ekroos et al., 2013; Williams et al., 2010);

iii) some closely-related species with similar traits could co-occur in given environments, therefore traits that are phylogenetically linked to response traits might also shift along environmental gradients (Hoiss et al., 2012; Sydenham et al., 2015). Alternatively, if the response and effect traits are not related, then environmental changes affecting the community should not alter ecosystem function on short timescales. This absence of a link could be caused if the community is randomly assembled in terms of sensitivity to environmental change and functional importance (Suding et al., 2008). However, it should be noted that the relationship between response and effect traits in this framework does not take into account species interactions such as resource partitioning or competition, and these could change the prediction of ecosystem functions in relation to changes in functional community structure (Kremen, 2005a; Larsen et al., 2005).

In this study, we aimed to explore the effect of habitat amount and fragmentation on the functional structure of wild bee communities, and whether the links among ecological traits revealed by landscape gradients were consistent between two regions with different species pools and different agricultural contexts. We examined the phylogenetic structure of wild bee communities along the landscape gradients (phylogenetic clustering), to detect if changes in some trait distributions were due to a direct effect of landscape variables or to a phylogenetic association among species, leading to similar shifts of true response traits and other functional traits (Webb et al., 2002). We explored the joint effects of habitat amount and fragmentation on bee communities as these two landscapes changes are often correlated in real-world landscapes and have contrasting effects on biodiversity (Fahrig, 2003). We studied shifts in body size, sociality, diet breadth, nest location, the duration and beginning of foraging season along gradients of habitat amount and isolation (Table 1). We predicted certain traits shifts along the gradient of habitat amount and fragmentation (e.g. reduced body size and occurrence of above-ground nesters in landscapes with low amounts and high fragmentation of semi-natural habitats, Table 1). We hypothesized that such correlated shifts in traits would be due to either i) an effect of landscape variables on one or more response traits that in turn influence the shift in other ecological traits, and could be caused by a) a correlation among traits at the species level or b) a phylogenetic structure in the community (closely related and functionally similar species respond similarly to landscape variables) leading to the phylogenetic association of several traits at the community level (co-occurrence of the values of different traits along the landscape gradients) or; ii) a direct effect of landscape variables on multiple traits.

Materials and methods

Study site and sampling design

1. SW France

The first part of this study was conducted in south-western France (Fig. 1a), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17’N, 0°54’E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al., 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

Within the studied region, we selected 80 cereal fields (40 different winter wheat and barley fields in each of 2013 and 2014 years) differing in the proportion of semi-natural habitats within a 500-m buffer, to cover independent gradients of woodland and grassland proportions. Preselection of sampling sites was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). In each field (hereafter sampling site), the sampling points were located near a field border that had a grassy margin, at least 100 m from a non-cropped area (woodland or built area). In each crop field, we established four sampling points: two 50 cm inside the field and 25 m apart from each other (field border transect), and two 25 m inside the field and parallel to the first two points (field interior transect). We sampled bees with six pan traps per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of four poles (one pole per sampling point), one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint, SparVar® Germany) and each pole had two different colors. The location of the trap colors was the same for each sampling site. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension. The poles were designed such that the height was adjustable to the crop canopy (10 to 120 cm). The traps were placed during two periods of 3 or 4 days per sampling site. The two sampling periods were from 22 April to 24 May and from 27 May to 21 June in 2013, and from 17 April to 12 May and from 22 May to 16 June in 2014. The number of individuals and the number of species determined for each sampling site represented the sum of all traps from the two sampling periods conducted in that site. Wild bee individuals (solitary and social species) were identified to species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than a direct effect of landscape structure. We also excluded cleptoparasitic bees because they do not provide pollination services.

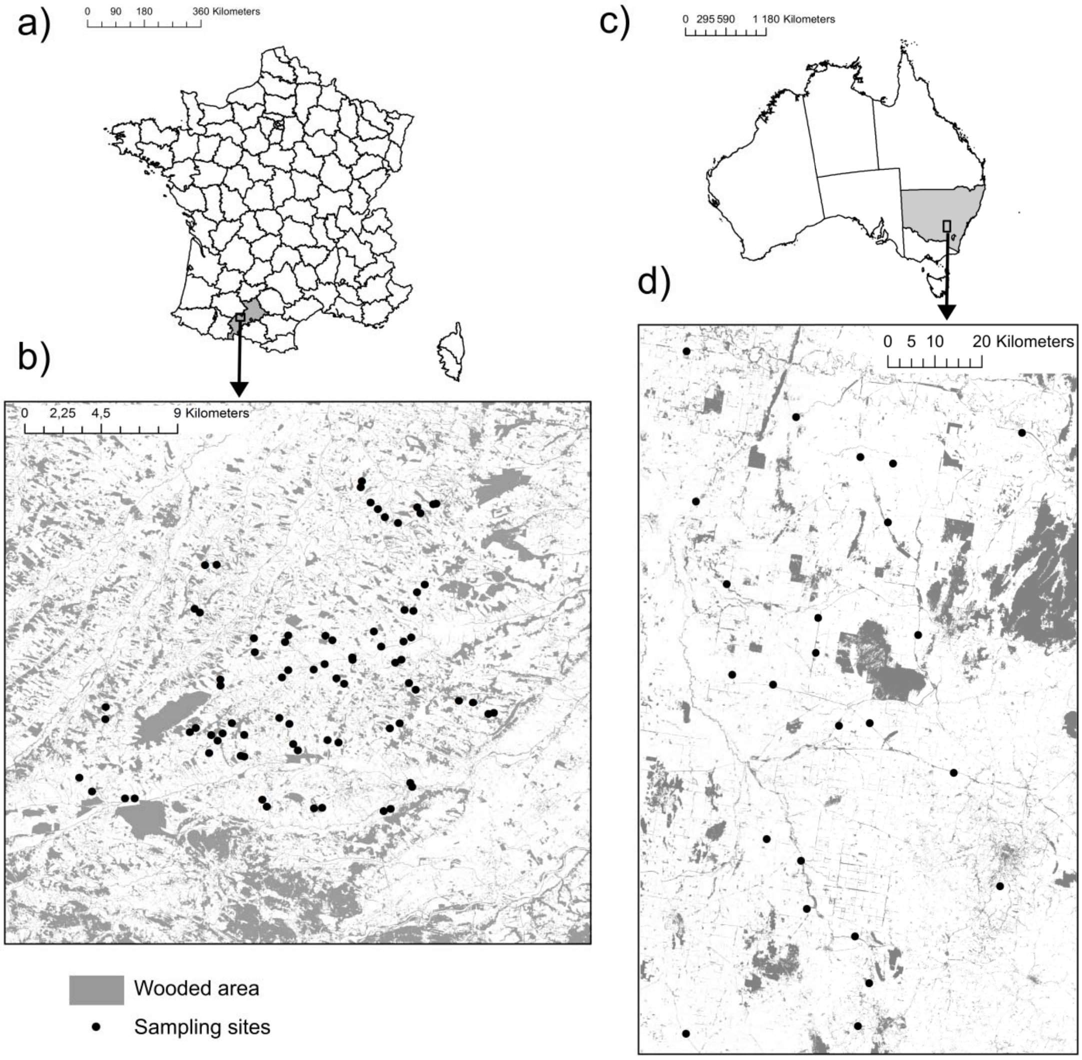

Figure 1 Maps showing (a, c) the French and Australian study areas, (b) the 78 sampled crop fields in SW France and (d) the 24 sampled crop fields in NSW Australia.

2. NSW, Australia

Wild bee communities were surveyed in the wheat-sheep belt of New South Wales, Australia (33–34°S and 147–148°E, Fig. 1c). This region is dominated by cereal and livestock production, with crop fields interspersed with linear remnants of native grassy box *Eucalyptus* woodlands dominated by Yellow box (*E. melliodora*), Grey box (*E. microcarpa*), White box (*E. albens*), Blakely's red gum (*E.*

blakelyi) and some White cypress pine (*Callitris columellaris*) (Lentini et al., 2012). Large scattered *Eucalyptus* can also be found throughout the fields.

Bees were sampled in 24 different annual crop fields (hereafter sampling sites) across the region, consisting of five native pastures, five agriculturally-improved pastures dominated by exotic grasses, five fields sown with lucerne (*Medicago sativa*) and/or clover (*Trifolium spp.*), six fields of wheat (*Triticum spp.*), and three fields of canola (*Brassica spp.*). Sampling points were located in isolated trees at 100, 200 and 400 m from an adjacent woodland remnant. Bees were surveyed using blue vane traps (SpringStar Inc., Woodinville, USA, 64 oz capacity, collecting jar: 15cm dia x 15 cm high, two blue vanes: 24 x 13 cm), which were hung in trees (a single trap per sampling point) located within the fields for a week-long period during two survey periods in spring/summer approximately two months apart (12th November – 8th December 2009, and 14th January – 9th February 2010). Wild bees were identified to species level and honey bees were excluded from the analysis for the same reason as in SW France. The number of individuals and the number of species determined for each site represented the sum of all traps from the two sampling periods conducted on that site. More detailed information about the sampling method can be found in Lentini et al. (2012).

Landscape variables

1. SW France

Landscape variables were calculated within a radius of 500 m centered on the field border transect in each site. The radius was chosen according to the results of previous studies on the functional scale of wild bees (Gathmann and Tscharntke, 2002; Holzschuh et al., 2010; Zurbuchen et al., 2010). Using aerial photographs (IGN, 2013) the different land covers (woodlands, hedgerows, permanent grasslands, crop fields and isolated trees) were digitalized using ArcGIS 10.2 (ESRI). Crop field and grassland boundaries were validated by ground surveys in July 2013, May 2014 and April 2015.

Four habitats were considered semi-natural: woodland edges, hedgerows and permanent grasslands. In each 500-m buffer (hereafter landscape), we calculated 6 variables measuring semi-natural habitat fragmentation (Table 1) using ArcGIS 10.2 (ESRI). We calculated the proportion of permanent grasslands and the length of woodland edges and hedgerows as a measure of habitat amount and we computed, for each habitat type, a proximity index as a measure of isolation or fragmentation of habitat patches. To calculate this proximity index, we created buffers around each habitat patch as an approximation of the maximum foraging distance (100 m) of the least mobile species that we captured (Greenleaf et al., 2007). We then calculated the proximity index, which was the proportion of overlapping zones amongst all the landscapes (proximity index= area of buffer overlap / total buffer area) to measure the zones in the landscapes where movements between habitat patches were possible for the whole bee community (Fig. 2).

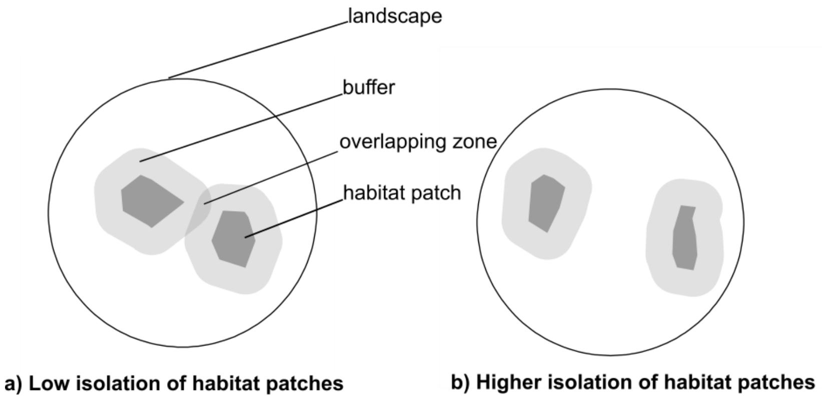

Figure 2 Calculation of the proximity index, showing examples of low habitat isolation (a) and high habitat isolation (b). A buffer zone was created around each habitat patch per habitat type which corresponded to the maximum foraging distance of the least mobile species captured in the traps (100m). The proximity index was the ratio of the area of buffer overlap / total buffer area. In this example the proximity index would be 4% for a) and 0% for b).

As some of the sampling sites were surveyed for a different study, sites were paired in such a way that they were at least 200 m apart. As a consequence, spatial autocorrelation of wild bee species richness and abundance was checked in the data. After a random resampling process, two buffers were finally removed from the analysis to minimize spatial autocorrelation (*Moran index* = 0.07, *p* = 0.19). Statistical analyses were then performed on the 78 remaining landscapes (Fig. 1b).

Table 1 Description of landscape variables used to assess habitat amount and habitat isolation.

	Code	Variable (units)	Mean (min–max)
SW France (n=78)			
Habitat amount	*hedge*	Length of hedgerows (m)	3,448 (881–7,655)
	woodland_edge	Length of woodland edges (m)	2,150 (0–5,494)
	grassland	Permanent grassland area (m²)	164,240 (0–471,640)
Habitat isolation	*prox_hedge*	Proximity of hedgerows (%)	58 (28–89)
	prox_woodland_edge	Proximity of woodland edges (%)	11 (0–35)
	prox_grassland	Proximity of permanent grasslands (%)	28 (0–64)
NSW Australia (n=24)			
Crop type	*crop*	Identity of the surveyed crop field	-
Habitat amount	*woodland_edge*	Length of woody vegetation edges (m)	3,271 (0–7,633)
	grassland	Native pasture area (m²)	31,854 (0–257,366)
Habitat isolation	*prox_woodland_edge*	Proximity of woody patches (%)	45 (0–88)
	prox_grassland	Proximity of native pastures (%)	4 (0–32)

2. NSW, Australia

Landscape variables were calculated within a 500 m radius centered between the 200 and 400 m trappings points in each sampled field. Using the “Land Use: New South Wales” spatial data set, dated 8th April 2011 and supplied by the NSW Department of Environment, Climate Change and Water, we calculated four landscape variables as a measure of semi-natural habitat amount and fragmentation (Table 1) using ArcGIS 10.2 (ESRI). We calculated the proportion of native pasture and the edge length of woody vegetation as a measure of habitat amount, and using the same method as for SW France and for each habitat type we computed a proximity index to quantify habitat fragmentation (Fig. 2).

Bee traits

Six ecological and life-history traits were chosen based on their knowledge in the literature regarding their potential to influence the response of wild bees to environmental changes (response trait) and/or affect pollination efficiency (effect trait) (Table 2). Some traits, such as body size, diet breadth, sociality, and timing of the foraging season, were considered both response and effect traits, based on previous studies (Table 1). Only nest location was considered to be only a response trait (Table 1). For bees in SW France, we sourced trait information from the ALARM project database (Settele et al. 2005), and from Michener (2000), Gathmann and Tscharntke (2002), Bommarco et al. (2010), Fortel et al. (2014) and Forrest et al. (2015). The beginning and duration of the foraging season in SW France was based on expert knowledge (David Genoud, pers. com.). For body size values in France, when no data were available on a particular taxon, ITD was measured on at least five female individuals per taxon, and queens were used for eusocial species. In NSW Australia, ITD was measured on one to ten female individuals per taxon. For both regions, social bees included species that live in a colony characterized by cooperative brood care, therefore including eusocial and primitively social species. Solitary bees included species that care only for their own offspring. If trait values compiled from the literature varied for a given taxon, the mean value was retained in our trait database. We were able to obtain traits for 60 of 111 species in SW France and for 29 of 30 species in NSW Australia (representing 97 and 99% of the sampled individuals respectively) (Supplementary material Appendix 1, Table A1; Appendix 2, Table A2). Species lacking trait values were excluded from the analyses. In SW France, we were able to include six traits in the analysis, whereas only two traits (body size and nest location) were used in NSW Australia. Indeed, the foraging period was unknown for every species and we excluded diet breadth and sociality as only one sub-dominant species was oligolectic (*Hylaeus albocuneatus*) and all the species were solitary (Table A2).

Table 2 Response and effect traits used in the analyses and their corresponding ecological roles. Trait type indicates if each trait was considered a response or an effect trait in the analyses.

Trait	Unit	Trait type	Tested in SW France	Tested in NSW Australia	Description and ecological implications
Inter-tegular distance (ITD)	mm	Response/Effect	X	X	Distance between the nearest edges of the tegulae (plates covering the wing bases), which measures body size. This measure is strongly correlated with bee foraging ranges (Greenleaf et al., 2007) and is likely to affect resource use in landscapes and response to habitat amount (Bommarco et al., 2010; Williams et al., 2010). Body size was also found to affect the efficiency of wild bee in depositing pollen, as large-bodied species tend to deposit more pollen grains on flower stigmas than small-bodied ones (Garibaldi et al., 2015; Larsen et al., 2005).
Diet breadth	Nominal (oligolectic, polylectic)	Response/Effect	X		Diet specialization defined by the number of plant families bees collect pollen from. Polylectic species (pollen generalists = several plant families) are more likely to pollinate a variety of plant species than oligolectic species (pollen specialists = one plant family) (Williams et al., 2010).
Sociality	Nominal (social, solitary)	Response/Effect	X		Sociality can affect bee response to habitat amount, but studies have found contradictory results regarding responses of solitary *vs.* social species (Hopfenmüller et al., 2014; Jauker et al., 2013; Williams et al., 2010). Sociality was found to affect the pollination efficiency of bee species but the relative effectiveness of solitary *vs.* social species seems to depend on plant species (Albrecht et al., 2012; Klein et al., 2003).
Beginning of the foraging season ; duration of the foraging season	Number of the start month (1-12); Number of months	Response/Effect	X		The beginning and the duration of the foraging season influences the temporal range of pollination activity and thus the correspondence of foraging period of bees with the flowering period of plants (Woodcock et al., 2014).
Nest location	Nominal (above-ground, below-ground)	Response	X	X	Nest location can affect the response of bees to habitat amount and disturbances (tillage regimes, deforestation, mowing regimes, overgrazing) (Kremen and M'Gonigle, 2015b; Shuler et al., 2005; Williams et al., 2010).

Statistical analyses

We used an RLQ analysis (Dolédec et al., 1996) to explore the covariance between the amount and isolation of semi-natural habitats (table R) and species trait values (table Q), constrained by their relative abundance (table L). Because it explores the joint structure of the three tables, RLQ analysis is particularly useful for exploring the link between environmental variables and multiple species traits (Barbaro and Van Halder, 2009; Duflot et al., 2014; Gámez-Virués et al., 2015; Trichard et al., 2013). As RLQ is an ordination analysis, this method reduces the number of environmental variables that influence community structure and is therefore useful when exploring the combined effect of correlated variables in real-world landscapes such as habitat amount and fragmentation (Fahrig, 2003). Indeed, in our study, habitat amount and inter-patch proximity were positively correlated in both SW France and NSW Australia (Table 3).

Table 3 Spearman rank correlations or Kruskal-Wallis chi-square statistics (italic) among landscape variables describing habitat amount and habitat isolation in the SW France region (n=78) and NSW Australia region (n=24) (*P*<0.05 *; *P*<0.01 **; *P*<0.001 ***).

SW France

	prox_hedge	*woodland_edge*	*prox_woodland_edge*	*grassland*	*prox_grassland*
hedge	0.84 ***	-0.31 **	-0.2	0.1	0.3 **
prox_hedge		-0.17	-0.14	0.15	0.33 **
woodland_edge			0.67 ***	0.32 **	0.23 *
prox_woodland_edge				0.26 *	0.16
grassland					0.76 ***

NSW Australia

	woodland_edge	*prox_woodland_edge*	*grassland*	*prox_grassland*
crop	*12.22 **	*7.22*	*7.8*	*6.12*
woodland_edge		0.62 **	0.68 ***	0.58 **
prox_woodland_edge			0.35	0.24
grassland				0.84 ***

RLQ analysis involves the selection of axes that maximize the covariance between linear combinations of the columns of R- and Q-tables (Dolédec et al., 1996). The R-table comprised the amount and proximity index of permanent grasslands, woodlands and hedgerows for SW France and of permanent grasslands and woody vegetation for NSW Australia (Table 2). In NSW, Australia, bees were surveyed in different crop types, so crop type was added in the R-table for to account for a local effect of crop type on bee functional structure (Table 2). The Q-trait table comprised body size, nest location, the beginning and duration of foraging season, diet breadth and sociality for SW France, and only body size and nest location for NSW Australia (Table 1). The three tables were analyzed separately first using ordination methods. The L-species table was analyzed using Correspondence Analysis (CA), and the R-environmental variables table using Principal Component Analysis (PCA), with the CA site scores being used as row weighting to couple R and L. The Q-trait table was analyzed by a Hill Smith PCA, which combines quantitative and qualitative variables, using CA species scores as a column weighting to couple Q and L. Second, the RLQ analysis was used to combine the three independent analyses in a single ordination (Barbaro and Van Halder, 2009; Gámez-Virués et al., 2015; Trichard et al., 2013). Finally, to test the significance of the link between traits and landscape variables, we used a two-step analysis (Gámez-Virués et al., 2015). First, we tested the link between site scores on the RLQ axes and landscape descriptors using Spearman correlations for continuous variables and Kruskal-Wallis tests for categorical variables (Gámez-Virués et al., 2015; Trichard et al., 2013). Second, we tested the link between species scores on the RLQ axes and corresponding trait values using Spearman correlations for continuous traits and Kruskal-Wallis tests for nominal traits (Trichard et al., 2013). Independently of the RLQ analysis, we used Spearman rank correlations to quantify the association between traits among species (Table 4), because the effect of one trait on the response to environmental change or on ecological function may not be biologically independent of others (Ekroos et al., 2013; Forrest et al., 2015; Williams et al., 2010). The same analysis was run on the two regions separately to maximize the number of traits in the analyses, as the number of available traits was different between the two study regions (six in SW France and two in NSW Australia).

We used a three-step analysis to check for a phylogenetic signal in wild bee communities along landscape gradients (Sydenham et al., 2015). First, we built a polytomous, ultrametric tree based on bee taxonomy for the two regions (Supplementary material Appendix 3, Fig. A3) using the R package *ape*. Branch lengths were calculated setting the p-parameter to 1 (Hoiss et al., 2012; Sydenham et al., 2015). Second, we checked for evidence of niche conservatism (i.e. that closely related species are ecologically similar and thus share similar trait values; Webb et al. 2002, Wiens et al. 2010). We used the phylogenetic independent contrasts (PIC, R package *picante*) for each trait to test if ecological traits displayed phylogenetic signals in the species pool. The observed PIC was compared to a null distribution generated by randomly shuffling taxa names across the phylogeny while leaving the ecological traits in place (Sydenham et al., 2015). We ran 10,000 iterations to obtain the null distribution. If the p-values of observed vs. random variance of PICs were lower than 0.05, we interpreted them as an evidence of non-random phylogenetic signal. Third, we calculated the net relatedness index (NRI) to quantify phylogenetic clustering at the community level (Webb et al., 2002). The null model for the NRI was generated by calculating for each site the mean and standard deviation of the phylogenetic distances expected for the number of taxa found on the site, based on a random selection of species from the regional species pool found in our study (10,000 iterations per site) (Hoiss et al., 2012) . As we assumed that the ability of a species to colonize a sampling site would be proportional to its frequency in the species pool, the random draws were weighted by the relative abundance of each species in the pool (Hoiss et al., 2012). Positive values of NRI indicate phylogenetic clustering and negative values phylogenetic over-dispersion. To test whether NRI significantly changed along landscape gradients, we performed linear regressions for the two regions with site scores from the RLQ as predictors and NRIs per site as response variables.

Results

Association among ecological traits at the species level

In both regions, above-ground nesters were significantly larger than below-ground nesters (Table 4). In the SW France region, body size was negatively correlated with the beginning of the foraging period (Table 4). Late-emerging species tended to forager for shorter periods than early-emerging species. Oligolectic species foraged for shorter periods and were mostly solitary compared to polylectic species.

Table 4 Spearman rank correlations among species traits for the SW France (n=60) and NSW Australia (n=28). For nominal traits, trait values were coded as 0 or 1 to allow for correlation calculation. Sociality: social=0, solitary=1; diet breadth: polylectic=0, oligolectic=1; nest location: below-ground=0, above-ground=1 (*P*<0.05 *; *P*<0.01 **; *P*<0.001 ***).

SW France

	Foraging duration	Beginning of foraging	Sociality	Diet breadth	Nest location
ITD	-0.07	-0.31 *	0.08	-0.03	0.31 *
Foraging duration		-0.41 **	-0.25 *	-0.39 **	0.04
Beginning of foraging			-0.17	0.02	-0.16
Sociality				0.34 **	0.17
Diet breadth					-0.09

NSW Australia

	Nest location
ITD	0.47 *

Identification of landscape gradients affecting the functional structure of bee communities

1. SW France

Even though the first two axes of the RLQ explained only 26% of the total joint inertia of the three tables, the analysis accounted for most of the variability explained by the separate analyses of landscape variables and trait data (65% for landscape and trait data). Therefore the covariance between the R-landscape variables and Q-trait table was well described in the RLQ analysis.

For each type of semi-natural habitat, habitat amount and isolation were correlated to the same axes of the RLQ analysis (Table 5). The first RLQ axis separated crop fields according to the amount and isolation of the surrounding hedgerows and permanent grasslands (Table 5), with a positive correlation between site scores of the first axis and the amount and proximity of grasslands and hedgerows. The second axis of the RLQ was positively associated with the amount and proximity of woodland edges (Table 5)

Body size, sociality and nest location were significantly associated with the first RLQ axis (Table 5). Small-bodied, solitary and below-ground nesting species were associated with the highest levels of amount and proximity of grasslands and hedgerows, whereas large-bodied, social and above-ground nesting species were associated with reduced amounts and proximity grasslands and hedgerows (Table 5, Fig. 3).

Table 5 Correlation coefficients between the environmental variables and traits with the first and second axis of the RLQ for the SW France and NSW Australia regions. Spearman correlation coefficients are for continuous variables and Kruskal-Wallis chi-squared statistics are for the categorical variables (marked with an "a"). The highest correlations are in bold.

		Axis 1	Axis 2
SW France			
Environmental variables	hedge	**0.69** ***	-0.26 *
	prox_hedge	**0.73** ***	-0.12
	woodland_edge	0.16	**0.93** ***
	prox_woodland_edge	0.29 **	**0.78** ***
	grassland	**0.65** ***	0.09
	prox_grassland	**0.74** ***	0
Traits	ITD	**-0.65** ***	**-0.54*****
	Sociality	**15.14** ***	**21.96** ***
	Diet breadth	2.83	**23.62** ***
	Foraging duration	-0.14	0.15
	Foraging beginning	0.26 *	**0.45** ***
	Nest location	**14.59** ***	**10.1** **
NSW Australia			
Environmental variables	crop[a]	**17.07** **	**15.71** **
	woodland_edge	0.43 *	**-0.85** ***
	prox_woodland_edge	0.13	**-0.81** ***
	grassland	0.45 *	**-0.66** ***
	prox_grassland	0.46 *	**-0.52** **
Traits	ITD	**0.95** ***	0.17
	Nest location	**11.61** ***	**16.55** ***

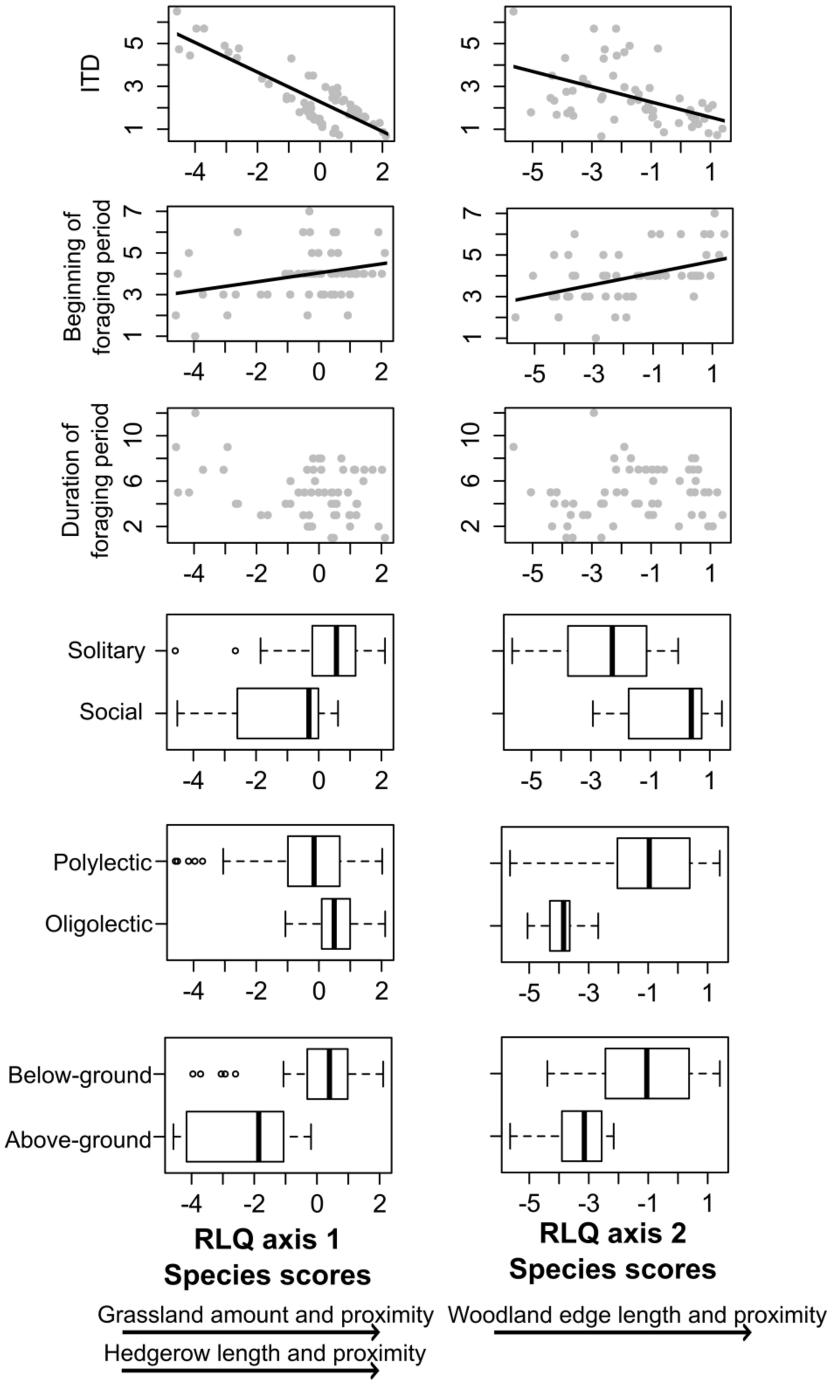

Figure 3 Correlation between trait values and species scores along the first and second axes of the RLQ for the SW France region. Regression lines for significant correlations are shown for illustrative purposes. Description of RLQ axes in terms of environmental gradients was added for interpretation purposes.

Body size, the beginning of foraging period, sociality, diet breadth and nest location were significantly associated with the second RLQ axis (Table 5). Indeed, the small-bodied, late foraging, social, polylectic and below-ground nesting species were associated with greater amounts and proximity of woodland edges. In contrast, the large-bodied, early foragers, solitary, oligolectic and above-ground nesting species were associated with reduced amounts and proximity of woodland edges (Table 5, Fig. 3). The duration of foraging season was not correlated with any of the two RLQ axes (Table 5).

2. NSW Australia

The first two axes of the RLQ explained 57% of the total joint inertia of the three tables. The variability explained by the separate analyses of landscape variables and trait data was conserved in the RLQ analysis (77% and 100% respectively). Therefore the RLQ analysis gave a good description of the covariance between the R-landscape variables and Q-trait table.

The first RLQ axis separated crop fields according to their identity (Table 5, Fig. 4), with sampling sites in canola fields having the lowest scores and the sites in lucerne having the highest scores on this axis. Wheat fields, mixed and exotic pastures were located at intermediate positions. The second axis of the RLQ was negatively associated with the amount and proximity of woody and grassy habitats (Table 5).

The first axis of the RLQ separated wild bee species according to their body size and nest location (Table 5). Small-bodied and below-ground nesting species were associated with sampling sites located in canola fields, whereas large-bodied and above-ground nesting species were associated with sampling points located in lucerne (Fig 5).

Only nest location was correlated with the second axis of the RLQ (Table 5), and to a greater extent than the first axis. Above-ground nesters were associated with landscapes that had a greater amount and proximity of semi-natural habitats, whereas below-ground nesters were dominant in more crop-dominated landscapes (Fig. 5).

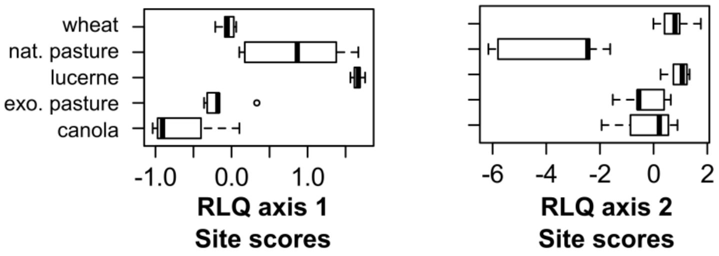

Figure 4 Correlation between crop type and site scores along the first (a) and second (b) axes of the RLQ for the NSW Australia region. These boxplots allow interpreting the directionality of the correlation between crop type (categorical variable) and RLQ axes. Correlation between continuous environmental variables and RLQ axes can be found in Table 5.

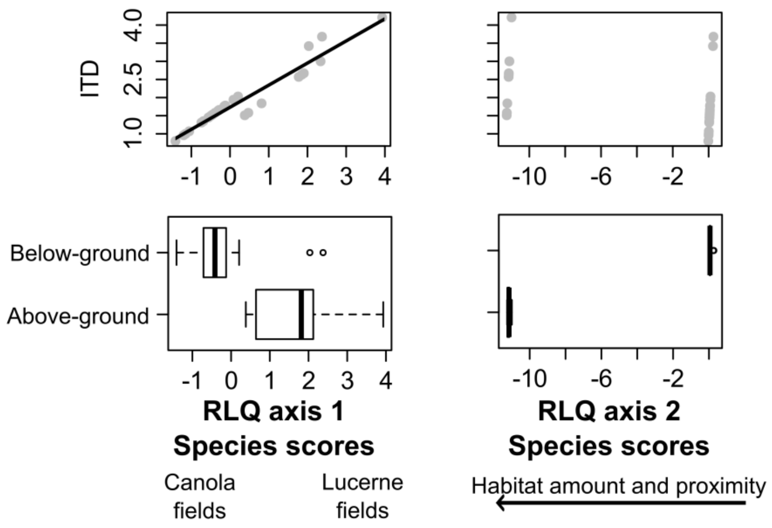

Figure 5 Correlation between trait values and species scores along the first and second axes of the RLQ for the NSW Australia region. Regression lines for significant correlations are displayed for illustration purposes. Description of RLQ axes in terms of environmental gradients was added for interpretation purposes.

Phylogenetic signal in species traits and bee communities

The majority of the traits showed significant phylogenetic signals in both regions (Table 6). In SW France, the largest bees were from the genus *Bombus*. Sociality was exclusive to the *Bombus*, *Halictus* and *Lasioglossum* (sub-genus *Evylaeus*) genera. Oligolectic species were all from the *Andrena* and *Eucera* genera. Above-ground nesters were found in *Xylocopa, Osmia* and *Bombus* genera (*B. sylvarum* and *B. ruderarius*). In NSW Australia, nest location showed a greater phylogenetic signal than body size (Table 6). Above-ground nesters were exclusive to the genera *Megachile* and *Hylaeus*, and species from the *Amegilla* and *Megachile* genera were the largest bees.

There was no significant association between relatedness of bees (NRI) and the landscape gradients in either of the two regions (Table 7).

Table 6 Phylogenetic signal in ecological traits of wild bee species for the SW France and NSW Australia regions. For nominal traits, trait values were coded as 0 or 1 to allow for the phylogenetic independent contrasts (PIC) (Sociality: social=0, solitary=1; diet breadth: polylectic=0, oligolectic=1; nest location: below-ground=0, above-ground=1). The test of the significance of the phylogenetic independent contrasts (PIC) were based on the comparison between the variance of the observed contrasts (PIC.var.obs) and the mean variance in contrasts obtained by randomizing the relationship between the trait and the phylogeny (null expectation, PIC.var.rnd.mean). The relationship between the variance of the observed and randomized PIC provided a z-value (PIC.var.Z). A smaller P-value than 0.05 is a sign of phylogenetic signal in ecological traits.

	Bloomberg K	PIC.var.obs	PIC.var.rnd.mean	P-value	PIC.var.Z
SW France (n=60)					
ITD	0.20	10.97	27.85	0.0001	-2.79
Foraging duration	0.15	44.67	81.89	0.0026	-2.22
Foraging beginning	0.16	12.06	21.30	0.0047	-2.07
Sociality	0.27	1.30	3.83	0.0001	-3.85
Diet breadth	0.20	0.99	2.51	0.0006	-2.87
Nest location	0.34	0.48	2.01	0.0003	-3.19
NSW Australia (n=28)					
ITD	0.57	1.77	3.83	0.0523	-1.15
Nest location	4.39	0.07	1.16	0.0001	-2.56

Table 7 Result of the linear regression testing the relationships between site scores on the RLQ axes and the net relatedness index (NRI). A significant trend in NRI along an environmental gradient indicates a phylogenetic clustering towards the negative values of the index.

	Estimate	SE	P-value
SW France			
Site scores axis 1	0.03	0.09	0.71
Site scores axis 2	0.08	0.12	0.53
NSW Australia			
Site scores axis 1	-0.24	0.26	0.36
Site scores axis 2	-0.03	0.11	0.79

Discussion

Relationships among ecological traits along the gradient of habitat amount and fragmentation in the landscapes

Our hypothesis that community-level covariation among ecological traits along the landscape gradients would be due to a correlation between these traits at the species level was not validated. Indeed, there were similarities in the associations of trait values at the species and community level for some traits (body size and nest location in SW France and NSW Australia, diet breadth and sociality in SW France, body size and beginning of the foraging season in SW France) but this pattern was not detected for all the traits. Indeed, some trait values were associated at the species level but did not co-occur along the landscape gradients (sociality and diet breadth, beginning and duration of foraging season, Table 4, Fig. 3) and some other traits shifted along landscape gradients without being associated at the species level (body size and sociality, body size and diet breadth, Table 4, Fig. 3). Therefore species-level association among traits seemed to be of minor importance in determining co-occurrence of trait values along the gradient of habitat amount and fragmentation.

Even though there were phylogenetic associations in species traits, we did not find significant correlations between phylogenetic relatedness (NRI) and landscape drivers (RLQ axes) for either region. This result is consistent with Sydenham et al. (2015), which found that the response of wild bees to landscape habitat diversity did not involve a phylogenetic clustering of wild bee communities.

Our results therefore suggest that neither species-level nor phylogenetic association among ecological traits seemed to strongly influence the shifts in multiple traits that were detected along the landscape gradients in both regions. The results thus suggest that such shifts were mainly due to a direct effect of landscape variables on multiple traits.

Changes in response trait distributions along the gradients of habitat amount and fragmentation

We found that body size was strongly correlated with environmental gradients in both regions. In SW France, body size was positively correlated to the RLQ axis describing the amount and isolation of grasslands and hedgerows, and to a lesser extent the axis describing woodland edge length and fragmentation. This result was consistent with our expectation that small-bodied species that have limited dispersal abilities and therefore need to nest closer to floral resources (Greenleaf et al., 2007), would be more abundant in landscapes with high amount and low fragmentation of semi-natural habitats compared to large species. Indeed, wild bee species in agricultural landscapes can benefit from semi-natural habitats such as hedgerows, permanent grasslands and woodland edges as they can provide critical feeding resources and nesting sites for both above- and below-ground nesting species

(Bailey et al., 2014; Forrest et al., 2015; Hopfenmüller et al., 2014; Morandin et al., 2007). Even though some crop fields can provide flowering resources for wild bees, such as mass-flowering crops or weeds (Bretagnolle and Gaba, 2015; Garibaldi et al., 2013), farmed areas are likely to be less suitable habitats for bee species that depend on semi-natural habitats (Westrich, 1996). Indeed, bees have been shown to move from semi-natural habitats into cropped areas to look for flowering resources, which explains the decrease in bee species richness and abundance with increasing isolation from semi-natural habitats (Albrecht et al., 2007; Bailey et al., 2014; Garibaldi et al., 2011; Steffan-Dewenter and Tscharntke, 1999). Species with limited dispersal abilities in the farmed area in SW France might therefore have benefitted from the large amount and the low isolation of semi-natural habitats, that might provide a high amount of available resources and opportunity for supplementation between habitats (Dunning et al., 1992; Fahrig, 2003). A decrease in the abundance of small-bodied species with decreasing habitat amount was also found in previous studies (Bommarco et al., 2010; Jauker et al., 2013; Williams et al., 2010). However, Larsen et al. (2005) found the opposite pattern as large-bodied species were more sensitive to habitat loss. Body size can be correlated with other traits such as diet breadth and sociality (Bommarco et al., 2010; Jauker et al., 2013), which also influence the response of bees to habitat amount. This may explain why studies not controlling for the correlation of body size with other traits, such as Larsen et al. (2005), found ambiguous results when studying the effect of habitat amount or fragmentation.

Contrary to our expectations, the body size of bee species was not linked to the amount and fragmentation of semi-natural habitats in NSW Australia (Table 5). The spatial extent of resource use by bees in this region therefore does not appear to influence community structure in response to habitat loss and fragmentation. However, there was a shift in body size at the community level along the first RLQ axis, which described the type of crop fields in which bees were captured (Table 5). Bee body size and proboscis length tend to be positively correlated (Cariveau et al., 2016), and our results show that short-tongued bees were more abundant in fields supporting crops with open and short corolla flowers (canola) whereas long-tongued species were associated with long and tubular flowering fields (Lucerne, Fig. 5). This is consistent with other studies that have found that proboscis length influences the flower choice of bee species (Cariveau et al., 2016; Garibaldi et al., 2015; Goulson et al., 2008). Therefore, the shift in bee body size observed along the first axis might have actually been due to the positive correlation between body size and tongue length, so tongue length seemed to be the actual response trait influencing bee functional community structure depending on crop type in NSW Australia.

As with body size, shifts in nest location along the gradients of habitat amount and fragmentation differed between the two regions. Contrary to our expectations, above-ground nesters in SW France were associated with landscapes with a low amount and high degree of isolation of semi-natural habitats (Fig. 3), whereas nesting sites for these species may be scarce in these crop-dominated landscapes (Potts et al., 2005; Williams et al., 2010). The shift in nest location along the landscape gradients that we detected in SW France may have actually been due to the positive effects of the amount and proximity of semi-natural habitats on the occurrence of below-ground nesters. Indeed, permanent grasslands and woodland edges can provide zones of undisturbed bare soil surrounded by sparse vegetation that can benefit below-ground nesting species (Bailey et al., 2014; Hopfenmüller et al., 2014; Potts et al., 2005). However, the opposite pattern was found in NSW Australia (Table 5). Above-ground nesters were associated with landscapes that were dominated by permanent woody and grassy vegetation, whereas below-ground nesters were more abundant in crop-dominated landscapes. This pattern can be explained by the fact that above-ground nesters nest in stems or existing holes using plant materials, and native vegetation such as trees, shrubs and permanent grassy areas would have allowed them to fulfil their nesting requirements (Potts et al., 2005; Williams et al., 2010). Nest location also shifted on the first axis of the RLQ in the Australian study, but this trend was likely to be a correlated response driven by the shift in body size, rather than differences among crops in nesting opportunities.

Such differences in the response of wild bee species to habitat amount and fragmentation among the two regions were mainly due to the differences in the regional species pools. Indeed, in SW France, we captured species from five different families, with contrasted trait values such as sociality and diet breadth (Supplementary material Appendix 1, Table A1). In NSW Australia, the captured bees had less contrasting ecological requirements and were from only four families (Supplementary material Appendix 2, Table A2). Moreover, the lack of knowledge in ecological trait values of Australian bee species (Batley and Hogendoorn, 2009) prevented us from testing all the associations among ecological traits that were tested in SW France. These differences in the regional species pools can be explained by several factors that were impossible to disentangle in this study. First, the trapping method might have influenced the diversity of captured species. Indeed, blue vane traps are particularly appropriate for capturing bee individuals in the presence of abundant flowering resources but the use of only one color might have reduced the diversity of captured species (Toler et al., 2005; Westphal et al., 2008). Pan traps are less efficient in capturing the functional association between bee species and local flower resources, but they are efficient to assess bee community structure when using different colors (Westphal et al., 2008). Moreover, species pools presumably differed between the two regions because traps were placed in different habitats. Even though isolated trees in NSW Australia were located in crop fields, this location may have selected specific species due to the floral and nesting sites that isolated trees can provide (Tscharntke et al., 1998), whereas annual, non-entomophilous, crop fields sampled in SW France were likely to provide fewer resources. Second, the differences in the species pool might be due to biogeographic history. Indeed, the families Andrenidae and Mellitidae are not found in Australia, whereas species from the family Colletidae are over-represented compared to Europe. Further, *Bombus* are not part of the Australian fauna except as an introduced species on the island of Tasmania (Batley and Hogendoorn, 2009; Hines, 2008). Third, differences in the species pools might be due to differences in the history and spatial extent of land-use change in the two regions. Indeed, in Australia the conversion of natural habitats to crop production took place 200 years ago during the European settlement and is thus recent compared to Europe (Benson, 1991). However, in France, wood cover reached its minimum extent at the end of the 19th century and has increased since to reach currently 30% of the land (Andrieu et al., 2011). Conversely, hedgerow cover reached its maximum extent in the late 19th century, and suffered from further fragmentation during the second post-war period (Burel and Baudry, 1990). As a result, south-western France has relatively denser wood cover and smaller mean field size than the Australian region (~4 ha in SW France, ~90 ha in NSW Australia). Therefore these relatively new and substantial land-use changes in NSW Australia compared to SW France may explain the lower bee species richness and the absence of relatively mobile species responding to landscape changes in the Australian landscapes.

In SW France, other response traits such as sociality, diet breadth and the beginning of foraging season shifted along the gradients of habitat amount and fragmentation. We found that social bees were dominant in landscapes with low amounts and high fragmentation of grasslands and hedgerows (Fig. 3), which is in line with a previous study that found that solitary species were more sensitive to the local loss of grassy permanent vegetation than social species (Jauker et al., 2013; Krauss et al., 2009). However, we found the opposite relationship along the gradient of length and isolation of woodland edges, with social species being associated with highly forested landscapes. This is in consistent with the meta-analysis of Williams et al. (2010), who found that social species in farmlands were more sensitive to the loss of natural habitats (mostly woody habitats) than solitary ones. The authors suggest that this was because social species need larger amount of floral resources to feed their numerous larvae. Our results therefore suggest that woodland edges provided critical resources for social bees, whereas solitary bees benefitted from grasslands and hedgerows. We also found that oligolectic species were associated with landscapes with low cover and high fragmentation of woodlands, which contradicted our expectations. This trend may be explained by the fact that the oligolectic species we captured in the SW France sites were dominated by species from the *Andrena* and *Eucera* genera, foraging principally on plants in the Brassicaceae and Fabaceae respectively, which can be easily found in the crop mosaic, as mass-flowering crops (oilseed rape) or weed species (clover or mustard) for example (Bretagnolle and Gaba, 2015; Le Féon et al., 2013; Rollin et al., 2016). As woodland and annual crop proportions were negatively correlated in the French landscapes ($r=-0.55$, $P<0.0001$), oligolectic species were less abundant in wooded landscapes, presumably because they found fewer suitable floral resources compared to less wooded landscapes.

In SW France, the beginning of the foraging period shifted along the gradient of woodland edge length and isolation, with early emerging species being favored in the least-forested landscapes. This trend is in accordance with previous studies on other taxa that found that early-active species were more abundant in open landscapes than in highly forested ones, presumably due to the fact that species may complete the majority of their life before the onset of agricultural disturbances in crop-dominated landscapes (Barbaro and Van Halder, 2009; Duflot et al., 2014). Therefore in the least-forested landscapes of our study, early-emerging species might have been favored due to their capacity to forage and reproduce before the main agricultural interventions that can impact bee survival, such as pesticide spraying, mowing or grazing in late spring (Gámez-Virués et al., 2015; Le Féon et al., 2010).

Potential influence of ecological trait shifts on pollination delivery

The majority of the ecological traits that we examined have been reported to affect pollination delivery in other studies. For example, body size can be an effect trait as large-bodied species have a greater chance of depositing pollen grains on flower stigmas (Hoehn et al., 2008; Larsen et al., 2005). However, the effect of body size on pollen deposition seems to depend on tongue length and on the plant species being considered (Garibaldi et al., 2015). Fruit set of crop plants with short corolla such as oilseed rape was found to increase with increasing abundance of large-bodied species with short mouthparts (Garibaldi et al., 2015). Measurement of mouthpart length and the exploration of the variation of this trait along our landscape gradients would help to determine if the shift in body size we detected could affect pollination provision in our study. Bee sociality might also influence pollination delivery, as Albrecht et al. (2012) found that social species visited *Raphanus sativus L.* more frequently than solitary ones and deposited more pollen grains. Conversely, Klein et al. (2003) found greater pollination efficiency of solitary bees in the case of coffee crops, therefore the pollination efficiency of social versus solitary bees may depend on the focal plant species or broader plant assemblages. The previous studies suggest that, in SW France, the pollination of plants with similar flower visitors as with *Raphanus sativus L.* would possibly decrease with increasing loss and fragmentation of woodlands but would increase as a function of loss and fragmentation of grasslands and hedgerows. Bee diet breadth might also influence pollination success as polylectic species are more likely to pollinate a variety of plant species (Williams et al., 2010). This could have important implications for pollination as plant-pollinator networks are asymmetric: specialist plants often rely on generalist pollinators and vice-versa (Memmott et al., 2004; Potts et al., 2010a). This could lead, in our case, to a depletion of pollen deposition on plants with specialized pollinator requirements at the plant community level in landscapes with few and highly fragmented woodlands, possibly causing a decrease in plant species richness. In SW France, we also found that the beginning of foraging season shifted along the gradient of woodland edge length and isolation, with late-foragers being favored over early ones in forested landscapes. Therefore, the amount and fragmentation of woodlands in the landscapes might influence pollination by determining the mean emergence date at the community level. This could in turn increase the risk of a mismatch between crop flowering phenology and the foraging season of wild bees (Blüthgen and Klein, 2011) and could cause a pollination depletion of late-flowering crops (such as sunflower) in crop-dominated landscapes or early-flowering crops (such as canola) in highly forested landscapes.

Conclusion

Our results clearly show that there was a strong shift in distribution of traits along the gradient of habitat amount and fragmentation across the two regions and, due to nature of these traits, this could influence pollination delivery for both cultivated and wild plants. However, links between trait distributions and pollination delivery is not always straightforward, as the predictive power of certain bee trait values in explaining pollination success depends on plant traits (Garibaldi et al., 2015) but also on the diversity of bee traits (Hoehn et al., 2008; Klein et al., 2008; Martins et al., 2015). Further research is thus needed to better describe bee species traits in a variety of agroecosystems and the dynamics of the functional links between these traits and pollination.

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Supplementary material Appendix 1, Table A1 List of bee species in the SW France dataset, corresponding abundance of individuals over all sites and trait values for bee species (females only).

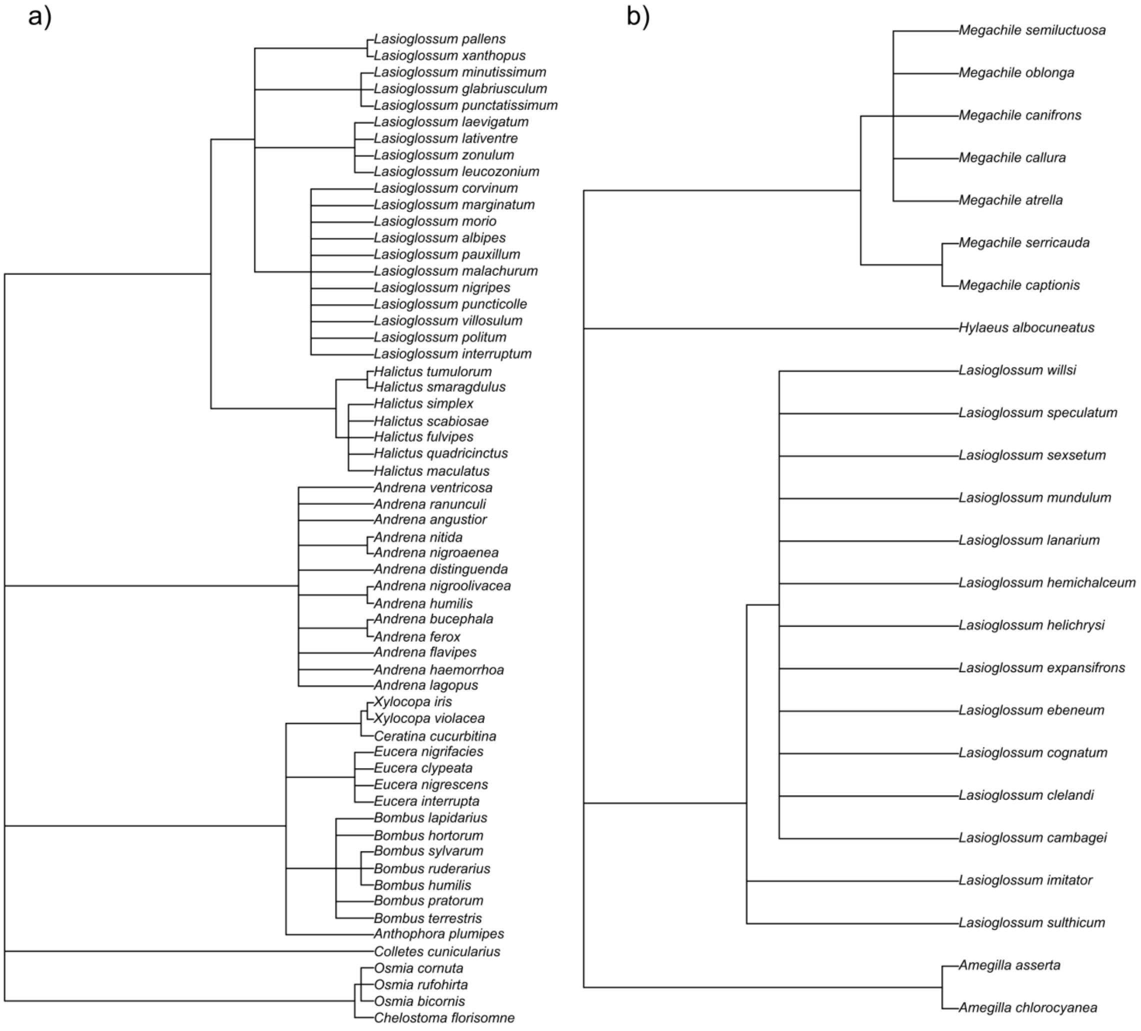
Species	ITD	Sociality	Diet breadth	Foraging duration (number of months)	Beginning of the foraging period	Nest location	Abundance
Andrena angustior	1.88	solitary	polylectic	3	april	below-ground	4
Andrena bucephala	2.15	solitary	polylectic	3	april	below-ground	2
Andrena distinguenda	1.68	solitary	oligolectic	5	february	below-ground	2
Andrena ferox	1.88	solitary	oligolectic	3	april	below-ground	1
Andrena flavipes	2.3	solitary	polylectic	8	march	below-ground	61
Andrena haemorrhoa	2.64	solitary	polylectic	4	april	below-ground	5
Andrena humilis	2.4	social	oligolectic	4	april	below-ground	22
Andrena lagopus	2.34	solitary	oligolectic	4	march	below-ground	5
Andrena nigroaenea	2.84	solitary	polylectic	4	april	below-ground	5
Andrena nigroolivacea	2.46	solitary	oligolectic	5	march	below-ground	10
Andrena nitida	2.97	solitary	polylectic	5	march	below-ground	6
Andrena ranunculi	1.75	solitary	oligolectic	2	march	below-ground	1
Andrena ventricosa	1.63	solitary	oligolectic	4	april	below-ground	3
Anthophora plumipes	4.3	solitary	polylectic	4	march	below-ground	6
Bombus hortorum	5.7	social	polylectic	7	march	below-ground	13
Bombus humilis	4.77	social	polylectic	4	june	below-ground	1
Bombus lapidarius	4.9	social	polylectic	7	march	below-ground	11
Bombus pratorum	4.6	social	polylectic	9	february	below-ground	6
Bombus ruderarius	4.73	social	polylectic	5	april	above-ground	5
Bombus sylvarum	4.44	social	polylectic	5	may	above-ground	9
Bombus terrestris	5.7	social	polylectic	12	january	below-ground	71
Ceratina cucurbitina	1.45	solitary	polylectic	8	april	above-ground	2
Chelostoma florisomne	1.79	solitary	oligolectic	5	april	above-ground	2
Colletes cunicularius	3.5	solitary	polylectic	2	february	below-ground	2
Eucera clypeata	2.75	solitary	oligolectic	1	may	below-ground	23
Eucera interrupta	0.67	solitary	oligolectic	1	may	below-ground	1
Eucera nigrescens	3.5	solitary	oligolectic	2	may	below-ground	20
Eucera nigrifacies	2.8	solitary	oligolectic	1	june	below-ground	123
Halictus fulvipes	2.13	social	polylectic	2	july	below-ground	1
Halictus maculatus	1.55	social	polylectic	7	april	below-ground	9
Halictus quadricinctus	2.93	solitary	polylectic	3	june	below-ground	57
Halictus scabiosae	2.44	social	polylectic	6	april	below-ground	524
Halictus simplex	1.9	social	polylectic	5	april	below-ground	750
Halictus smaragdulus	1.03	social	polylectic	3	june	below-ground	1
Halictus tumulorum	1.49	social	polylectic	6	april	below-ground	3
Lasioglossum albipes	1.64	social	polylectic	5	april	below-ground	4
Lasioglossum corvinum	1.29	solitary	polylectic	2	june	below-ground	459
Lasioglossum glabriusculum	0.73	social	polylectic	5	may	below-ground	134
Lasioglossum interruptum	2.23	social	polylectic	3	june	below-ground	68
Lasioglossum laevigatum	1.84	solitary	polylectic	4	april	below-ground	9

Lasioglossum lativentre	1.55	solitary	polylectic	7	april	below-ground	13
Lasioglossum leucozonium	1.91	solitary	polylectic	7	april	below-ground	37
Lasioglossum malachurum	1.79	social	polylectic	7	april	below-ground	359
Lasioglossum marginatum	1.59	social	polylectic	3	march	below-ground	182
Lasioglossum minutissimum	0.86	solitary	polylectic	7	april	below-ground	21
Lasioglossum morio	1.1	social	polylectic	8	march	below-ground	14
Lasioglossum nigripes	1.97	social	polylectic	2	june	below-ground	216
Lasioglossum pallens	1.59	solitary	polylectic	6	april	below-ground	48
Lasioglossum pauxillum	1.24	social	polylectic	7	april	below-ground	144
Lasioglossum politum	0.82	social	polylectic	5	april	below-ground	455
Lasioglossum punctatissimum	1.23	solitary	polylectic	7	april	below-ground	26
Lasioglossum puncticolle	1.49	social	polylectic	5	may	below-ground	341
Lasioglossum villosulum	1.33	social	polylectic	8	april	below-ground	133
Lasioglossum xanthopus	2.37	solitary	polylectic	7	april	below-ground	3
Lasioglossum zonulum	1.95	solitary	polylectic	7	april	below-ground	82
Osmia bicornis	3.1	solitary	polylectic	3	march	above-ground	9
Osmia cornuta	3.36	solitary	polylectic	3	march	above-ground	2
Osmia rufohirta	2.53	solitary	polylectic	4	april	above-ground	5
Xylocopa iris	4.33	solitary	polylectic	4	march	above-ground	2
Xylocopa violacea	6.5	solitary	polylectic	9	february	above-ground	7

Supplementary material Appendix 2, Table A2 List of bee species in the NSW Australia dataset, corresponding abundance of individuals over all sites and trait values for bee species (females only).

Species	ITD (mm)	Sociality	Diet breadth	Nest location	Abundance
Amegilla asserta	3.42	solitary	polylectic	below-ground	1
Amegilla chlorocyanea	3.68	solitary	polylectic	below-ground	303
Homalictus sphecodoides	0.96	solitary	polylectic	below-ground	44
Homalictus urbanus	1	solitary	polylectic	below-ground	8
Hylaeus albocuneatus	1.58	solitary	oligolectic	above-ground	1
Lasioglossum cambagei	1.64	solitary	polylectic	below-ground	276
Lasioglossum clelandi	1.94	solitary	polylectic	below-ground	10
Lasioglossum cognatum	1.31	solitary	polylectic	below-ground	219
Lasioglossum ebeneum	1.77	solitary	polylectic	below-ground	32
Lasioglossum expansifrons	1.53	solitary	polylectic	below-ground	577
Lasioglossum helichrysi	1.5	solitary	polylectic	below-ground	9
Lasioglossum hemichalceum	1.07	solitary	polylectic	below-ground	108
Lasioglossum imitator	1.45	solitary	polylectic	below-ground	206
Lasioglossum lanarium	2.03	solitary	polylectic	below-ground	377
Lasioglossum mundulum	1.35	solitary	polylectic	below-ground	3
Lasioglossum sexsetum	0.8	solitary	polylectic	below-ground	2
Lasioglossum speculatum	1.58	solitary	polylectic	below-ground	1
Lasioglossum sulthicum	1.78	solitary	polylectic	below-ground	2
Lasioglossum willsi	1.66	solitary	polylectic	below-ground	9
Lipotriches flavoviridis	1.45	solitary	polylectic	below-ground	4
Lipotriches moerens	1.76	solitary	polylectic	below-ground	90
Megachile atrella	2.57	solitary	polylectic	above-ground	1
Megachile callura	1.51	solitary	polylectic	above-ground	1
Megachile canifrons	3	solitary	polylectic	above-ground	3
Megachile captionis	2.67	solitary	polylectic	above-ground	4
Megachile oblonga	1.84	solitary	polylectic	above-ground	6
Megachile semiluctuosa	4.21	solitary	polylectic	above-ground	1
Megachile serricauda	2.63	solitary	polylectic	above-ground	1

Supplementary material Appendix 3, Figure A3 Polytomous, ultrametric tree of bee species captured in SW France (a) and NSW Australia (b), based on their taxonomy.



Partie B : Réponse des communautés d'abeilles sauvages à l'hétérogénéité « cachée » des paysages agricoles.

Chapter 3: Interactive effects of landscape-wide intensity of farming practices and landscape complexity on wild bee diversity

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Abstract

Context: The local intensity of farming practices is considered as an important driver of biodiversity in agricultural landscapes and its effect on biodiversity has been shown to interact with landscape complexity. But the influence of landscape-wide intensity of farming practices on biodiversity and its combined effect with landscape complexity have been little explored.

Objective: In this study, we tested the interactive effect of the landscape-wide intensity of farming practices and landscape complexity on the local species richness and abundance of farmland wild bee communities.

Methods: We captured wild bees in 96 crop fields and explored the effect of landscape-wide intensity of various farming practices along a gradient of landscape complexity.

Results: We found that species richness and abundance of wild bees were more positively influenced by permanent grassland proportion in highly sprayed and ploughed landscapes than in less intensively managed landscapes. We also found that the effect of woodland edges on wild bee species richness changed with the intensity of herbicide application in the farmed areas. Dominant bee species benefited from woody habitats, but were not affected by intensive practices. In contrast, sub-dominant species responded to the combined effects of landscape-wide intensity of farming practices and landscape complexity.

Conclusions: Our study demonstrates the interactive effects of landscape-wide farming intensity and landscape complexity in shaping the diversity of farmland wild bee communities. We conclude that landscape-wide extensification of farming practices could mitigate the effects of habitat loss on wild bee decline and would help to maintain pollination services in agricultural landscapes.

Introduction

Agricultural intensification over the past 60 years has been identified as the main cause of biodiversity decline in temperate agricultural landscapes, causing habitat fragmentation, degradation of habitat quality and landscape simplification (Krebs et al., 1999; Potts et al., 2010a; Robinson and Sutherland, 2002; Tilman et al., 2002). This intensification was characterized by the loss of semi-natural habitats, an increase in field and farm sizes, reduced crop diversity, and an increase in the use of pesticides and fertilizers (Benton et al., 2003; Robinson and Sutherland, 2002; Tilman et al., 2002). Therefore, agricultural intensification affected biodiversity through the simplification of landscape structure and changes in local farming practices (Firbank et al., 2008; Kleijn et al., 2009).

The role of landscape complexity on biodiversity is a standing issue in landscape ecology (Fahrig, 2003, 2013; Garibaldi et al., 2011; Steffan-Dewenter et al., 2002; Tscharntke et al., 2005): the proportion of semi-natural habitats in the landscapes, a widespread measure of landscape complexity, is associated with greater diversity of many taxa, such as birds, arthropods and plants. These habitats, such as hedgerows, permanent grasslands or woodlands, can provide feeding and nesting resources (Morandin and Kremen, 2013; Steffan-Dewenter et al., 2006) as well as promoting the dispersal of individuals by contributing to landscape connectivity (Cranmer et al., 2012; Krewenka et al., 2011). The intensity of local farming practices also affects biodiversity: when compared to conventionally managed fields, organic fields are associated with a higher species richness and abundance for a wide range of taxa (Batáry et al., 2011; Bengtsson et al., 2005) because they provide more diverse and abundant resources due to a reduced use of herbicides and fertilizers (Batáry et al., 2011; Bengtsson et al., 2005; Holzschuh et al., 2007; Roschewitz et al., 2005a). However, the strength of the effect of local farming practices on biodiversity depends also on the landscape context: extensive farming practices increase local biodiversity in simple but not in complex landscapes (Batáry et al., 2011; Tuck et al., 2014). Indeed, in homogeneous landscapes, organic farming increases biodiversity because this system, by increasing local diversity and abundance of resources, may compensate for the low amount of non-crop habitats in the vicinity of crop fields (Benton et al., 2003; Holzschuh et al., 2007). In complex landscapes, crop fields are in the direct vicinity of semi-natural habitats and the constant spillover of arthropods and plants from these source habitats may mitigate negative effects of intensive local management (Batáry et al., 2011; Roschewitz et al., 2005; Rundlöf et al., 2008).

However, by considering farming practices in a binary way (conventional *vs.* organic), these studies have not considered the relative impact of different farming practices on biodiversity and have not taken into account the diversity of practices and levels of intensity the organic and conventional farming systems encompass (Puech et al., 2014; Vasseur et al., 2012). Moreover, the effect of farming practices has mainly been studied at the local scale whereas the changes in the intensity of agricultural practices occur at the landscape scale (Herzog et al., 2006; Roschewitz et al., 2005b) and are likely to alter functional biodiversity and ecological processes (Hendrickx et al., 2007; Le Féon et al., 2010; Vasseur et al., 2012). The few studies that explored a landscape-scale effect of farming practices on biodiversity used a global intensity index (Gabriel et al., 2010; Hendrickx et al., 2007; Holzschuh et al., 2008; Le Féon et al., 2010; Rundlöf et al., 2008a) and thus have not addressed the effect of the intensity of a specific farm practice. The landscape-wide intensity of farming practices, by changing the distribution of resources in the landscapes (indirect effect) and by disturbing populations due to lethal or sub-lethal effects (direct effect), is likely to modulate the effect of landscape complexity on biodiversity (Vasseur et al., 2012).

Wild bees are ecologically and economically important in agroecosystems, contributing to crop production (Garibaldi et al., 2013; Klein et al., 2007) and to wild plant pollination (Kremen et al., 2007b; Memmott et al., 2004). They are affected by the intensification of agriculture and the loss of semi-natural habitats (Garibaldi et al., 2011; Le Féon et al., 2010; Winfree et al., 2009), however the interactive effect of these environmental factors remains poorly understood. Moreover, the effect of habitat loss on species richness of wild bees depends on species identity (Kleijn et al., 2015; Williams et al., 2010) and dominant bee species in agricultural landscape are less affected by habitat loss than sub-dominant species (Kleijn et al., 2015). In addition, different types of semi-natural habitats such as woody or grassy permanent vegetation might have contrasting effects on wild bee species depending on the resources they provide and on bee ecological requirements (Bailey et al., 2014; Forrest et al., 2015; Hopfenmüller et al., 2014; Morandin et al., 2007) but their relative effects on wild bee communities are still unclear. Therefore exploring whether the interactive effect of farming intensity at the landscape scale and landscape complexity on wild bee diversity depends on the type of semi-natural habitats deserves consideration.

The objective of this study was to explore whether the intensity of farming practices – pesticide, fertilizer use and tillage frequency – measured at the landscape scale, modulated the effect of landscape complexity on farmland wild bee communities. We captured wild bees in annual crop fields within landscape contexts contrasted in terms of landscape complexity – measured as the independent proportions of various types of semi-natural habitats– and of heterogeneity of crop mosaic, which was shown to be correlated with landscape-wide intensity of farming practices. We then characterized landscape-wide intensity of farming practices using farm interviews. We first expected that landscape-wide intensity of farming practices interacted with the proportions of semi-natural habitats to explain variations in species richness and abundance of wild bees. Second, we expected that two types of interactive effect between landscape-wide intensity (LWI) of farming practices and proportions of multiple semi-natural habitats (SNHs) occurred, depending on the type of farming practice and SNH: (a) the positive effect of the proportions of SNHs on wild bee diversity or abundance is stronger for high than low levels of LWI of farming practices, suggesting that SNHs would be the principal source of bees in intensively managed landscape due to the constant spill-over of pollinators from these habitats into the farmed area (Tscharntke et al., 2012) whereas in extensively managed landscapes, this spill-over would be less important in determining local species richness in annual fields as farmed areas would also provide flowering resources (Holzschuh et al., 2007; Roschewitz et al., 2005a) (Fig. 1a); (b) the positive effect of the proportions of SNH on wild bee diversity and abundance is stronger for low than high levels LWI of farming practices (Fig. 1b), suggesting that in extensively managed landscapes, farmed area and SNHs would provide complementary resources (e.g. specific flowering resources in crop mosaics and nesting sites in SNHs) that sustain local bee populations (Holzschuh et al., 2007; Tscharntke et al., 2012), whereas in intensively managed landscapes, farmland wild bees would lack critical resources leading to low bee species richness and abundance irrespective of the proportion of SNHs in the landscapes. Third, we expected that these relationships differed according to the dominance of wild bee species in the agricultural landscapes, with dominant species being less affected by the amount of SNHs (Kleijn et al., 2015) and LWI of farming practices than sub-dominant species, due to a particular set of trait values that would make them relatively insensitive to farming intensity and habitat loss (Williams et al., 2010).

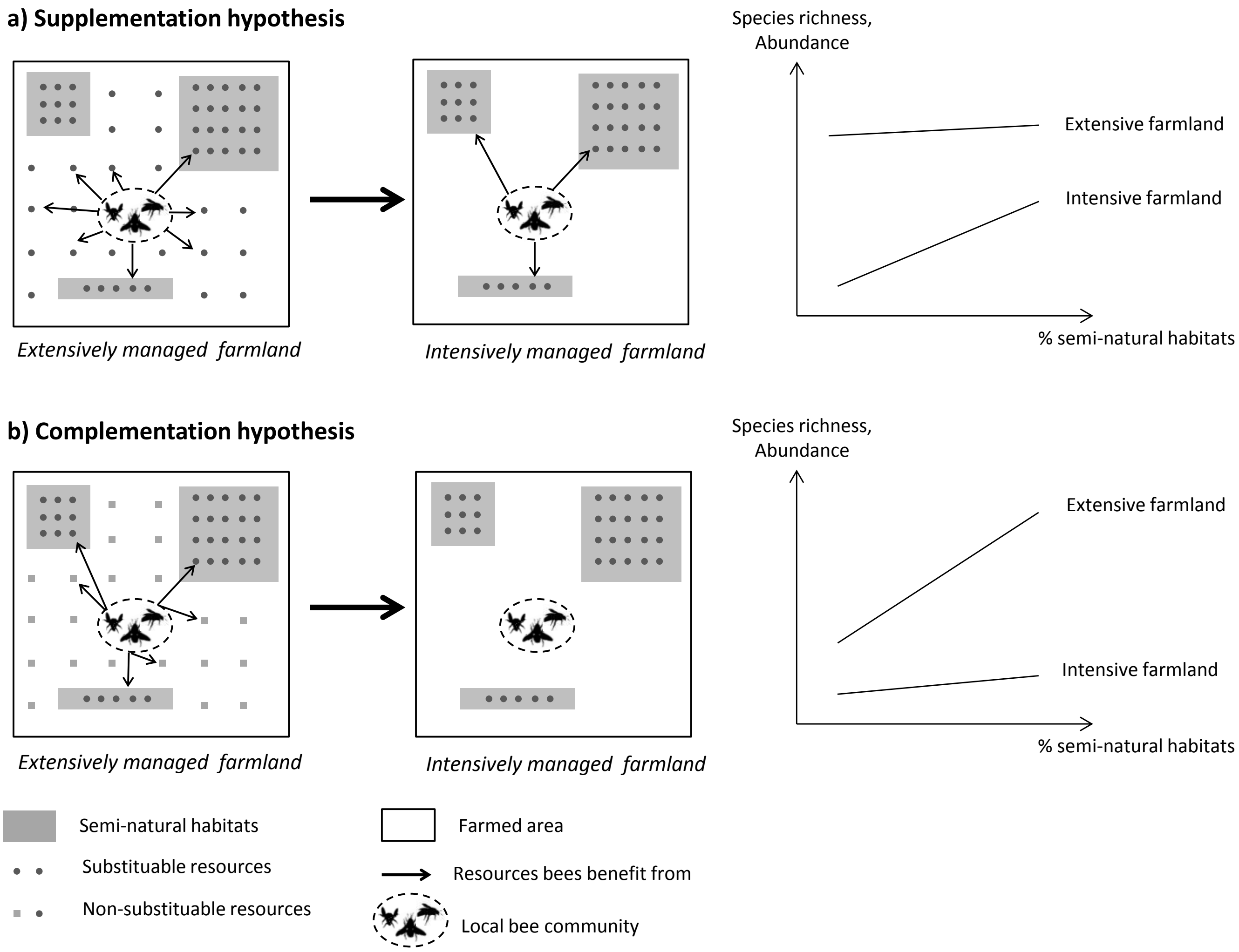

Figure 1 Predictions of the supplementation (a) and the complementation hypotheses (b). Both models rely on the common hypothesis that bees nest in semi-natural habitats and can forage in the surrounding farmed area. In the case a, when cropped area is intensively managed, semi-natural habitats provide the majority of foraging resources for farmland bees because crop fields cannot sustain wild bee populations. Therefore, increasing the proportion of semi-natural habitats (SNHs) in intensively managed landscapes would result in an increased species richness or abundance of farmland wild bees due to a larger carrying capacity of SNHs (habitat amount) and a reduced isolation of crop fields from SNHs. In extensively managed landscapes, as crop fields can also provide supplementary flowering resources, the proportion of SNHs is much less important in determining local species richness and abundance of farmland bees. In the case b, when cropped area is extensively managed, wild bee populations might benefit from complementation effects between cropped area and SNHs (Dunning et al., 1992) due to the diversity of resources provided by these two types of habitats (example: specific flowering resources in crop fields and nesting sites in semi-natural habitats). Therefore, increasing the proportion of semi-natural habitats (SNHs) in extensively managed landscapes would result in an increased species richness or abundance of farmland wild bees due to a reduced isolation of crop fields from SNHs and among SNHs. In intensively managed landscapes, farmland wild bees would lack critical resources and their species richness and abundance would be low irrespective of the proportion of SNHs as complementation would not occur.

Materials and methods

Study site and sampling design

This study was conducted in south-western France (Fig. 2a), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² area (43°17’N, 0°54’E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on the steep slopes, whereas annual crop fields (winter cereals, rapeseed, maize and sunflower) tend to be situated in the valleys (Choisis et al., 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

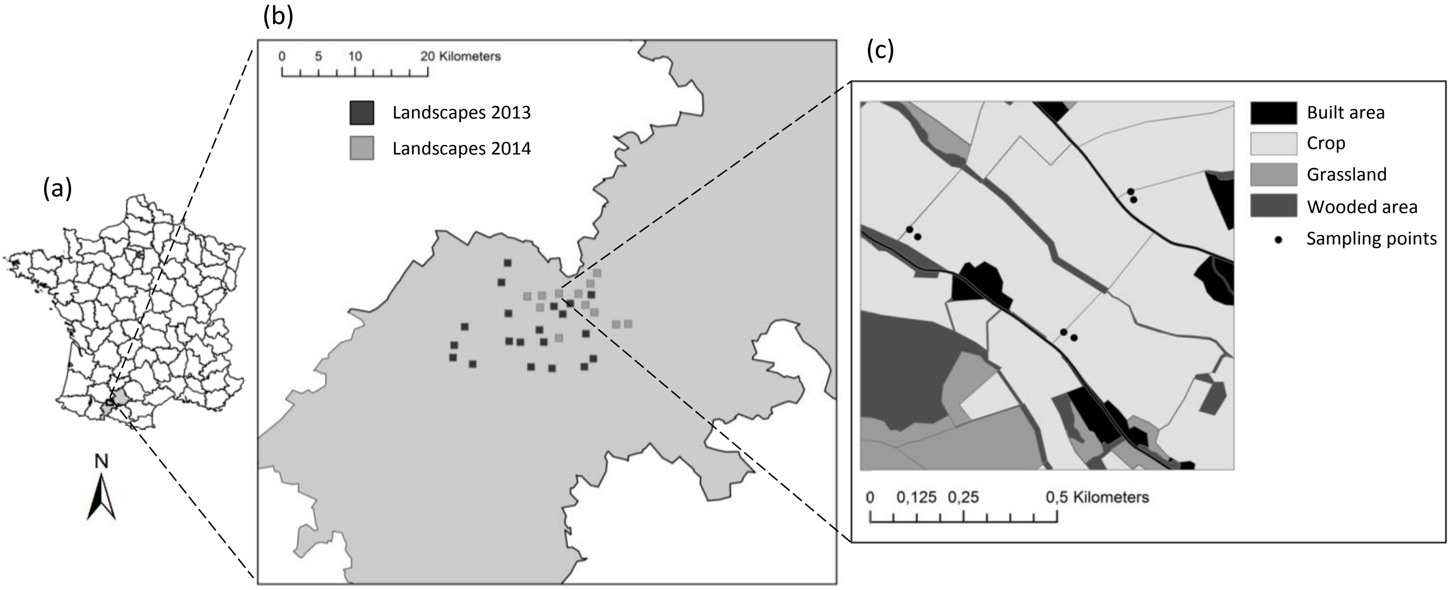

Figure 2 Maps showing (a) the study area, (b) the 32 landscapes sampled in 2013 and 2014 and (c) the location of the sampling points (transect) within three crop fields in one of the 32 landscapes.

We selected 1x1-km squares (hereafter landscapes) based on land cover maps of the main crops of the study region (wheat, maize, sunflower and grasslands) derived from a multispectral satellite image (Spot 5; Gleyzes et al. 2003). We selected 32 landscapes (Fig. 2b) from the results of a moving window analysis to cover independent gradients of crop diversity (Shannon diversity of crops), mean field size and woody habitat cover (Fragstats software; McGarigal et al. 2002), in areas dominated by agricultural land use (agricultural cover ranged from 70 to 90% for each landscape). More detailed information about the sampling design can be found in Pasher et al. (2013) and Fahrig et al. (2015). The proportion of grassy habitats and the landscape-wide intensity of farming practices were not taken into account in the landscape selection process, however our approach ensured low correlation between these two factors as the mean field size in landscapes were shown to be correlated with landscape-wide intensity of farming practices (Herzog et al., 2006; Roschewitz et al., 2005b) and crop diversity was negatively correlated with the proportion of permanent grasslands (r=-0.38, *P*=0.032).

Inside each landscape, we selected three crop fields (sampling sites), two winter cereal fields and one spring crop field (maize or sunflower), representing the dominant crops in the landscapes. They were at least 200 m apart (Fig. 2c), for a total of 96 sampled fields (60 in 2013: 40 wheat fields and 20 spring crop fields, and 36 in 2014: 24 wheat fields and 12 spring fields). In each field, the sampling points were located at the vicinity of a field border that consisted of grassy margins, at least 100 m apart from a non-cropped area (woodland or built area) to avoid any local effect on the bee sampling. In each crop field, 6 pan traps (colored plastic cups) were placed at the top of 4 poles, 1 or 2 traps per pole, with the poles placed at the end and the center of two transects (two poles at 50 cm of the grassy margin and two poles 25 m inside the crop field, the poles from the same transect being 25 m away from each other; Fig.2c). We used three colors of pan traps (white, yellow and blue UV color paint), and each pole had one or two different colors. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension (Westphal et al., 2008). The poles were designed such that the height was adjustable to the crop canopy. The traps were placed during two periods of 3 or 4 days during the 2013 and 2014 summers. The two sampling periods were from 22 April to 24 May and from 27 May to 21 June in 2013, and from 17 April to 12 May and from 22 May to 16 June in 2014. The number of individuals and the number of species determined for each field represented the sum of all traps from the two sampling periods conducted on that field. Wild bee individuals (solitary and social species) were identified to the species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than the result of a direct effect of landscape structure.

Landscape variables

Farming practices were evaluated in each landscape by standardized interviews with 73 farmers. Interviews were conducted to obtain information about local management intensity for each sampling site and to assess landscape-wide intensity of practices for crop fields around the sampling sites. In each landscape, 2 to 5 farmers were interviewed, who together managed on average 56.6% of the agricultural land in the landscapes (min=34.2%, max=85.2%). For each type of crop, we collected information on nitrogen input to arable crops, herbicide and insecticide application intensity, superficial tillage frequency and ploughing frequency. To calculate herbicide and insecticide application intensity, we asked farmers about the applied doses per hectare of arable area and the frequency of application. We then compared the applied doses of each chemical product to the maximum allowed doses by the French Ministry of Agriculture (E-phy 2015) and then calculated the ratio “applied dose/maximum allowed dose” to take into account dose-dependent effects on biodiversity. This ratio was then multiplied, for each crop type of each farmer, to the application frequency of the given chemical product. This index was then summed for each type of pesticide (herbicide and insecticide) at the farm level. To calculate the amount of nitrogen input, we asked the farmers about the frequency and the doses of mineral and organic fertilizers for the complete crop cycle and the amount of nitrogen was calculated using reference tables. The ploughing and superficial tillage frequency was calculated by summing up the number of these two types of tillage for the complete crop cycle.

Six indicators of landscape-wide intensity of farming practices were then calculated at the landscape extent: mean nitrogen input, mean herbicide and insecticide application frequency, mean superficial tillage frequency and mean ploughing frequency (Table 1). Following (Herzog et al., 2006) , we calculated these indicators, consisting in the weighted mean of each indicator (1) taking into account the different levels of intensity and associated crop area.

$$I_{mean} = \frac{Area_{field\ 1} \times I_{field\ 1} + \cdots + Area_{field\ n} \times I_{field\ n}}{Area_{total,known\ in\ the\ landscape}} \qquad (1)$$

Table 1 Description of landscape variables assessing landscape-wide intensity of agricultural practices and proportions of semi-natural habitats

Name	Scale of measurement	Code	Units	Mean	Min	Max	SE
Nitrogen input	Local (crop field)	N.qty	kg/ha/year	160.07	0	1380	17.75
Herbicide input		Herbicide.local	/year	1.17	0	5	0.10
Insecticide input		Insecticide.local	/year	0.31	0	7.08	0.10
Superficial tillage frequency		Nb.sup	/year	1.83	0	5	0.11
Ploughing frequency		Nb.plough	/year	0.38	0	1	0.05
Mean nitrogen input	Landscape	N.landscape	kg/ha/year	148.87	36.85	449.42	18.09
Mean herbicide application		Herbicide.landscape	/year	1.03	0	2.88	0.11
Mean insecticide application		Insecticide.landscape	/year	0.31	0	2.04	0.10
Mean superficial tilling frequency		superficial.landscape	/year	1.65	0.04	2.97	0.11
Mean ploughing frequency		plough.landscape	/year	0.37	0	1	0.05
Grassy strip cover		Grassy_edge	%	0.76	0.14	1.74	0.07
Grassland cover		Grassland	%	24.29	0.64	60.85	3.11
Woodland edge cover		Woodland_edge	%	2.18	0.34	4.78	0.21
Hedgerow cover		Hedgerow	%	2.82	0.46	9.28	0.38

Using aerial photographs (IGN, 2013), the different land covers (woodlands, hedgerows, permanent grassland and crop fields) were digitalized using ArcGIS 10.2 (ESRI) and were validated by ground surveys in July 2013 and May 2014. We calculated the proportion of four semi-natural habitats (woodland edges, hedgerows, permanent grasslands and grassy strips) in each landscape as a measure of landscape complexity (Table 1). The total proportion of semi-natural habitats ranged from 5.2% to 64.1%.

Statistical analyses

All analyses were performed using R 3.0.2 (R Development Core Team, 2011). To test the level of collinearity in our models, we followed Smith et al. (2009) by calculating Spearman rank correlations among variables and the variance inflation factor (VIF) for each variable (Table S1). Even though some variables were correlated (*Insecticide.local* and *Insecticide.landscape*, $r = 0.57$, $P < 0.001$), the VIF of all the variables were far below the threshold of 10 and all $|r| < 0.7$, indicating low collinearity in our models (Dormann et al., 2013; Smith et al., 2009). Thus, all the local and landscape variables were included in the same statistical models and were standardized to better assess their relative effects on the response variables.

#Table 2 approximately here#

We built generalized linear mixed-effect models to test the effect of semi-natural habitats (SNH) and landscape-wide intensity (LWI) of farming practices on local bee diversity, assuming Poisson error distribution (log-link function) to model variations in bee abundance and bee species richness, with the R *lme4* package. A landscape random factor was included to account for spatial autocorrelation of sampling sites located in the same landscapes and a sampling site random factor nested into the landscape random factor to account for possible overdispersion in the data (Lee and Nelder, 2000). First, we tested the interactive effect of the proportion of each type of SNH and LWI of farming practices on total bee species richness and abundance. To limit the number of variables in our models, we didn't include the interactions between local farming intensity and the proportions of SNHs as the variance of wild bee species richness and abundance explained simultaneously by local and landscape interaction was insignificant (Appendix S1, Fig. S1). Even if we would not lose information about the pure effect of landscape interactions without including local interactions, we included local intensity of farming practices (individual effect) as covariates in the models to control for this local effect on wild bee abundance and species richness. Therefore we considered the effect of local intensity of farming practices on wild bees as a confounding factor. A significant interaction term between the proportions of SNHs and landscape-wide intensity of practices in the models indicated that the effect of the proportions of SNHs on local wild bee communities was modulated by farming practices at the landscape scale. To test whether the landscape-wide intensity of agricultural practices modulated the effect of SNH on wild bees depending on their dominance status, the same models were used for all bee species (dominant and sub-dominant species), and for dominant and sub-dominant species separately. Dominant crop visitors were shown to be highly adapted to landscapes dominated by agriculture and less dependent on the proportion of less disturbed habitats, like SNH, in the landscapes (Kleijn et al., 2015). The other, less common, bee species were shown to be largely dependent on the proportion of SNH and might be less tolerant to disturbances due to farming practices. Therefore bee species were classified according to their total abundance (Fig. 3) and we selected species representing 80% of the total number of individuals as being the most common bee species (Kleijn et al., 2015). We used R^2 calculated for fixed effects using the *MuMin* package as a goodness of fit of the models (Nakagawa and Schielzeth, 2013). For all the models, we plotted the significant interaction terms to analyze the changes in the strength of the relationship between the proportions of SNHs and wild bee communities depending on the level farming intensity. To do so, we isolated the slope of the effect of the proportions of SNHs on the response variable considering the principal effect of the proportions of SNHs (β_1) and the interaction term between SNH proportions and LWI of farming practices (β_3) estimated by the statistical models. The formula (2) gives the detail of the calculation for an example with only one variable describing the proportions of SNHs and one variable describing LWI of farming practices.

$$\begin{aligned} \text{Response} &= \mu + \beta_1.\text{SNH} + \beta_2.\text{LWI} + \beta_3.(\text{SNH}.\text{LWI}) + \varepsilon \qquad (2) \\ &= \mu + \beta_2.\text{LWI} + (\beta_{1+}\,\beta_3.\text{LWI}).\text{SNH} + \varepsilon \end{aligned}$$

The slope of the effect of the proportions of SNHs ($\beta_{1+}\,\beta_3$.LWI) on the response variable (species richness or abundance) was then displayed for the range of LWI values measured in the landscapes. The graphs were then used to interpret the changes in the strength of the relationship between the proportions of SNHs and species richness of abundance of wild bees depending on the values of LWI of farming practices.

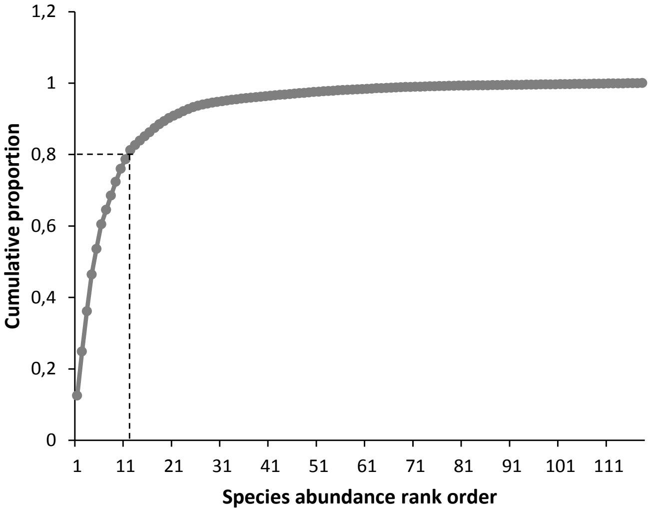

Figure 3 Relationship between cumulative proportions of captured wild bee individuals and species abundance rank order. The 12 dominant species represented 80% of the capture individuals in crop fields.

Results

A total of 5300 individuals belonging to 120 species was sampled across the 96 sampling sites. The 12 most dominant species (Fig. 3) comprised eleven species from the Halictidae family and one from the Apidae family (*Eucera nigrifacies*). These species were all ground-nesting and polylectic bee species, except *Eucera nigrifacies* (oligolectic on plants from the Dipsacaceae family).

Interactive effect of landscape-wide intensity of farming practices and SNH on total wild bee species richness and abundance

The proportion of three semi-natural habitat types significantly interacted with landscape-wide intensity (LWI) of farming practices when considering variations in species richness (Table 2). The effect of woodland edge proportion on bee diversity depended on LWI of herbicide application, the effect of hedgerow proportion on LWI of herbicide application and on LWI of ploughing frequency, the effect of grassland proportion on LWI of herbicide and insecticide application and LWI of ploughing frequency. When considering the slopes of the effect of SNH proportions on species richness (Fig. 4), three types of variations could be detected: a stronger and positive effect of the proportions of SNHs on wild bee species richness as LWI increased, only for permanent grassland proportion (*grassland x insecticide, grassland x ploughing*, Fig. 4d, 4g); a negative effect of the proportions of SNHs whatever level of LWI (*hedgerow x herbicide,* Fig. 4b); a change in the direction of the effect of the proportion of SNHs depending on LWI level (*woodland edge x herbicide*, *grassland x herbicide, hedgerow x ploughing,* Fig. 4a, 4c, 4f). For this latter type of interaction, the sign of the relationship between the proportion of SNH and species richness depended on the values of LWI of farming practices. Indeed, for low values of LWI of herbicide application, woodland edge proportion had a positive effect on species richness (Fig. 4a). However, for high values of LWI of herbicide application, species richness decreased with increasing woodland edge proportion (Fig. 4a). There was an opposite trend for hedgerow proportion: the effect of hedgerow proportion on species richness was positive for high values of LWI of ploughing frequency, whereas it was negative for lower values of LWI of ploughing intensity (Fig. 4f). There was the same trend for grassland proportion, even if the effect of grassland proportion on species richness was negative or neutral for extremely low values of LWI of herbicide application (Fig. 4c).

Table 2 Results of the generalized linear mixed models testing the interaction effects between landscape-wide intensity of crop practices and SNH to explain the variation in wild bee total species richness and total abundance. Only landscape variables and significant interactions are displayed.

Response variable	R^2 (fixed effects)	Variables	Estimate	SE	P value
Species richness	0.61	Herbicide.landscape:Woodland_edge	-0.49	0.20	0.012
		Herbicide.landscape:Hedgerow	-0.22	0.10	0.037
		Herbicide.landscape:Grassland	0.37	0.17	0.028
		Insecticide.landscape:Grassland	0.48	0.19	0.012
		plough.landscape:Hedgerow	0.59	0.16	0.000
		plough.landscape:Grassland	0.26	0.13	0.041
Abundance	0.53	Herbicide.landscape:Grassland	0.72	0.35	0.038
		plough.landscape:Grassland	0.53	0.25	0.033

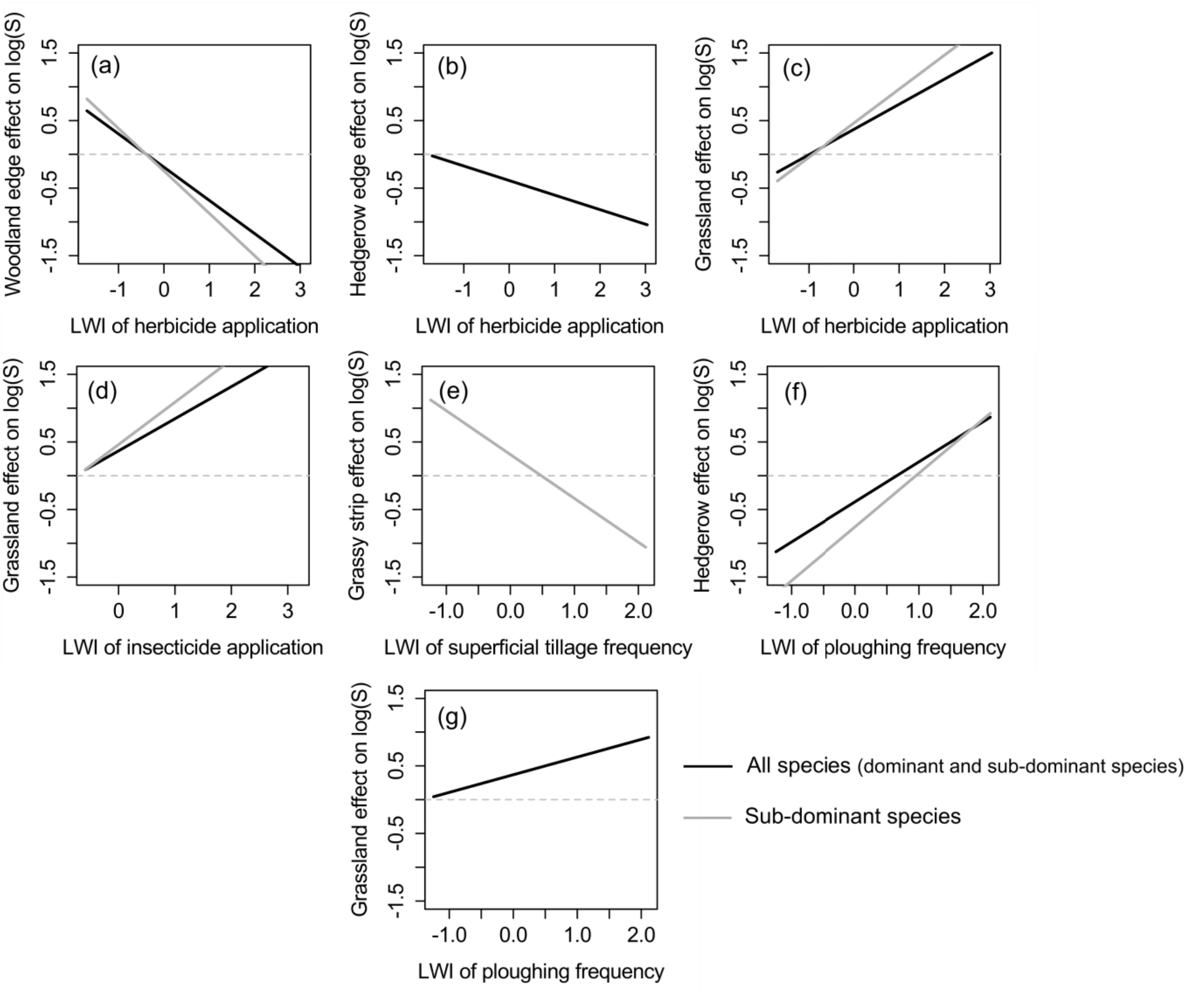

Figure 4 Slopes of the effects of the proportions of semi-natural habitats on expected values of log-transformed species richness (y axis) depending on values of landscape-wide intensity of farming practices (x-axis). The y-axis is the slope of the poisson regression of species richness against SNH proportion (see equation 2). Only significant interactions from Tables 3 and 4 are displayed. a) Woodland edge area x Landscape-intensity of herbicide application; b) Hedgerow area x Landscape-intensity of herbicide application; c) Permanent grassland area x Landscape-intensity of herbicide application; d) Permanent grassland area x Landscape-intensity of insecticide application; e) Grassy strip area x Landscape-intensity of superficial tillage frequency; f) Hedgerow area x Landscape-intensity of ploughing frequency; g) Permanent grassland area x Landscape-intensity of ploughing frequency. All predictors were kept in a standardized form in the graphs. All species, black solid lines; only subdominant species, grey solid lines.

Only the effect of permanent grassland proportion on total wild bee abundance was modulated by LWI of practices (Table 2). The effect of grassland proportion on wild abundance was stronger as LWI of herbicide application and of ploughing frequency increased (Fig. 5c, 5f), however the effect of grassland proportion on total abundance was slightly negative for the lowest value of LWI of herbicide application (Fig. 5c). These trends were consistent with the ones found on wild bee species richness considering the same landscape variables (Fig. 4c, 4g).

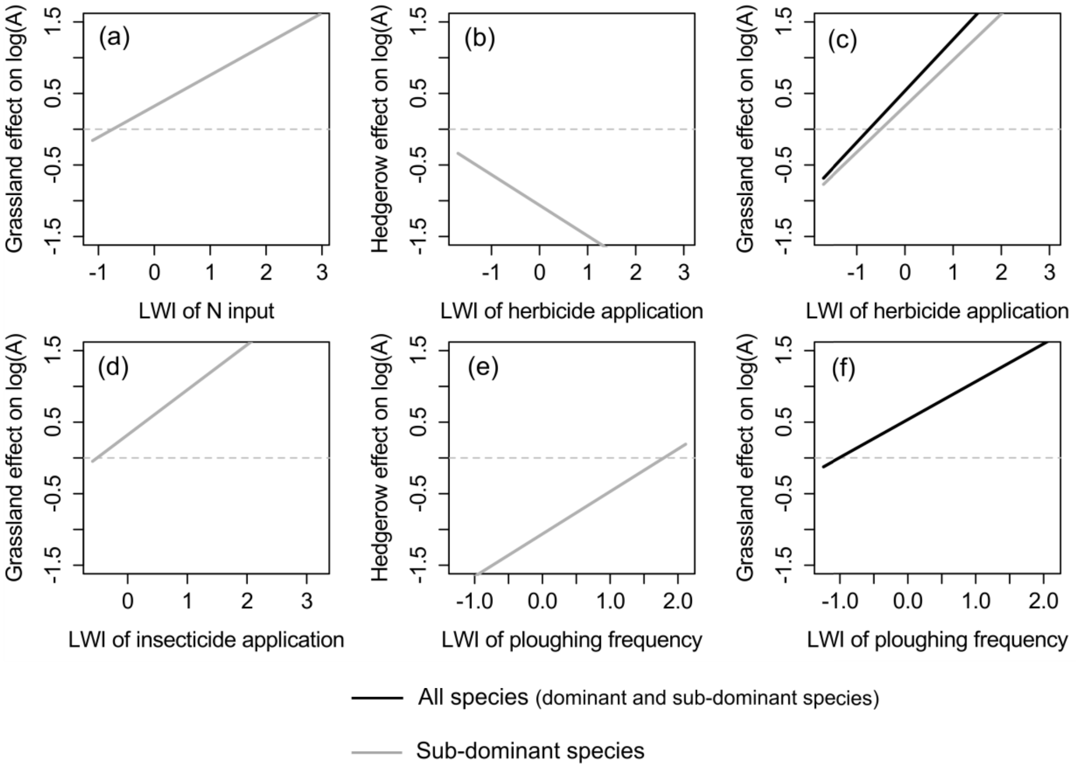

Figure 5 Slopes of the effects of the proportions of semi-natural habitats on expected values of log-transformed species abundance (y axis) depending on values of landscape-wide intensity of farming practices (x-axis). The y-axis is the slope of the poisson regression of species abundance against SNH proportion (see equation 2). Only significant interactions from Tables 3 and 4 are displayed. a) Permanent grassland area x Landscape-intensity of nitrogen input; b) Hedgerow area x Landscape-intensity of herbicide application; c) Permanent grassland area x Landscape-intensity of herbicide application; d) Permanent grassland area x Landscape-intensity of insecticide application; e) Hedgerow area x Landscape-intensity of ploughing frequency; f) Permanent grassland area x Landscape-intensity of ploughing frequency. All predictors were kept in a standardized form in the graphs. All species, black solid lines; only subdominant species, grey solid lines.

Interactive effect of landscape-wide intensity of farming practices and SNH on dominant and sub-dominant wild bee species

LWI of farming practices did not interacted with the proportions of SNHs to explain variations in species richness and abundance of dominant wild bee species (Table 3). After removing the interactions from the models to explore the principal effects, the only environmental variable that explained the variations in abundance and species richness was the proportion of woody SNH (Table 4, Fig. 6).

Table 4 Results of the generalized linear mixed models testing the effects of variables related to landscape-wide intensity of crop practices and SNH on the variations in wild bee species richness and abundance for dominant species. Only significant effects of landscape variables are displayed.

Response variable	R^2 (fixed effects)	Variable	Estimate	SE	P value
Species richness	0.20	Woodland_edge	0.14	0.05	0.008
		Hedgerow	0.12	0.05	0.016
Abundance	0.34	Woodland_edge	0.43	0.12	0.000

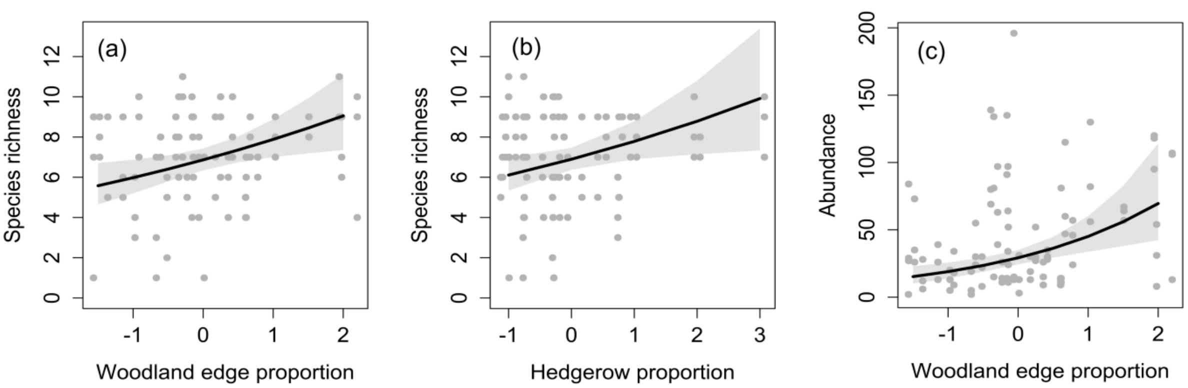

Figure 6 Response of species richness to woodland edge and hedgerow proportion (a, b) and of abundance to woodland edge proportion (c) of dominant bee species. Only significant relationships from Tables 5 are displayed. All predictors were kept in a standardized form in the graphs. Grey zones indicate 95% confidence envelopes.

Species richness of dominant species increased with increasing area of hedgerow and woodland edges (Fig. 6a, 6b) and their abundance increased with increasing woodland edge only (Fig. 6c), and to a larger extent than for species richness. However, several indices of LWI of farming practices interacted significantly with the proportions of SNHs of sub-dominant species. For the species richness of sub-dominant bee species, we nearly found the same interactive effects as for the models fitted on total wild bee richness (Table 2), except for the *grassland x ploughing* and *hedgerow x herbicide* interactions that disappeared for sub-dominant species and for the *grassy strips x superficial tillage* interaction that was only present for rare species. The common interactive effects between analyses on total wild bee species richness and species richness of sub-dominant species followed the same trends (Fig. 4). For the *grassy strips x superficial tillage* interaction, the proportion of grassy strips had a positive effect on species richness of sub-dominant species for low values of LWI of superficial tillage frequency, but had a negative effect for high values of this index (Fig. 4e). More indices of LWI of farming practices interacted with SNH to explain variation in abundance of sub-dominant species than total wild bee abundance (Table 2, 4). The effect of grassland proportion on sub-dominant bee abundance depended on LWI of nitrogen input, herbicide and insecticide application. The effect of hedgerow proportion depended on LWI of herbicide application and of ploughing frequency. When considering the slopes of the effect of the proportions of SNHs on abundance of sub-dominant species (Fig. 5), the same types of variations could be detected: a stronger and positive effect of the proportions of SNHs on abundance as LWI increased (*grassland x nitrogen, grassland x insecticide*, Fig. 6a, 6d); a negative effect of the proportions of SNHs whatever level of LWI (*hedgerow x herbicide, hedgerow x ploughing,* Fig. 5b, 5e); a change in the direction of SNH depending on LWI level (*grassland x herbicide,* Fig. 5c). This latter *grassland x herbicide* interaction, found for the total community abundance and for the abundance of rare species, followed the same trends than for the one found to explain variations in total species richness and species richness of sub-dominant species (Fig. 4c).

Discussion

In this study, we showed that the strength of the influence of the proportion of SNHs on farmland wild bee communities depended on the level of LWI of farming practices. Importantly, we found that even the most common bee species in the farmed area of the studied region relied on woody perennial elements but were less affected by the LWI of farming practices. In contrast, the patterns detected for the whole community, as well as for less common species, demonstrate a reliance on several SNH types and a stronger response to different components of landscape-wide farmland intensity.

Our hypothesis about the modulation of the positive effect of SNH proportions on wild bee species richness and abundance is validated. Indeed, we found i) that the strength of the positive effect of permanent grassland proportion on species richness of wild bees depended on the level of LWI of herbicide and insecticide application and of ploughing frequency and ii) for total wild bee abundance, that the positive effect of grassland proportion was only modulated by the LWI of herbicide application (Table 2). The intensity of herbicide application is detrimental to the abundance and diversity of weed species in cereal fields (Holzschuh et al., 2007; Marshall et al., 2006) and a change in the flower resources provided by weed species due to herbicide use affects the local species richness and abundance of wild bees (Holzschuh et al., 2007) as many weed species are used as nectar and pollen sources by bees (Biesmeijer et al., 2006; Bretagnolle and Gaba, 2015; Potts et al., 2010a; Westrich, 1996). Also, insecticide application has direct effects on wild bees via lethal or sub-lethal effects (Brittain and Potts, 2011; Desneux et al., 2007; Whitehorn et al., 2012) and is likely to cause local species extinctions. The intensity of soil tillage can have direct and indirect effects on wild bee species: the increase in tillage frequency is usually associated with a decrease in local weed species diversity (Murphy et al., 2006) and can also cause nest destruction or disturbance for ground-nesting bee species (Kim et al., 2006; Shuler et al., 2005; Williams et al., 2010).

Our results are consistent with other studies that found that a decrease in the global intensity of farming practices at the landscape scale, promoting flower resources in crop fields and limiting direct disturbances to species, positively influences the diversity and abundance of wild bees in crop fields (Holzschuh et al., 2008; Le Féon et al., 2010). However, here we found that local bee richness and abundance within cropped areas depended more on the proportion of grasslands in landscapes with intensively managed crop mosaic than in extensively managed ones. Moreover, this pattern was mainly explained by the variation in abundance and species richness of sub-dominant bee species in agricultural landscapes. This relationship suggests that permanent grasslands acted as population sources for sub-dominant farmland bees in the landscapes and that the strength of this source effect depended on the intensity of farming practices in the whole crop mosaic. Indeed, permanent grasslands are known to harbor a wide variety of wild bee species as they provide abundant nesting sites and long-lasting feeding resources (Hopfenmüller et al., 2014; Jauker et al., 2013; Öckinger and Smith, 2007) and because of their high carrying capacity, spill-over of individuals from the grasslands to the crop fields regularly occurs (Albrecht et al., 2007; Öckinger and Smith, 2007; Ricketts et al., 2008). The proportion of permanent grasslands did not have any effect on bee abundance and diversity for low values of LWI of herbicides, insecticides application and ploughing frequency as species might have found enough resources to complete their life cycles within the crop mosaic. Conversely, the variation in the proportion of permanent grasslands in landscapes with high chemical inputs was more important in determining observed species richness. For higher values of LWI of herbicides, insecticides application and ploughing frequency, permanent grasslands became more important in sustaining local species richness and abundance, suggesting that in intensively farmed landscapes, local farmland bee assemblages and abundance depended largely on species immigration from the surrounding permanent grasslands. Our results are thus consistent with previous studies that found that landscape complexity is more important in determining local species richness of wild bees in intensively than in extensively managed crop fields (Batáry et al., 2011; Holzschuh et al., 2007; Tuck et al., 2014), and support that this relationship might also be true when considering intensity of farming practices at the landscape scale.

However, other SNHs than permanent grasslands interacted differently with LWI of farming practices and showed opposite effect on local community structure depending on landscape-intensity levels. The proportion of woodland edges in the landscapes had positive effects on bee species richness for the lowest value of LWI of herbicides and this relationship was due to sub-dominant bee species (Fig. 4a). This suggests that these sub-dominant bee species, in cropped areas with low herbicide application tended to benefit from the resources found both in crop fields and woodland edges. Our hypothesis about the increased importance of landscape complexity in determining local bee species richness in extensively managed landscapes is thus validated. Indeed, woodland edges can provide nesting and feeding resources for farmland wild bees (Bailey et al., 2014). As a decrease in the use of herbicides may have increased the flowering resources within the crop mosaic (Holzschuh et al., 2007; Roschewitz et al., 2005a), wild bee species might have benefited from a landscape complementation effect between cropped areas and woodland edges. The same trend was observed with the proportion of hedgerows and the LWI of ploughing frequency (Fig. 5f). This phenomenon, in a context of low intensity of farming practices, was already observed for some butterfly and carabid species in modeling studies (Aviron et al., 2007; Vasseur et al., 2012). Indeed, extensively managed crop mosaics have been shown to increase the quality of crop fields as habitats for these species and allowed the populations to disperse through the landscapes (Vasseur et al., 2012). However, we found that linear elements such as woodland edges and hedgerows had increased negative effects on local bee abundance and species richness for increasing herbicide application. This relationship suggests that in highly sprayed landscapes, these elements exerted a barrier effects on farmland bees coming from permanent grasslands, which were population sources of bees for cropped areas in these landscape contexts.

Moreover, for low values of LWI of ploughing frequency, the proportion of hedgerows had a negative effect on species richness, suggesting again a barrier effect (Fig. 4f, inversion of the sign of the effect of hedgerow proportion depending on the LWI of ploughing frequency). But the opposite relationship emerged for higher proportions of ploughed fields in the landscapes with a positive role of the proportion of hedgerows on local bee species richness. As hedgerows can promote above and below-ground nesting species in agricultural landscapes by the provision of flower resources and nesting sites (Forrest et al., 2015; Kremen and M'Gonigle, 2015a; Morandin et al., 2007), these SNHs might have provided these critical resources in landscapes where crop fields could not offer them because of intense soil tillage (Kim et al., 2006; Shuler et al., 2005; Williams et al., 2010). Overall, our results suggest that hedgerows are sub-optimal habitats for farmland bees in the studied region, as they acted as barriers in resource-rich landscapes, but tended to be used as habitats in landscapes where the crop mosaic was intensively ploughed and was presumably devoid of feeding or nesting resources.

Our results also supported our hypothesis concerning the difference of sensitivity to farming practices according to the dominance of bee species. None of the indices of local or landscape-wide intensity of farming practices affected the abundance or species richness of dominant bee species at this scale of measurement (Table 4). Wild bees species respond differently to agricultural intensification depending on their traits (Williams et al., 2010). The dominant species we captured were dominated by polylectic species, which are known to be more tolerant to farming practices reducing floral resources in crop fields and adjacent field margins (Williams et al., 2010). All the dominant species were ground-nesters but were not affect by the intensity of soil tillage at the local and landscape level (Table 4), contrary to other studies (Kim et al., 2006; Shuler et al., 2005; Williams et al., 2010). However, these dominant species benefited from the proportion of wooded semi-natural habitats in the landscapes and may have thus found critical nesting sites and flower resources in these habitats (Bailey et al., 2014; Morandin and Kremen, 2013). Our findings on dominant bee species at this spatial scale are contradictory with the study of Kleijn et al. (2015), who found that the abundance of dominant crop-visiting bee species was not affected by the proportion of SNHs but could be enhanced by a local extensification of farming practices. The differences observed between our results and the ones from Kleijn et al. (2015) may arise from differences in the protocols. Indeed, the mass-flowering crops sampled by Kleijn et al. (2015) may have provided enough resources for dominant bee species irrespective of surrounding SNHs. On the contrary, we sampled bees in crop fields which provided flower resources only via the weed plant community and not by the crops themselves (Holzschuh et al., 2007). These differences may explain why the dominant bee species in our studied region depended on other habitats such as hedgerows and woodland edges to complete their life cycle, due to the relative scarcity of the weed flora in cereal fields compared to resources found in mass-flowering crops. Moreover, the dominant species in the study of Kleijn et al. (2015) and in the present one are not similar and might have emphasized the differences in the effect of habitat amount. Indeed, only five species out of the eleven dominant species we captured were in common with the European dominant crop visitors in the study of Kleijn et al. (2015), and there was no species from the *Bombus* genus in this study contrary to the Kleijn's one. Pan traps tend to under-sample large-bodied individuals (Westphal et al., 2008) and might explain the relative rarity of bumblebee species in the present study compared to the dataset of Kleijn et al. (2015) obtained with field observations. As a result, the dominant species in our dataset were smaller than the ones in Kleijn et al. (2015). and thus had a smaller foraging range (Greenleaf et al., 2007). Therefore, the two studies had dominant bee species differing in body size and ecological requirements and this might explain the stronger effect of semi-natural habitat amount in our study than in (Kleijn et al., 2015).

Conclusion

Our study suggests that the landscape-wide intensity of farming practices modulates the effect of landscape complexity on the species richness and abundance of sub-dominant farmland wild bees. Our results highlight the role of farming practices in the whole crop mosaic in shaping the local community structure of farmland bees and show that a low intensity of agricultural practices at a larger scale than the crop field could contribute to the conservation of farmland wild bee species. More specifically, a low level of farming intensity at the landscape level could buffer the negative effect of habitat loss on bee species richness and abundance but could also promote a positive complementary effect of semi-natural habitats and agroecosystems in promoting rich wild bee communities.

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Supplementary information

Table S1 Spearman rank correlations among landscape variables assessing landscape-wide intensity of agricultural practices and proportions of semi-natural habitats. Numbers in parentheses are the variance inflation factors (VIF) for each variable ($P<0.05$ *; $P<0.01$ **; $P<0.001$ ***).

	N.qty	Herbicide.local	Insecticide.local	Nb.sup	Nb.plough	N.landscape	Herbicide.landscape	Insecticide.landscape	superficial.landscape	plough.landscape	Grassy_edge	Hedgerow	Grassland	Woodland_edge
N.qty	(1.43)	0.18	0.33 **	0.04	-0.14	0.47 ***	0.1	0.25 *	-0.06	0.01	0.13	-0.23 *	-0.03	0
Herbicide.local		(2.18)	0.29 **	0.07	-0.22 *	0.01	0.52 ***	0.21 *	0.07	-0.24 *	0.34 ***	-0.18	-0.39 ***	0
Insecticide.local			(1.51)	0.18	-0.02	0.16	0.26 *	0.57 ***	0.1	-0.13	0.08	-0.23 *	-0.23 *	0.12
Nb.sup				(1.58)	-0.39 ***	-0.16	-0.09	0.03	0.38 ***	-0.11	-0.02	0.05	0.03	0.29 **
Nb.plough					(1.55)	0.04	0.01	0.09	-0.08	0.44 ***	-0.1	-0.09	0.16	-0.1
N.landscape						(1.68)	-0.04	0.31 **	-0.03	-0.05	-0.07	-0.26 **	0.05	-0.01
Herbicide.landscape							(2.37)	0.29 **	0.01	-0.02	0.23 *	-0.24 *	-0.52 ***	-0.09
Insecticide.landscape								(2.51)	0.18	0.1	0.07	-0.29 **	-0.31 **	0.14
superficial.landscape									(1.65)	-0.11	-0.11	-0.06	-0.08	0.24 *
plough.landscape										(1.40)	-0.01	0.03	0.11	0.03
Grassy_edge											(1.53)	0.21 *	-0.31 **	-0.29 **
Hedgerow												(1.74)	0	-0.38 ***
Grassland													(1.48)	0.07
Woodland_edge														(1.70)

Appendix S1 Variance partitioning of wild bee species richness and abundance

We used a variance partitioning approach to determine the amount variance in abundance and species richness of wild bees explained by local and landscape-wide intensity of farming practices. As the effect of local and landscape-wide intensity of farming practices on local biodiversity was likely to interact with proportion of semi-natural habitats (SNH) in the landscapes, the partition of variance was conducted by separating the effect of local interactions (local intensity of farming practices x proportions of SNHs) from the landscape interactions (landscape-wide intensity of farming practices x proportions of SNHs). We fitted partial models (regressing abundance or species richness with only local interactions, only landscape interaction and both local and landscape interaction) and estimated the R^2 of fixed effects for each model using the *MuMIn* package (Nakagawa and Schielzeth, 2013). As generalized linear models with random factors were used to fit the models, the amount of unexplained variance is not known (Araújo et al., 2014). The pure effect of local interaction variables was calculated as $R^2_{pure.local} = 1 – R^2_{landscape}$. The pure effect of landscape interaction variables was calculated as $R^2_{pure.landscape} = 1 – R^2_{local}$ and the shared effect of local and landscape interactions was calculated as $R^2_{shared.local.landscape} = 1 – R^2_{pure.local} – R^2_{pure.landscape}$. We used the package *modEvA* for the variance partitioning.

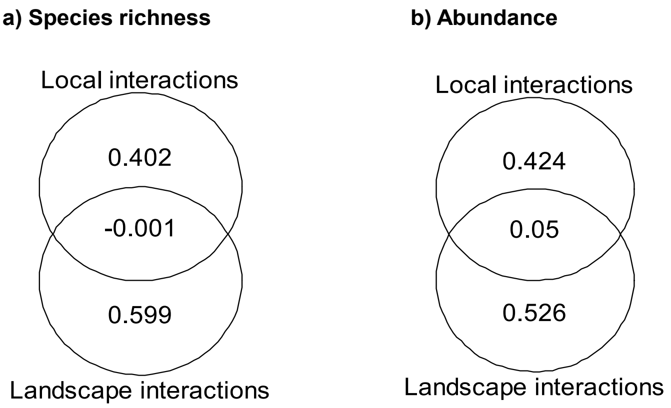

Figure S1 Variance partitioning of wild bee (a) species richness and (b) abundance. The values on the graphs are the percentage of variance explained exclusively by interactive effects of local farming intensity and the proportions of SNHs (local interactions), by the interactive effects of landscape-wide farming intensity and the proportions of SNHs (landscape interactions) and the shared variance explained simultaneously by the two factors.

Chapter 4: Bee diversity in crop mosaic is affected by remotely-sensed nesting resources in surrounding permanent grasslands

Article en préparation

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Abstract

Landscape heterogeneity is an important driver of biodiversity in agroecosystems. However, the functional heterogeneity of agricultural landscapes, taking into account the different resources that habitat patches can provide to species, has rarely been studied. In this study, we explored the effect of landscape-scale nest availability provided by permanent grasslands on wild bee communities captured in cereal fields. Wild bees were sampled in 44 cereal fields in south-western France along differing in the surrounding proportion of permanent grasslands. We assessed the availability of ground-nesting resources by assessing the slopes and the proportion of sparse vegetation in permanent grasslands, derived from remote sensing data. We found that both surrogates of ground-nesting resources affected the abundance of wild bees in cereal fields, and that this influence depended on bee traits. Below-ground nesting bees, with high dispersal capacities were positively affected by the proportion of sparse vegetation and high slopes in surrounding grasslands. Other ground-nesting species, with specialized flower requirements, were also positively affected by the two surrogates of nesting resources. Our results suggest that landscape-scale availability of nesting resources provided by grasslands affect bee communities in agricultural landscapes and can help to sustain functionally diverse bee assemblages. By using simple remote sensing tools, this study highlights the importance of considering nesting resources in agricultural landscapes to conserve wild bees in farmlands.

Keywords: Wild bees, ground nests, permanent grasslands, agricultural landscapes.

Introduction

Wild bees are key providers of pollination services (Garibaldi et al., 2013; Klein et al., 2007) and the conservation of diverse wild bee assemblages in agroecosystems is therefore a critical issue. However wild bees are threatened throughout western countries, due to the degradation and loss of habitats (Biesmeijer et al., 2006; Potts et al., 2010a). To reverse this decline, new strategies based upon habitat management in agricultural landscapes are needed (Kremen, 2005a; Kremen et al., 2007a).

Among the habitats in agricultural landscapes that wild bees can benefit from, permanent grasslands are of major importance (Gámez-Virués et al., 2015; Jauker et al., 2013; Steffan-Dewenter et al., 2001). At the local scale, the quality of grasslands can influence bee assemblages (Hopfenmüller et al., 2014) and local resource availability can be increased by changes in farming practices (Gámez-Virués et al., 2015). Moreover, the role of grasslands as a source of bee populations for crop mosaic in agricultural landscapes (Hopfenmüller et al., 2014; Steffan-Dewenter et al., 2002; Steffan-Dewenter and Tscharntke, 1999) suggest that a change in the resources they can provide would have important implications for wild bees visiting crop fields. These open and grassy permanent habitats can offer diverse flowering resources and below-ground nesting sites for wild bees (Hopfenmüller et al., 2014; Jauker et al., 2013; Ingolf Steffan-Dewenter and Tscharntke, 2000). Moreover, even if they are mowed or grazed, permanent grasslands can offer long-lasting flowering resources and zones of undisturbed grounds, contrary to annual crops (Gámez-Virués et al., 2015; Hopfenmüller et al., 2014; Rollin et al., 2013). Indeed, soil tillage in annual crops is known to have a negative impact on the nest density of below-ground nesters, due to nest destruction by agriculture machinery (Kim et al., 2006; Shuler et al., 2005). As the majority of wild bees are below-ground nesters (Danforth, 2007), nesting sites provided by permanent grasslands are of critical importance. Other traits than nest location (below-ground/above ground nests) could determine the response of wild bees to landscape-scale nesting resources. Indeed, as wild bees are central-place foragers, they need to have access to flowering resources within their foraging range (Westrich, 1996; Zurbuchen et al., 2010). Therefore grasslands providing nesting sites could promote ground-nesting bee species with specialized flower requirements (oligolectic ground nesters) in crop mosaic, by providing both flowering and nesting resources.

Habitat quality is often characterized locally in bee studies, in terms of nesting and flowering resources, and rarely assessed at the landscape scale (Holzschuh et al., 2007; Hopfenmüller et al., 2014; Kim et al., 2006). In landscape scale studies, all patches with the same cover type are considered equal in terms of resource provision, and the functional heterogeneity – heterogeneity based on the different uses of cover types by species – is ignored (Fahrig et al., 2011). There is therefore a substantial scope to determine the landscape-level effect of changes in the resources provided by permanent grasslands on farmland wild bees. The assessment of grassland nesting resources would help to understand the positive landscape-scale effect of permanent grasslands on the diversity of crop-visiting wild bees (Holzschuh et al., 2007; Morandin et al., 2007; Steffan-Dewenter and Tscharntke, 1999).

However the assessment of habitat quality on large spatial extent, by field surveys of farmer interview, is a time-consuming task. Remote sensing is a promising solution to have access this information on broad geographic extents (Kerr and Ostrovsky, 2003). For example, remotely sensed habitat diversity in agricultural landscapes, based on vegetation structure, was shown to effectively predict butterfly species richness (Kerr et al., 2001) and bird diversity (Sheeren et al., 2014). However, the ecological application of remote-sensing is only possible when an a priori knowledge of species habitat requirements is available. In the case of wild bees, steep slopes and areas of bare grounds can influence nest densities of below-ground nesters (Potts et al., 2005; Sardiñas and Kremen, 2014). Indeed, the area of exposed earth makes the nest excavation easier for below-ground nesters (Potts et al., 2010a) and steep slopes can increase solar radiation on south exposed slopes compared to flat grounds (Hopfenmüller et al., 2014; Potts and Willmer, 1997; Sardiñas and Kremen, 2014). Indeed, As these two types of ground configuration are easily detected using remote sensing (Kerr and Ostrovsky, 2003), such tools could be used to detect the occurrence of potential nesting sites for bee species on large spatial extents.

In this study, we aimed to determine if the availability of remotely-sensed nesting sites in permanent grasslands could effectively predict changes in the diversity of wild bees captured in crop fields. We expected that : i) the grassland quality in terms of nesting site availability could better predict changes in wild bee diversity than the total proportion of permanent grasslands; ii) effect of nesting resource availability on wild bees depend on species traits. We indeed expected that below-ground nesters, low dispersing species with specialized flower requirements would be more affected by nesting resource availability than other species.

Materials and methods

Study site and sampling design

This study was conducted in south-western France (Fig. 1a), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17’N, 0°54’E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al., 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

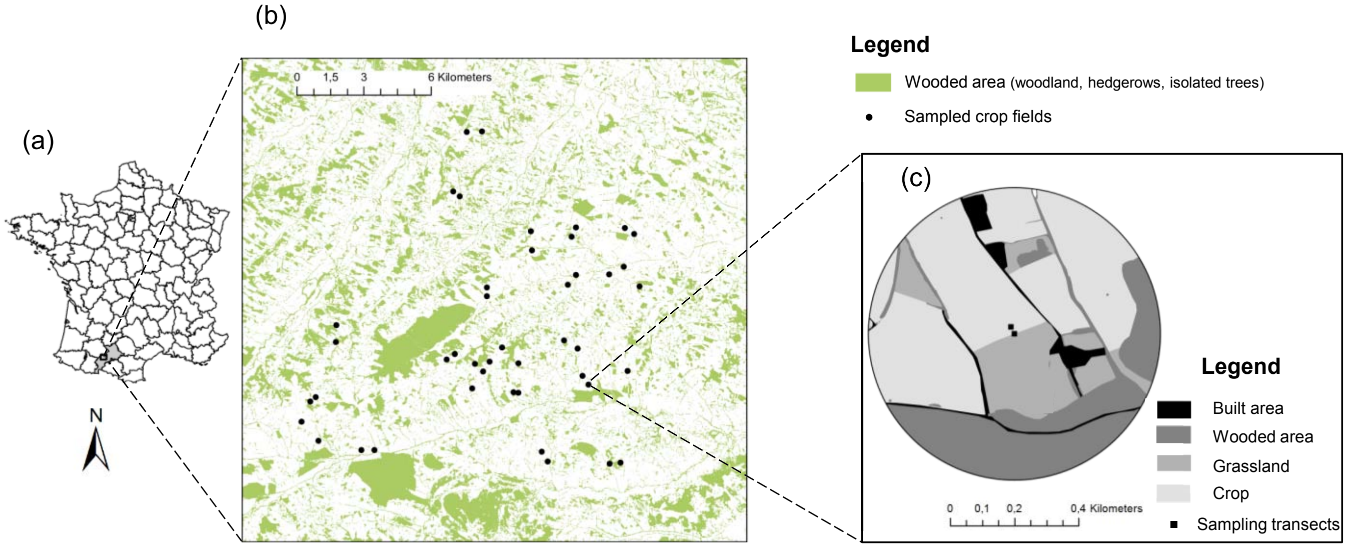


Figure 1 Maps showing (a) the location of the study area in south-western France, (b) the 44 sampled crop fields and (c) the location of the 2 sampling transects (3 traps per transect) within one sampled crop.

Within the studied region, we selected 44 cereal fields (29 in 2013 and 15 in 2014, consisting in wheat and barley fields, Fig. 1b) differing in the proportion of semi-natural habitats within a 500-m buffer centered on the field border (see the landscape characterization section), to cover independent gradients of woodland and permanent grassland proportions (0-3% of woodland edges, 0-42% of grassland proportion). Preselection of sampling sites was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). As some of the sampling sites were from another sampling procedure, some sampling sites were paired and sites from a pair were at least 200 m apart. In each field (hereafter sampling site), the sampling points were located near a field border that had a grassy margin, at least 100 m from a non-cropped area (woodland or built area, Fig. 1c). In each sampling site, we established four sampling points: two on the field border transect, 50 cm inside the field and 25 m apart from each other, and two on the field interior transect, 25 m inside the field and parallel to the first transect (Fig. 1c). We sampled bees with six pan traps per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of four poles (one pole per sampling point), one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint, SparVar® Germany) and each pole had two different colors. The location of the trap colors was the same for each sampling site. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension. The poles were designed such that the height was adjustable to the crop canopy (10 to 120 cm). The traps were placed during two periods of 3 or 4 days per sampling site. The two sampling periods were from 22 April to 24 May and from 27 May to 21 June in 2013, and from 17 April to 12 May and from 22 May to 16 June in 2014. Wild bee individuals (solitary and social species) were identified to species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than a direct effect of landscape structure. We also excluded cleptoparasitic bees because they do not provide pollination services. The number of individuals and the number of species determined for each sampling site represented the sum of all traps from the two sampling periods conducted in that site.

Bee traits

Five ecological and life-history traits were chosen according to their implication in the response of wild bees to environmental changes and because of their availability in the literature (Table 1): body size (measured as inter-tegular distance or ITD), sociality, nest location, diet breadth, and emergence date (Williams et al. 2010; Forrest et al. 2015; Kremen and M'Gonigle 2015). Sources for trait information were the ALARM project database (Settele et al. 2005), Michener (2000), Gathmann and Tscharntke et al. (2002), Bommarco et al. (2010), Fortel et al. (2014) and Forrest et al. (2015). For body size values, when no data were available on a particular taxon, ITD was measured on at least five female individuals per taxon, and queens were used for eusocial species. Social bees were defined as species that live in colonies characterized by cooperative brood care, therefore including eusocial and primitively social species. Solitary bees were defined as species that care only for their own offspring. The beginning of the foraging season (or emergence date) was based on expert knowledge (David Genoud, pers. com.). We were able to obtain traits for 59 of 81 species in our data (representing 98.7% of the sampled individuals). The 22 species for which insufficient trait information was available were removed from the trait analysis.

Table 1 Ecological traits used in the analyses

Trait	Unit
Body size = Inter-tegular distance (ITD)	mm. Nominal form: very small (<1 mm, 4 sp.), small (1-1.5 mm, 14 sp.); medium (1.6-2 mm, 14 sp.); large (2.1-3mm, 15 sp.); very large (>3mm, 12 sp.)
Nest location	Nominal. Below-ground nesters (49 sp.); Above-ground nesters (7 sp.)
Diet breadth	Nominal. Oligolectic (9 sp.); Polylectic (47 sp.)
Sociality	Nominal. Social (23 sp.); Solitary (29 sp.)
Emergence date	Number of the start month (1-12). Nominal form: winter (Jan-Feb, 4 sp.); early spring (Mar, 11 sp.); late spring (Apr-May, 32 sp.); summer (Jun-Jul, 7 sp.).

Semi-natural habitats were mapped within 500-m buffers (hereafter landscapes) centered on the field border transect of each sampling site, using ArcGIS 10.2 (ESRI). Grassland boundaries were validated by ground surveys in July 2013, May 2014 and April 2015.

We isolated grassland polygons and we removed their margins by using inner buffers of 10 m, to avoid neighboring effects on the number of vegetation classes (extra classes due to the presence of hedgerows, woodland edges or shadows). We used a multispectral Pleiade satellite image (four bands: blue, green, red and near infrared) with a spatial resolution of 2x2 m (one pixel = 2x2 m on the ground) taken at the 12 October 2013, covering an area of 354 km². The use of an image taken during winter season allowed us to better detect zones of bare grounds. We performed a non-supervised classification on the multispectral image by only considering the grassland polygons, using Gaussian mixture models (Fraley and Raftery, 1998). To determine the best number of clusters, we used the BIC (Bayesian Information Criterion) using a two-step procedure. First, we performed the clustering with fixed number of clusters, from 4 to 24 clusters (hereafter called class). For each round of clustering, 25 random starts (model initialization) were performed, and the best result was chosen among the 25 runs (the best result was given by the lowest BIC). Second, to determine the best number of classes, a graph showing the BIC in relation to the number of classes was built (Fraley and Raftery, 1998). According to this graph, we retained 10 classes as there was a break in the slope for 10 clusters (Fig. 2).

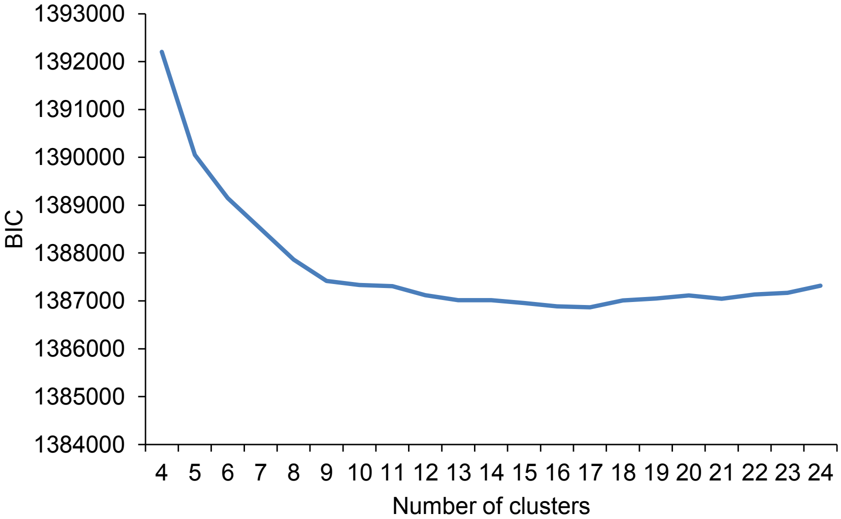
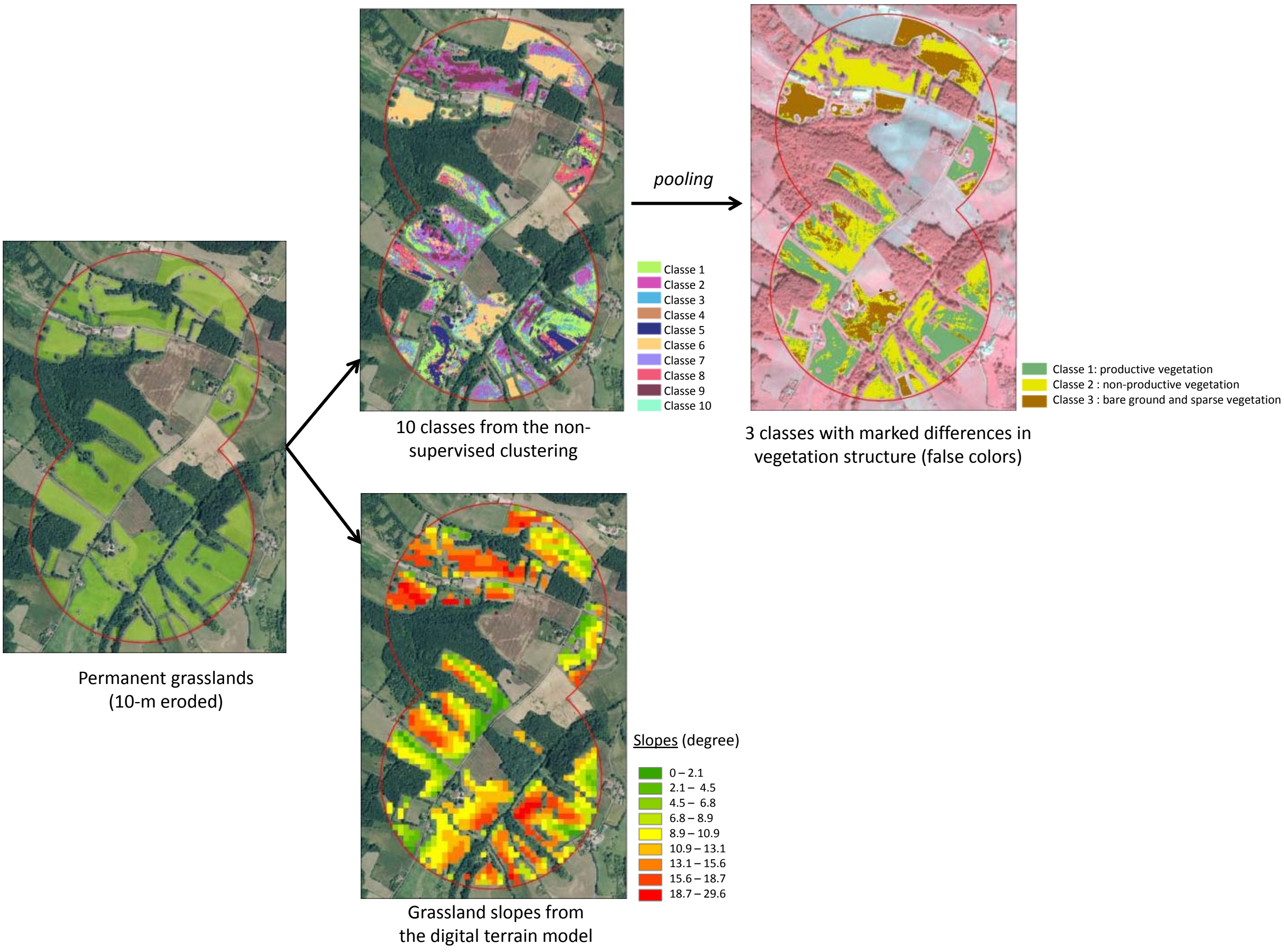


Figure 2 Bayesian information criterion (BIC) in relation to the number of clusters in the Gaussian mixture models. The best clustering is given by the lowest BIC. To avoid overfitting (too many classes), we chose the first inflexion point in the BIC variation, reached for 10 classes.

Many of these different vegetation classes were associated along the gradient of grassland proportion (Table S1) and were difficult to interpret in terms of bee habitats. We therefore decided to pool some classes to decorrelate their occurrence along the landscape gradient and to better describe vegetation patches differing in structure (Fig. 3). Using the false colors of the Pleida image, the 10 classes were gathered into 3 new classes that differentiated patches of productive, unproductive and bare ground/sparse vegetation (Fig. S2), based on typical spectral signatures (red = productive vegetation, usually reflects in the near infrared ; blue-green = very low vegetation cover, reflects , Kerr and Ostrovsky, 2003). Then, the proportions of these three classes were calculated at the landscape scale for the 44 landscapes (Table 2).

Grassland slopes were extracted from a digital terrain model provided by IGN (BD ALTI®), with a 25x25 m resolution (Fig. 3). We then calculated the mean slopes of grasslands at the landscape scale to have a second surrogate of grassland nesting resources (Table 2).



10 classes from the non-supervised clustering

3 classes with marked differences in vegetation structure (false colors)

Permanent grasslands (10-m eroded)

Grassland slopes from the digital terrain model

Figure 3 Principal steps of the classification procedure to obtain data on grassland vegetation structure and grassland slope. Grassland polygons were 10-m eroded to avoid any border effect. To obtain data on grassland vegetation structure, a non-supervised clustering was performed on the Pleiade images. According to the BIC criterion, 10 classes were retained. However, many classes had correlated occurrences across the landscape gradient and were very similar in terms of vegetation structure. To gather associated and similar classes, we pooled them based on their correlation coefficient and on a visual inspection of Pleidade images using false colors (red = plant canopy, blue-green = very low vegetation cover, Kerr and Ostrovsky, 2003). To obtain data on grassland slopes, slopes were extracted from the digital terrain model and were averaged at the landscape scale.

Table 2 Description of landscape variables assessing the proportion of different grassland vegetation classes, mean slopes of grasslands and the proportion of woodland edges and permanent grasslands (n=44).

	Code	Variable (units)	Mean (min–max)
Remotely sensed variables at the landscape scale	*p_prod*	Proportion of class 1 (%) : productive vegetation	7.6 (0.07–27.9)
	p_unprod	Proportion of class 2 (%) : unproductive vegetation	5.9 (0.05–18.1)
	p_sparse	Proportion of class 3 (%) : bare ground to sparse vegetation	4.4 (0.005–15.8)
	mean_slope	Mean slope of grasslands at the landscape scale (degree)	7.8 (0.7–11.8)
Landscape composition variables	*p_wood_edge*	Proportion of woodland edges (%)	1.3 (0–3.1)
	p_grassland	Proportion of permanent grasslands (%)	15.8 (0.18–42)

Statistical analyses

All analyses were performed using R 3.0.2 (R Development Core Team 2011). To test the level of collinearity in our models, we calculated Spearman rank correlations, and the variance inflation factor (VIF) was computed for each variable (Table 3). Even though some variables were correlated (*p_prod* and *p_sparse*, r = 0.68, $P < 0.001$), the VIFs of all the variables were far below the threshold of 10 and all $|r| \leq 0.7$, indicating low collinearity in our models (Smith et al. 2009; Dormann et al. 2013). Thus, all the landscape variables were included in the same statistical models and were standardized to better assess their relative effects on the response variables.

Table 3 Spearman rank correlations among environmental variables describing the remotely sensed vegetation structure in grasslands (p_prod: productive vegetation, p_unprod: unproductive vegetation, p_sparse: bare ground/sparse vegetation), mean slope of grasslands (mean_slope) and the proportion of woodland edges (p_wood_edge) (n=44). Numbers in parentheses are the variance inflation factors for each variable (P<0.05 *; P<0.01 **; P<0.001 ***).

	p_prod	p_unprod	p_sparse	p_wood_edge	mean_slope
p_prod	(1.62)	0.58 ***	0.68 ***	0.05	-0.06
p_unprod		(2.86)	0.69 ***	0.31 *	0.58 ***
p_sparse			(2.30)	0.36 *	0.26
p_wood_edge				(1.55)	0.46 **
mean_slope					(2.35)

We first checked if the remotely-sensed nesting resources in grasslands were not correlated with the availability of flowering resources. Indeed, sparse vegetation could be composed of flower rich-patches due to competitive release. Using flowering plant surveys performed on a subset of remotely sensed grasslands, we calculated the correlation between flowering plant richness (including only insect-pollinated species) and habitat quality of grasslands in terms of nesting sites. We found no significant correlations between indicators of flowering resources and nesting resources in permanent grasslands (Table S3, Fig. S4). Therefore in this study, we characterized variations in the availability of remotely-sensed nesting resources independently of flowering resources.

To test the effect of the availability of grassland nesting resources on bee diversity and abundance, we used generalized linear mixed models (GLMM) assuming Poisson error distribution (log-link function) with the R *lme4* package. A landscape random factor was included in the models to account for a possible non-independency of paired sampling sites for species that forage over distances greater than 200 m (minimum distance between two sampling sites). We added a sampling site random factor nested into the landscape random factor to account for possible overdispersion in the data (Lee and Nelder 2000). Fixed factors were the proportion of the different vegetation classes (p_prod: productive vegetation, p_unprod: unproductive vegetation, p_sparse: bare ground/sparse vegetation) and the mean slope of grasslands. We also added the proportion of woodland edges as fixed effect as this variable is known to influence bee diversity in crop fields (Bailey et al., 2014a; Garibaldi et al., 2011). Response variables were the total species richness and abundance of bees.

To test whether trait abundance distributions of wild bee communities shifted in response to the availability of landscape-scale nesting resources, we used the same structure of models (GLMM with log-link function). For each trait value, trait abundance was calculated by summing the abundances of all the species with this given trait value (Hopfenmüller et al., 2014). Fixed factors were the proportion of the different vegetation classes, mean slope of grasslands and the proportion of woodland edges. Response variables were the abundance of bees within a given trait category (oligolectic/polylectic, social/solitary, etc.). As some traits were continuous (body size and emergence date), we created trait categories (Table 2) to fit models for each type of category.

We then tested if the models taking into account landscape-scale quality of permanent grasslands ("resource-based" models, quantifying the cover of vegetation classes and mean grassland slopes) better predicted variations in bee diversity in crop mosaic than models taking only into account the proportion of permanent grasslands ("habitat-proportion based" models). To do so, for each response variable (total abundance/species richness or abundance per each trait category), we run new models that only took into account the proportion of permanent grasslands and woodland edges as explanatory variables (fitted with the same structure of random effects and the same link function). We then compared the R^2 of the "resource-based" models (called "R^2 nest" in the following tables) to R^2 of the "habitat-proportion based" models (called "R^2 habitat"). R^2 were calculated with the R *MuMIn* package.

Results

A total of 2605 individuals belonging to 81 species were sampled across the 44 sampling sites (Table S1).

The proportion of productive vegetation in permanent grasslands negatively affected wild bee species richness and abundance, but the other landscape variables were not correlated to wild bee community structure (Table 4, Fig 4).

Table 4 Results of the generalized linear mixed models testing the effects of the proportion of the three classes of vegetation structure in grasslands (p_prod: productive vegetation, p_unprod: unproductive vegetation, p_sparse: sparse vegetation), mean slope of grasslands and the proportion of woodland edges on species richness and abundance of wild bees. "R^2_{nest}" (coefficient of determination) are given for each model. "$R^2_{habitat}$" is the coefficient of determination for the models with the proportion of permanent grasslands and woodland edges as explanatory variables. Significant coefficients are in bold.

	Species richness					Abundance				
Predictor	Estimate	SE	P-value	R^2_{nest}	$R^2_{habitat}$	Estimate	SE	P-value	R^2_{nest}	$R^2_{habitat}$
p_prod	**-0.15**	**0.07**	**0.0437**	0.21	0.05	**-0.49**	**0.13**	**0.0002**	0.40	0.06
p_unprod	-0.02	0.09	0.8528			0.09	0.17	0.5971		
p_sparse	0.07	0.08	0.3992			0.15	0.15	0.3198		
mean_slope	0.10	0.09	0.2285			0.23	0.16	0.1475		
p_wood_edge	-0.02	0.06	0.7332			-0.15	0.12	0.2202		

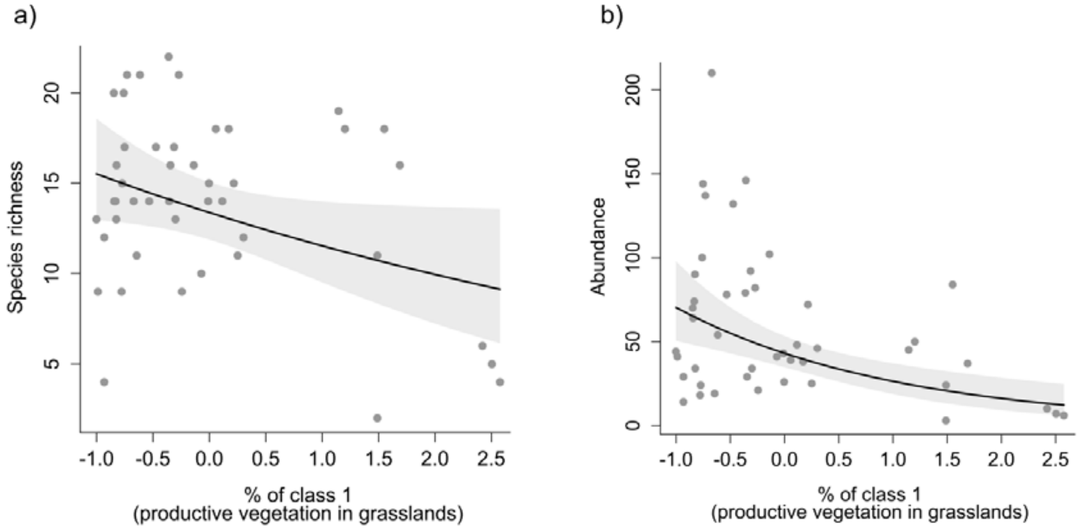


Figure 4 Effect of the proportion of productive vegetation in grasslands on species richness (a) and abundance (b) of wild bees. All predictors are shown in a standardized form in the graphs.

Mean slope of grasslands had a positive effect on the abundance of large bees, solitary bees and oligolectic species but did not affect the abundance of other traits (Table 5, Fig. 5a & Fig. 6c). Wild bee species significantly differed in their response to variations in the vegetation structure of permanent grasslands depending of their traits (Table 5). Overall, the abundances of nearly all traits were negatively affected by the proportion of productive grassland vegetation (p_prod), except for oligolectic bees, large bees, solitary bees or above-ground nesting species. The proportion of sparse vegetation had a positive effect on the abundance of very small species or large-bodied species and on the abundance of oligolectic species. Oligolectic bees, very small bees and large bees were the most affected by the different grassland descriptors (Table 5). The factor that most positively influenced the abundance of oligolectic bees and very small-bodied bees was the proportion of sparse vegetation in grasslands (Table 5, Fig. 5c, Fig. 6b), and it was the mean slope of grasslands for large species (Table 5, Fig. 6c).

The proportion of woodland edges in the landscapes had a positive effect on the abundance of species emerging in early spring, but negatively influenced the abundance of oligolectic bees and large-bodied bees (Table 5).

Table 5 Results of the generalized linear mixed models testing the effects of the proportion of the three classes of vegetation structure in grasslands (p_prod: productive vegetation, p_unprod: unproductive vegetation, p_sparse: sparse vegetation) mean slope of grasslands and the proportion of woodland edges on the abundance of species traits. A model was fitted for each trait value and this table only displays significant coefficients in the full models. "R^2_{nest}" (coefficient of determination) are given for each model. "$R^2_{habitat}$" is the coefficient of determination for the models with the proportion of permanent grasslands and woodland edges as explanatory variables. Significant coefficients are in bold.

Trait	Trait value	Predictor	Estimate	SE	P-value	R^2_{nest}	$R^2_{habitat}$
body size	*very_small*	p_prod	-0.62	0.23	0.0066	0.32	0.06
		p_sparse	0.67	0.23	0.0035		
	small	p_prod	-0.54	0.23	0.0184	0.23	0.07
	medium	p_prod	-0.48	0.22	0.0275	0.17	0.01
	large	p_sparse	0.36	0.12	0.0020	0.51	0.03
		mean_slope	0.68	0.14	0.0000		
		p_wood_edge	-0.34	0.09	0.0002		
	very_large	-	-	-	-	-	-
nest location	*above-ground*	-	-	-	-	-	-
	below-ground	p_prod	-0.52	0.13	0.0001	0.42	0.06
sociality	*social*	p_prod	-0.58	0.15	0.0001	0.42	0.06
	solitary	mean_slope	0.51	0.18	0.0051	0.33	0.06
diet breadth	*oligolectic*	mean_slope	0.78	0.31	0.0120	0.39	0.08
		p_unprod	-0.96	0.38	0.0117		
		p_sparse	1.14	0.32	0.0003		
		p_wood_edge	-0.86	0.27	0.0014		
	polylectic	p_prod	-0.58	0.15	0.0001	0.43	0.07
emergence date	*early_spring*	p_wood_edge	0.36	0.16	0.0288	0.29	0.10
	late_spring	p_prod	-0.33	0.15	0.0275	0.25	0.10
	summer	-	-	-	-	-	-

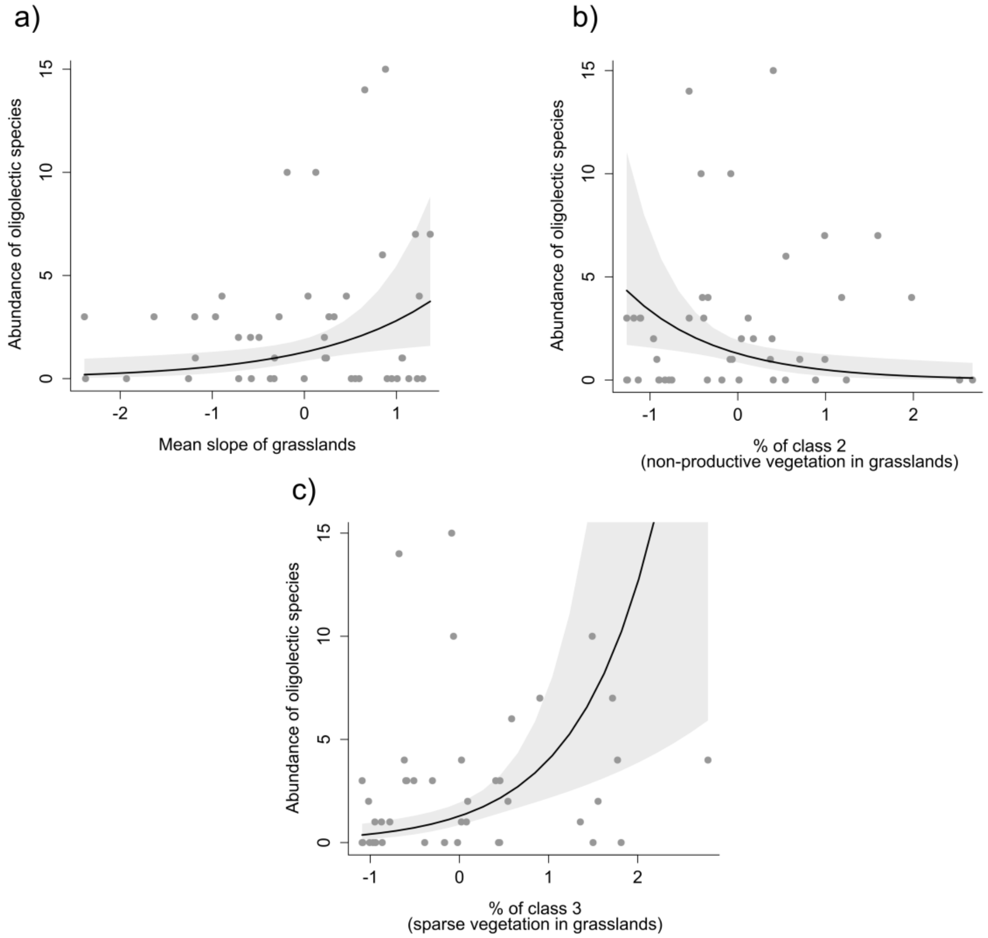


Figure 5 Effect of the mean slope of grasslands (a), proportion of non-productive vegetation (b) and sparse vegetation (c) in grasslands on the abundance of oligolectic species. All predictors are shown in a standardized form in the graphs.

Overall, landscape descriptors of grassland vegetation structure had a better predictive power of wild bee species richness or abundance than the models only taking the proportion of permanent grasslands into account (Tables 4 & 5).

When comparing models quantifying the changes in grassland vegetation structure to those accounting for changes in grassland proportion, R^2 were 4.2 and 6.7 times higher for models explaining variations in species richness and abundance respectively, and from 1.3 to 21 times higher for models explaining changes in trait abundances.

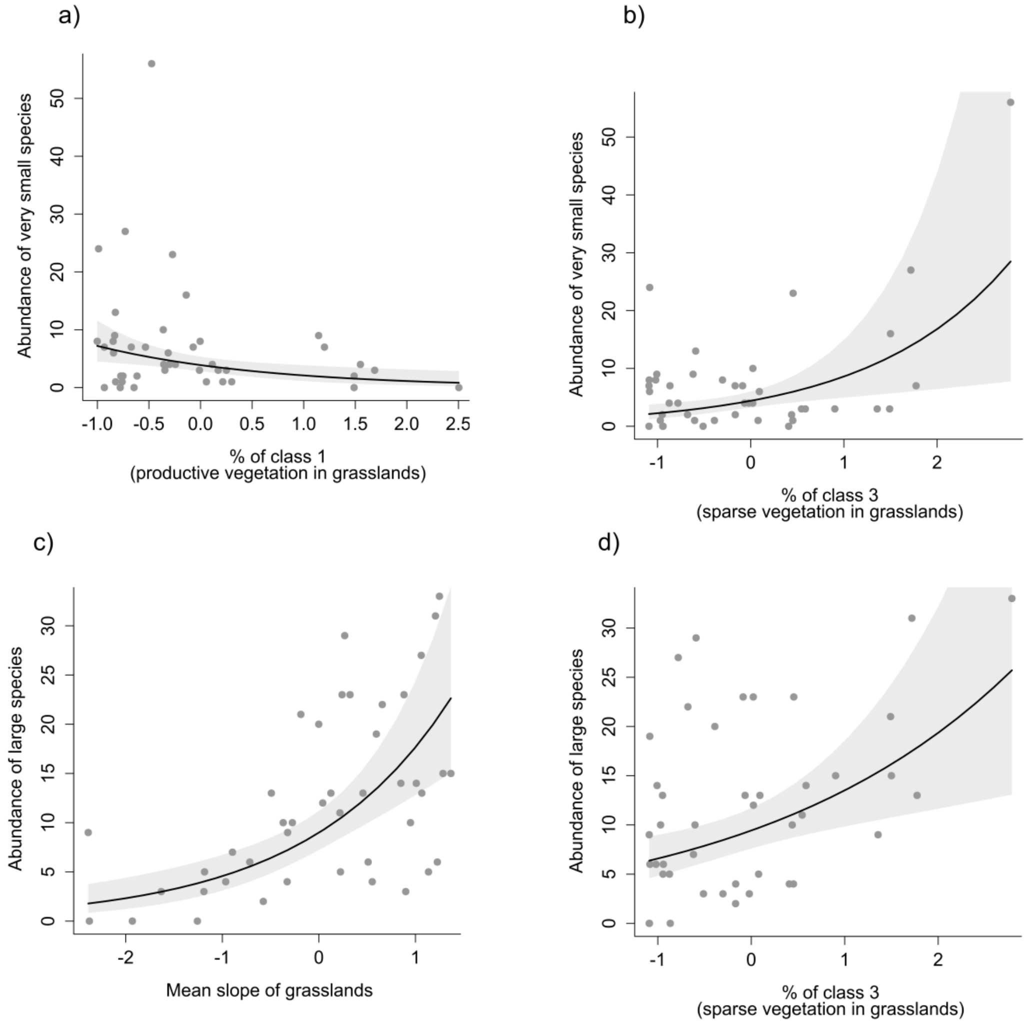


Figure 6 Effect of proportion of productive (a) and sparse vegetation (b) in grasslands on the abundance of very small-bodied species and of mean slope of grasslands (c) and proportion of sparse vegetation in grasslands (d) on the abundance of large-bodied species. All predictors are shown in a standardized form in the graphs.

Discussion

In this study, we investigated the effect of nesting resource availability provided by permanent grasslands on farmland wild bees. We used remote sensing to detect two types of ground characteristics in permanent grasslands (slope and areas of sparse vegetation) that are known to affect nest densities of below-ground nesters (Hopfenmüller et al., 2014; Potts et al., 2005; Sardiñas and Kremen, 2014). We showed that these two surrogates of nesting resources in grasslands, measured at the landscape scale, effectively influenced the abundance of wild bees in annual crop fields.

Our first hypothesis stating that the availability of landscape-scale nesting resources in grasslands could better predict wild bee abundance and species richness than the proportion of permanent grasslands was validated. Indeed, we found that models measuring the impact of remotely-sensed nesting resources in grasslands ("resource-based" models) performed better than models measuring the effects of grassland proportion ("habitat proportion-based" models). The goodness of fit of "resource-based" models compared to "habitat proportion-based" models was 6.7 times higher in average. Our results confirm the benefit of considering the functional heterogeneity of agricultural landscapes, by defining the resources species can benefit from in habitat patches that are usually considered as equivalent (Fahrig et al., 2011). By using simple remote sensing tools, we had access to the vegetation structure and ground topography of permanent grasslands on large spatial extents (5,000,000 m² of grasslands) with a relatively high precision. Such an amount of data, necessary to conduct landscape-scale studies of functional heterogeneity, would have been extremely time-consuming to obtain using ground surveys.

Our study also confirms that an increase in the amount of grasslands in landscapes is not a synonym of increased resource availability (Roulston and Goodell, 2011). Indeed, we found that productive vegetation patches of grasslands had a negative effect on the abundance of many species groups. These patches, probably made of productive graminoids (such as rye grass (*Lollium sp.*) or cocksfoot grasses (*Dactylis glomerata*)), may have negatively affected bee abundance because they were devoid of flower resources due to high grazing, high fertilisation and/or mowing frequencies (Gámez-Virués et al., 2015). The variability in the vegetation structure and topography among different grasslands presumably explained the poor effect of the amount of permanent grasslands *per se* on wild bee communities.

Contrary to our expectation, we found that nest location alone did not determine the response of wild bee species to the availability of nesting sites (sparse vegetation or steep slopes) in permanent grasslands. However, other traits determined the response of wild bees to this landscape variable. Indeed, we found that oligolectic bees, solitary bees, very small and large-bodied species were favored by the high availability in nesting sites surrounding crop fields, whereas other traits did not respond to this landscape variable. However, all these species were ground-nesting species (Table S5), suggesting that it was a combination of trait values which was decisive in the response of wild bees to the availability of grassland nesting sites, and not nest location *per se* (below-ground/above-ground nest). Body size, sociality and diet specialization were not correlated among species (Table S6), suggesting that these traits influenced the response of species to nest availability independently of each other.

Large ground-nesting bees were the most affected species by the availability of nesting resources in permanent grasslands (R^2=0.51, Table 5). Large-bodied species are long-distance foragers (Greenleaf et al., 2007) and thus can easily move between habitat patches in agricultural landscapes (Bommarco et al., 2010; Zurbuchen et al., 2010). The substantial effect of nest availability on long-distance foragers suggests that nesting and foraging resources they used were spatially segregated in the studied landscapes and that large species used several habitats (including grasslands) in a complementary way (Dunning et al., 1992). This complementation effect may also have happened for oligolectic ground-nesting species, which have good dispersal abilities (medium to large-bodied species, Table S5). Oligolectic bees are known to be more sensitive to the local loss of herbaceous habitats than polylectic bees due to their high floral requirements (Hopfenmüller et al., 2014; Steffan-Dewenter et al., 2006). Here, our result suggests that, in addition to floral resources, the landscape-scale availability of ground-nesting sites can also affect oligolectic species.

We found that the availability of grassland nesting sites positively affected the occurrence of small ground-nesting species in crop fields. As short-dispersers need to have their nests and foraging resources in a close distance (Zurbuchen et al., 2010), increasing the availability of nesting sites could decrease the isolation between bee nests and crop fields and thus could lead to higher crop visitations (Garibaldi et al., 2011).

Other species of ground-nesting bees (medium-sized polylectic species for example) did not respond to the availability of nesting sites provided by permanent grassland in our dataset. Other semi-natural habitats, such as woodland edges, hedgerows or ditches, containing undisturbed areas of bare grounds, may have provided nesting sites for these species (Bailey et al., 2014; Kremen and M'Gonigle, 2015b; Morandin and Kremen, 2013).

Conclusion

Our study provides the evidence that simple remote-sensing tools can be used better characterize the effect of habitat quality on wild bees in agricultural landscapes. The local availability of nesting resources is known to affect bee community structure (Potts et al., 2005; Sardiñas and Kremen, 2014) but due to their dispersal capacities, local resource depletion does not necessarily indicates resource limitation for wild bee populations (Roulston and Goodell, 2011). Our results suggest that the availability of nesting resources at the landscape scale can also structure bee communities in crop fields. Indeed, we found that crop fields surrounded by few nesting resources had low abundances of large-bodied bees and oligolectic bees compared to other species, suggesting that a loss in these resources can potentially homogenize local bee assemblages. This functional homogenization has the potential to alter ecosystem functions in agroecosystems (Albrecht et al., 2012; Hoehn et al., 2008; Martins et al., 2015). It is therefore necessary to consider the availability of nesting resources in agricultural landscapes, in addition to the usual focus on flower resources, for the management of wild bee communities.

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Supplementary information

Table S1 Spearman rank correlations among the landscape proportions of the 10 classes of vegetation structure obtained from the non-supervised clustering. Correlation coefficient >0.7 are in red. The occurrence of many vegetation classes were highly correlated along the landscape gradient, which prevented us to included them as explanatory variables in a linear model (Zuur et al., 2010).

	c2	c3	c4	c5	c6	c7	c8	c9	c10
c1	0.36 *	**0.84 *****	0.36 *	**0.82 *****	0.58 ***	0.41 **	**0.79 *****	0.54 ***	0.47 **
c2		0.63 ***	0.61 ***	0.31 *	0.63 ***	0.35 *	0.52 ***	**0.84 *****	0.48 ***
c3			0.59 ***	**0.7 *****	**0.75 *****	0.41 **	**0.79 *****	**0.71 *****	0.54 ***
c4				0.49 ***	0.64 ***	0.32 *	0.56 ***	**0.74 *****	0.5 ***
c5					0.57 ***	0.33 *	**0.84 *****	0.59 ***	0.37 *
c6						0.56 ***	0.69 ***	0.68 ***	0.66 ***
c7							0.43 **	0.39 **	0.58 ***
c8								0.66 ***	0.66 ***
c9									0.44 **

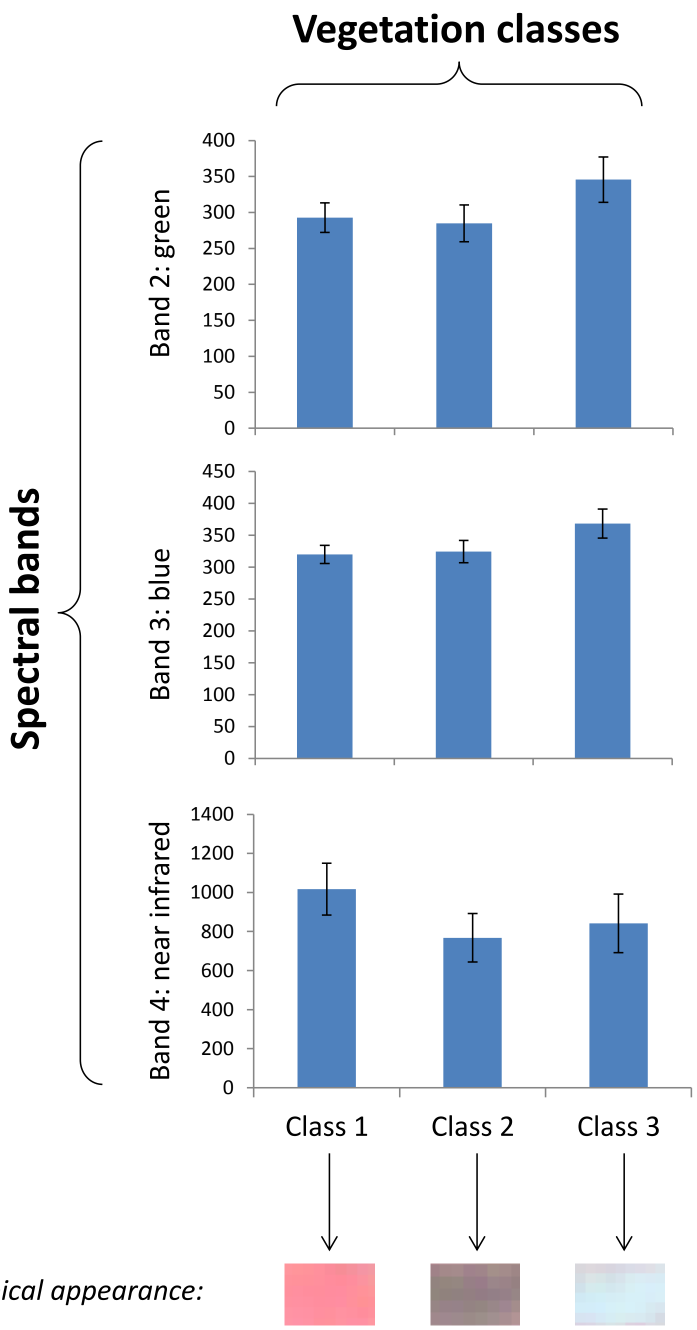

Figure S2 Spectral description of the three vegetation classes and their typical appearance in false colors. Class 1 reflects principally in the near infrared, which is typical of productive plant canopy (red in false colors). Class 3 reflects green and blue wavelengths and is typically associated with bare grounds and zones of bare vegetation (blue-green in false colors). Class 2 has the same spectral signature than the productive vegetation in the bands 2 and 3, but doesn't reflect much in the near infrared (grey-red in false colors). Class 2 is thus typical of vegetation patches that do not produce high levels of biomass.

Table S3 Spearman rank correlations between variables describing the availability of remotely sensed nesting resources (p_sparse: % of bare ground/sparse vegetation per grassland, mean slope of grassland) and the observed availability in flowering resources per grassland (n=63). Only mean slope and flower richness of grasslands were weakly correlated (Fig. S3), suggesting no relationship between remotely sensed nesting resources and flowering resources.

	mean_slope	flower richness	flower cover
p_sparse	0.2	0.02	-0.12
mean_slope		0.26 *	-0.06
flower richness			0.35 **

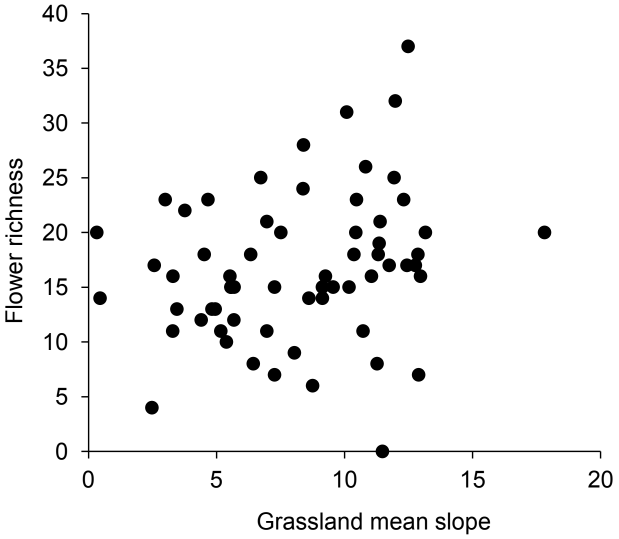

Figure S4 Association between mean slope and the species richness of flowering plants in grasslands (n=63). The weak correlation coefficient between these two parameters suggests that they were not associated across permanent grasslands in the studied region.

Table S5 Bee abundance and trait assignment per species (females only).

Species	Abundance	ITD	Coded ITD	Sociality	Nest location	Diet breadth	Emergence date
Andrena bucephala	2	2.15	large	solitary	below-ground	polylectic	april
Andrena distinguenda	1	1.68	medium	solitary	below-ground	oligolectic	february
Andrena flavipes	42	2.3	large	solitary	below-ground	polylectic	march
Andrena haemorrhoa	3	2.64	large	solitary	below-ground	polylectic	april
Andrena humilis	22	2.4	large	social	below-ground	oligolectic	april
Andrena lagopus	1	2.34	large	solitary	below-ground	oligolectic	march
Andrena nigroaenea	4	2.84	large	solitary	below-ground	polylectic	april
Andrena nigroolivacea	8	2.46	large	solitary	below-ground	oligolectic	march
Andrena ranunculi	1	1.75	medium	solitary	below-ground	oligolectic	march
Andrena ventricosa	2	1.63	medium	solitary	below-ground	oligolectic	april
Anthophora plumipes	1	4.3	very_large	solitary	below-ground	polylectic	march
Bombus hortorum	3	5.7	very_large	social	below-ground	polylectic	march
Bombus lapidarius	6	4.9	very_large	social	below-ground	polylectic	march
Bombus pratorum	2	4.6	very_large	social	below-ground	polylectic	february
Bombus ruderarius	4	4.73	very_large	social	above-ground	polylectic	april
Bombus sylvarum	6	4.44	very_large	social	above-ground	polylectic	may
Bombus terrestris	39	5.7	very_large	social	below-ground	polylectic	january
Ceratina cucurbitina	1	1.45	small	solitary	above-ground	polylectic	april
Eucera clypeata	14	2.75	large	solitary	below-ground	oligolectic	may
Eucera nigrescens	10	3.5	very_large	solitary	below-ground	oligolectic	may
Eucera nigrifacies	62	2.8	large	solitary	below-ground	oligolectic	june
Eucera taurica	2	3.6	very_large	NA	NA	NA	NA
Halictus maculatus	4	1.55	medium	social	below-ground	polylectic	april
Halictus patellatus	2	2.38	large	NA	below-ground	polylectic	july
Halictus quadricinctus	32	2.93	large	solitary	below-ground	polylectic	june
Halictus scabiosae	264	2.44	large	social	below-ground	polylectic	april
Halictus simplex	393	1.9	medium	social	below-ground	polylectic	april
Halictus smaragdulus	1	1.03	small	social	below-ground	polylectic	june
Halictus tumulorum	2	1.49	small	social	below-ground	polylectic	april
Lasioglossum albipes	2	1.64	medium	social	below-ground	polylectic	april
Lasioglossum corvinum	133	1.29	small	solitary	below-ground	polylectic	june
Lasioglossum crassepunctatum	1	1.41	small	NA	NA	NA	NA
Lasioglossum glabriusculum	73	0.73	very_small	social	below-ground	polylectic	may
Lasioglossum griseolum	2	0.93	very_small	NA	below-ground	polylectic	april
Lasioglossum interruptum	63	2.23	large	social	below-ground	polylectic	june
Lasioglossum laevigatum	6	1.84	medium	solitary	below-ground	polylectic	april
Lasioglossum lativentre	9	1.55	medium	solitary	below-ground	polylectic	april
Lasioglossum leucozonium	27	1.91	medium	solitary	below-ground	polylectic	april
Lasioglossum malachurum	305	1.79	medium	social	below-ground	polylectic	april
Lasioglossum marginatum	109	1.59	medium	social	below-ground	polylectic	march
Lasioglossum mesosclerum	1	1.31	small	NA	below-ground	polylectic	NA
Lasioglossum minutissimum	2	0.86	very_small	solitary	below-ground	polylectic	april

Lasioglossum morio	9	1.1	small	social	below-ground	polylectic	march
Lasioglossum nigripes	212	1.97	medium	social	below-ground	polylectic	june
Lasioglossum pallens	20	1.59	medium	solitary	below-ground	polylectic	april
Lasioglossum pauperatum	1	1.14	small	NA	NA	NA	NA
Lasioglossum pauxillum	69	1.24	small	social	below-ground	polylectic	april
Lasioglossum politum	229	0.82	very_small	social	below-ground	polylectic	april
Lasioglossum punctatissimum	9	1.23	small	solitary	below-ground	polylectic	april
Lasioglossum puncticolle	211	1.49	small	social	below-ground	polylectic	may
Lasioglossum subhirtum	1	1.2	small	NA	below-ground	polylectic	april
Lasioglossum tricinctum	5	1.25	small	solitary	below-ground	polylectic	NA
Lasioglossum villosulum	77	1.33	small	social	below-ground	polylectic	april
Lasioglossum xanthopus	2	2.37	large	solitary	below-ground	polylectic	april
Lasioglossum zonulum	43	1.95	medium	solitary	below-ground	polylectic	april
Osmia bicornis	8	3.1	very_large	solitary	above-ground	polylectic	march
Osmia rufohirta	4	2.53	large	solitary	above-ground	polylectic	april
Xylocopa iris	1	4.33	very_large	solitary	above-ground	polylectic	march
Xylocopa violacea	3	6.5	very_large	solitary	above-ground	polylectic	february

Table S6 Spearman rank correlations among species traits (n=59). For nominal traits, trait values were coded as 0 or 1 to allow for correlation calculation. Sociality: social=0, solitary=1; nest location: above-ground=1, below-ground=0; diet breadth: oligolectic=0, polylectic=1; (P<0.05 *; P<0.01 **).

	Sociality	Nest location	Diet breadth	Emergence date
Body size (ITD)	0.09	0.31 *	-0.01	-0.25 *
Sociality		0.16	-0.35 **	-0.17
Nest location			0.08	-0.18
Diet breadth				0.01

Partie C : Lien fonctionnel entre structure des communautés d'abeilles sauvages et pollinisation le long de gradients paysagers

Chapter 5: Combined effects of local farming intensity and habitat amount and fragmentation on wild bee diversity and pollination

Article en préparation

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Abstract

Understanding the influence of landscape heterogeneity and intensity of farming practices on the relationship between pollinators and pollination delivery is critical to maintain pollination services in agricultural landscapes. In this study, we investigated the relative effects of the proportion of semi-natural habitats and local intensity of farming practices on wild bee diversity and pollination delivery and we explored the occurrence of two stabilizing mechanisms – density compensation and response diversity – that could possibly buffer pollination delivery against bee species loss. We measured pollination success of potted petunia plants and bee community structure along independent gradients of local intensity of farming practices and habitat amount/fragmentation. We found a strong correlation between the abundance of dominant bee species and pollination success, suggesting that dominant bee species were the most functionally important species compared to sub-dominant ones. The abundance of dominant species was equally and negatively influenced by the local intensity of farming practices and loss/fragmentation of surrounding permanent grasslands, with no effect on pollination success. This unexpected absence of variation in pollination success along the environmental gradients was presumably due to the fact that dominant species were not impacted enough to cause pollination depletion. However, the absence of stabilizing mechanisms within dominant species suggest that further grassland fragmentation and intensification of farming practices could potentially endanger pollination services provided by wild bees.

Keywords: Pollination, wild bees, habitat loss and fragmentation, farming intensity, stabilizing mechanisms

Introduction

Understanding the relationship between biodiversity and ecosystem functioning is a standing issue in ecology (Hooper et al., 2005; Kremen, 2005a; Loreau et al., 2001). Insect-mediated pollination is a pivotal function in agroecosystems, which is mainly provided by wild bees (Garibaldi et al., 2013). By visiting cultivated and wild plants, they provide crop pollination services but also sustain other ecosystem services that rely on wild plant communities such as biological pest control (Kremen et al., 2007b; Memmott et al., 2004; Scherber et al., 2010). However, agricultural intensification, through the loss and fragmentation of semi-natural habitats and increase in the use of chemical inputs, has led to a dramatic decline in wild bee diversity (Biesmeijer et al., 2006; Potts et al., 2010a).

Wild bee diversity is affected by the amount and fragmentation of habitats and also by the intensity of farming practices (Batáry et al., 2011; Winfree et al., 2009). Indeed, an increase in the amount and proximity of semi-natural habitats such as woodland edges or permanent grasslands in the landscapes promote wild bee diversity by increasing the diversity and availability of critical resources but also promoting the dispersal of individuals though the landscape (Garibaldi et al., 2011; Winfree et al., 2009). The intensity of local farming practices also affects bee diversity: when compared to conventionally managed fields, organic fields are associated with a higher bee species richness and abundance (Batáry et al., 2011; Bengtsson et al., 2005) because they are less sprayed with insecticides and provide more diverse and abundant resources due to a reduced use of herbicides and fertilizers (Batáry et al., 2011; Bengtsson et al., 2005; Holzschuh et al., 2007; Roschewitz et al., 2005a). However, little is known about the relative effects of these two factors on pollination. The amount of semi-natural habitats is known to increase the pollination success of many cultivated and wild plants (Garibaldi et al., 2011; Steffan-Dewenter et al., 2001; Steffan-Dewenter and Tscharntke, 1999). Different types of semi-natural habitats such as woody or grassy permanent vegetation might have contrasting effects on wild bee species and pollination success depending on the resources they provide and on bee ecological requirements (Bailey et al., 2014a; Forrest et al., 2015; Hopfenmüller et al., 2014; Morandin et al., 2007) but their relative effects on wild bee communities and pollination services have been poorly investigated. Moreover, the effect of the intensity of crop management on pollination delivery by wild bees is still unclear as previous studies have found that an increase in farming intensity decreased (Andersson et al., 2012; Gabriel and Tscharntke, 2007; Kremen et al., 2002) or did not affect pollination success (C. Brittain et al., 2010; Kremen et al., 2004). In addition, little is known about the underlying functional mechanisms linking bee diversity and pollination success across gradients of habitat amount, fragmentation and local land use intensity (Kremen et al., 2007b). Changes in pollination delivery along environmental gradients is not as sharp as changes in wild bee diversity (Garibaldi et al., 2011) suggesting that the diversity-pollination link in bee communities is complex. Indeed, ecological theory predicts that a decrease in diversity would not always lead to a decrease in a given function if stabilizing mechanisms occur in the community and buffer pollination delivery against bee species loss (Blüthgen and Klein, 2011; Loreau et al., 2001). For example, in case of density compensation, species loss could lead to a competitive release in communities, therefore other less competitive species may compensate for the loss of the competitors by increasing their density and the provision of the ecosystem function would fluctuate less (Kremen, 2005a; Tilman, 1996). Some empirical studies have found evidence for response diversity (Cariveau et al., 2016; Winfree and Kremen, 2009) – differential response to environmental changes among species contributing to the same function – but no density compensation along gradients of habitat amount in agricultural landscapes (Winfree and Kremen, 2009). But the actual implication of these mechanisms in stabilizing pollination along agricultural intensity gradients remains unclear (Cariveau et al., 2013; Winfree, 2013), as only few studies estimated pollination success along with changes in wild bee community structure (Cariveau et al., 2013). As only a subset of dominant bee species might provide the totality of pollination delivery in bee communities in some cases (Kleijn et al., 2015; Winfree et al., 2015), these stabilizing mechanisms may only hold for dominant species in agroecosystems. But dominant and sub-dominant species respond to different environmental factors (Kleijn et al., 2015), therefore the factors affecting bee species richness in agricultural landscapes might not be relevant to explain variations in pollination success in this case. As real-world communities have strong dominance (McGill et al., 2007) and as species usually contribute to a function depending on their abundance (mass ratio hypothesis, Grime, 1998), testing if the environment-pollinator-pollination relationship differs depending on dominance status deserves consideration.

The aim of this study was to explore the combined effects of habitat amount, fragmentation and local intensity of farming practices on bee diversity and pollination success and to test for the occurrence of two stabilizing mechanism – density compensation and response diversity – that could buffer pollination delivery against environmental changes. We also tested if the functionally important species were the dominant bee species in the community and if they responded differently to the environmental gradients compared to sub-dominant species.

We expected that i) local intensity of farming practices would decrease bee diversity and pollination success to the same rate as habitat loss and fragmentation, ii) pollination success would be positively correlated with bee diversity, iii) the most functionally important bee species would be the dominant ones, iv) response diversity but not density compensation would buffer pollination success against bee diversity changes along the gradient of habitat amount/fragmentation and local intensity of farming practices.

Materials and methods

Study site and sampling design

This study was conducted in south-western France (Fig. 1), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17'N, 0°54'E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al., 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5◦C; mean annual precipitation, 750 mm).

We selected 40 cereal fields (winter wheat and barley) differing in the proportion of semi-natural habitats (woodlands and permanent grasslands) within a radius of 500 m centered on the sampling point (see the landscape characterization section). Preselection of cereal fields (hereafter sampling site) was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). As some of the sampling sites were from another sampling procedure, sampling sites were paired and sites from a pair were at least 200 m apart. In each field sampling site, the sampling point was located in a grassy of a winter cereal field, at least 100 m from other non-cropped area (woodland or built area). One third of the cereal fields were organic fields, randomly chosen along the landscape gradients to try to avoid correlation between the amount of semi-natural habitat and local farming intensity as much as possible.

In each crop field, we established four sampling points: two 50 cm inside the field and 25 m apart from each other (field border transect), and two 25 m inside the field and parallel to the first two points (field interior transect). We sampled bees with six pan traps per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of four poles (one pole per sampling point), one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint, SparVar® Germany) and each pole had two different colors. The location of the trap colors was the same for each sampling site. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension. The poles were designed such that the height was adjustable to the crop canopy (10 to 120 cm). The traps were placed during two periods of 3 days per sampling site. The two sampling periods were from 17 April to 12 May and from 22 May to 16 June in 2014. The number of species and the number of individuals per species determined for each sampling site represented the sum of all traps from the two sampling periods conducted in that site. Wild bee individuals (solitary and social species) were identified to species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than a direct effect of landscape structure. We also excluded cleptoparasitic bees because they do not provide pollination services.

We experimentally assessed pollination success using potted plants placed in each sampling sites. Potted petunia plants were bought the 09 July 2014 and all open flowers – potentially already pollinated – were removed from the plants. Potted plants were placed under insect-proof tents inside a greenhouse before the exposition in the fields. The use of potted plants allowed for standardized growing conditions for all the plants. Even if petunia plants were already use to measure pollination success in previous studies (C. Brittain et al., 2010), we decided to test the degree of pollinator dependence by placing one bagged potted plant with insect-proof gauze (Climabio, Nortene®) per field, as petunia plants can be both self-incompatible and self-compatible (Tsukamoto et al., 2003). Each flower that had opened in the greenhouse was marked with waterproof tape a day before the field exposure. In each field, three potted plants – two unbagged pots with open flowers and one bagged pot – were placed next to the field border at the same location as the border sampling transect of bees, during a period of 3 days, from 18 July to 21 July 2014. The three potted plants were placed in plastic trays which were filled with one liter of water. After the field exposure, flowers that had opened in the field were marked and potted plants were stored again under insect-proof tents until the seed harvesting. Between the 18 and 21 August 2014, all the marked flowers were harvested. Pollination success was estimated using the mean number of seed per fruit (seed set) and the proportion of flowers that developed into fruits (fruit set) at the field level. As petunia fruits contained many small seeds, seed set was assessed for each fruit by weighing all the seeds and ten seeds chosen randomly. We combined the two types of flowers – that had opened in the greenhouse or in the field – to assess pollination success.

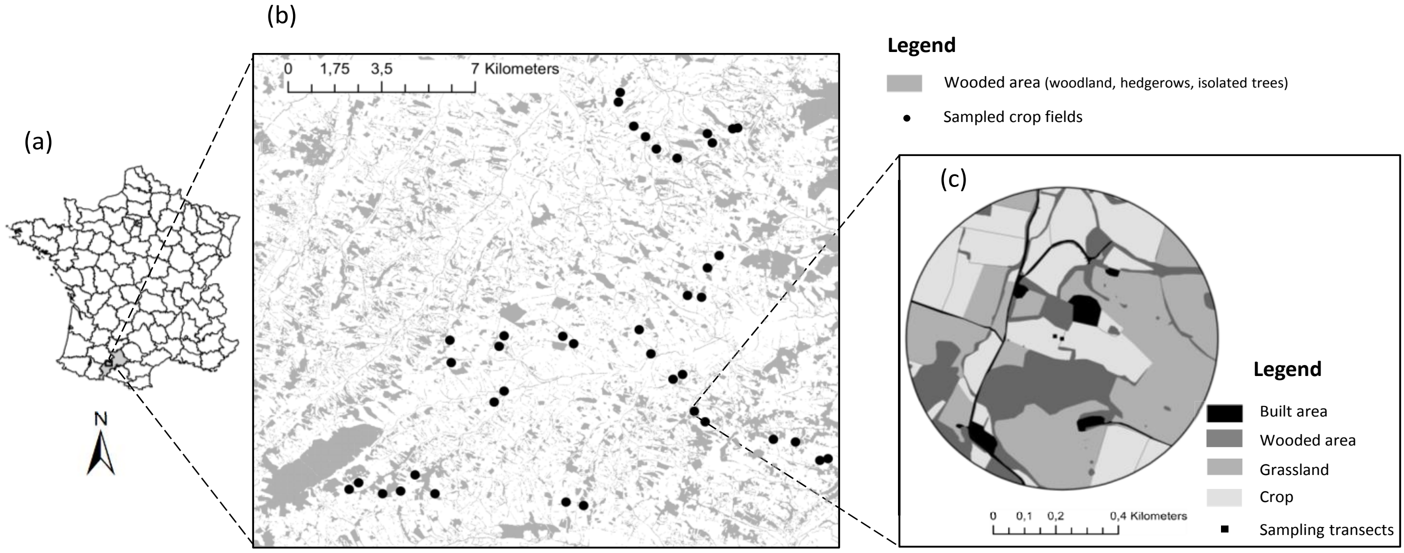

Figure 1 Maps showing (a) the study area, (b) the 40 sampled crop fields and (c) the location of the transects (three traps per transect) within a crop field in one of the 40 landscape sector.

Local and landscape variables

Landscape variables were calculated within a radius of 500 m centered on the field border transect in each site. This radius was chosen according to the results of previous studies on the functional scale of wild bees (Gathmann and Tscharntke, 2002; Holzschuh et al., 2010; Zurbuchen et al., 2010). Using aerial photographs (IGN, 2013) the different land covers (woodlands, hedgerows, permanent grasslands, crop fields and isolated trees) were digitalized using ArcGIS 10.2 (ESRI). Crop field and grassland boundaries were validated by ground surveys in May 2014 and April 2015.

Three habitats were considered as semi-natural: woodland edges, hedgerows and permanent grasslands. In each 500-m buffer (hereafter landscape), we calculated 6 variables measuring semi-natural habitat amount and fragmentation (Table 1) using ArcGIS 10.2 (ESRI). We calculated the proportion of permanent grasslands and the length of woodland edges and hedgerows as a measure of habitat amount and we computed, for each habitat type, a proximity index as a measure of isolation or fragmentation of habitat patches. To calculate this proximity index, we created buffers around each habitat patch as an approximation of the maximum foraging distance (100 m) of the least mobile species that we captured (Greenleaf et al., 2007). We then calculated the proximity index, which was the proportion of overlapping zones amongst all the landscapes (proximity index= area of buffer overlap / total buffer area) to measure the zones in the landscapes where movements between habitat patches were possible for the whole bee community.

Table 1 Description of environmental variables used to assess local intensity of farming practices, habitat amount and habitat fragmentation (n=40).

	Code	Variable (units)	Mean (min–max)
Local crop management	*LLUI*	Index of intensity of farming practices	21 (5–49)
Habitat amount	*hedge*	Length of hedgerows (m)	3,254 (1410–6,680)
	woodland_edge	Length of woodland edges (m)	2,295 (0–5,494)
	grassland	Permanent grassland area (m²)	128,572 (3,697–466,211)
Habitat fragmentation	*prox_hedge*	Proximity of hedgerows (%)	56 (28–85)
	prox_woodland_edge	Proximity of woodland edges (%)	13 (0–29)
	prox_grassland	Proximity of permanent grasslands (%)	23 (0–59)

Because of our sampling design, whereby the two crop fields were at least 200m apart, many of the landscape sectors overlapped each other. As a consequence, spatial autocorrelation of wild bee species richness and abundance was checked in the data. We found no evidence of spatial autocorrelation in the dataset (*Moran index species richness* = 0.07, $P = 0.09$, *abundance* = 0.07, $P = 0.11$).

Interviews were conducted with 26 farmers to obtain information about local management intensity for the 40 sampled crop fields. For each type of crop, we collected information on nitrogen input, herbicide and insecticide application intensity and tillage frequency. To calculate herbicide and insecticide application intensity, we asked farmers about the applied doses per hectare of arable area and the frequency of application. We then compared the applied doses of each chemical product to the maximum allowed doses by the French Ministry of Agriculture (E-phy 2015) and then calculated the ratio "applied dose/maximum allowed dose" to take into account dose-dependent effects on biodiversity. This ratio was then multiplied, for each crop type of each farmer, to the application frequency of the given chemical product. This index was then summed for each type of pesticide (herbicide and insecticide). To calculate the amount of nitrogen input, we asked the farmers about the frequency and the doses of mineral and organic fertilizers for the complete crop cycle and the amount of nitrogen was calculated using reference tables. The total tillage frequency was calculated by summing up the number of ploughing and superficial tillage interventions for the complete crop cycle. Following Herzog et al. (2006), we condensed these indicators of management intensity into one global indicator of local land-use intensity index (LLUI) using the formula (1).

$$LLUI = \frac{\sum_{i=1}^{n}(y_i - y_{max})/(y_{min} - y_{max})}{n} \times 100 \qquad (1)$$

Where LLUI is the overall local land-use intensity index, y_i is the observed value, y_{min} and y_{max} are the minimum and maximum observed values respectively and n is the number of individual indicators (in our case, n=4) (Herzog et al., 2006).

Statistical analyses

We calculated the associations among environmental variables using Spearman rank correlations (Table 2).

Our objective was to analyze the effect of joint effect of habitat amount and fragmentation on bee diversity and pollination success as these two landscapes variables are often correlated in real-world landscapes and have contrasting effects on biodiversity (Fahrig, 2003). Indeed, these two variables were correlated in our dataset for all the SNHs (Table 2), therefore we needed to create new integrative variables to describe both the amount and the fragmentation of SNHs. We used a principal component analysis (PCA) to reduce the number of variables and to obtain independent axes describing variations in habitat amount and fragmentation of various types of semi-natural habitats (SNHs) as well as local intensity of farm management. This is a common method to deal with collinearity in multiple regression models in ecology (Dormann et al., 2013; Essl and Dirnböck, 2012). However, when considering all the types of SNHs, the PCA failed to separate the variations in the amount/fragmentation of permanent grasslands and woodland edges (Fig. S1) even though the correlations of habitat amount and fragmentation were low between these two types of SNHs (Table 2). Therefore two separate PCA were conducted to deal with the effect of grassland amount/fragmentation on one side, and of woodland edge length/fragmentation on the other. All other variables – hedgerow length/fragmentation and LLUI – were kept in the two PCAs to describe grassland or woodland edge amount/fragmentation independently of hedgerow length/fragmentation and LLUI.

Table 2 Spearman rank correlations among environmental variables describing habitat amount, habitat isolation and local intensity of farming practices (n=40).

	prox_hedge	*woodland_edge*	*prox_woodland_edge*	*grassland*	*prox_grassland*	*LLUI*
hedge	0.95 ***	-0.21	-0.02	-0.02	0.17	-0.21
prox_hedge		-0.13	0.05	0.06	0.23	-0.13
woodland_edge			0.73 ***	0.41 **	0.39 *	0.11
prox_woodland_edge				0.58 ***	0.45 **	0.18
grassland					0.75 ***	0.01
prox_grassland						-0.11

To test for the degree of pollinator dependence for petunia plants, we explored the differences in seed set and fruit set between bagged and open-pollinated potted plants using a Kruskal-Wallis test. The difference between bagged and open-pollinated flowers was significant for seed set and fruit set (Fig. 2). Open-pollinated plants produced 2.5 times more seeds per fruit and twice as more fruits per total flowers in average than bagged ones (Fig. 2). Moreover, to control for the effect of local microclimatic effects on pollination delivery and better assess the contribution of pollinators to pollination success, we corrected the seed set and fruit set per site by subtracting the seed set and fruit set of open pollinated plants by the one of bagged plants.

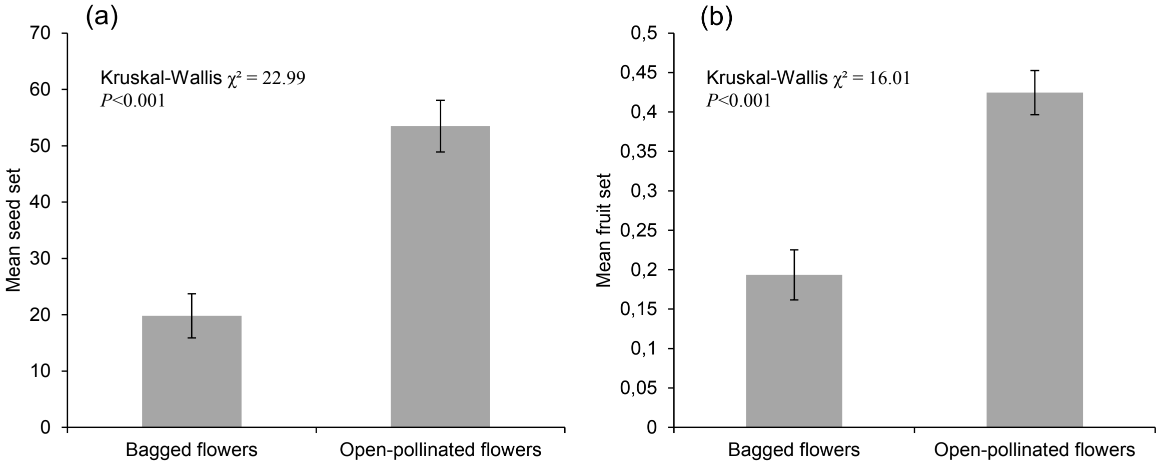

Figure 2 Mean seed set (a) and fruit set (b) for bagged and open-pollinated flowers. Standard errors are represented at the top of each bar.

The effects of SNH amount/fragmentation and LLUI on wild bee species richness, abundance and pollination success was then tested using generalized linear models (GLM), with a quasipoisson error distribution to account for possible overdispersion in the data. The explanatory variables were the scores of the different sampling sites on the PCA axes describing SNH amount/fragmentation and LLUI. These scores were standardized to better assess their relative effects on the response variables. This procedure was used for the two PCAs, therefore there were two GLM for each response variable.

The effect of wild bee species richness /abundance on pollination success was tested using GLM with a quasipoisson error distribution.

To test for differences in the response of bees to environmental variables depending on dominance status, we repeated the same previous tests – bee and pollination response to environmental variables, link between abundance/species richness and pollination success– for dominant and sub-dominant bee species respectively. To quantify species contribution to petunia pollination, we ordered bee species depending on their cumulated frequency in the dataset and calculated the correlation between species richness and pollination success across all sites for increasing number of species ordered by their cumulated frequency – the first species being the most abundant, the last one the rarest. The most contributive species were then chosen when the correlation coefficient peaked. A graph with no unique peak would indicate that dominance status of bee species is not important in determining the link between species richness and pollination success.

To test for density compensation across sampling sites, we used a visualization technique by plotting the frequency distribution of all pairwise correlation coefficients (Spearman's *r*) between the abundances of dominant and thus functionally important species (Winfree and Kremen, 2009). In this plot, density compensation would be indicated by a distribution shifted to negative values (negative covariance among the abundances of wild bee species). To test for response diversity, we tested the

interaction between species identity (categorical variable) and the different axes of the PCA to explain variations in the abundance of individual species. The response variable was thus the number of individuals captured per species. To avoid collinearity effects due to the inclusion of interaction terms, we tested the effect of each PCA axis in separate models. Significant interaction terms would indicate that bee species varies in their response to environmental factors, suggesting the presence of response diversity. We used a GLM with a quasipoisson error distribution for this latter test.
All analyses were performed using R 3.0.2 (R Development Core Team, 2011).

Results

A total of 2538 individuals belonging to 86 wild bee species was sampled across the 40 sampling sites (Table S1). There were six species that contributed the most to petunia pollination success, as the correlation coefficient between the variation of species richness and pollination success across all sites peaked for this species group compared to others, when bee species were ordered by their abundance rank (Fig. 3).

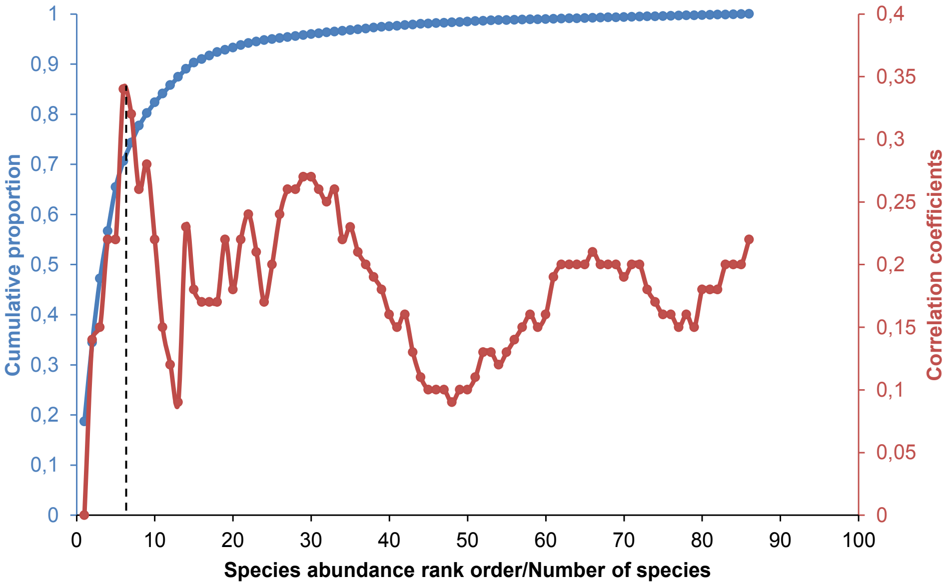

Figure 3 Relationship between cumulative proportions of captured wild bee individuals and species abundance rank order (blue line) and Spearman correlation coefficients between the number of species and pollination success across all sites (red line) for an increasing number of species taken from the total species pools, in which species were ordered by their abundance rank. The maximum correlation between species richness and pollination success is reached when the six dominant bee species are considered.

They were all from the Halictidae family and were dominated by individuals from the *Lasioglossum* genus. These species were all ground-nesting and polylectic bee species but had contrasted body sizes.

There were all primitively social species except for *Lasioglossum corvinum*. These six species accounted for 71% of the total bee abundance and were thus classified as dominant bee species.

The three PCA axes of the two PCAs accounted for 94% of the total variance in the environmental variables. In the two PCAs, the first axis was associated with the level of hedgerow length/proximity and the third one described the local intensity of farming practices (Table 3a). In the first PCA, the second axis described variations in woodland edge length/proximity but was associated with the level of permanent grassland amount/proximity in the second PCA (Table 3b).

Table 3 Coordinates of the environmental variables in the PCA axis for the two PCAs. These coordinates show the degree of association between environmental variables and the axes of the PCA. Variables describing hedgerow length and fragmentation and local intensity of farming practices were included in both PCAs. The first PCA included woodland edge length and fragmentation (a) and the second one grassland amount and fragmentation (b). The highest associations are in bold.

(a)

	PCA #1 axis 1	PCA #1 axis 2	PCA #1 axis 3
woodland_edge	-0,52	**0,76**	-0,18
prox_woodland_edge	-0,31	**0,88**	0,03
LLUI	-0,43	-0,02	**0,90**
hedge	**0,91**	0,32	0,22
prox_hedge	**0,88**	0,42	0,12

(b)

	PCA #2 axis 1	PCA #2 axis 2	PCA #2 axis 3
grassland	0.23	**0.91**	0.07
prox_grassland	0.55	**0.75**	-0.03
LLUI	-0.42	0.11	**0.90**
hedge	**0.88**	-0.36	0.25
prox_hedge	**0.93**	-0.29	0.17

Response of bee diversity and pollination success to the intensity of farming practices and the amount and fragmentation of semi-natural habitats

Total bee species richness was negatively influenced by hedgerow length and proximity but decreased with decreasing grassland amount and proximity (Table 4a, Fig. 4). When considering dominant and sub-dominant species separately, only species richness of sub-dominant species followed the same trend as for total bee community (Table 4b, Fig. 5). Total bee abundance was negatively influenced by local LLUI and positively affected by grassland amount/proximity, and to the same extent for these two factors (Table 4a, Fig. 4). Only abundance of dominant bee species followed the same trend as for total bee community (Table 4b, Fig. 5). The length and proximity of woodland edges did not influence any the components of bee diversity (Table 4a)

Neither SNH amount/proximity nor local LLUI influenced petunia seed set or fruit set (Table 5).

Table 4 Results of the generalized linear models testing the effects PCA axes describing SNH amount/fragmentation and local intensity of management practices on total species richness and abundance (a) and on species richness and abundance of dominant and sub-dominant species (b). PCA axis 1 is positively correlated with hedgerow length and proximity and axis 3 with the intensity of farming practices for the two PCAs (Table 3). The axis 2 of the first PCA is positively correlated with woodland amount and proximity and the axis 2 of the second PCA is positively correlated with grassland amount and proximity (Table 3). Significant probabilities are in bold (*P*<0.05 *; *P*<0.01 **; *P*<0.001 ***).

(a)

	Total species richness		**Total abundance**	
	Coef	SE	Coef	SE
PCA #1 axis 1	**-0.12****	**0.04**	-0.1	0.09
PCA #1 axis 2	-0.01	0.04	-0.06	0.08
PCA #1 axis 3	-0.03	0.04	**-0.18***	**0.09**
PCA #2 axis 1	**-0.08***	**0.04**	-0.05	0.08
PCA #2 axis 2	**0.09***	**0.04**	**0.18***	**0.08**
PCA #2 axis 3	-0.03	0.04	**-0.19***	**0.08**

(b)

	Species richness				**Abundance**			
	Dominant species		Sub-dominant species		Dominant species		Sub-dominant species	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE
PCA #1 axis 1	-0.02	0.03	**-0.17****	**0.05**	-0.01	0.10	**-0.22***	**0.11**
PCA #1 axis 2	0.01	0.03	-0.02	0.05	-0.04	0.09	-0.09	0.11
PCA #1 axis 3	-0.02	0.03	-0.04	0.05	**-0.22***	**0.10**	-0.14	0.11
PCA #2 axis 1	-0.01	0.03	**-0.12***	**0.05**	0.05	0.09	-0.19	0.11
PCA #2 axis 2	0.04	0.03	**0.12***	**0.05**	**0.19***	**0.08**	0.17	0.10
PCA #2 axis 3	-0.02	0.03	-0.03	0.05	**-0.23***	**0.09**	-0.14	0.11

Table 5 Results of the generalized linear models testing the effects PCA axes describing SNH fragmentation and local intensity of management practices on petunia seed set and fruit set. PCA axis 1 is positively correlated with hedgerow length and proximity and axis 3 with the intensity of farming practices for the two PCAs (Table 3). The axis 2 of the first PCA is positively correlated with woodland amount and proximity and the axis 2 of the second PCA is positively correlated with grassland amount and proximity (Table 3). Significant probabilities are in bold (*P*<0.05 *; *P*<0.01 **; *P*<0.001 ***).

	Seed set		**Fruit set**	
	Coef	SE	Coef	SE
PCA #1 axis 1	0,01	0,14	-0,09	0,16
PCA #1 axis 2	0,14	0,15	0,07	0,16
PCA #1 axis 3	-0,26	0,15	-0,23	0,16
PCA #2 axis 1	0,09	0,15	-0,01	0,04
PCA #2 axis 2	0,08	0,14	0,02	0,04
PCA #2 axis 3	-0,25	0,16	-0,05	0,04

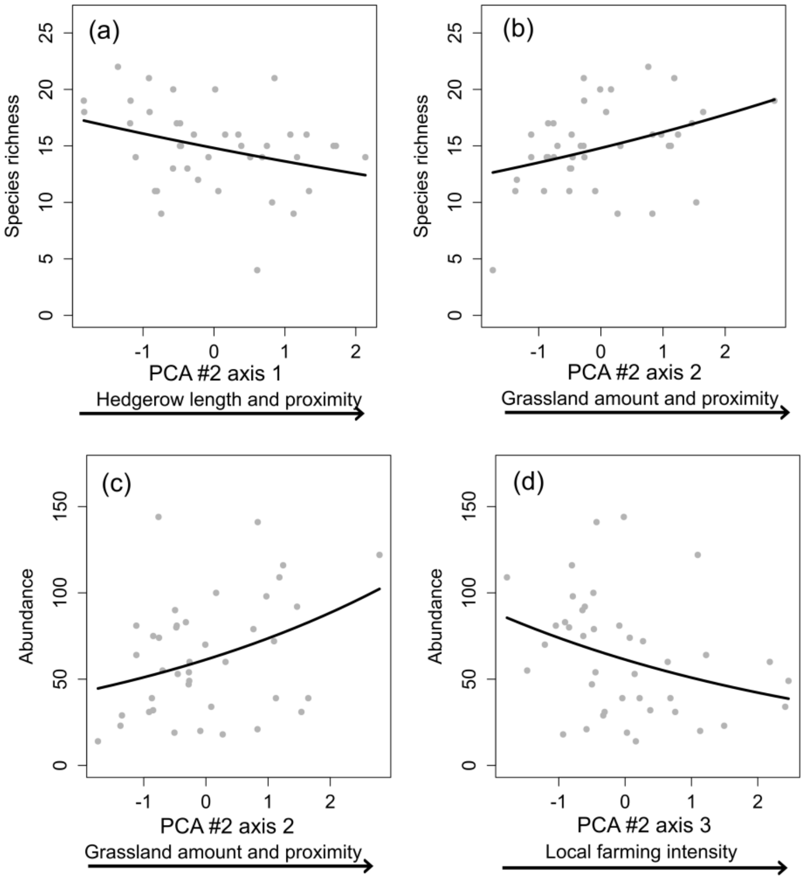

Figure 4 Effects of hedgerow (a) and grassland amount/proximity (b) on total bee species richness, and effects of grassland amount/proximity (c) and local farming intensity (d) on total bee abundance. Only significant relationships from the Table 4a are displayed.

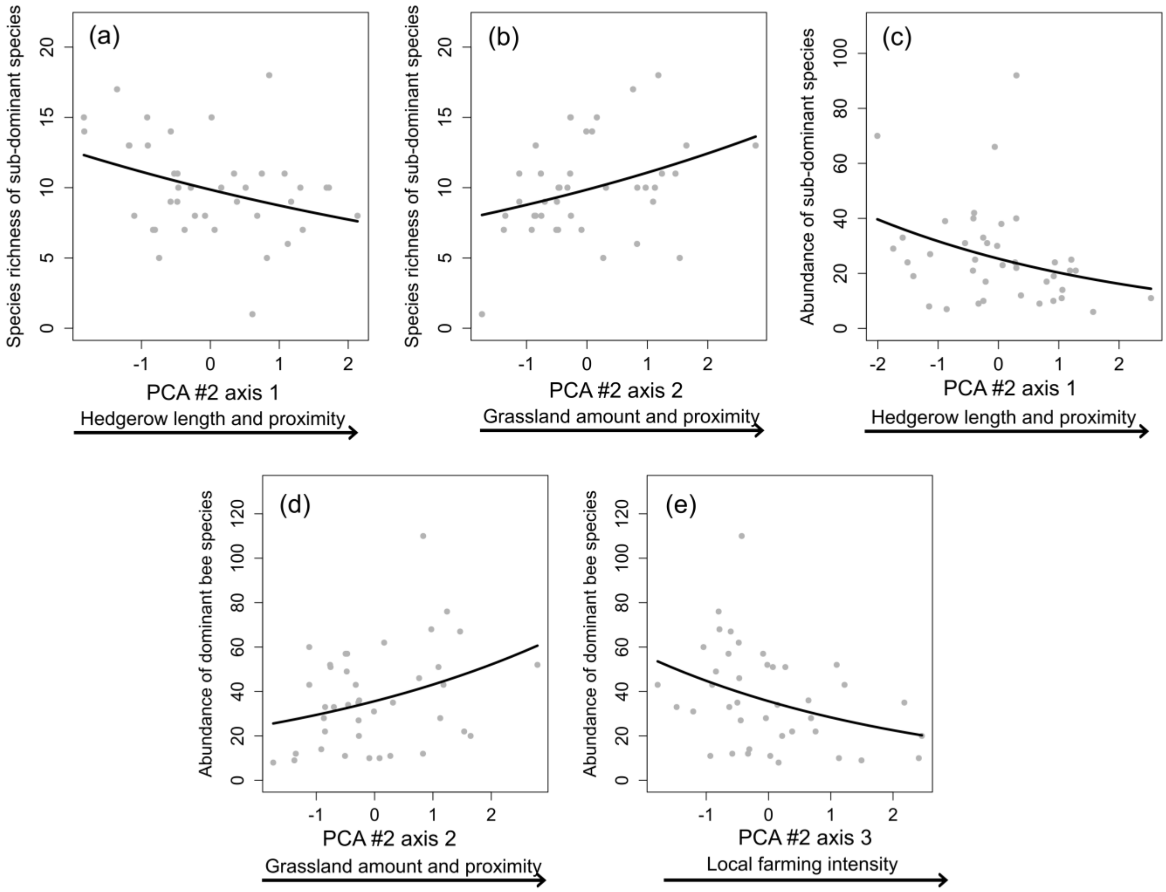

Figure 5 Effects of hedgerow length/proximity (a, c) and grassland amount/proximity (b) on the species richness or abundance of sub-dominant bee species, and effects of grassland amount/proximity (d) and local farming intensity (e) on the abundance of dominant bee species. Only significant relationships from the Table 4b are displayed.

Relationship between bee diversity and pollination success

Petunia seed set was positively correlated to total bee abundance but not to total bee species richness (Table 6). The species richness and abundance of dominant species were also positively correlated to pollination success (Table 6). However, petunia seed set was not correlated to the abundance or species richness of sub-dominant species (Table 6).

Contrary to seed set, petunia fruit set was not correlated to total bee abundance or species richness, even when considering dominant and sub-dominant species separately (Table 6).

Table 6 Results of the GLM testing the effects of the species richness and abundance of total bee community or dominant and sub-dominant species on seed set and fruit set. Significant probabilities are in bold.

Dependant	Independant	Coef	SE	*P*-value
Seed set	Total species richness	0,2	0,15	0,193
Seed set	Total abundance	**0,29**	**0,13**	**0,031**
Fruit set	Total species richness	0,03	0,04	0,391
Fruit set	Total abundance	0,06	0,03	0,084
Seed set	Species richness of dominant species	**0,3**	**0,15**	**0,047**
Seed set	Abundance of dominant species	**0,3**	**0,12**	**0,0195**
Seed set	Species richness of sub-dominant species	0,13	0,15	0,398
Seed set	Abundance of sub-dominant species	0,16	0,13	0,219
Fruit set	Species richness of dominant species	0,18	0,14	0,182
Fruit set	Abundance of dominant species	0,22	0,12	0,0569
Fruit set	Species richness of sub-dominant species	0,07	0,13	0,59
Fruit set	Abundance of sub-dominant species	0,11	0,12	0,36

Stabilizing mechanisms for dominant bee species

We found no evidence for density compensation as the correlations among the abundances of dominant bee species across sites were globally positive (Fig. 6).

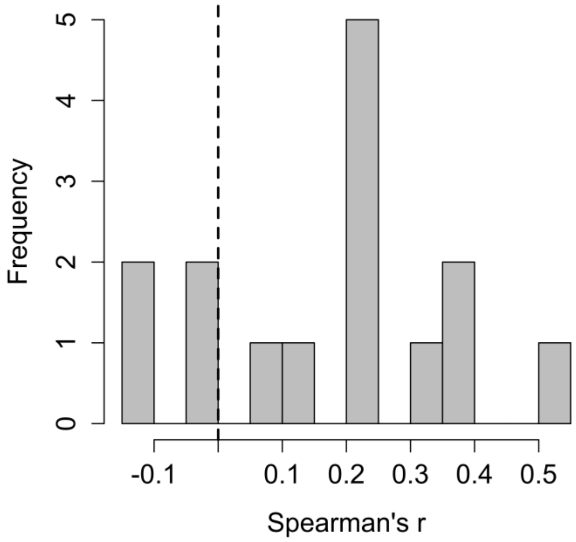

Figure 6 Frequency distribution of Spearman's r values calculated among the abundances across sites of dominant bee species that were found to be the most functionally important species. The frequency distribution is shifted to the right of zero, indicating no density compensation in the dataset.

Similarly, we found no significant interactions between environmental gradients and bee species to explain abundances of dominant bee species (Table 7), which means that there was no response diversity to any of the environmental variables.

Table 7 Results of the GLM for the analysis of response diversity in dominant bee species for the two PCAs. No significant interactions between bee species and environmental variables were found and this suggests the absence species response diversity for this variable.

	d.f.	F	*P*-value
bee species	5	16.33	<0.0001
PCA #1 axis 1	1	0.025	0.87
bee species x PCA #1 axis 1	5	1.5	0.19
bee species	5	15.93	<0.0001
PCA #1 axis 1	1	0.197	0.66
bee species x PCA #1 axis 2	5	1.47	0.2
bee species	5	16.15	<0.0001
PCA #1 axis 1	1	7.77	0.006
bee species x PCA #1 axis 3	5	0.23	0.95
bee species	5	15.93	<0.0001
PCA #2 axis 1	1	0.36	0.55
bee species x PCA #2 axis 1	5	1.23	0.3
bee species	5	16.89	<0.0001
PCA #2 axis 1	1	6.83	0.01
bee species x PCA #2 axis 2	5	0.58	0.72
bee species	5	16.19	<0.0001
PCA #2 axis 1	1	8.22	0.005
bee species x PCA #2 axis 3	5	0.44	0.82

Discussion

Our hypothesis about the decrease of wild bee diversity and pollination along the gradient of intensity of farming practices and habitat amount and fragmentation is not validated. Indeed, we found that only wild bee abundance and richness responded to local and landscape variables whereas pollination success remained unaffected by these factors. We found that grassland amount and proximity positively influenced total bee species richness and abundance. The loss and fragmentation of permanent grasslands might have therefore decreased the abundance and diversity of wild bees by decreasing the availability and diversity of high quality resources they provide for wild bees (Hopfenmüller et al., 2014; Jauker et al., 2013; Öckinger and Smith, 2007) as well as limited the opportunity for spill-over from these habitats to focal crop fields due to increased habitat isolation (Albrecht et al., 2007; Öckinger and Smith, 2007; Ricketts et al., 2008). Moreover, the amount and proximity of hedgerows was negatively correlated to total abundance and species richness of bee species, suggesting a barrier effect. Other studies have also found that hedgerows can reduce arthropod movements between crop fields, for carabid beetles for example (Mauremooto et al., 1995). Even if hedgerows can provide critical resources for farmland wild bees (Kremen and M'Gonigle, 2015a; Morandin and Kremen, 2013), our results suggest that a dense hedgerow network in agricultural landscapes may not be beneficial for them. As permanent grasslands were population sources of bees to crop fields in the studied region, hedgerows might have impeded wild bee movements between grasslands and annual crops. We also found that an increase in the local intensity of farming practices reduced the abundance but not the species richness of wild bee species captured in the crop fields.

The intensity of herbicide application is detrimental to the abundance and diversity of weed species in cereal fields (Holzschuh et al., 2007; Marshall et al., 2006) that can in turn affect the local species richness and abundance of wild bees (Holzschuh et al., 2007) as many weed species are used as nectar and pollen sources by bees (Biesmeijer et al., 2006; Bretagnolle and Gaba, 2015; Potts et al., 2010a; Westrich, 1996). Insecticides are known to be detrimental to bee species through lethal and sub-lethal effects (Brittain and Potts, 2011; Desneux et al., 2007; Whitehorn et al., 2012). The intensity of soil tillage can have direct and indirect effects on wild bee species, via the decrease in weed species diversity (Murphy et al., 2006) of below-ground nest destruction (Kim et al., 2006; Shuler et al., 2005; Williams et al., 2010). Our result suggest that bee population size was negatively influenced by the local intensity of farming practices, but as species richness remained unchanged along the intensity gradient, farming intensity might have not caused species loss.

As expected, the species that contributed the most to pollination delivery, measured by seed set, were dominant in bee communities. Even if the result we found was only correlative, the correlation we found between species richness of dominant species and pollination success, compared to other species groups, was strong enough to draw this conclusion. These results are in accordance with previous studies that found that pollination services were driven by variations in the abundance of dominant species (Kleijn et al., 2015; Winfree et al., 2015). Globally, the distribution of species' abundances is skewed in real-world communities (Kleijn et al., 2015; McGill et al., 2007; Winfree et al., 2015) and our results confirm the mass ratio hypothesis – the contribution of a given species to a function is proportional to its relative abundance (Grime, 1998) – as dominant species seemed to contribute more to pollination than sub-dominant ones in our dataset. In accordance with other studies on wild bees, we found that changes in abundance of dominant species strongly influenced the variations of total bee abundance, whereas the changes in species richness of sub-dominant species explained the variations of species richness in response to the environment (Winfree et al., 2015). Due to their low population size, the number of sub-dominant species is more likely to fluctuate due to environmental or statistical reasons, whereas dominant species are less likely to contribute to species richness variations due to their high occurrence along environmental gradients (Johnson, 1998; Winfree et al., 2015). Here we found that the species richness of sub-dominant species was negatively affected by grassland loss fragmentation but did not respond to variations in crop management intensity. Conversely, the abundance of dominant species was negatively correlated with the intensity of crop management. This result is in accordance with Kleijn et al. (2015) as they found that dominant bee species in farmland, more adapted to landscapes dominated by agricultural land use, could be enhanced though the adoption of agri-environment schemes and therefore responded to the in-field variations in resource availability and level of disturbance. Our results also suggest that sub-dominant species preferentially use semi-natural habitats to complete their life cycle and are relatively unaffected by the variation of resources in crop fields that are influenced by crop management, which is also in line with Kleijn et al. (2015). However, contrary to Kleijn et al. (2015), we found that dominant bee species were negatively affected by grassland loss and fragmentation and to the same extent as local farming intensity, suggesting that the dependence of dominant species on semi-natural habitats may depend on the species pool and agricultural context.

Yet, even if dominant species abundance was correlated to petunia seed set and responded negatively to the local intensity of farming practices and grassland loss/fragmentation, these two environmental factors did not affect petunia pollination success across the study sites. Moreover, there was no evidence of stabilizing mechanism among dominant species against grassland loss and fragmentation or increase in local intensity of crop management. Altogether, our results suggest that the decrease in abundance of dominant species along the gradient of grassland loss/fragmentation and farming intensity was not strong enough to negatively impact pollination success and that these dominant species were abundant enough in each study sites to fully pollinate petunia flowers. However, the absence of stabilizing mechanisms such as response diversity and density compensation, that could buffer pollination delivery in case of bee species loss (Cariveau et al., 2013; Winfree and Kremen, 2009), suggest that in a context of further grassland loss/fragmentation or local farming intensification, a decrease in population sizes of dominant species that would in turn decrease their species richness might potentially alter pollination delivery. Also, the lack of link between pollination success and environmental variables may arise from the scale of measurement of landscape variables. Indeed, functionally important species had different body sizes and thus had contrasting foraging ranges (Greenleaf et al., 2007), making them sensitive to habitat loss and fragmentation at different spatial scales (Steffan-Dewenter et al., 2002). Therefore in our study, the spatial scale at which we measured landscape variables might have been relevant for quantifying landscape effects of wild bee communities but not for explaining variations in pollination delivery. Moreover, similarly to the study of Steffan-Dewenter et al. (2001), the absence of relationship between the proportion of SNHs and pollination success may arise from unquantified processes in this study, such as changes in foraging behaviors of wild bees along the landscape complexity gradient or from the contribution of other wild pollinator guilds such as hoverflies, butterflies or beetles. Indeed, these different pollinator guilds have been shown to contribute significantly to the pollination of many crop plants, irrespective of the proportion of SNH around crop fields (Rader et al., 2016). In addition, the lack of relationship between landscape variables and petunia seed set could be due to the exotic character of petunia plants. Indeed, petunia species are native from south America (Tsukamoto et al., 2003) and are thus likely to be pollinated by specific bee assemblages from this region. However, we detected a high contribution of insect pollination in this study and other studies reported that petunia flowers with large corolla were visited by social and solitary bees (Ando et al., 2001; Hoballah et al., 2007). These two considerations therefore suggest that the exogenous character of petunia plants was not responsible for the lack of effect of landscape context on petunia pollination success.

Conclusion

We found that bee diversity, via sub-dominant species, was positively correlated to the amount and proximity of permanent grasslands. However, functionally important species, dominant in the communities, were enhanced by this same factor but were also influenced by local intensity of farming practices. Yet, we have not found any link between pollination delivery and gradients of farming intensity or habitat loss and fragmentation, presumably because our measurements of the diversity-function relationship were only correlative. However, the absence compensatory mechanisms among functionally important bee species across the studied sites suggests that landscape simplification and local intensification of farming practices might potentially endanger pollination services provided by wild bees to the same extent.

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Appendices

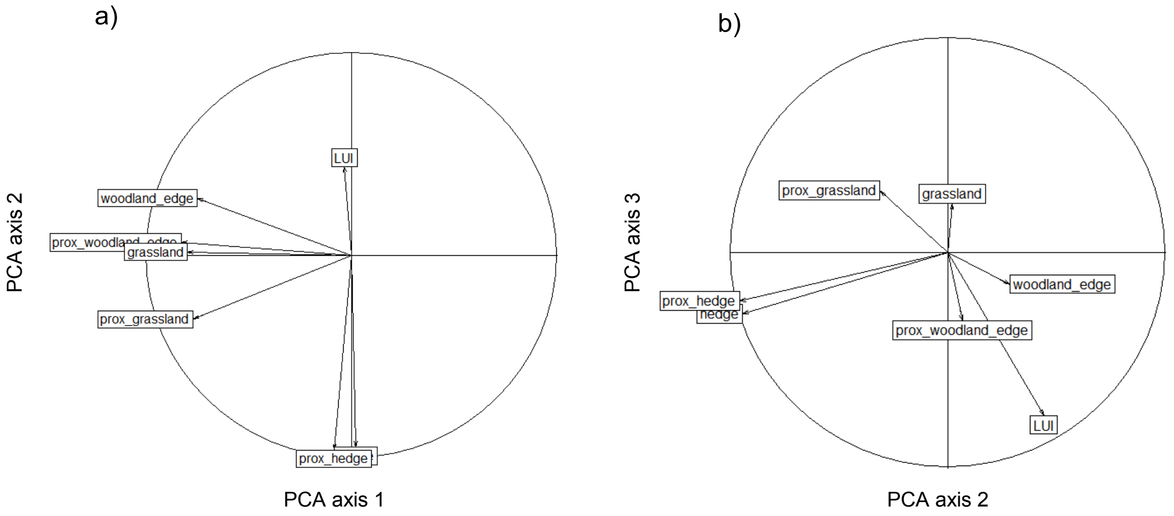

Figure S1 Correlation circles summarizing the coordinates of the local and landscape variables in the PCA axes 1 and 2 (a) and 2 and 3 (b).

Table S1 List of bee species in the dataset and corresponding summed abundance of individuals over all sites

Species	Abundance
Andrena agilissima	1
Andrena angustior	4
Andrena bicolorata	1
Andrena bucephala	2
Andrena chrysopyga	1
Andrena ferox	1
Andrena flavipes	31
Andrena gravida	1
Andrena haemorrhoa	2
Andrena humilis	4
Andrena lagopus	4
Andrena livens	4
Andrena minutula	3
Andrena nigroaenea	4
Andrena nigroolivacea	2
Andrena nitida	3
Andrena nitidula	1
Andrena ranunculi	1
Andrena rhenana	1
Andrena ventricosa	3

Anthophora plumipes	5
Bombus hortorum	12
Bombus humilis	1
Bombus lapidarius	4
Bombus lucorum	2
Bombus pascuorum	1
Bombus pratorum	3
Bombus ruderarius	4
Bombus ruderatus	1
Bombus sylvarum	4
Bombus sylvestris	1
Bombus terrestris	45
Ceratina cucurbitina	1
Eucera clypeata	7
Eucera nigrescens	10
Eucera nigrifacies	42
Eucera taurica	6
Halictus corvinum	2
Halictus fulvipes	1
Halictus maculatus	4
Halictus quadricinctus	41
Halictus scabiosae	324
Halictus simplex	474
Halictus smaragdulus	1
Halictus subauratus	1
Halictus tumulorum	1
Hylaeus confusus	1
Hylaeus cornutus	1
Hylaeus dilatatus	1
Hylaeus euryscapus	1
Lasioglossum albipes	1
Lasioglossum corvinum	400
Lasioglossum crassepunctatum	12
Lasioglossum discum	2
Lasioglossum glabriusculum	64
Lasioglossum griseolum	17
Lasioglossum interruptum	5
Lasioglossum laevigatum	1
Lasioglossum laticeps	1
Lasioglossum lativentre	5
Lasioglossum leucozonium	8
Lasioglossum malachurum	132
Lasioglossum marginatum	94
Lasioglossum minutissimum	18
Lasioglossum morio	5
Lasioglossum nigripes	12

Lasioglossum pallens	3
Lasioglossum pauxillum	85
Lasioglossum politum	222
Lasioglossum punctatissimum	18
Lasioglossum puncticolle	241
Lasioglossum pygmaeum	1
Lasioglossum tricinctum	1
Lasioglossum truncaticolle	1
Lasioglossum villosulum	42
Lasioglossum xanthopus	1
Lasioglossum zonulum	54
Melecta italica	1
Osmia aurulenta	1
Osmia bicornis	2
Osmia brevicornis	1
Osmia cornuta	1
Osmia rufohirta	1
Xylocopa iris	2
Xylocopa valga	2
Xylocopa violacea	5

Chapter 6: Assemblages of uncommon bee species affect pollination success along a gradient of landscape complexity

Article en préparation

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Abstract

Landscape simplification, through the loss of semi-natural habitats, can have detrimental effects on bee diversity and pollination delivery. Ecological theory and empirical studies have proposed that pollination delivery can be affected by abundance fluctuations of dominant bee species or changes in functional diversity of bee communities. There is still little knowledge on the relative importance of these two mechanisms in real-world landscapes. In this study, we explored the effect of landscape complexity on pollination success, and we assessed whether pollination success was better predicted by functional diversity or abundance of dominant bee species. In 20 cereal fields differing in the surrounding proportion of semi-natural habitats (landscape complexity), we sampled wild bees and estimated pollination success using potted mustard plants. We found that neither bee functional diversity nor abundance of dominant species affected pollination success along the gradient of landscape complexity. However, variations in the occurrence of six uncommon species accounted for most of the variation of pollination success, and landscape complexity positively affected the occurrence of these six species. Our study suggests that uncommon bee species can drive pollination delivery in agroecosystems and highlights the importance of landscape complexity for the management of pollination services.

Keywords: Pollination, landscape complexity, biodiversity-ecosystem function, wild bees.

Introduction

Insect-mediated pollination is a pivotal ecosystem function in agroecosystems, contributing to the maintenance of plant biodiversity and crop production (Biesmeijer et al., 2006; Klein et al., 2007). Pollination services are mostly provided by bees (Klein et al., 2007), and the declines of the managed hives of the honeybees (*Apis mellifera*) throughout western countries stresses the need for strategies to increase pollination services provided by wild bees (Breeze et al., 2014; Ellis et al., 2010; Garibaldi et al., 2013; Potts et al., 2010b).

Recent studies have related pollination delivery to the diversity of bee communities and suggested that bee functional diversity – diversity of traits within bee communities – was a good predictor of pollination success. Indeed, bee species with different trait combinations are likely to have different foraging behaviors and morphological features (spatio-temporal complementarity, contrasting pollen deposition) that each contribute in a complementary way to the overall pollination success (Albrecht et al., 2012; Blüthgen and Klein, 2011; Cardinale et al., 2012). However, other studies have found that only one or a few dominant bee species may predominantly contribute to pollination in agroecosystems (Garibaldi et al., 2015; Kleijn et al., 2015; Winfree et al., 2015) so that pollination success was better predicted when considering the traits of these dominant species - community trait values - rather than the functional diversity of the whole bee community (Garibaldi et al., 2015; Winfree et al., 2015). Globally, the distribution of species' abundances is skewed in real-world communities (Kleijn et al., 2015; McGill et al., 2007; Winfree et al., 2015) and the contribution of a species to an ecosystem function is often a function of its abundance. Apart from bee conservation issues, the management of only a few dominant species would therefore be enough to maximize the provision of crop pollination in agroecosystems (Kleijn et al., 2015). There is therefore a substantial scope to determine the relative influence of functional diversity and community mean trait values on pollination success in different agroecosystems (Garibaldi et al., 2015) and whether their relative importance depends on environmental conditions (Hooper et al., 2005).

The diversity of farmland wild bees are positively affected by landscape complexity, usually measured as the proportion of semi-natural habitats in the landscapes (Batáry et al., 2011; Garibaldi et al., 2011; Winfree et al., 2009). Indeed, these habitats provide critical resources to wild bees such as nesting sites and floral resources and their availability around crop fields are critical to sustain pollinator diversity and crop pollination (Bailey et al., 2014a; Roulston and Goodell, 2011; Steffan-Dewenter et al., 2002). Landscape complexity was reported elsewhere to increase functional diversity of farmland bees (Klein et al., 2008; Martins et al., 2015) but also the abundance of species with specific traits (Klein et al., 2008; Williams et al., 2010). Therefore landscape diversity has the potential to affect pollination success via changes in bee functional diversity and community trait values (abundance of specific trait values). The aim of this study was to assess whether trait diversity and/or mean trait values explained the variation in pollination delivery along a gradient of landscape complexity, measured as the proportion of non-crop habitats. We sampled bee communities and experimentally assessed pollination success using potted mustard plants along a gradient of landscape complexity. We expected that i) pollination success would be positively correlated with landscape complexity, ii) the abundance of dominant species with similar trait would better explain variations in pollination success than functional diversity, iii) the abundance of dominant species would be positively correlated with landscape complexity.

Materials and methods

Study site and sampling design

This study was conducted in south-western France (Fig. 1), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17'N, 0°54'E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al., 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

We selected 20 cereal fields (winter wheat and barley) differing in the proportion of semi-natural habitats (woodlands and permanent grasslands) within a radius of 500 m centered on the sampling point (see the landscape characterization section). Preselection of cereal fields (hereafter sampling site) was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). In each field sampling site, the sampling point was located in a grassy of a winter cereal field, at least 100 m from other non-cropped area (woodland or built area).

We sampled bees with three pan traps per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of two poles per sampling point, one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint, SparVar® Germany), one trap per color. Traps were 2/3 filled with water, with a small amount of soap (Teepol® Multipurpose detergent) to break surface tension. The poles were designed such that the height was adjustable to the plant canopy. The traps were placed during one period of four days from 8 to 12 June 2015. The number of species and the number of individuals per species determined for each sampling site represented the sum of all traps in that site. Wild bee individuals (solitary and social species) were identified to species level. We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than a direct effect of landscape structure. We also excluded cleptoparasitic bees because they do not provide pollination services.

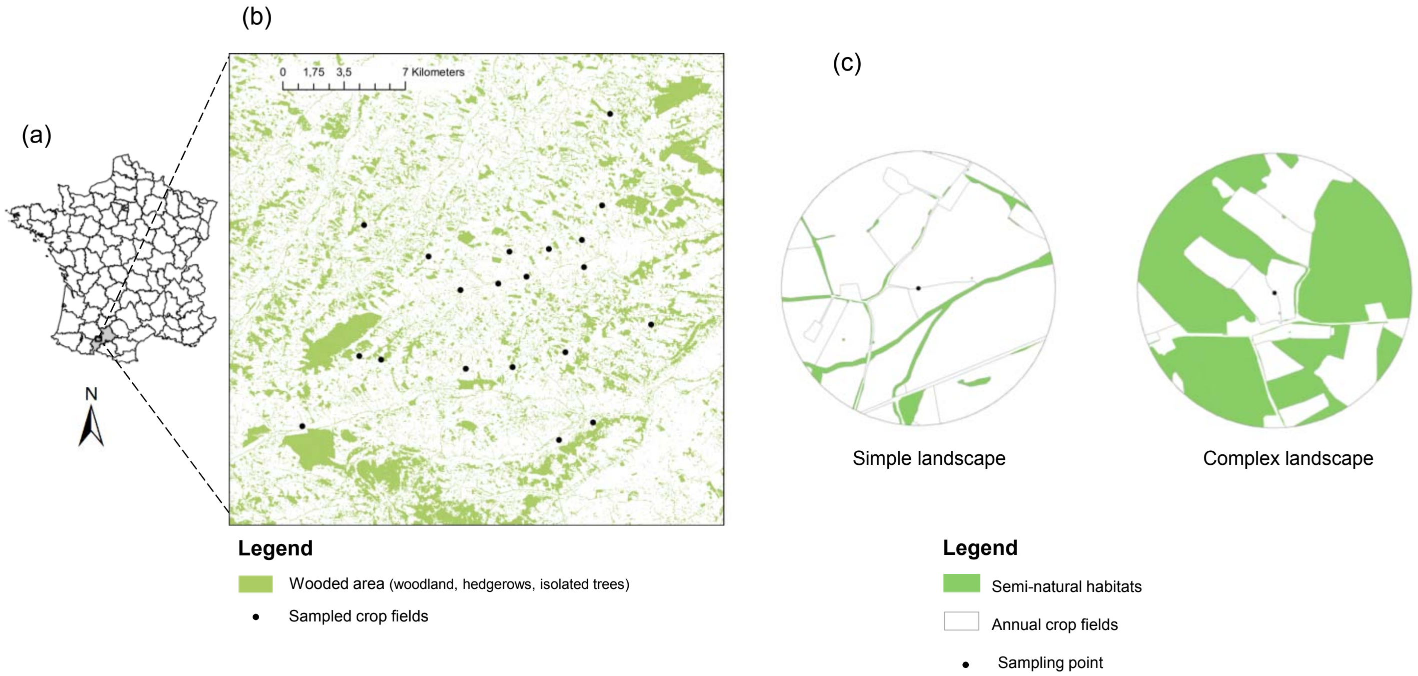

Figure 1 Maps showing (a) the study area, (b) the 44 sampled crop fields and (c) two extremes examples in terms of landscape complexity.

We experimentally assessed pollination success using potted plants placed in each sampling sites. Seeds of white mustard (Sinapis alba L.) were sown the 24 April 2015 and were grown in greenhouse in pots of standardized garden soil (3 L). Before the onset of flowering, potted plants were placed in insect-proof tents until the exposure in the fields. A day before field exposure, the last opened flower of each stem was marked with waterproof tape. In each field, three potted plants – two pots with open flowers and one with bagged flowers – were placed in the field margin, 10m away from the bee sampling point, during the same 4-day period (from 8 to 12 June 2015). The pots with bagged flowers (insect-proof gauze, Climabio, Nortene®) were used to test de degree of pollinator dependence. The three potted plants were placed in plastic trays which were filled with one liter of water. After the field exposure, flowers that had opened in the field were marked and potted plants were stored again under insect-proof tents until the seed harvesting. Between the 8 and 10 July 2015, all the marked flowers were harvested. Pollination success was estimated using the mean number of seed per fruit (seed set) at the field level. To calculate mustard seed set, we considered only the flowers that were pollinated on the field, which comprised flowers that open before and during field exposure. Moreover, to control for the effect of local microclimatic effects on pollination success and better assess the contribution of pollinators to pollination success, we corrected the seed per site by subtracting the seed set of open pollinated plants by the one of bagged plants. Unfortunately, the mustard plants in three sampling sites were damaged by pollen beetles. Therefore pollination success could be statistically analyzed using 17 sites.

Landscape characterization

Landscape context was characterized within a radius of 500 m centered on the sampling point (field margin) in each site. This radius was chosen according to the results of previous studies on the functional scale of wild bees (Gathmann and Tscharntke, 2002; Holzschuh et al., 2010; Zurbuchen et al., 2010). Using aerial photographs (IGN, 2013) the different land covers (woodlands, hedgerows, permanent grasslands, crop fields and isolated trees) were digitalized using ArcGIS 10.2 (ESRI). Crop field and grassland boundaries were validated by ground surveys in April 2015. The proportion of non-crop habitat (a measure of landscape complexity, Batáry et al., 2011; Holzschuh et al., 2010) was calculated for each site [(total area – farmed area)/total area] and ranged from 11 to 68%. The proportion of woodlands and permanent grasslands were positively correlated to the proportion of non-crop habitats (Spearman correlations: $r=0.89$, $P<0.001$ and $r=0.91$, $P<0.001$ respectively).

Bee traits

Five ecological and life-history traits were chosen based on their knowledge in the literature regarding their potential to influence the response of wild bees to environmental changes (response trait) and/or affect pollination efficiency (effect trait) (Table S1). We sourced trait information from the ALARM project database (Settele et al., 2005), Bommarco et al. (2010), Forrest et al. (2015), Fortel et al. (2014), Gathmann and Tscharntke (2002) and Michener (2000). The beginning and duration of the foraging season in SW France was based on expert knowledge (David Genoud, pers. com.). For body size values, when no data were available on a particular taxon, ITD was measured on at least five female individuals per taxon, and queens were used for eusocial species.

Statistical analyses

1. *Assessing functional diversity and species assemblages*

Bee diversity was characterized using species richness, total abundance and trait functional dispersion. Functional dispersion is a good proxy of functional diversity, as this metrics takes trait richness and relative abundance of species into account (Laliberté and Legendre, 2010). To test whether only a few species explained variations in pollination success, we calculated several indices. First, to detect shifts in the dominance of traits in bee communities, we calculated community weighted means (CWMs) for continuous traits and abundance-weighted frequencies (proportion of individuals per trait category) for binary traits. We estimated statistical association between traits among species with Spearman rank correlations (Table 1), because the effect of one trait on response to environmental change may not be biologically or statistically independent of others (Ekroos et al., 2013; Forrest et al., 2015; Williams et al., 2010).

Table 1 Spearman rank correlations among species traits (n=35). For nominal traits, trait values were coded as 0 or 1 to allow for correlation calculation. Sociality: solitary=0, social=1; diet breadth: oligolectic=0, polylectic=1 ($P<0.01$ **; $P<0.001$ ***).

	Sociality	Diet breadth	Foraging duration	Beginning of foraging period
ITD	0.08	-0.29	-0.13	0.06
Sociality		0.29	0.05	-0.02
Diet breadth			0.5 **	-0.18
Foraging duration				-0.8 ***

Second, to detect whether an assemblage of species explained variations in pollination success, we conducted a species association analysis to look for significant associations among species (Legendre, 2005). Correlation matrix of species abundances was computed for all the species (Spearman correlations). Then, a hierarchical clustering using the Ward distance was used on this correlation matrix (Hellinger transformed) to create groups of co-occurrent species. The silhouette information was used to find the optimal number of groups (Rousseeuw, 1987). To check for the significance of associations among species in these groups, the Kendall (W) coefficient of concordance and the associated *P*-values were computed, based on 10,000 permutations. Then, for each group of co-occurrent species, we searched for the species assemblage that most explained the variations in pollination success. To do so, we computed all the possible combinations of species for each possible number of species (based on 10,000 or 20,000 random draws, depending on species number) and calculated the Spearman correlation coefficient between species richness in the assemblage and pollination success. The best assemblage for a given number of randomly drawn species was the assemblage for which the maximum correlation coefficient between species richness and pollination success was reached.

2. *Testing the links between landscape complexity, pollination success, bee community structure and bee assemblages*

To test for the degree of pollinator dependence for mustard plants, we explored the differences in seed set between bagged and open-pollinated potted plants using a Kruskal-Wallis test.

Linear models were used to test the relationships between landscape complexity, seed set and bee community structure (functional structure and bee assemblages). Response variables such as abundance, species richness or seed set were log-transformed [log(x+1)] to meet the assumptions of the ANOVA.

First, we tested the relationship between landscape complexity and mustard seed set. Second, in separate models, we tested the effect of bee diversity (abundance, species richness), functional diversity and mean trait values on mustard seed set. In other set of separate models, we then tested the response of bee diversity, functional diversity and mean trait values to variations in landscape diversity.

Then, only for species assemblages that significantly explained variations in seed set, we tested the links between their species richness and seed set, and between landscape complexity and species richness. We also tested these relationships when several assemblages were considered together.

All analyses were performed using R 3.0.2 (R Development Core Team, 2011).

Results

Effect of landscape complexity on pollination success

Mustard seed set was lower in bagged flower than in open flowers (χ^2=4.6, *P*=0.03, Fig. 2), confirming that mustard plants benefited from the exposure to pollinators.

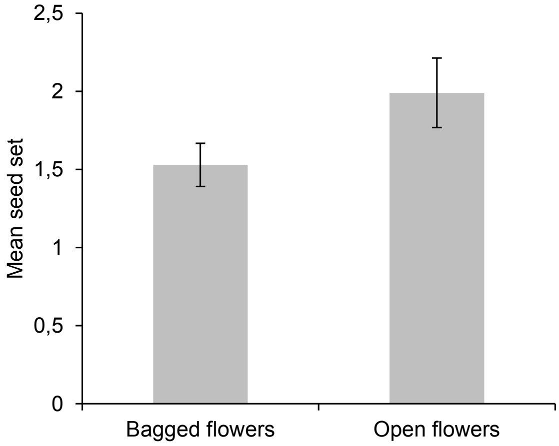

Figure 2 Mean seed set (± SE) for bagged and open-pollinated flowers.

Mustard seed set was positively related to the proportion of non-crop habitats in the landscapes (*F*=14.67, *P*=0.0016, R^2=0.49), which was 2.5 higher in the most complex landscapes when compared to the simplest ones (Fig. 3).

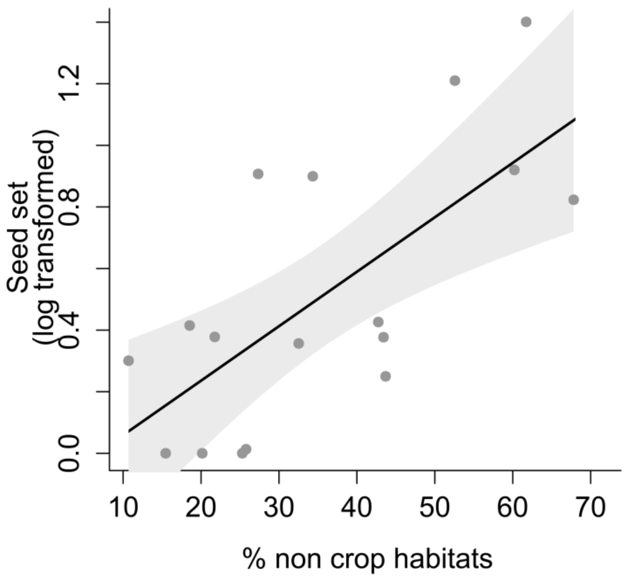

Figure 3 Relationship between seed set (log-transformed) and the proportion of non-crop habitats in the 17 landscapes. Solid black lines and dark grey-shaded areas represent model predictions and corresponding standard errors.

Relationships between landscape complexity, bee community structure and seed set

A total of 549 individuals belonging to 38 species were sampled across the 20 sampling sites (Supplementary material Table S1).

There was no significant relationship between seed set and bee diversity, functional dispersion or mean community trait values (Table 2). The proportion of non-crop habitats did not influence variations in bee diversity, functional dispersion or mean community trait values (Table 2).

Table 2 Results of the linear models testing the effects of several variables quantifying the community structure of wild bees on mustard pollination success, and the effect of landscape complexity on these latter variables. Species richness, abundance and seed set were log-transformed when treated as response variables. Each line corresponds to a single model.

Response variable	Explanatory variable	d.f.	*F*	*P*-value	R²
Seed set	Species richness	15	0.06	0.814	0
	Abundance	15	2.3	0.15	0.13
	Functional dispersion	15	0.12	0.732	0.01
	Mean ITD	15	0.05	0.832	0
	Proportion of social	14	0.22	0.649	0.02
	Proportion of oligolectic	14	0.32	0.581	0.02
	Mean foraging duration	15	0.55	0.469	0.04
	Mean beginning of foraging period	15	0.04	0.839	0
Species richness	% non-crop habitats	15	0.02	0.886	0
Abundance		15	0.9	0.359	0.06
Functional dispersion		15	0.95	0.344	0.06
Mean ITD		15	0.03	0.869	0
Proportion of social		14	0.36	0.559	0.03
Proportion of oligolectic		14	0.52	0.484	0.04
Mean foraging duration		15	2.65	0.124	0.15
Mean beginning of foraging period		15	0.42	0.526	0.03

Bee assemblages correlated to seed set

We found five groups of bee species for which species occurrences were significantly associated across sampling sites (Table 3; Supplementary material Fig. S2).

Table 3 Results of the concordance analysis, showing the Kendall's coefficient of concordance (W), the Friedman chi-square statistic used in the permutation test of W and the associated corrected *P*-values. A lower *P*-value than 0.05 indicates that the group contains species that significantly co-occur along the gradient of landscape complexity.

	Group 1	Group 2	Group 3	Group 4	Group 5
Kendall's W	0.46	0.12	1	0.39	0.27
Chi2	43.69	32.46	76	44.29	46.41
P-value	0.005	0.02	0.005	0.005	0.005

We discarded the group 3 because species from this group were only found in one site (*L. subhirtum, L. pygmaeum, A. propinqua* and *B. lapidarius*). Among the four remaining groups, only two had species assemblages for which variations in species richness significantly explained changes in mustard seed set (Fig. 4, Table S3). In the group 2, the correlation between species richness and seed set peaked when three species were considered (*A. humilis, L. lativentre* and *L. punctatissimum*). In the group 5, the correlation peaked also for three species (*L. crassepunctatum*, *L. minutissimum* and *L. zonulum*).

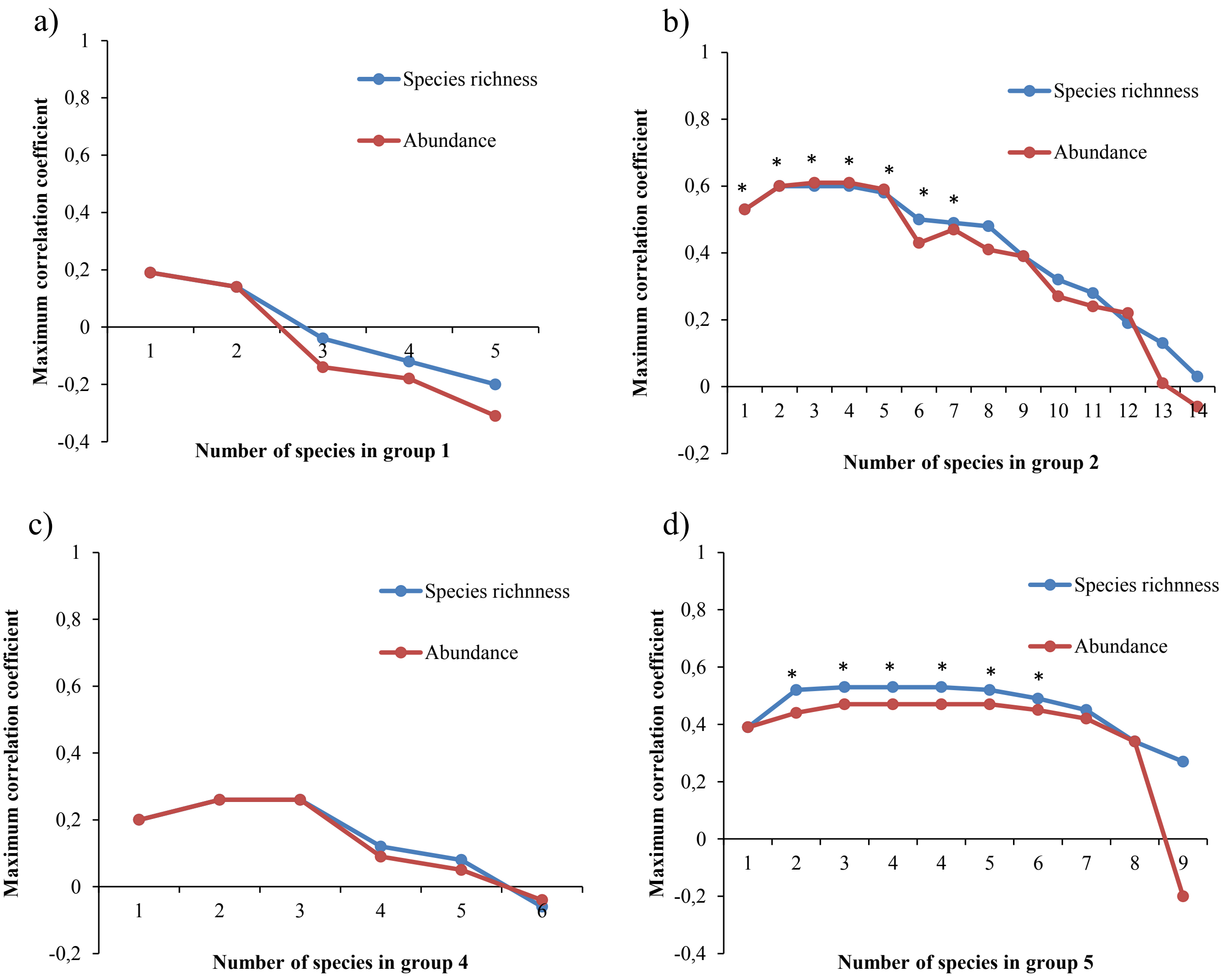

Figure 4 Maximum correlation coefficients between the species richness/abundance of assemblages (among all possible combinations of species for a given number of species) and seed set as a function of the number of species in the assemblages for group 1 (a), 2 (b), 4 (c) and 5 (d). The stars indicate the correlations that were significant (* $P<0.05$).

Species richness of each of the two groups was positively related to seed set, but species richness of group 2 explained more variation in seed set than group 5 (Table 4). There was a significant relationship between species richness in group 2 and the proportion of non-crop habitats, whereas species richness of group 5 remained unaffected by this landscape variable (Table 4).

When considering the two groups together, species richness influenced positively mustard seed set and was a better predictor of pollination success than the species richness of the groups considered separately (Table 4, Fig. 5a). Landscape complexity positively affected the species richness of the pooled two groups (Table 4, Fig. 5b).

Table 4 Results of the linear models testing the effects of functionally important and co-occurrent species richness on mustard pollination success, and the effect of landscape complexity on these latter variables. Species richness was log-transformed when treated as response variables. Each line corresponds to a single model**.** Significant relationships are in bold.

Response variable	Explanatory variable	d.f.	*F*	*P*-value	R²
Seed set	Species richness gp. 2	**15**	**9.52**	**0.008**	**0.39**
	Species richness gp. 5	**15**	**4.38**	**0.054**	**0.23**
	Species richness gr. 2 and 5	**15**	**26.61**	**<0.001**	**0.64**
Species richness gp. 2	% non-crop habitats	**15**	**4.17**	**0.059**	**0.22**
Species richness gp. 5		15	2.78	0.117	0.16
Species richness gr. 2 and 5		**15**	**9.18**	**0.008**	**0.38**

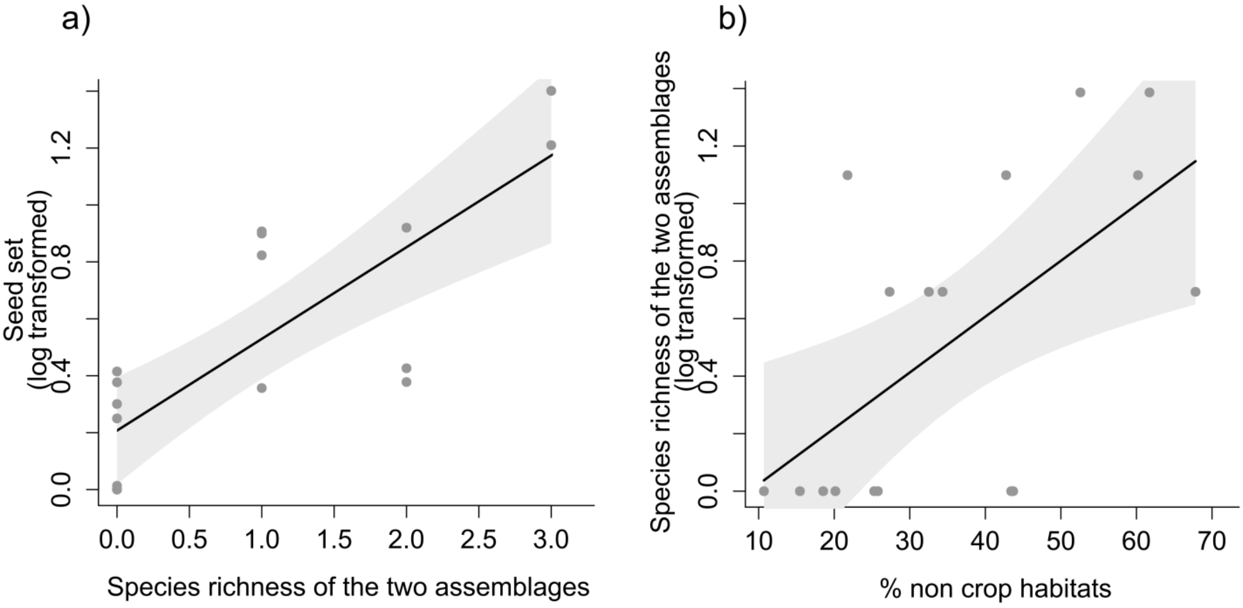

Figure 5 Relationship between seed set (log-transformed) and the species richness of two functionally important assemblages (a) and between species richness of these assemblages and the proportion of non-crop habitats in the landscapes (b). Solid black lines and dark grey-shaded areas represent model predictions and corresponding standard errors.

Discussion

In this study, we confirmed that landscape complexity, i.e. the proportion of non-crop habitats, could positively affect pollination success. However, the functional relationship between landscape complexity and pollination success did not involve the two major mechanisms linking bee diversity and pollination tested in previous studies, i.e. variations in functional diversity or community mean trait values.

First, our first hypothesis about the positive relationship between landscape complexity and pollination success was validated. Our results are consistent with previous studies which found a negative effect of isolation from semi-natural habitats and crop pollination (Garibaldi et al., 2011; Kremen et al., 2002; Martins et al., 2015).

Second, our hypothesis stating that a few dominant species with similar traits would be responsible for the variations in pollination success is not validated. Indeed, mean community trait values were not correlated to pollination success and trait values were not affected by landscape complexity. This result contradicts recent studies that found that the abundance of few dominant species with similar trait values explained variations in pollination provision (Garibaldi et al., 2011; Winfree et al., 2015). Shifts in trait values are the result of changes in the abundance of dominant species (Garibaldi et al., 2015), as real-world communities always display skewed species-abundance distributions (strong dominance of few species (Kleijn et al., 2015; McGill et al., 2007; Winfree et al., 2015). The mass-ratio hypothesis, stating that only few dominant species would contribute to a function in proportion of their abundance (Grime, 1998), was validated for some pollination systems (Cariveau et al., 2013; Garibaldi et al., 2015; Winfree et al., 2015).

The alternative hypothesis, stating that functional diversity, rather than trait abundance, would enhance pollination success (Hoehn et al., 2008; Klein et al., 2008; Martins et al., 2015) was not validated in our study. We found that neither bee diversity nor trait diversity was correlated to pollination success or landscape complexity. As neither trait abundances nor trait diversity responded to landscape complexity or explained variation in pollination success, our study suggest that none of the two drivers of pollination delivery examined in pollination studies (species complementarity or functional dominance) explained the relationship we observed between landscape complexity and pollination success.

We found that two assemblages of sub-dominant species (6 species representing 5.5% of total bee abundance) explained most of the variation in mustard seed set. The positive effects of this 6 co-occurrent species on pollination success could be due to two mechanisms: i) these 6 species would be complementary to dominant species that are found in all the sampling sites. That is to say that dominant species would provide a “baseline” pollination, and variation in pollination success would be the consequence of the occurrence of these 6 uncommon species; ii) these 6 species be the most functionally important species and the other species would only have a marginal impact on pollination success. When examining the variation in pollination success in relation to landscape complexity, an important proportion of sites have very low pollination success (four sites with null seed set, Fig. 3), and these situation correspond to sites where the 6 species from the two assemblages were absent (Fig. 5a). Therefore these results suggest that these six uncommon species contributed to the pollination seed set and that other species were less functionally important.

The species group for which species richness was the most correlated to seed set variations was the most sensitive to changes in landscape complexity, and may explained the positive correlations we found between species richness for the combined two groups and landscape complexity. Our result suggest that these two groups contributed in a complementary way to pollination, as these two groups occurred in contrasted landscape contexts (Blüthgen and Klein, 2011). Even if most of the studies demonstrated that common species make most of the contribution to ecosystem function, some studies have reported that less common species can also be functionally important, for ecosystem functions such as primary productivity, nutrient cycling and resistance to plant invasion (Hooper et al., 2005; Lyons et al., 2005). The effect of sub-dominant species on ecosystem function was reported to be even stronger when they are aggregated (Lyons et al., 2005), confirming the result of our study. Indeed, only the occurrence of some sub-dominant co-occurrent species was correlated to pollination success, suggesting that not all rare species contributed to pollination delivery. The six species from these two groups were all below-ground nesters, but differed in terms of body size, sociality and diet breadth (Supplementary material, Table S1). In our landscape gradient, the increase in landscape complexity was correlated to an increase in the proportion of semi-natural habitats such as permanent grasslands and woodlands, which can provide nesting sites and flowering resources for wild bees (Bailey et al., 2014; Hopfenmüller et al., 2014). Landscape complexity may have favored the six sub-dominant species by provides critical resources but also by reducing the isolation between crop fields and semi-natural habitats, as most of these species were small-bodied and thus had small foraging ranges (Greenleaf et al., 2007).

Our conclusions are contradiction with the meta-analysis of Kleijn et al. (2015), which found that the most functionally important species in intensive agroecosystems were the dominant ones and that pollination provision would not drastically change in function of the proportion of semi-natural habitats. Such differences may arise from the sampling design that differed between our study and the meta-analysis. First, we used a passive sampling technique (pan traps) which is useful for assessing bee diversity along environmental gradients (Westphal et al., 2008) and measured pollination success with potted plants. Even if this method did not provide any information on pollinator species that actually visited mustard flowers, the colors of the traps and the period of sampling (4 days for each site) allow to capture a wide variety of species including uncommon specimens (Westphal et al., 2008). The use of pan traps is also a good method to capture small-bodied specimens, which are usually missed during transect walks. In the meta-analysis of Kleijn et al. (2015), the use of transect walk allowed for the identification of the main flower visitors, but the shorter sampling period and the risk to miss small-bodied and rare species. Second, Kleijn et al. (2015) used the frequency of flower visitation as a measure of pollination success as they showed that visitation frequency was correlated to total pollen deposition (visitation frequency x pollen deposition per visit). However, as this proxy is based on single-visit experiments of virgin flowers, it is likely to miss species interaction that may influence pollination delivery such as species complementarity (Winfree et al., 2015). Another reason for such differing results is the differences in agricultural contexts. Indeed, our study region is characterized by a mosaic of crop and non-crop habitats, with small crop fields surrounded by a relatively high proportion of semi-natural habitats compared to other agricultural temperate regions (Choisis et al., 2010). Comparatively to the studied regions retained in Kleijn et al. (2015), our region is made of complex and extensive landscapes, which are likely to host a relatively rich species pool (Tscharntke et al., 2012). In the studied regions of Kleijn et al. (2015), agricultural landscapes – with a relative high number of sites in USA and Canada – might have been too simplified to sustain rich species pools and only contained common species adapted to intensive agricultural contexts (Tscharntke et al., 2012). The positive effect of landscape complexity on pollination success we detected in our study may thus arise from the fact that our region was complex enough to host a diversity of species that actually benefit from the presence of semi-natural habitats.

Conclusion

Our results suggest that landscape complexity can act on pollination success through changes in the occurrence of a subset of sub-dominant species. This study therefore highlights the fact that the measurement of functional diversity or trait distribution in communities does not always help to predict ecosystem functions. The contribution of less common species to ecosystem functions is still little studied (Hooper et al., 2005; Lyons et al., 2005) and the present study, even though only correlative, highlights the need for more studies on the aggregated role of rare species assemblages on ecosystem functions.

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Supplementary materials

Table S1 List of bee species, corresponding abundance of individuals over all sites and trait values for bee species (females only).

Species	Abundance	ITD	Sociality	Nest location	Diet breadth	Beginning of foraging season	Duration of foraging season
Andrena flavipes	2	2.3	Solitary	Below-ground	Polylectic	March	8
Andrena humilis	2	2.4	Social	Below-ground	Oligolectic	April	4
Andrena propinqua	1	2.04	NA	NA	NA	NA	NA
Andrena ventricosa	1	1.63	Solitary	Below-ground	Oligolectic	April	4
Bombus humilis	2	4.77	Social	Below-ground	Polylectic	June	4
Bombus lapidarius	2	4.9	Social	Below-ground	Polylectic	March	7
Bombus lucorum	2	NA	NA	NA	NA	NA	NA
Bombus pascuorum	3	NA	NA	NA	NA	NA	NA
Bombus sylvarum	1	4.44	Social	Above-ground	Polylectic	May	5
Bombus terrestris	8	5.7	Social	Below-ground	Polylectic	January	12
Ceratina cyanea	2	1.32	Solitary	Above-ground	Polylectic	NA	NA
Eucera clypeata	8	2.75	Solitary	Below-ground	Oligolectic	May	1
Eucera nigrifacies	20	2.8	Solitary	Below-ground	Oligolectic	June	1
Eucera taurica	2	3.6	NA	NA	NA	NA	NA
Halictus scabiosae	9	2.44	Social	Below-ground	Polylectic	April	6
Halictus simplex	17	1.9	Social	Below-ground	Polylectic	April	5
Hylaeus annularis	1	1.32	NA	NA	NA	NA	NA
Lasioglossum angusticeps	1	NA	NA	NA	NA	NA	NA
Lasioglossum corvinum	26	1.29	Solitary	Below-ground	Polylectic	June	2
Lasioglossum crassepunctatum	17	1.41	NA	NA	NA	NA	NA
Lasioglossum glabriusculum	3	0.73	Social	Below-ground	Polylectic	May	5
Lasioglossum interruptum	4	2.23	Social	Below-ground	Polylectic	June	3
Lasioglossum lativentre	1	1.55	Solitary	Below-ground	Polylectic	April	7
Lasioglossum leucozonium	14	1.91	Solitary	Below-ground	Polylectic	April	7
Lasioglossum malachurum	163	1.79	Social	Below-ground	Polylectic	April	7
Lasioglossum minutissimum	2	0.86	Solitary	Below-ground	Polylectic	April	7
Lasioglossum morio	30	1.1	Social	Below-ground	Polylectic	March	8
Lasioglossum nigripes	1	1.97	Social	Below-ground	Polylectic	June	2
Lasioglossum pauperatum	2	1.14	NA	NA	NA	NA	NA
Lasioglossum pauxillum	90	1.24	Social	Below-ground	Polylectic	April	7
Lasioglossum politum	3	0.82	Social	Below-ground	Polylectic	April	5
Lasioglossum punctatissimum	3	1.23	Solitary	Below-ground	Polylectic	April	7
Lasioglossum puncticolle	49	1.49	Social	Below-ground	Polylectic	May	5
Lasioglossum pygmaeum	1	1.32	NA	NA	NA	NA	NA
Lasioglossum subhirtum	1	1.2	NA	Below-ground	Polylectic	April	3
Lasioglossum villosulum	47	1.33	Social	Below-ground	Polylectic	April	8
Lasioglossum zonulum	5	1.95	Solitary	Below-ground	Polylectic	April	7
Tetralonia malvae	3	2.61	Solitary	Below-ground	NA	NA	NA

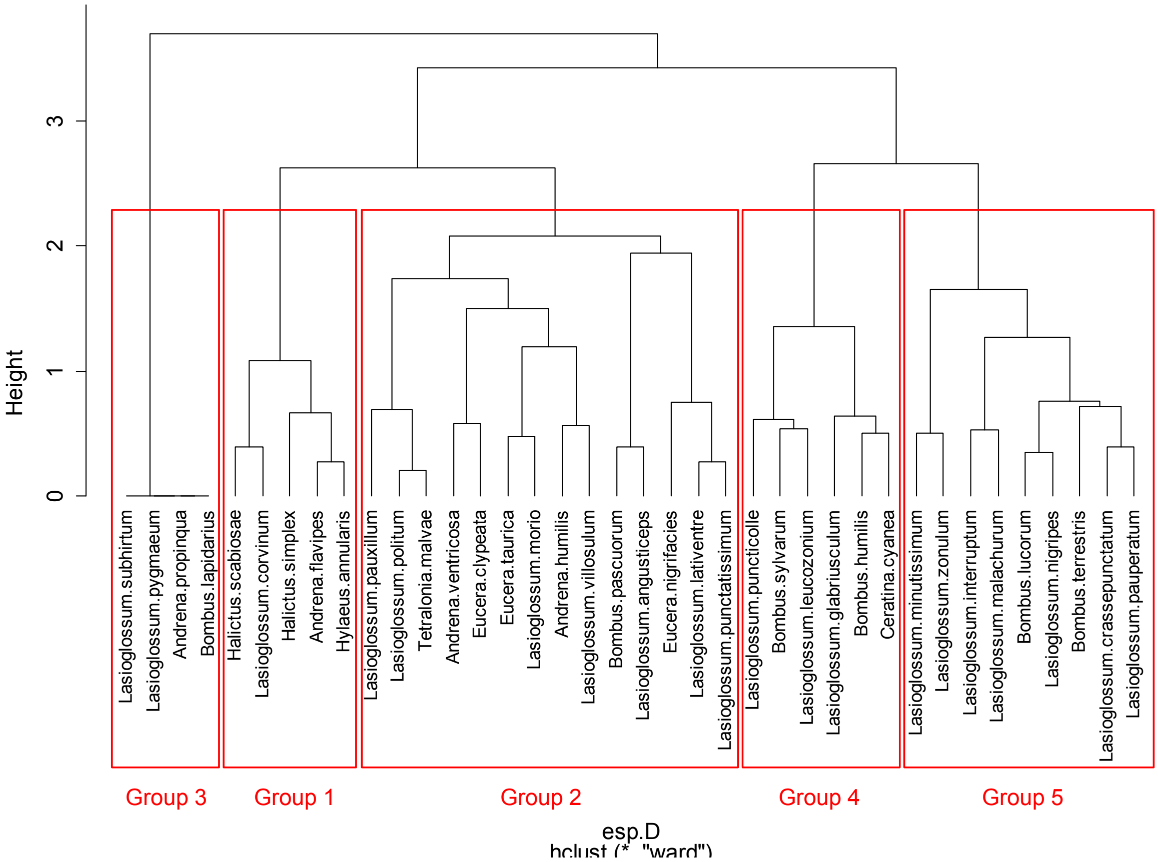

Figure S2 Hierarchical clustering of bee species based on their abundances along the landscape gradients. The clustering was processed on the correlation matrix of species abundances. Each group contains species that co-occurred in at least on site of the study.

Table S3 Maximum Spearman correlation coefficient seed set and between species richness/abundance for each assemblage tested in the study, for every group of co-occurrent species. The best assemblages (which maximize the correlation between seed set and species richness/abundance) are indicated in green (P<0.05 *; P<0.01 **). Even if species were chosen randomly in each group, there was a nested structure in the different assemblages.

	Nb species	Assemblages	Coef. Seed set~Species richness	Coef. Seed set~Abundance
Group #1	2	*A. flavipes+H. annularis*	0.14	0.14
	3	*A. flavipes+H. annularis+L. corvinum*	-0.04	-0.14
	4	*A. flavipes+H. scabiosae+H. annularis+L. corvinum*	-0.12	-0.18
	5	*A. flavipes+H. scabiosae+H. simplex+H. annularis+L. corvinum*	-0.2	-0.31
Group #2	2	*A. humilis+L. punctatissimum*	0.6 *	0.6 *
	3	*A. humilis+L. lativentre+L. punctatissimum*	0.6 *	0.61 **
	4	*A. humilis+A. ventricosa+L. lativentre+L. punctatissimum*	0.6 *	0.61 **
	5	*A. humilis+A. ventricosa+E. taurica+L. lativentre+L. punctatissimum*	0.58 *	0.59 *
	6	*A. humilis+A. ventricosa+E. taurica+L. lativentre+L. punctatissimum+L. villosulum*	0.5 *	0.43
	7	*A. humilis+A. ventricosa+E. clypeata+E. taurica+L. angusticeps+L. lativentre+L. punctatissimum*	0.49 *	0.47
	8	*A. humilis+A. ventricosa+E. clypeata+E. taurica+L. angusticeps+L. lativentre+L. punctatissimum+L. villosulum*	0.48	0.41
	9	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. taurica+L. angusticeps+L. lativentre+L. punctatissimum+L. villosulum*	0.39	0.39
	10	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. nigrifacies+E. taurica+L. angusticeps+L. lativentre+L. punctatissimum+L. villosulum*	0.32	0.27
	11	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. nigrifacies+E. taurica+L. angusticeps+L. lativentre+L. politum+L. punctatissimum+L. villosulum*	0.28	0.24
	12	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. nigrifacies+E. taurica+L. angusticeps+L. lativentre+L. politum+L. punctatissimum+L. villosulum+T. malvae*	0.19	0.22
	13	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. nigrifacies+E. taurica+L. angusticeps+L. lativentre+L. pauxillum+L. politum+L. punctatissimum+L. villosulum+T. malvae*	0.13	0.01
	14	*A. humilis+A. ventricosa+B. pascuorum+E. clypeata+E. nigrifacies+E. taurica+L. angusticeps+L. lativentre+L. morio+L. pauxillum+L. politum+L. punctatissimum+L. villosulum+T. malvae*	0.03	-0.06
Group #4	2	*B. sylvarum+C. cyanea*	0.26	0.26
	3	*B. humilis+B. sylvarum+C. cyanea*	0.26	0.26
	4	*B. humilis+B. sylvarum+C. cyanea+L. leucozonium*	0.12	0.09
	5	*B. humilis+B. sylvarum+C. cyanea+L. leucozonium+L. puncticolle*	0.08	0.05
	6	*B. humilis+B. sylvarum+C. cyanea+L. glabriusculum+L. leucozonium+L. puncticolle*	-0.06	-0.04
Group #5	2	L. crassepunctatum+L. zonulum	0.52 *	0.44
	3	L. crassepunctatum+L. minutissimum+L. zonulum	0.53 *	0.47
	4	L. crassepunctatum+L. minutissimum+L. nigripes+L. zonulum	0.53 *	0.47
	5	B. lucorum+L. crassepunctatum+L. minutissimum+L. nigripes+L. zonulum	0.52 *	0.47
	6	B. lucorum+L. crassepunctatum+L. minutissimum+L. nigripes+L. pauperatum+L. zonulum	0.49 *	0.45
	7	B. lucorum+L. crassepunctatum+L. interruptum+L. minutissimum+L. nigripes+L. pauperatum+L. zonulum	0.45	0.42
	8	B. lucorum+B. terrestris+L. crassepunctatum+L. interruptum+L. minutissimum+L. nigripes+L. pauperatum+L. zonulum	0.34	0.34
	9	B. lucorum+B. terrestris+L. crassepunctatum+L. interruptum+L. malachurum+L. minutissimum+L. nigripes+L. pauperatum+L. zonulum	0.27	-0.2

Discussion générale

I- Réponse des communautés d'abeilles sauvages et de la pollinisation à l'hétérogénéité des paysages et aux pratiques agricoles

1- Une approche fonctionnelle pour une vision plus mécaniste du lien entre paysage et diversité des abeilles sauvages

a- L'hétérogénéité du paysage peut jouer le rôle de filtre des espèces d'abeilles sauvages selon leurs traits

Nos résultats ont permis de mettre en évidence que la composition des paysages en milieux semi-naturels peut jouer le rôle de filtre sur les communautés d'abeilles sauvages, en excluant les espèces oligolectiques dans les paysages fortement boisés (Chapitre 1). Ces espèces oligolectiques, spécialisées dans le butinage de plantes de la famille des Brassicacées et Fabacées, peuvent facilement trouver ces ressources au sein de la mosaïque cultivée, sous forme sauvage (adventices des bordures de champs, dans les parcelles) ou cultivée (moutarde, colza, soja, féverole, pois, etc.) (Bretagnolle and Gaba, 2015). Dans les paysages fortement boisés, les parcelles contenant ces ressources utiles aux espèces oligolectiques dans la mosaïque cultivée tendent à être plus rares mais aussi isolées spatialement. Les abeilles aux exigences trophiques spécialisées ont tendance à être défavorisées comparativement aux espèces généralistes dans des contextes paysagers où les ressources sont rares et peu accessibles (Bommarco et al., 2010; Williams et al., 2010). Notre étude confirme donc que la faible disponibilité en ressources peut filtrer les espèces spécialistes capturées dans les parcelles agricoles. Contrairement à ce qui était attendu, les variables paysagères ont filtré des espèces dépendantes de ressources fournies par la mosaïque cultivée plutôt que des espèces dépendantes des milieux semi-naturels. Cette absence de filtres liée à la quantité de milieux semi-naturels est sûrement due au fait que nous n'avions pas de situations où des paysages étaient dénués de tout milieu semi-naturel.

L'étude des effets de filtres a été possible via l'utilisation de modèles nuls, permettant de confronter des patrons observés d'occurrences d'espèces à des patrons théoriques. Les modèles nuls permettent de créer, à partir des données disponibles, des distributions aléatoires d'espèces dans les limites d'une hypothèse nulle bien définie (Gotelli, 2001). L'hypothèse nulle doit être définie afin d'exclure de façon délibérée le mécanisme d'intérêt à l'étude. La différence entre la distribution générée par le modèle nul et la distribution observée permet donc de statuer sur la présence non aléatoire d'un patron de distribution et d'inférer sur le mécanisme sous-jacent (Gotelli, 2001; Gotelli and Ulrich, 2012). Dans notre étude, l'hypothèse nulle consistait à supposer que les espèces n'étaient pas filtrées le long des gradients paysagers et était donc formulée ainsi : « les occurrences des espèces sont distribuées de façon aléatoires le long des gradients paysagers, indépendamment de leurs traits ou de l'environnement ». Une différence significative entre les occurrences observées et prédites, via le calcul d'une statistique de test appropriée, nous a donc permis d'inférer sur la présence d'un effet de filtre de l'environnement sur des valeurs de traits données. En cela, les modèles nuls peuvent donner des indices sur la présence de processus, tels que des filtres écologiques ou la percolation d'individus au travers des paysages, à partir de patrons observés de distributions d'espèces (Turner, 1989). L'utilisation de modèles nuls est donc une façon de rendre l'écologie du paysage plus prédictive et d'approfondir les connaissances sur des processus écologiques à partir de patrons observés (Turner, 1989).

Notre étude confirme l'hypothèse selon laquelle la structure des paysages peut contraindre les assemblages locaux des espèces en filtrant les espèces non aptes à survivre dans un contexte paysager donné (Tscharntke et al., 2012). Cependant nos résultats suggèrent que l'effet de filtre a une portée relativement faible sur les changements de distribution des valeurs de traits le long de gradients paysagers (Chapitre 1). Les mécanismes jouant sur les abondances relatives des espèces sont d'ordres abiotiques (tolérance différentes suivant les espèces à une condition climatique donnée par exemple) ou biotique (partition des ressources, dominance de stratégies compétitives) (Bernard-Verdier et al., 2012; Cornwell and Ackerly, 2009; Kraft et al., 2015). Cependant, les effets de filtres et les mécanismes jouant sur les abondances relatives des espèces n'agissent pas de manière indépendante dans les écosystèmes (Bernard-Verdier et al., 2012; Cornwell and Ackerly, 2009; Hoiss et al., 2012). En effet, ils peuvent agir de façon concomitante sur la structure des communautés, et traduire le degré de réponse des communautés à un changement de l'environnement (Hoiss et al., 2012; Kraft et al., 2015). En effet, des conditions extrêmes de l'environnement sont à même de réduire fortement la taille des populations d'une espèce sensible à ces variations, jusqu'à l'extinction locale de l'espèce en question. Ainsi, l'exclusion de certaines espèces dans des conditions environnementales données peut être considérée comme une réponse extrême des espèces à l'environnement (« hard edge », Kraft et al., 2015). Il sera donc moins aisé de détecter des effets de filtre le long d'un gradient de conditions environnementales peu contrastées, puisque le filtrage des espèces a tendance à s'observer dans des conditions extrêmes de l'environnement (Hoiss et al., 2012; Kraft et al., 2015; Sydenham et al., 2015). Par conséquent une variable n'influençant que l'abondance relative des espèces dans un contexte donné sera peut-être identifiée comme filtrant des espèces dans un autre (Fig. 1). De plus, il est important de noter que des processus comme la compétition, qui influence l'équitabilité des espèces, peut aller jusqu'à exclure (filtrer) certaines espèces (Bernard-Verdier et al., 2012; Kraft et al., 2015).

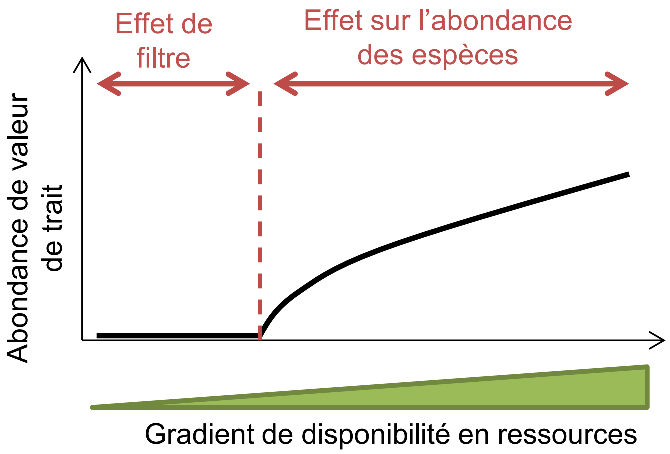

Figure 1 Illustration des effets de filtre et de la fluctuation de l'abondance de traits le long d'un gradient de disponibilité en ressources. Les effets de filtres peuvent être compris comme une réponse extrême des espèces à l'environnement. Ainsi, les conditions de l'environnement sont tellement défavorables qu'elles peuvent mener à l'extinction locale des espèces. Pour des études utilisant un gradient environnemental comprenant des situations peu contrastées et où la quantité de ressources est non limitante (partie droite du gradient), une variable de l'environnement ne sera pas identifiée comme jouant le rôle de filtres sur certaines espèces. Au contraire, pour des études utilisant un gradient de disponibilités en ressource très contrastées, l'effet de filtre de l'environnement sera plus à même d'être détecté.

b- Les changements d'abondances de traits révèlent des utilisations des milieux semi-naturels contrastées suivant les espèces

Nous avons détecté des patrons différents de variation de la structure fonctionnelle des communautés d'abeilles sauvages entre les chapitres 1 et 2, pourtant basés sur les mêmes données. En effet, nous avons détecté dans le chapitre 2 que les gradients paysagers influençaient la distribution d'un plus grand nombre de traits que dans le chapitre 1. Cette différence peut potentiellement provenir de :

i) **La différence dans la caractérisation de la composition et de la configuration des milieux semi-naturels** (MSN). En effet dans le chapitre 1, la composition des paysages était mesurée par la proportion des différents MSN, alors que la configuration était évaluée par la quantité d'interface entre un MSN donné et la mosaïque cultivée. Cependant, dans le chapitre 2, nous avons mesuré l'effet conjoint de la composition et de la configuration des MSN en créant des variables combinant l'effet de la quantité de MSN et l'isolement des différentes taches de MSN (fragmentation). Nous avons montré dans le chapitre 1 que la quantité d'interfaces MSN/mosaïque cultivée influençait minoritairement la structure fonctionnelle des communautés d'abeilles sauvages. Cependant, nous avons trouvé qu'un plus grand nombre de traits variaient le long des gradients paysagers dans le chapitre 2, suggérant que les effets combinés de l'isolement et de la quantité des taches de MSN structurent plus les communautés que la quantité d'interface MSN/zones cultivées et la proportion de MSN étudiées séparément.

ii) **La différence dans la caractérisation de la distribution des traits.** En effet, nous avons considérés chaque trait de façon indépendante dans le chapitre 1, alors que l'approche d'ordination dans le chapitre 2 nous a permis de rendre compte de variations dans la distribution de multiples traits le long des gradients paysagers. La méthode RLQ (ordination de trois tableaux relevés d'espèces-traits-environnement) utilisée dans le chapitre 2 permet de trouver une combinaison linéaire de variables environnementales et de traits qui maximise leur covariation. En cela, elle semble plus efficace pour trouver les relations principales entre traits et environnement, conditionnées par les abondances relatives des espèces et ce même en cas de corrélation entre traits (Dray et al., 2014). Le fait de considérer chaque trait de façon indépendante nous a empêché de prendre en compte la covariation qui peut exister entre les espèces le long de gradient environnementaux (Ekroos et al., 2013; Hopfenmüller et al., 2014; Suding et al., 2008) et a sûrement masqué certaines relations entre traits et environnements. La RLQ semble donc plus appropriée pour détecter des changements de distribution d'abondance de traits. Cependant les deux approches statistiques sont complémentaires puisque les modèles développés dans le chapitre 1, indépendamment sur chaque trait, nous ont permis de détecter des effets de filtres, impossible à détecter avec une analyse RLQ.

La distribution de plusieurs traits variait le long des gradients de proportion et de fragmentation des prairies permanentes et des bois (Chapitre 2). Nos résultats suggèrent que ces variations conjointes de traits ne sont pas systématiquement contraintes par la corrélation entre traits des espèces et ne sont pas le résultat de la réponse aux variables paysagères d'un groupe d'espèces phylogénétiquement proches, partageant des valeurs de traits communes du fait de leur parenté. Par conséquent, les traits écologiques qui répondent aux variations de structure des paysages semblent être en majorité des traits de réponse dans cette étude (effet direct de l'environnement sur la distribution de ces traits) et ne varient pas en raison de corrélations entre traits écologiques et traits de réponse (Suding et al., 2008).

Cette étude a été réalisée en collaboration avec une équipe de chercheurs australiens, et leur jeu de données issues d'une étude menée en Nouvelle-Galles du Sud, Australie, a montré des résultats similaires au sein d'une région agricole abritant des espèces différentes des Coteaux de Gascogne. La distribution des traits écologiques variait donc le long des gradients paysagers du fait de l'implication de ces traits dans la réponse des espèces au contexte paysager. Cependant, nous avons trouvés que les traits impliqués dans la réponse à la quantité et la fragmentation des milieux semi-naturels sont différents suivant les deux régions étudiées. En effet, la taille du corps détermine fortement la réponse des espèces à la quantité et la fragmentation des MSN dans les Coteaux de Gascogne, tandis que c'est la localisation de nid (terricole, cavicole) en Australie. Ces résultats suggèrent que dans les Coteaux de Gascogne, les MSN permettent de promouvoir, au sein des parcelles agricoles, des espèces aux capacités de dispersion faibles, tandis qu'en Australie les MSN favorisent la présence d'espèces aux exigences écologiques spécifiques (nids localisés dans des substrats boisés), sans relation à leur capacité de dispersion. Ces résultats montrent qu'il est important de prendre en compte l'effet du pool régional d'espèce dans les études multi-sites, et qu'il est parfois peu pertinent de généraliser des résultats à d'autres régions.

Dans les Coteaux, nous avons donc détecté de forts changements dans la distribution de traits de réponse le long des gradients de composition et/ou configuration des milieux semi-naturels (Chapitre 1 et 2). Les traits de réponses aux variations de la quantité et de la configuration des prairies permanentes sont la taille du corps, la localisation du nid et la socialité, tandis que la date d'émergence, la spécialisation alimentaire et la socialité déterminent plutôt la réponse des espèces à la composition et configuration des zones boisées (Chapitre 1 et 2). En effet, la quantité et la proximité des prairies ont un effet positif sur l'abondance d'espèces de petites tailles, terricoles et solitaires. Il a déjà été montré que les prairies permanentes sont des habitats critiques pour les espèces d'abeilles solitaires (Jauker et al., 2013; Krauss et al., 2010) et terricoles (Hopfenmüller et al., 2014), dans les paysages agricoles. Ces espèces d'abeilles ont probablement bénéficié de la proximité des différentes prairies dans les paysages peu fragmentés, qui a favorisé les échanges d'individus entre prairies et donc l'accès à des ressources similaires (supplémentation) ou de natures différentes (complémentation) (Dunning et al., 1992). Les lisières forestières ont pu favoriser l'occurrence d'espèces précoces et sociales (fortes exigences en ressources nectarifères, Williams et al., 2010) en fournissant des ressources florales diversifiés et disponibles avant la floraison des cultures entomophiles (Bailey et al., 2014; Bretagnolle and Gaba, 2015; Williams et al., 2010).

2- Les prairies permanentes sont des habitats clés des d'abeilles sauvages dans les paysages agricoles

a- Les prairies permanentes jouent le rôle d'habitats « sources » d'abeilles sauvages dans les paysages des Coteaux de Gascogne

Nous avons montré que la proportion et l'isolement des prairies permanentes influencent la distribution de certains traits dans les communautés d'abeilles sauvages des parcelles agricoles. D'autres tests ont permis de mieux connaitre les déterminants de cet effets paysager des prairies permanentes sur les abeilles sauvages capturées dans les parcelles. En effet, le long de gradients de proportions de différent MSN (bois et prairies permanentes) et d'intensité locale des pratiques agricoles (application de pesticides, fertilisation et travail du sol), les prairies permanentes étaient les seuls milieux semi-naturels qui ont influencé la diversité et l'abondance des abeilles sauvages en parcelles de céréales (chapitre 5). La proportion et la proximité des prairies permanentes dans les paysages avaient un effet positif sur l'abondance d'espèces dominantes (qui représentent plus de 80% de tous les spécimens capturés) et sur la diversité d'espèces sub-dominantes (ou rares). Cette étude confirme donc le rôle important des prairies permanentes dans la conservation des abeilles sauvages en permettant le maintien d'espèces peu communes à l'intérieur et en bordure de parcelles de céréales (Morandin et al., 2007; Steffan-Dewenter et al., 2002; Steffan-Dewenter and Tscharntke, 1999), suggérant que :

i) Les prairies permanentes fournissent des ressources critiques aux abeilles sauvages qui permettent de maintenir une diversité importante d'espèces aux exigences écologiques variées. Des études au sein de prairies permanentes ont mis en évidence que les abeilles terricoles et certaines espèces de bourdons pouvaient y trouver des ressources abondantes en nids (Hopfenmüller et al., 2014; Svensson et al., 2000). La richesse spécifique et la couverture locale des plantes à fleurs dans les prairies permanentes a aussi un effet significatif sur la richesse spécifique des abeilles sauvages (Batáry et al., 2010; Ebeling et al., 2008), suggérant un rôle majeur dans la provision de ressources trophiques.

ii) Les prairies permanentes sont des sources d'abeilles sauvages pour les parcelles agricoles environnantes (Albrecht et al., 2007; Morandin et al., 2007; Steffan-Dewenter and Tscharntke, 1999), expliquant l'effet positif de la proportion de prairies sur la diversité des abeilles sauvages dans les parcelles agricoles. Dans les paysages à forte couverture en prairies, les opportunités de spill-over (débordement) vers les zones cultivées seraient plus importantes du fait de la plus grande proximité entre les parcelles focales (échantillonnées) et les prairies mais aussi du fait de la plus grande « capacité d'accueil » des prairies. Cette capacité d'accueil est plus importante pour des prairies de grande taille et faiblement isolées (Hopfenmüller et al., 2014; Jauker et al., 2013).

Dans le chapitre 5, notre objectif était de savoir si la disponibilité des ressources en nids au sein des prairies permanentes pouvait influencer la diversité des abeilles sauvages dans les parcelles agricoles. Deux facteurs sont connus pour influencer localement la densité des nids d'espèces terricoles au sein des prairies: la quantité de zones de sols nus/végétation éparse et de pentes fortes (Hopfenmüller et al., 2014; Potts et al., 2005; Sardiñas and Kremen, 2014). Nous avons évalué par télédétection, en collaboration avec des chercheurs géomaticiens du laboratoire, l'occurrence à l'échelle du paysage de ces deux indicateurs de la qualité nidicole des prairies. Ces deux indicateurs étaient indépendants de la quantité et de la diversité des ressources en fleurs, évaluées grâce à des relevés botaniques sur une partie des prairies analysées par télédétection. Notre hypothèse était que, puisque la disponibilité des ressources en nid dans les prairies a un effet positif sur l'abondance et la diversité locale des abeilles terricoles qu'elles abritent (Hopfenmüller et al., 2014), la quantité de ressources en nid dans toutes les prairies des paysages devrait en partie expliquer l'abondance et la diversité des abeilles, en particulier terricoles, capturées dans les parcelles agricoles. Nos résultats ont prouvé que ces deux indicateurs influencent positivement l'abondance des abeilles terricoles et de grande taille (à forte capacité de dispersion) et aussi les espèces terricoles et oligolectiques. Il semblerait aussi que la pente des prairies influence plus l'abondance des abeilles sauvages des parcelles agricoles que les zones prairiales clairsemées. Nos résultats suggèrent donc que ces deux proxys des ressources en nid ont une influence paysagère sur les abeilles sauvages capturées dans les parcelles agricoles. Notre étude suggère aussi que les prairies permanentes jouent un rôle source d'abeilles sauvages pour la mosaïque cultivée en raison des ressources en nid qu'elles fournissent, et ce indépendamment des ressources florales. Cet effet positif des ressources en nid sur des espèces pouvant avoir accès à des taches de ressources isolées (espèces de grande taille, Greenleaf et al., 2007) et sur des espèces aux exigences florales importantes, suggère la présence d'un effet de complémentation entre ressources florales et nidicoles fournies par différentes prairies (Dunning et al., 1992). Cependant, pour confirmer cette tendance, il faudrait pouvoir quantifier les ressources florales sur un nombre important de prairies et tester l'effet indépendant des deux types de ressources sur les communautés d'abeilles sauvages.

b- Le rôle d'habitat source des prairies est modulé par les pratiques agricoles dans la mosaïque cultivée

La prise en compte de l'effet des pratiques agricoles sur la biodiversité est un enjeu fort en agroécologie, puisque si un tel effet est avéré, les changements de pratiques pourraient constituer un levier important pour maintenir voire atteindre un certain niveau de biodiversité en contexte agricole (Bengtsson et al., 2005; Kremen et al., 2007b). Alors que l'intensification des pratiques agricoles s'effectue à l'échelle des paysages et des territoires (Burel and Baudry, 1990; Herzog et al., 2006; Robinson and Sutherland, 2002), son effet sur la biodiversité est souvent étudié à l'échelle parcellaire (Batáry et al., 2010; Bengtsson et al., 2005). Pour des groupes fonctionnels mobilisant des ressources à l'échelle paysagère comme les abeilles sauvages, il est nécessaire de mieux connaître l'effet de l'intensité pratiques agricoles à l'échelle paysagère sur leur diversité (Kremen et al., 2007b).

Nous avons montré, dans le chapitre 3, que la proportion en MSN et l'intensité paysagère des pratiques agricoles agissaient en interaction sur la diversité des abeilles sauvages dans les parcelles agricoles, indépendamment de l'intensité locale des pratiques. Un des principaux résultats est que l'effet positif de la proportion en prairies permanentes sur la diversité des abeilles est plus important dans les paysages avec de forts apports de pesticides et une proportion forte de parcelles labourées (Fig. 2).

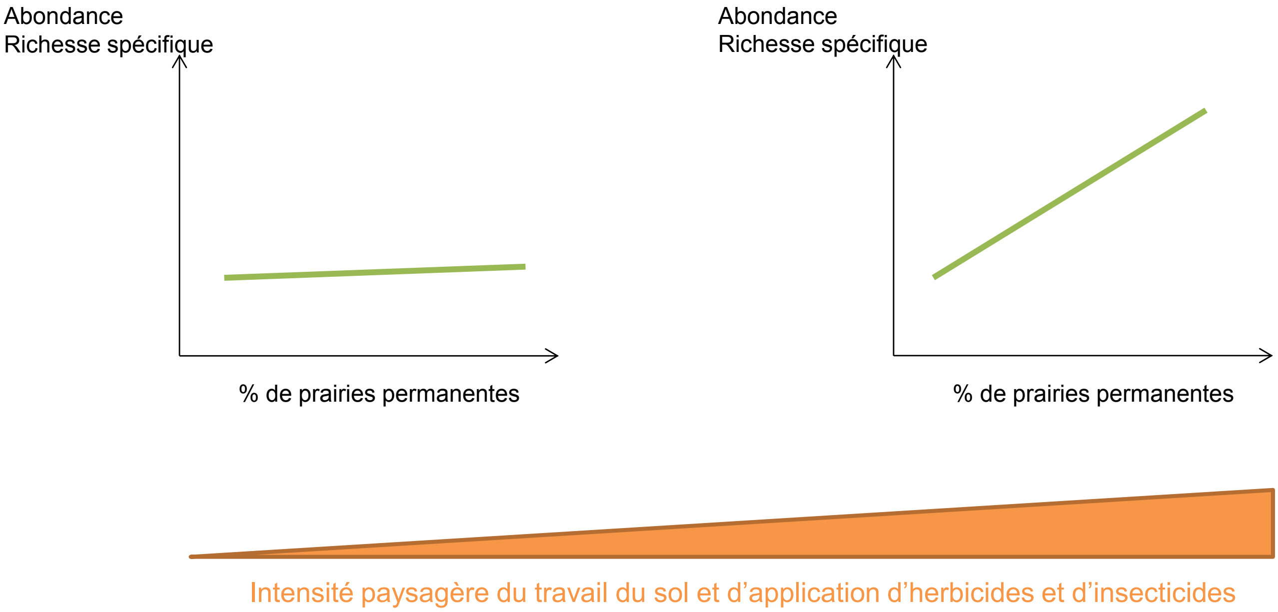

Figure 2 Représentation schématique de l’effet interactif de la proportion de prairies permanentes et des pratiques agricoles sur la diversité locale des abeilles sauvages en parcelles agricoles (chapitre 3). Cette interaction montre que la proportion de prairies influence fortement la diversité locale des abeilles sauvages dans des paysages où la mosaïque agricole est gérée de façon intensive, mais a peu d’effet dans les paysages gérés de façon extensive.

Une tendance similaire a été trouvée dans d’autres études en considérant l’intensité des pratiques agricoles à l’échelle locale, avec un effet positif important de la complexité paysagère sur la diversité locale des abeilles sauvages pour des parcelles gérées de façon intensive, comparativement à des parcelles aux pratiques extensives (Batáry et al., 2010). Notre étude confirme que cette relation est aussi vérifiée en considérant l’intensité des pratiques à l’échelle du paysage.

Un autre résultat du chapitre 3 est que cet effet interactif concerne majoritairement les espèces d’abeilles sauvages sub-dominantes (peu communes). Les espèces dominantes ne semblent pas être influencées par l’intensité des pratiques agricoles à l’échelle du paysage.

En reliant ces résultats à ceux des chapitre 4 et 5, on peut en déduire que l’effet source des prairies permanentes en abeilles sauvages pour les parcelles cultivées est modulé par l’intensité paysagère des pratiques agricoles. Les pratiques telles que l’utilisation d’herbicide et le travail profond du sol sont connues pour réduire la diversité et l’abondance des adventices au sein des parcelles agricoles (Holzschuh et al., 2007; Marshall et al., 2006; Murphy et al., 2006) et le labour ou l’application d’insecticides peuvent affecter directement les abeilles sauvages (C. A. Brittain et al., 2010; Whitehorn et al., 2012; Woodcock et al., 2016). Puisque les ressources florales au sein des parcelles agricoles peuvent représenter une source trophique importante pour les abeilles sauvages (Bretagnolle and Gaba, 2015), les paysages ayant une forte intensité des pratiques agricoles présentent probablement une faible qualité de la mosaïque cultivée en tant qu’habitat pour les abeilles sauvages. Nos résultats suggèrent donc qu’en contexte intensif, les parcelles agricoles auraient tendance à plus dépendre de l’immigration d’individus depuis les prairies permanentes qu’en contexte extensif. Dans les paysages extensifs, les parcelles semblent soutenir une diversité importante d'espèces d'abeilles, rendant les MSN moins déterminants pour la diversité des abeilles sauvages en parcelles agricoles. Dans notre étude comme dans d'autres dispositifs, ce sont les espèces rares qui expliquent les variations de richesse spécifique totale (Hooper et al., 2005; Winfree et al., 2015). En effet, les espèces dominantes ont plus de chance d'être présentes dans tous les sites échantillonnés, tandis que l'occurrence d'espèces peu communes a plus de chance de fluctuer le long d'un gradient environnemental, pour des raisons écologiques ou d'échantillonnage (Winfree et al., 2014, 2015). L'intensité des pratiques au sein de la mosaïque cultivée, en plus de la quantité de milieux semi-naturels, apparait donc comme un facteur déterminant de l'occurrence d'espèces rares dans les parcelles agricoles. Il semble donc essentiel de considérer le « paysage des pratiques agricoles » pour conserver les abeilles sauvages en zones agricoles.

3- Influence de la structure des communautés d'abeilles sauvages sur le succès de pollinisation

Nous avons trouvé, dans les chapitres 5 et 6, que la structure des communautés d'abeilles sauvages influençait différemment le succès de pollinisation selon l'espèce de plante considérée. Dans le cas où nous avons utilisé les pétunias comme phytomètre pour estimer le succès de pollinisation (nombre de graines par fruit), nous avons montré que l'abondance d'espèces dominantes était fortement corrélée à la pollinisation. Cependant, dans le cas où les phytomètres étaient des plants de moutardes, l'abondance d'espèces dominantes n'était pas un facteur déterminant le succès de pollinisation (Fig. 3).

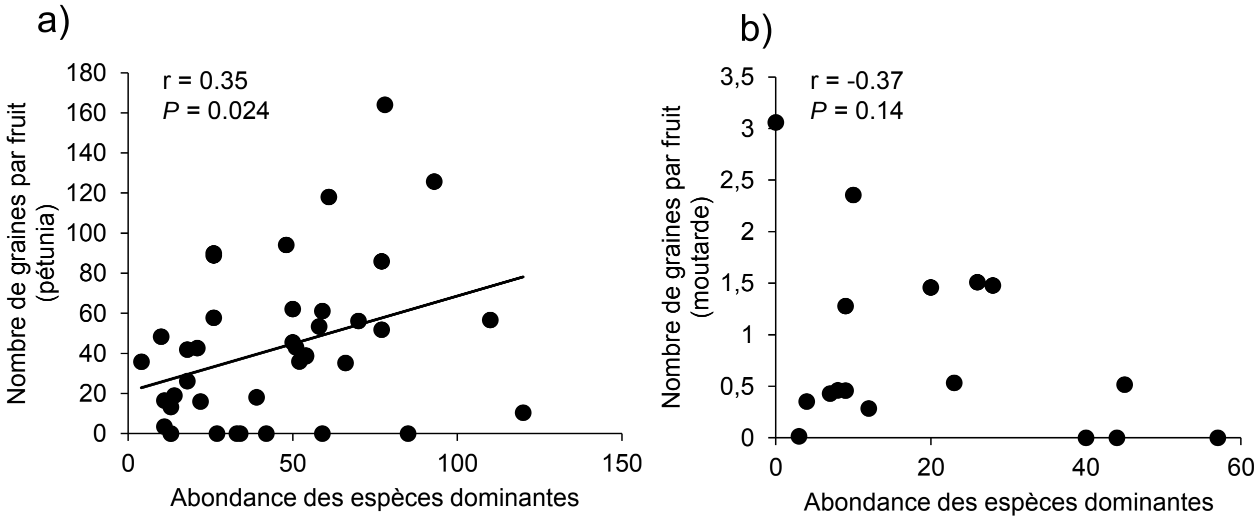

Figure 3 Corrélation de Spearman entre abondance des espèces dominante et succès de pollinisation pour les expérimentations menées avec plants de pétunia (a) et de moutarde (b).

Dans le cas des expérimentations avec les plants de pétunia, c'est l'hypothèse du « mass-ratio » qui s'est vérifiée, qui stipule que les espèces contribuent à une fonction proportionnellement à leur abondance (Grime, 1998; Hooper et al., 2005). Selon cette hypothèse, ce sont les fluctuations d'abondance des espèces dominantes qui déterminent les variations d'intensité d'une fonction écologique (Winfree et al., 2015). Les espèces d'abeilles dominantes étaient toutes sociales, polylectiques et terricoles (chapitre 5). L'absence de relation entre richesse spécifique totale et succès de pollinisation des fleurs de pétunia suggère que la complémentarité fonctionnelle entre espèces d'abeilles sauvages n'influençait pas le niveau de pollinisation dans les parcelles.

Cependant, dans le cas des expérimentations menées avec les plants de moutarde, ni l'abondance des valeurs de traits ni la diversité fonctionnelle n'étaient corrélées au succès de pollinisation (chapitre 6). Ces résultats suggèrent que ni l'hypothèse du « mass-ratio », ni celle de la complémentarité fonctionnelle ne sont vérifiées le long du gradient de complexité paysagère. Cependant, nous avons trouvé que l'occurrence de 6 espèces, faisant partie de deux assemblages de trois espèces co-occurrentes, explique une forte part de la variation de pollinisation le long du gradient paysager étudié. Les résultats démontrent que les espèces d'un des deux assemblages sont sensibles aux variations de complexité du paysage (pourcentage de milieux semi-naturels), tandis que les autres ne répondent pas au contexte paysager. Ces 6 espèces ont des abondances très faibles dans le jeu de données et sont donc considérées comme peu communes. De plus, nous avons trouvé que les succès de pollinisation dans les parcelles où ces espèces sont absentes sont très faibles voire nuls. Cela laisse à penser que c'est bien la co-occurrence de ces espèces rares et non un effet de complémentarité entre ces espèces rares et d'autres espèces plus communes qui gouverne la fourniture en pollinisation. Ces résultats permettent de reconsidérer le rôle des espèces rares dans la fourniture de services écosystémiques. En effet, de nombreuses études ont montré que la pollinisation des cultures était assurée par des espèces dominantes dans les agroécosystèmes (Kleijn et al., 2015; Winfree et al., 2015) et que l'effet généralement positif de la diversité des abeilles sauvages sur la pollinisation (Garibaldi et al., 2013) est dû à un effet d'échantillonnage (plus il y a d'espèce et plus il y a de chance qu'une ou des espèces fonctionnellement efficaces soient présentes) (Hooper et al., 2005; Loreau et al., 2001). De plus, il a été montré que les espèces communes, fonctionnellement importantes, dans les paysages agricoles n'étaient pas influencées par la proportion de milieux semi-naturels (Kleijn et al., 2015). Nos résultats concernant les plants de moutarde sont en contradiction avec ces deux points, puisque ils suggèrent que dans certaines situations, les espèces peu communes peuvent être fonctionnellement importantes et que le pourcentage de milieux semi-naturels a un rôle significativement positif sur la pollinisation.

La différence de résultats entre ces deux expérimentation menées dans la même zone d'étude peut être expliquée par :

- **La différence de cortèges de pollinisateurs des fleurs de pétunia et de moutarde**. Contrairement aux fleurs de pétunia, la complexité du paysage avaient un effet positif sur le succès de pollinisation des fleurs de moutarde (Fig. 4). Ces résultats confortent l'hypothèse selon laquelle les fleurs de pétunia ne seraient pas uniquement pollinisées par des abeilles sauvages le long des gradients paysagers étudiés. En effet, les résultats montrent une contribution significative de la pollinisation entomophile pour les fleurs de pétunia en comparant fleurs ensachées et fleurs ouvertes (chapitre 5). Or, la proportion de prairies influençait positivement la diversité en espèces d'abeilles rares et l'abondance d'espèces d'abeilles dominantes, mais sans influencer la pollinisation. D'autres espèces que les abeilles sauvages, qui ne sont pas négativement influencées par la perte de milieux semi-naturels environnants, peuvent significativement contribuer à la pollinisation des cultures (Rader et al., 2016). Ces insectes non-apiformes ont donc pu compenser les variations d'abondance et de diversité des abeilles sauvages le long des gradients paysagers et ainsi fournir un dépôt de pollen efficace dans une majorité de sites de mesure. Pour les fleurs de moutarde, nous avons aussi trouvé une contribution significative de la pollinisation entomophile. La contribution d'autres pollinisateurs que les abeilles sauvages n'est donc pas exclue, mais la relation forte que nous avons trouvée entre l'occurrence des 6 espèces d'abeilles sauvages et le succès de pollinisation des fleurs de moutarde suggère que ce sont des abeilles sauvages qui y ont majoritairement contribué. Cette différence dans les cortèges de pollinisateurs peut s'expliquer par de possibles différences dans la qualité du nectar et du pollen fournies par les fleurs de moutarde et de pétunia, deux facteurs qui peuvent conditionner le choix des espèces florales visitées par les pollinisateurs (Muth et al., 2016; Somme et al., 2015).

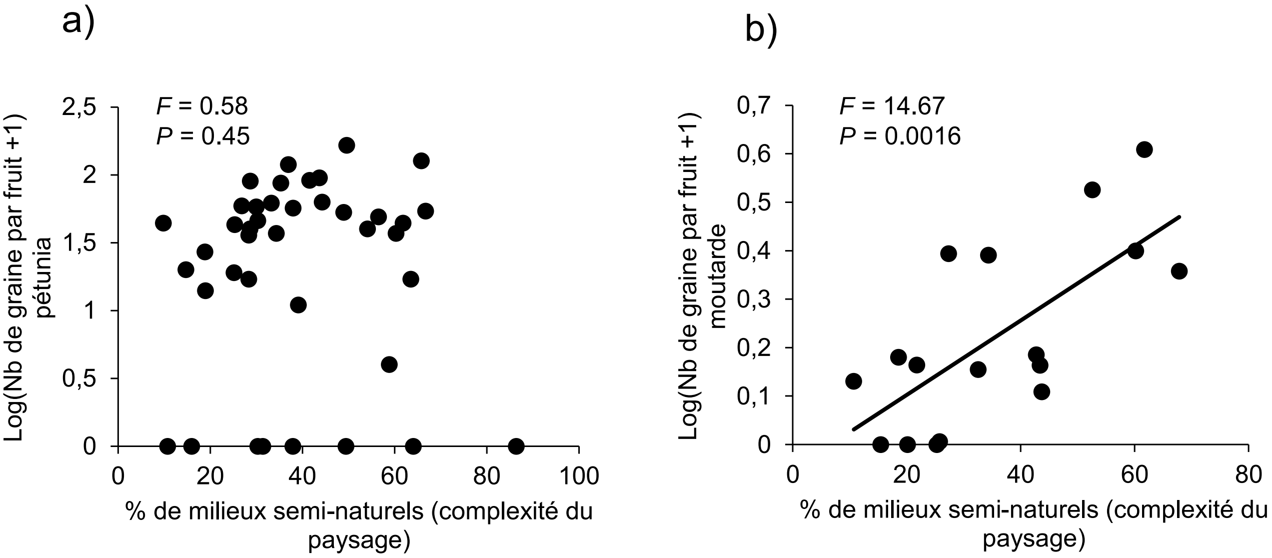

Figure 4 Effet de la complexité du paysage (% de milieux semi-naturels) sur le succès de pollinisation des fleurs de pétunia (a) et de moutarde (b) (mesuré par le nombre de graine moyen par fruit). Les nombre de graines par fruit a été transformé au log pour pourvoir réaliser les régressions linéaires.

- **La variabilité temporelle de l'importance fonctionnelle des espèces**. Les pools d'espèces capturées pendant les expérimentations de 2014 et 2015 étaient différents, probablement dû aux fluctuations des paramètres climatiques et de la disponibilité en ressource entre les deux années. La composition spécifique et l'abondance relative des espèces est très variable suivant les années (Kremen et al., 2002; Williams et al., 2001) et ces changements inter-annuels dans la structure des communautés peut faire varier la contribution relative des espèces à la pollinisation des cultures (Fig. 5, Kremen et al., 2002). En effet, des espèces fonctionnellement importantes une année donnée (espèce n° 13 année 2000, points noirs) peut ne plus contribuer aussi fortement l'année suivante (année 2001, points gris), et inversement (Fig. 5). Cependant, le succès de pollinisation des cultures dépend aussi du comportement de butinage des espèces (temps de butinage par fleurs, nombre de fleurs visitées, espèces visitées, Bretagnolle and Gaba, 2015; Hoehn et al., 2008; Martins et al., 2015) qui n'est souvent pas quantifié dans les expérimentations. Or, le comportement de butinage dépend fortement de la disponibilité des ressources mais aussi d'interactions biotiques entre espèces. Il a été en effet démontré que la fréquence de visite d'espèces de plante à corolle profonde par des espèces d'abeilles à longue langue diminuait en fonction de la proportion de colza dans les paysages, alors que le vol de nectar augmentait par les espèces à langue courtes (Diekötter et al., 2010). Ces résultats suggèrent la présence d'un effet de compétition entre espèces d'abeilles à langues longues et courtes, modulé par la quantité de ressources fournies par les parcelles de colza. De même, il a été montré, au sein de parcelles de tournesol, que la présence d'abeilles sauvages pouvait induire un comportement d'évitement chez les abeilles domestiques, qui se traduisait par un changement plus fréquent d'inflorescences visitées chez le tournesol (Greenleaf and Kremen, 2006). Cet évitement avait donc un effet significativement positif sur la pollinisation du tournesol, du fait que la présence d'abeilles sauvage augmentait indirectement la pollinisation croisée des fleurs de tournesol réalisée par les abeilles domestiques.

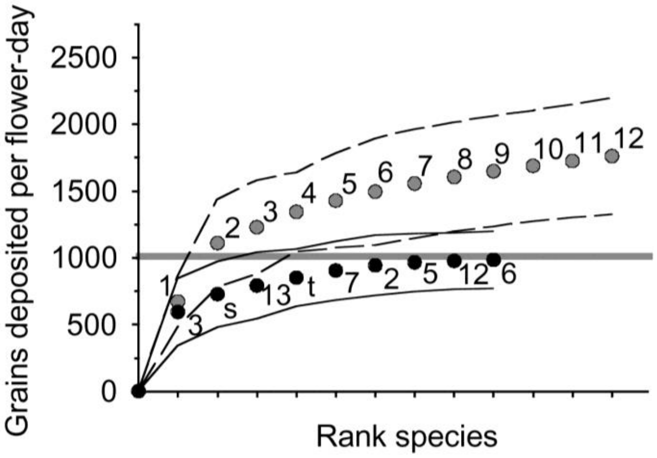

Figure 5 Moyennes (et erreurs standards) de la contribution cumulée des espèces d'abeilles sauvages au dépôt de pollen sur les stigmates de fleurs de pastèque pendant l'année 2000 (points noirs) et l'année 2001 (points gris) sur les mêmes fermes en Californie. Les lettres et les chiffrent correspondent à des espèces différentes. La ligne horizontale grise représente le dépôt de pollen minimal permettant de produire des pastèques commercialisables (extrait de Kremen et al., 2002)

Cependant, en dépit de ces différences de cortèges, nous pouvons nous demander pourquoi, dans le cas de la moutarde, ce ne sont pas les espèces dominantes qui ont préférentiellement contribué à son succès de pollinisation. L'efficacité de pollinisation de l'assemblage des 6 espèces identifiées pourrait provenir de leurs traits. En effet, ces 6 espèces avaient toutes des traits ayant favorisé leur efficacité en tant que pollinisatrices des fleurs de moutardes : elles ont des langues courtes, leur activité de butinage commence à la fin du printemps et ce pendant une longue période (7 mois). En effet les corolles de fleurs de moutardes sont peu profondes et ouvertes et donc préférentiellement visitées par des espèces d'abeilles à langue courte (Cariveau et al., 2016; Garibaldi et al., 2015). Cependant, les principales espèces dominantes capturées lors de l'expérimentation ont exactement ces même caractéristiques (*L. malachurum, L. pauxillum, L. puncticolle* : langue courte, période longue et tardive de butinage) et leurs abondances le long du gradient auraient dues être corrélées à la pollinisation de la moutarde. Une différence importante entre ces 6 espèces peu communes et les espèces dominantes était la socialité (6 espèces rares : solitaires, espèces dominantes : sociales). Or, la socialité peut influencer l'efficacité de pollinisation des espèces d'abeilles sauvages pour des plantes comme les radis (Albrecht et al., 2012) ou le café (Klein et al., 2003) mais les déterminants biologiques de ces différences d'efficacité restent peu étudiés. Klein et al. (2003) évoquent que la différence d'efficacité peut provenir de différences comportementales, les espèces solitaires récoltant plus de pollen et provoquant plus de contact entre corps et stigmate que les espèces sociales. Des connaissances plus approfondies sur le comportement de butinage et les traits des 6 espèces concernées nous permettraient de confirmer cette hypothèse.

Ainsi, les succès de pollinisation des fleurs de moutarde et de pétunia ne sont pas influencés de la même manière par les communautés d'abeilles sauvages. Ce résultat est sûrement à l'origine de la différence d'effet de l'hétérogénéité des paysages sur le succès de pollinisation des deux plantes (Fig. 4).

Nous avons donc trouvé que la présence de milieux semi-naturels pouvait, dans certains cas, avoir un effet positif sur la pollinisation. Pour confirmer les hypothèses que nous avons émises quant à l'effet contrasté des milieux semi-naturels sur la pollinisation, il est nécessaire de répliquer la démarche utilisée dans cette thèse dans d'autres paysages et d'autres régions. En répertoriant les cas où la structure des paysages influence ou pas la pollinisation, la compréhension des processus paysagers à l'œuvre permettra de mieux optimiser la fourniture de services de pollinisation.

L'approfondissement des connaissances quant à l'utilisation de leviers paysagers pour maximiser la pollinisation devra passer par :

- La vérification de la contribution des insectes (apiformes ou non) à la pollinisation des plantes cultivée ou sauvages étudiées. En effet, pour le moment, les méta-analyses étudiant la pollinisation entomophile des cultures n'ont pas pris en compte des phénomènes comme l'autopollinisation ou l'anémophilie, ni les effets des ressources en eaux ou minéraux des cultures (Garibaldi et al., 2011, 2013; Kleijn et al., 2015; Rader et al., 2016). Ces effets peuvent influencer la formation et le remplissage des graines et ainsi biaiser le lien entre structure des paysage et niveau de pollinisation (Garibaldi et al., 2011). L'utilisation de fleurs ensachées « témoins » ainsi que la standardisation des ressources hydrominérales apportées aux plants étudiés permettraient de répondre à ses objectifs.
- L'exploration fine des mécanismes à l'échelle des communautés de pollinisateurs pouvant possiblement expliquer les variations de pollinisation. En effet, la majorité des méta-analyses étudiant le lien entre pollinisateurs et pollinisation explorent les effets de la richesse spécifique (Garibaldi et al., 2011, 2013) ou de la contribution individuelle des espèces d'abeilles sauvages sur la pollinisation des cultures (Kleijn et al., 2015; Rader et al., 2016; Winfree et al., 2015). Notre travail de thèse montre que dans certains cas, le nombre d'espèces de pollinisateurs n'est pas un bon prédicteur du succès de pollinisation. De plus, les études explorant la contribution individuelle des espèces à la pollinisation évaluent le succès de pollinisation par la quantité de pollen déposé sur des fleurs « vierges » pour une visite unique d'un individu d'une seule espèce. Ce protocole ne permet pas de détecter des effets d'interactions entre espèces sur la pollinisation, telles que complémentarité spatiale ou

temporelles (Blüthgen and Klein, 2011; Winfree et al., 2015). Aussi, ces études se basent sur le dépôt de pollen, qui est corrélé à la formation des graines ou des fruit, mais de façon asymptotique (Aizen and Harder, 2007). Cette corrélation asymptotique signifie qu'à partir d'un certain seuil de quantité de pollen déposé, une espèce déposant plus de pollen qu'une autre ne contribuera pas plus à la pollinisation de la plante. Même si ces études apportent des informations capitales sur l'importance fonctionnelle des différentes espèces de pollinisateurs, la complexité des relations écologiques menant à l'élaboration du succès de pollinisation dans des contextes agricoles variés est encore à étudier.

II- Vers une gestion des paysages agricoles pour la conservation des abeilles sauvages et le maintien des services de pollinisation

1- Implications des résultats de la thèse pour la gestion de la biodiversité des abeilles sauvages dans les paysages agricoles

a- Cibler des habitats prioritaires pour la conservation des abeilles sauvages

Nos résultats suggèrent que les prairies permanentes ainsi que les lisières forestières ont un effet positif sur la diversité et l'abondance des abeilles sauvages, et en particuliers des espèces à faible capacité de dispersion et les espèces terricoles. La surface en prairies environnantes peut jouer un rôle positif sur la diversité des abeilles en parcelles agricoles, à condition qu'elles fournissent une quantité importante de sites de nidification en plus des ressources en fleurs.

La prise en compte des pollinisateurs dans les politiques publiques en France est récente (Plan national d'actions « France, terre de pollinisateurs », 2016). Un constat important qui a été fait est que les mesures ayant pour objectif la conservation de la biodiversité dans les paysages agricoles (MAE, Trame Verte et Bleue, sites Natura 2000) n'intègrent pas la préservation des pollinisateurs. Cependant, certains enjeux de la Trame Verte et Bleue (TVB, Grenelle de l'Enrivonnement) peuvent influencer positivement la diversité et l'abondance des abeilles sauvages, comme « le maintien et le développement d'une activité agricole organisée spatialement pour contribuer à une certaine hétérogénéité des paysages, et attentive au maintien ou au rétablissement […] des prairies naturelles ». Les mesures en places ne profiteraient pas forcément aux pollinisateurs du fait d'un manque de cohérence entres les différentes mesures (Plan national d'actions « France, terre de pollinisateurs », 2016). En effet, alors que les prairies semi-naturelles sont ciblées comme habitats bénéfiques dans la TVB, elles ne sont pas présentes dans les surfaces d'intérêt écologique (SIE) de la PAC (Politique Agricole Commune). Un point positif est la prise en compte des alignements d'arbres dans les SIE, dont font partie les lisières forestières, et de leur impact positif sur la biodiversité. L'intégration des prairies permanentes dans les SIE, qui reviendrait à promouvoir l'élevage extensif dans les territoires agricoles, serait un premier pas vers une conservation efficace des abeilles sauvages (Plan national d'actions « France, terre de pollinisateurs », 2016). L'utilisation de ces mesures incitatives pourrait permettre d'enrayer le retournement des prairies permanentes, constaté dans les Coteaux de Gascogne (Choisis et al., 2010; Faïq et al., 2013).

Actuellement, il y a un manque de prise en compte de la dimension paysagère dans la préservation de la biodiversité au niveau Européen. Des premières mesures de verdissement de la PAC permettent d'inciter à la conservation ou l'implantation de SIE à hauteur de 5% de la SAU (surface agricole utile) dans les exploitations agricoles. Cependant, est-ce que les 5 % de SIE par exploitation permettent de participer à l'accroissement de l'hétérogénéité des paysages ? Ne faudrait-il pas mettre des priorités sur certains types de SIE (sachant que certains SIE comme les cultures mellifères permettent d'attirer des pollinisateurs sauvages mais ne sont pas des habitats « sources », Holzschuh et al., 2016) ?

L'efficacité des politiques publiques actuelles quant à la conservation de la biodiversité, en particulier des abeilles, doit maintenant être évaluée. De plus, des études à large échelle pour la création de connaissances et d'outils sont nécessaires pour aider à piloter la gestion des paysages pour une meilleure conservation des abeilles sauvages.

b- Une possibilité de gestion paysagère des abeilles sauvages via les pratiques agricoles

Nos résultats suggèrent que l'intensité des pratiques agricoles, mesurée à l'échelle paysagère (supra-parcellaire), affecte fortement les abeilles sauvages. Ils suggèrent que les parcelles agricoles incluses dans une mosaïque cultivée gérée de façon extensive possèdent une diversité d'abeilles plus importante que dans des mosaïques intensives. L'apport de cette thèse réside dans la prise en compte de la diversité des pratiques et de la proportion de différents milieux semi-naturels. En effet, nous avons montré que l'intensité de certaines pratiques influence préférentiellement la diversité des abeilles, comme l'application d'herbicides et le travail du sol. Nous avons aussi montré que l'intensité des pratiques à l'échelle du paysage module l'effet des milieux semi-naturels sur la diversité des abeilles sauvages, en particulier pour les prairies permanentes.

Notre étude démontre l'importance de mesurer l'effet de l'intensité des pratiques agricoles à une échelle paysagère, et que les changements de pratiques doivent se faire à l'échelle des paysages et territoires. Nos résultats suggèrent en effet qu'une faible intensité des pratiques, dans plusieurs parcelles agricoles au sein de secteurs de 1 km², est associée à une diversité en abeille plus importante. Les changements de pratiques, sur plusieurs exploitations contiguës, permettraient donc de conserver les abeilles sauvages dans les paysages agricoles. Cependant il est nécessaire d'étudier si un changement dans les pratiques agricoles à l'échelle paysagère peut représenter un levier mobilisable pour gérer la biodiversité et les services écosystémiques. Ainsi, des travaux de modélisation d'accompagnement sont en cours au laboratoire Dynafor. Ces travaux permettront de valider si une démarche de concertation entre agriculteurs d'un même territoire et des prises de décisions collectives permettraient de mieux gérer la biodiversité fonctionnelle et les services écosystémiques dans les paysages agricoles.

c- Maintenir des milieux semi-naturels pour assurer un certain niveau de pollinisation

Nous avons montré que la complexité des paysages agricoles (mesurée par le pourcentage de MSN) avait un effet positif sur la pollinisation mesurée par des phytomètres. Dans le chapitre 6, nous n'avons pas pu séparer les effets du pourcentage de bois et de prairies sur la pollinisation, mais ces résultats suggèrent que ces deux types de milieux semi-naturels peuvent être importants pour assurer un fort niveau de pollinisation. En effet, les lisières forestières et les prairies permanentes peuvent fournir des ressources florales complémentaires, via des espèces de plantes différentes aux périodes de floraisons contrastées (Mallinger et al., 2016), mais aussi des ressources en nid complémentaires (Bailey et al., 2014; Hopfenmüller et al., 2014). Dans le chapitre 5, nous avons montré que même si la fragmentation des prairies n'avait pas un effet sur la pollinisation mesurée en parcelles agricoles, elle pourrait potentiellement l'affecter négativement pour des niveaux de fragmentations plus forts. Notre étude confirme donc que le maintien des milieux semi-naturels est essentiel pour la conservation des abeilles sauvages et que cela peut parfois se traduire en bénéfice pour la pollinisation.

2- Limites de cette étude et perspectives de recherche

a- Limite des études corrélatives le long de gradients pour la prédiction des effets des changements paysagers sur la biodiversité

Dans cette thèse, nous avons étudié des corrélations entre des gradients paysagers et des patrons de structures de communautés. Nous avons inféré, à partir de ces patrons, l'existence de processus écologiques grâce aux connaissances des espèces concernées. Cependant, une limite importante de ces études corrélatives est le manque de connaissances sur la relation de cause à effet entre les variables paysagères et patrons écologiques. En effet, nous avons fait l'hypothèse sous-jacente, comme la majorité des études en écologie du paysage, que la distribution des espèces capturées était le résultat de l'effet des patrons paysagers actuels (Sirami, 2016). Or, il s'avère qu'une perte d'habitat dans les paysages peut engendrer un délai de réponse des espèces à ces changements, appelée « dette d'extinction » (Herrault et al., 2016; Krauss et al., 2010; Kuussaari et al., 2009). Ainsi, la diminution de la taille d'un habitat pourrait engendrer une extinction d'espèces avec un certain délai (Essl et al., 2015; Piqueray et al., 2011). A l'opposé, l'augmentation de la richesse spécifique après restauration d'un habitat peut se produire avec un certain délai, appelé « crédit de colonisation » (Essl et al., 2015). Ces délais de réponse peuvent être favorisés par différents mécanismes, tels que la limitation des capacités de dispersion, des cycles de vie longs des espèces ou des fonctionnements en métapopulations (Essl et al., 2015).

Par conséquent, même si nous avons trouvé une corrélation positive entre la proportion de prairies permanentes et la diversité des abeilles sauvages capturées en parcelles agricoles, nous ne pouvons pas en déduire qu'une augmentation de la proportion de prairies permanentes augmenterait nécessairement la diversité des abeilles dans les parcelles agricoles. De par ces effets de délais de réponses, mais aussi du fait du manque de connaissances sur les dynamiques d'assemblage des communautés d'abeilles sauvages, ces relations de causalité sont encore à préciser. En particulier, le processus de « désassemblage » des communautés d'abeilles sauvages (perte d'espèces) et ses conséquences fonctionnelles, toujours étudiés le long de gradients spatiaux, est peu connu dans sa dimension temporelle (Cariveau et al., 2013; Larsen et al., 2005; Winfree and Kremen, 2009). Cependant, les études corrélatives le long de gradients spatiaux (études synchroniques) apportent des informations importantes quant aux facteurs écologiques pouvant jouer sur des patrons de distributions d'espèces. La multiplication des études corrélatives dans de « vrais » paysages, complétées par des études manipulatoires et de modélisation peuvent permettre de réduite les incertitudes sur la causalité de la relation entre changements paysagers et biodiversité (Kremen, 2005b).

b- Accroitre les connaissances sur les traits des espèces d'abeilles sauvages pour mieux prédire les relations entre paysage-biodiversité-pollinisation

Notre travail de thèse a permis de montrer qu'avec l'inclusion des traits écologiques dans les modèles statistiques, qui décrivent la niche écologique des espèces, nous décrivons de façon plus mécaniste la relation entre paysage – biodiversité, mais aussi la relation biodiversité – fonction écologique. Au contraire d'autres taxa comme les plantes (TRY) ou les carabes (Carabids), il n'y a pas de base de données internationale sur les traits des espèces d'abeilles sauvages. Même si nous avons pu rassembler des traits pour un maximum d'espèces, la phénologie, le statut social et la spécialisation alimentaire étaient inconnus pour un nombre importants d'espèces peu communes. Il est crucial d’encourager les initiatives visant à augmenter les connaissances écologiques des espèces d’abeilles sauvages, pour des traits déterminant l’utilisation des ressources, le comportement de butinage, mais aussi les relations interspécifiques (capacité compétitives). De façon surprenante, les connaissances concernant l’écologie des abeilles sauvages sont relativement faibles par rapport à leur importance écologique et agronomique, mais aussi par rapport à l’urgence de trouver des solutions pour enrayer leur déclin (Klein et al., 2007; Potts et al., 2010a; Woodcock et al., 2016).

c- Des fonctions écologiques aux services écosystémiques

Il y a un consensus fort dans la littérature scientifique sur l’intérêt de la biodiversité pour maintenir un niveau important et stable de fonctionnement des écosystèmes (Hooper et al., 2005; Loreau et al., 2001; Naeem et al., 2002). Cependant, il y a une confusion importante dans une majorité d’études sur les termes de fonctions écologiques et services écosystémiques (Tscharntke et al., 2005; Wood et al., 2015). Alors que les deux termes désignaient des concepts distincts dans les premiers essais de conceptualisation des services écosystémiques (Costanza et al., 1997), ce glissement sémantique dans la littérature écologique peut être source de confusion.

Les fonctions écologiques désignent des processus dans les écosystèmes, qui participent au transfert de matières, d’énergie et à la stabilité des écosystèmes (Costanza et al., 1997; Zhang et al., 2007). Les services écosystémiques sont les fonctions écologiques qui apportent un bénéfice à l’humanité (Costanza et al., 1997; Kremen, 2005b). Si on se réfère à cette définition, il devient compliqué de trouver des règles générales qui maximisent la provision de services écosystémiques, puisque la valeur des services dépend de l’échelle d’études et des acteurs concernés (Kremen et al., 2007b). En effet pour la pollinisation, une métrique couramment utilisée est le rendement des cultures, mesurée par le poids des fruits ou le nombre de graines par fruit (Liss et al., 2013). Du point de vue du marché économique, une augmentation du rendement représente un bénéfice en termes de volume de production commercialisable. Du point de vue de la population, le volume disponible est important, mais la diversité des produits l’est tout autant (Kremen et al., 2007b). Du point de vue de l’agriculteur, le revenu net issu d’une culture semble plus important que le rendement seul, puisque des pertes de rendement dues à une pratique agricole alternative peuvent être compensées par un moindre recours aux intrants. Par exemple, il a été montré que la présence d’adventices dans les parcelles de tournesol pouvait attirer les pollinisateurs sauvages et pousser les abeilles domestiques à polliniser les tournesols plutôt que les adventices (Carvalheiro et al., 2011). Dans ce cas-ci, le potentiel effet négatif des adventices sur les rendements pourrait être compensé par une pollinisation plus efficace par les abeilles, maximisant la formation des graines. Une comparaison des revenus nets dans cette étude aurait montré qu’à rendements équivalents, les agriculteurs ayant limité leur recours aux herbicides auraient eu un revenu net plus important par hectare de tournesol. Il est donc nécessaire d'intégrer la perception de la valeur des services écosystémiques par la multiplicité des acteurs dans la gestion des paysages.

Maximiser la provision d'un service est donc complexe, mais la maximisation de plusieurs services l'est aussi. En effet dans cette thèse, nous avons étudié les déterminants écologiques de fonctions écologiques (maintien de la diversité des abeilles sauvages, fonction de pollinisation), sous-tendant la production des services (biodiversité des abeilles, services de pollinisation), en nous concentrant uniquement sur les abeilles sauvages. Cependant, au sein des paysages agricoles, de multiples fonctions écologiques influencent la fourniture d'une diversité de services (de Groot et al., 2010; Kremen et al., 2007b). Or, il est possible que la maximisation d'un service écosystémique (production de denrées alimentaires) puisse mener à une réduction d'autres services (qualité de l'eau) (Bennett et al., 2009). Il est donc indispensable d'analyser les synergies et les antagonismes entre différents services dans des projets de gestions des paysages agricoles (Bennett et al., 2009; de Groot et al., 2010). Dans notre cas par exemple, une proportion plus importante de milieux semi-naturels était corrélée à de plus forts niveaux de pollinisation. Or, il s'avère que les syrphes aphidiphages, des ennemis naturels des pucerons des céréales, utilisent à la fois les lisières forestières et les champs cultivés comme habitats (Alignier et al., 2014; Sarthou et al., 2005). On pourrait donc se demander quelle serait la proportion de milieux semi-naturels optimale pour maintenir une forte provision de services de pollinisation et de régulation des ravageurs.

Une autre perspective de recherche sur le lien entre structure des paysages et pollinisation est l'exploration de la relation entre services de pollinisation et d'autres services dépendant des communautés végétales. En effet, des changements dans la provision de services de pollinisation pourraient avoir des effets en cascade sur d'autres services (capacité des prairies naturelles à stocker du carbone ou à réguler l'érosion des sols, via un effet sur la diversité des couverts végétaux, Memmott et al., 2004; Soliveres et al., 2016). De même, une diminution de la diversité végétale dans les bords de champs ou lisières forestières due à un manque de pollinisation pourrait réduire l'abondance et la diversité des auxiliaires des cultures utilisant ces ressources florales (comme les syrphes aphidiphages ou les guêpes parasitoïdes des pucerons). Une approche qui considèrerait l'apport des services de pollinisation dans le maintien de la multifonctionnalité des paysages agricoles (Soliveres et al., 2016), et pas seulement pour la pollinisation des cultures (Kleijn et al., 2015), permettrait de piloter au mieux la gestion de la biodiversité des pollinisateurs dans les paysages agricoles.

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Annexes

Annexe 1 : Liste des publications et communications associées à ce travail de thèse.

Publications à comité de lecture international

Carrié, R., Andrieu, E., Cunningham, S.A., Lentini, P.E., Loreau, M., Ouin, A. (2016) Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. *Ecography* (in press, DOI: 10.1111/ecog.02632)

Publications en préparation

Carrié, R., Andrieu, E., Ouin, A., Steffan-Dewenter, I. Interactive effects of landscape-wide intensity of farming practices and landscape complexity on wild bee diversity (soumis à Landscape Ecology)

Carrié, R., Ouin, A., Andrieu, E. Functional responses of wild bee communities to the heterogeneity of agricultural landscapes

Communication orales

Carrié, R., Ouin, A., & Andrieu, E. (2015). Landscape composition and configuration as ecological filters of wild bee functional diversity. IALE World, Portland 2015.

Poster

Carrié, R., Ouin, A., & Andrieu, E. (2014). Abeilles sauvages et pratiques agricoles à l'échelle paysagère. 7èmes Journées françaises de l'Ecologie du Paysage, IALE France, Dijon 2014

Résumé

L'importance écologique et agronomique des abeilles sauvages dans les paysages agricoles rend cruciale la gestion de ces insectes pollinisateurs. Les abeilles sauvages utilisent plusieurs habitats dans les paysages agricoles, comme les milieux semi-naturels (bois, haies, prairies permanentes), mais aussi les parcelles agricoles. L'objectif de ce travail est de caractériser la structure des communautés de pollinisateurs et le succès de pollinisation le long de gradients de composition et de configuration des milieux semi-naturels ainsi que d'intensité des pratiques agricoles à l'échelle paysagère. Par une approche basée sur les traits écologiques, traduisant des différences d'utilisation des ressources par les abeilles sauvages, nous avons mis en évidence que i) les abeilles sauvages peu mobiles, les espèces solitaires mais aussi les espèces terricoles (nids souterrains) sont plus abondantes dans des parcelles agricoles entourées d'une forte proportion de prairies permanentes faiblement fragmentées, ii) les parcelles entourées d'une forte quantité de lisières forestières présentent une abondance plus importante d'espèces peu mobiles, d'espèces tardives, sociales et polylectiques, iii) les espèces oligolectiques sont filtrées (exclues) dans les paysages fortement boisés car ce sont des espèces profitant de ressources fournies par la mosaïque cultivée. Nous avons aussi mis en évidence que l'effet positif de la proportion en milieux semi-naturels sur la diversité des abeilles sauvages était plus important dans des paysages à la mosaïque agricole gérée de façon intensive. Nous montrons par ailleurs que l'intensité locale des pratiques agricoles peut autant influencer la diversité des abeilles sauvages que la proportion de milieux semi-naturels environnants. Enfin, nous montrons que, suivant les situations, l'abondance des espèces d'abeilles sauvages dominantes ou la présence d'un assemblage d'espèces peu communes peut expliquer le succès de pollinisation. Il semblerait que, dans le cas où le succès de pollinisation répond à l'occurrence d'espèces peu communes, la proportion de milieux semi-naturels aurait une influence positive sur le succès de pollinisation par les abeilles sauvages. Ce travail de thèse démontre l'importance d'espèces peu communes, dépendantes des milieux semi-naturels, pour le succès de pollinisation mais aussi la relation positive entre l'abondance de certains groupes d'espèces et la proportion de milieux semi-naturels. Ce travail permet donc de soutenir l'hypothèse selon laquelle les milieux semi-naturels sont garants du maintien de la diversité des abeilles sauvages et des services rendus par ces dernières. Cependant, l'effet positif des milieux semi-naturels sur la diversité des abeilles sauvages est variable, puisque il dépend des pratiques agricoles à l'échelle locale et paysagère. Les préconisations d'aménagement paysager et de modifications des pratiques ne peuvent donc être faites indépendamment les unes des autres.

Mots clés : Hétérogénéité des paysages, abeilles sauvages, pollinisation, pratiques agricoles, traits écologiques, paysages agricoles

Abstract

The ecological and agricultural importance of wild bees in farmlands stresses the needs for management strategies for these insect pollinators. Wild bees use multiple habitats in agricultural landscapes, such as semi-natural habitats (woodlands, hedgerows, permanent grasslands) and crop fields. This study aims to characterize the community structure of wild bees and assess pollination delivery along gradients of landscape heterogeneity – based on the composition and configuration of semi-natural habitats – and landscape-wide intensity of farming practices. Using a trait-based approach, based on traits determining resource-use by wild bee species, we showed that i) the least mobile species, solitary bees and ground-nesting species were more abundant in crop fields surrounded by large amounts of little-fragmented permanent grasslands, ii) crop fields surrounded by high amount of woodland edges supported a greater abundance of little-mobile bee species, late-emerging bees, social bees and polylectic bees, iii) oligolectic bee species were filtered out in highly forested landscapes, because these species could thrive on resources provided by the crop mosaic. We also found that the positive effect of the proportion of semi-natural habitats on bee diversity was greater in landscapes with intensively managed crop mosaic. Moreover, we showed that the local intensity of farming practices had as much influence on bee diversity as the proportion of semi-natural habitats. Finally, we showed that, depending on situations, the abundance fluctuations of dominant bee species or the occurrence of an assemblage of uncommon bee species can explain variations in pollination success. In the cases where pollination success responded to the occurrence of uncommon species, the proportion of semi-natural habitats had a positive influence on pollination delivery provided by wild bees. This study shows the importance of some uncommon species, dependent on semi-natural habitats, for pollination delivery but also the positive relationship between the abundance of some species groups and the proportion of semi-natural habitats. This work therefore confirms the hypothesis that semi-natural habitats sustain the diversity of wild bee communities and pollination delivery. However, the positive effect of semi-natural habitats on bee diversity depends on farming practices at the local and landscape scale. Therefore, recommendations on the management of landscape heterogeneity and changes in farming practices cannot be given independently from each other.

Keywords: Landscape heterogeneity, wild bees, pollination, farming practices, ecological traits, agricultural landscapes