



HAL
open science

Effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales

Léa Uroy

► **To cite this version:**

Léa Uroy. Effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales. Sciences agricoles. Université de Rennes, 2020. Français. NNT : 2020REN1B030 . tel-04306446

HAL Id: tel-04306446

<https://theses.hal.science/tel-04306446>

Submitted on 25 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THESE DE DOCTORAT DE

L'UNIVERSITE DE RENNES 1

ECOLE DOCTORALE N° 600

Ecole doctorale Ecologie, Géosciences, Agronomie et Alimentation

Spécialité : Ecologie et Evolution

Par

Léa UROY

Effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales

Thèse présentée et soutenue à Rennes, le 24 novembre 2020

Unité de recherche : UMR CNRS 6553 ECOBIO & UMR 0980 BAGAP

Rapporteurs avant soutenance

Marie-Josée Fortin	Professeure, Université de Toronto
François Munoz	Professeur, Université Grenoble Alpes

Composition du Jury

Président	Edith Le Cadre	Professeure, Agrocampus Ouest
Rapporteurs	Marie-Josée Fortin François Munoz	Professeure, Université de Toronto Professeur, Université Grenoble Alpes
Examineurs	Laurent Bergès Guillaume Decocq	Ingénieur de recherche, INRAE Professeur, Université de Picardie Jules Verne
Directeur de thèse	Cendrine Mony	Maître de conférences, Université de Rennes 1
Co-directeurs de thèse	Audrey Alignier Aude Ernoult	Chargée de recherche, INRAE Maître de conférences, Université de Rennes 1

Projet
soutenu par

Fondation
de
France

Cette thèse a été préparée au sein des unités mixtes de recherche Ecosystèmes, Biodiversité, Evolution (UMR CNRS 6553 ECOBIO, Université de Rennes 1) et Biodiversité, AGroécologie et Aménagement du Paysage (UMR 0980 BAGAP, Agrocampus Ouest/l'institut Agro-ESA-INRAE), grâce au support financier du programme Agroforesterie de la **Fondation de France**.



Remerciements

Au cours de ces trois années de thèse, j'ai souvent pensé à ce moment où je devrais écrire mes remerciements. Ce temps est maintenant arrivé, et je ne sais si les lignes qui suivent suffiront à exprimer l'immense gratitude que j'éprouve envers toutes les personnes qui m'ont accompagnée dans cette aventure.

Avant tout, je pense bien évidemment à mes trois encadrantes : Cendrine, Audrey, et Aude. S'il m'est difficile de trouver les mots justes, c'est probablement parce que je ne vous remercierai jamais assez pour tout ce que vous m'avez apporté. Merci d'avoir été non seulement des encadrantes à toute épreuve (... et c'est peu de le dire), mais aussi des personnes extraordinaires et inspirantes. Je mesure la chance d'avoir croisé votre chemin, et j'espère sincèrement qu'ils se croiseront de nouveaux. Merci.

Je souhaite remercier chaleureusement les membres du jury qui ont accepté d'évaluer mon travail : Marie-Josée Fortin, François Munoz, Laurent Bergès, Guillaume Decocq et Edith Le Cadre. Mes remerciements vont également aux membres de mon comité de thèse : Déborah Closset-Kopp, Jean-Christophe Foltête, Sabrina Gaba et Vincent Jung, pour la pertinence de leurs conseils.

Même si « la connectivité, c'est pas sorcier ! » (Ernault 2018), je remercie vivement Jean-Nabucet, Charlotte Brabant, Tamara Alcalá-Jimenez et Yann Rantier pour leur initiation aux joies de la photo-interprétation, et pour leur aide en SIG. Merci à eux, et à Kemap pour leur travail sur les données cartographiques. Merci également à Hugues pour sa disponibilité et sa réactivité quant à l'utilisation du logiciel Chloé. Mes remerciements se tournent à nouveau vers Jean-Christophe Foltête pour les discussions et réflexions quant à la caractérisation de la connectivité. Merci également d'avoir accepté d'apporter votre expertise et vos connaissances pour la revue littéraire synthétisant les méthodes d'évaluation de la dynamique temporelle de connectivité. Speaking of collaboration, thank you to Santiago Saura, and, more recently, Marie-Josée Fortin, Alexandre C. Martensen and Jun-Long (Mark) Huang for your availability and enthusiasm to extend the spatio-temporal connectivity modelling to multiple time steps, and further. It was a real chance for me to discuss it with you.

Je remercie l'ensemble des agriculteurs de la Zone Atelier Armorique de Pleine-Fougères pour leur bienveillance. Merci non seulement à ceux qui m'ont autorisée à échantillonner leurs parcelles, mais aussi à tous ceux qui ont dû supporter mes nombreuses

allées et venues ! Merci de m'avoir toujours reçue avec le sourire, et d'avoir pris le temps de répondre à mes questions. Un merci tout particulier à Mr. Jean-Yves Éon d'avoir sauvé notre V3, qui a, malencontreusement atterri dans le fossé, à Mr. Jean-Luc Gauthier, le fameux !, mais aussi à Karine, pour nous avoir acceptés, parfois tout boueux, au « Ty Coat » de Trans-La-Forêt. Si le terrain fut, sans conteste, l'un des meilleurs moments de ma thèse, c'est, en grande partie grâce à vous.

Mais c'est aussi grâce à tous mes compagnons de terrains, qui ont accepté de sillonner la ZA avec moi, depuis la prospection jusqu'à l'échantillonnage, parfois au péril de leur vie... mais aussi à tous ceux qui se sont lancés (à corps perdu !) dans l'aventure de la banque de graines. Je pense bien évidemment à : Arnaud, Audrey, Aude, Benoit, Cendrine, Olivier, Rémi, Romain, Valérie mais aussi à tous mes stagiaires : Ophélie, Louise, Léo, Mathieu, Clément, Kévin et Maxime. Je garde de fabuleux souvenirs avec vous, crapahutant dans la ZA pour chercher des parcelles, mais aussi des agriculteurs, pour échantillonner les plantes ou encore carotter le sol... et ce, sous la neige, la pluie ou sous un soleil de plomb ! Bien évidemment, le tamisage et le suivi des plantules sous serre, bien que laborieux, reste également inoubliable. Merci à Jef et à Jean-Pierre pour les prototypes et la réalisation des carotteurs de l'extrême. Merci encore à Rémi, mais aussi à Thierry pour l'arrosage ! Merci aussi à Vincent, Simon, et Bernard Clément d'avoir toujours accepté de nous aider dans l'identification des plant(ule)s les plus « récalcitrantes » !

Une pensée nouvelle pour mes stagiaires, qui, en plus d'avoir été d'une aide plus que précieuse, ont dû subir, en parallèle, mes premiers pas de « maître de stage » (ohlàlà !). Merci pour votre enthousiasme et votre curiosité, vous avez été géniaux. J'espère sincèrement avoir été à la hauteur de vos espérances, et de vous avoir transmis autant de choses que vous m'en avez appris... Bonne continuation à vous tous ! Une pensée également à tous les anciens étudiants de Licence et de Master qui ont eu la lourde tâche de m'avoir en tant qu'enseignante pendant non pas une, ni deux, mais trois années consécutives. Merci à toutes les personnes avec lesquelles j'ai eu la joie d'enseigner, mais aussi à toutes les personnes qui m'ont fait confiance, Cédric, André-Jean, voire beaucoup confiance... n'est-ce pas Aude (les codes couleurs parfois trompeurs, le relookage *mint*) et Cendrine (*rou-rouou-rou-rou... -ru... désolée je n'arrive plus à m'arrêter...*) ?

Merci à l'équipe Paysaclim pour son accueil, aux habitués des (ex-)cafets' du 14a, de la nouvelle cafet' (Eco... fet', Eco... lax' ?), et plus généralement à toutes les personnes d'Ecobio que j'ai côtoyées, aussi bien *intra-* qu' *extra-muros*. Je pense à Aude et Cendrine (et à leur petite

famille), mais aussi à Cécile Le Lann, Simon, Vincent, Philippe... et bien évidemment aux doctorants (oui, je parle enfin de vous !) du bureau 112 et d'ailleurs. Par ordre de passage successifs dans le bureau, je nomme : Manon, Lou (désormais exilé dans le bureau de Aude) et Alice – puis, viennent les membres TERRIBLES du bureau 112 girl power (ou presque) – Eve, Lorine, Marine, Lucie, Claire, Victor et Solène... qui s'est déjà échappée ! Mille mercis pour tout. Jamais je n'oublierai toute l'entraide, tout le soutien qu'il y a eu dans ce bureau. S'il y a eu quand même un peu de science, il y a surtout eu des discussions incroyables, des potins, des fous-rires et des pleurs, du fameux « renwouennage », des karaokés, des danses et même de la gymnastique (enfin, surtout pour Marine). Jamais je ne n'aurais tenu trois ans sans vous. A ce sujet, merci Yann d'un côté et merci Isabelle de l'autre, de ne vous être jamais plaints... Bien évidemment, un immense merci à Maxime, parti bien trop tôt (avec ses gâteaux) pour les contrées Niçoises, non seulement pour son amitié et son soutien, mais aussi pour son aide inimaginable en statistiques, ou encore de m'avoir initiée à l'écologie urbaine... à récolter des trèfles, des trèfles, et... encore des trèfles pour le *GLUE* project ! Merci aussi à Loïs pour son aide précieuse sur le traitement des valeurs de traits de TRY, mais aussi pour toutes les discussions et prises de têtes qu'il a générées ! Enfin, un immense merci à l'équipe administrative pour leur travail, leur efficacité, leur patience et surtout leur bonne humeur à toute épreuve : Isabelle, Bertrand, Patricia et Valérie, mais aussi Sandra du temps de sa présence à Ecobio.

Merci également à toute la fine équipe de BAGAP ! Si vous ne m'avez pas beaucoup vu pendant ces trois années, c'était parce que je gardais le meilleur pour la fin ! Un immense merci à vous tous de m'avoir supporté, dans tous les sens du terme, lors de cette dernière ligne droite. Mes pensées se dirigent naturellement vers Audrey, qui m'a intégrée dans l'unité, mais aussi à Stéphanie A., Eloïse, Arnaud, Jean-Luc, Hugues, Paul, Claudine, Alexandra, Alexandre, Jacques, Stéphanie Q., Philippe (la nouvelle recrue !), et à ceux qui nous ont quitté entre temps, Gérard, Pierline et Béné. Une pensée particulière pour Tristan, Alejandro et Lily, qui se sont occupés de moi après ma fameuse chute, mais aussi pour Audrey, qui a eu la chance inouïe d'apercevoir l'os de mon menton, et oui... ! Enfin, Eloïse, je suis ravie d'avoir passé ce dernier été de thèse à tes côtés. Il fut plein de bons moments, de confidences, mais aussi de mots croisés... Prends soin de toi, mais aussi de la cafetière... Tâche d'être particulièrement attentive à la consommation de Hugues !

Je ne serais certainement pas arrivée jusqu'ici si mon chemin n'avait pas croisé celui de certains enseignants, tout autant passionnés qu'exigeants. Merci à eux. En particulier, j'ai une pensée affectueuse envers Maryvonne Charrier et Frédéric Ysnel, qui, de par leur implication au sein du master PNB, et leurs nombreux conseils, m'ont donné toutes les chances de réaliser une thèse.

Si la thèse m'a beaucoup éloigné de vous, sachez, mes amis, que je suis loin de vous avoir oubliés. Une pensée particulière pour mon grand ami, Paul, que je n'ai pas vu depuis beaucoup trop longtemps, mais aussi à Diane et à Mégane, qu'il me tarde d'appeler et de voir depuis des lustres ! Un grand merci à Camille, qui a bougé ses fesses jusqu'à Rennes, mais qui a aussi saisi la moindre occasion de me voir lors de mes passages éclairs à Caen. Merci aux copains qui sont venus à Rennes, pour tous les bons moments passés ensemble : Audresy et Arthur, Aurélien, Thomas et Bastien.

Enfin, je dédie ces trois ans de thèse à mes parents, pour tout ce qu'ils ont fait pour moi, malgré tout. De tout mon cœur, merci.

Je terminerai en remerciant Jib, qui est le premier à avoir perçu que la recherche était faite pour moi. En revanche, je n'aurais jamais cru que lorsque je terminerais ma thèse, tu commencerais la tienne... Merci d'avoir été toujours là.

Tables des matières

Introduction générale.....	1
1. De la fragmentation des habitats à l'importance de la dispersion pour les communautés végétales	2
2. La connectivité, une composante essentielle des paysages déterminant la dispersion entre tâches d'habitat	20
Article 1. How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review.....	33
3. Effet de la connectivité sur la structure des communautés végétales	53
Article 2. Effect of landscape connectivity on plant communities: a review of response patterns	57
4. Problématique et organisation de la thèse	87
Partie I : Elements méthodologiques.....	91
1. Le site agricole « de Pleine-Fougères » de la Zone Atelier Armorique, un site d'étude à l'histoire paysagère mouvementé	93
2. Sélection des tâches d'habitat.....	97
3. Echantillonnage des communautés végétales	99
Partie II : Connectivité fournie par les différents types d'habitat et communautés végétales.....	101
1. Contexte scientifique.....	103
2. Objectifs.....	104
3. Démarches mises en œuvre	105
4. Principaux résultats	105
Chapitre 1 : Effet de la connectivité fournie par les différents types d'habitat sur la similarité de composition des communautés végétales.....	107
Article 3. Additive effects of connectivity provided by different habitat types drive plant assembly.....	109

Chapitre 2 : Effets de la quantité d'habitat et de la connectivité sur la diversité spécifique et l'abondance totale des espèces adventices au sein des cultures céréalières : une approche taxonomique et fonctionnelle.....	137
Article 4. Using the response-effect trait framework reveals that high habitat connectivity reduces weed abundance in winter cereals.....	139
Partie III : Dynamique temporelle de connectivité et communautés végétales	171
1. Contexte scientifique.....	173
2. Objectifs.....	174
3. Démarche mise en œuvre.....	175
4. Principaux résultats.....	175
Chapitre 3 : Effet de la dynamique temporelle de connectivité opérée au cours des sept dernières décennies sur la diversité spécifique et la structure fonctionnelle des communautés végétales boisées actuelles	177
Article 5. Unveiling the ghosts of landscapes past: changes in landscape connectivity over the last decades are still shaping current woodland plant assemblages	179
Partie IV : Discussion générale.....	201
1. La connectivité, un phénomène complexe agissant dans l'espace et dans le temps, pour déterminer l'assemblage des communautés végétales.....	203
2. La considération conjointe des différents types d'habitat et de la dynamique temporelle, une voie vers une méthodologie pertinente de l'évaluation de la connectivité pour les communautés végétales	211
3. Implications pour la conservation de la biodiversité floristique au sein des paysages agricoles.....	218
4. Conclusion	223
Annexes.....	225
Article A1. Small but not the least: transient changes in landscape patterns drive grassland plant aboveground and seed bank assemblages	227
Article A2. Ecological corridors for the invisibles.....	229

Chapitre A1. The role of hedgerows to support biodiversity and associated ecosystem services in intensive agricultural landscapes	245
List of publications.....	269
Références	271

Introduction générale

1. De la fragmentation des habitats à l'importance de la dispersion pour les communautés végétales
2. La connectivité, une composante essentielle des paysages déterminant la dispersion entre tâches d'habitat
3. Effet de la connectivité sur la structure des communautés végétales
4. Problématique et organisation de la thèse

Depuis des milliers d'années, les Hommes interagissent avec le paysage et les organismes qui le composent. Les activités humaines, en altérant les paysages à un rythme sans précédent, sont aujourd'hui largement responsables du déclin de la biodiversité mondiale, désormais reconnu comme la sixième crise d'extinction de la biodiversité (Barnosky *et al.* 2011; Ceballos *et al.* 2015).

Opérée au cours du dernier siècle pour faire face à des besoins alimentaires croissants, l'intensification de l'agriculture est l'une des principales causes de ce déclin planétaire (Matson *et al.* 1997; Tilman *et al.* 2001). L'intensification des pratiques agricoles, notamment à travers le développement d'engrais chimiques, des produits phytosanitaires, et l'avènement de la mécanisation des outils, a été accompagnée d'une profonde transformation des paysages (Tscharrntke *et al.* 2005). En Europe, et notamment en France, les paysages agricoles sont devenus simplifiés par la destruction des habitats semi-naturels tels que les petits bois, les haies et les prairies permanentes au profit de grandes parcelles de monocultures et de prairies temporaires, selon les régions (Meeus 1993; Baudry & Papy 2001; Stoate *et al.* 2001; Robinson & Sutherland 2002). Cette perte d'habitat a entraîné la division des habitats semi-naturels en fragments (ci-après dénommés tâches d'habitat) de plus en plus petits et isolés au sein d'une matrice destinée à la production alimentaire (Tilman *et al.* 2001; Benton *et al.* 2003; Tscharrntke *et al.* 2005). Désormais, près de la moitié des terres de l'Union Européenne sont cultivées (Commission Européenne 2017).

L'ensemble de ces modifications ont considérablement appauvri la biodiversité des paysages agricoles, notamment pour les plantes (Andreasen *et al.* 1996; Stoate *et al.* 2001; Kleijn *et al.* 2009), les insectes (Biesmeijer *et al.* 2006) et les oiseaux (Krebs *et al.* 1999; Donald *et al.* 2001). Dans ces paysages, le déclin de la biodiversité est devenu une préoccupation majeure, non seulement pour des raisons intrinsèques mais également pragmatiques. La biodiversité soutient, en effet, le fonctionnement des écosystèmes et fournit des services écosystémiques utiles à l'Homme (Hooper *et al.* 2005). De nombreux services écosystémiques, définis comme les biens et services que les hommes peuvent tirer des écosystèmes, directement ou indirectement, pour assurer leur bien-être (Millennium Ecosystem Assessment 2005), tels que le contrôle biologique des ravageurs des cultures (Rusch *et al.* 2016) ou la pollinisation des cultures (Garibaldi *et al.* 2011; Deguines *et al.* 2014), sont ainsi menacés par l'intensification de l'agriculture. De cette façon, la préservation et la restauration de la biodiversité, en particulier au sein des agrosystèmes, sont des enjeux sociétaux majeurs.

Tandis que les niches climatiques des espèces se déplacent de plus en plus rapidement face au changement climatique (Thomas *et al.* 2004), les paysages agricoles contraignent une majorité d'espèces à survivre dans des petites tâches d'habitat isolées les unes des autres. Pour les plantes, organismes sessiles, la survie au sein de ces paysages dits fragmentés, qui ne leur permettent plus de se disperser facilement et ainsi, de s'adapter en réorganisant leurs aires de répartition, est un réel défi. Pour enrayer la perte de biodiversité, des continuités écologiques, éléments paysagers reliant entre elles des tâches d'habitat autrement isolées, ont ainsi été déployées sous l'impulsion des politiques publiques pour restaurer la connectivité, c'est-à-dire le degré avec lequel le paysage facilite les mouvements de dispersion des espèces entre tâches d'habitat (Taylor *et al.* 1993). En France, cette stratégie s'est traduite par la mise en place opérationnelle de la Trame Verte et Bleue (TVB, lois Grenelle I, 2009 et II, 2010). Définie comme l'un des projets phares du Grenelle de l'Environnement, la TVB vise à identifier et à maintenir les éléments paysagers constitutifs des continuités écologiques au sein des territoires afin de favoriser la protection des réservoirs de biodiversité et les échanges entre ces réservoirs.

1. De la fragmentation des habitats à l'importance de la dispersion pour les communautés végétales

1.1. Définitions du processus de fragmentation des habitats

La perte d'habitat et la fragmentation qui en résulte constituent les principales menaces qui pèsent sur la biodiversité (Pereira *et al.* 2010; Haddad *et al.* 2015), bien que les processus à l'origine de leurs effets font l'objet de nombreux débats (Fahrig 2003, 2013, 2017; Hanski 2015; Fletcher *et al.* 2018; Fahrig *et al.* 2019; Miller-Rushing *et al.* 2019).

A l'origine, la fragmentation de l'habitat se définit comme la division de l'habitat en tâches de plus en plus petites et isolées les unes des autres au sein d'une matrice différente de l'habitat originel (Wilcove *et al.* 1986). Selon cette définition, les trois conséquences du processus de fragmentation sont : (i) la réduction de la quantité d'habitat, (ii) la diminution de la surface des tâches d'habitat et (iii) l'augmentation de l'isolement entre tâches d'habitat (Fahrig 2003). La quantité d'habitat étant inévitablement corrélée avec la surface des tâches d'habitat et l'isolement entre celles-ci, Fahrig (2003) a proposé, plus récemment, de distinguer la perte d'habitat (i.e. la réduction de la quantité d'habitat) de la fragmentation *per se* (i.e. la division de l'habitat pour une quantité d'habitat donnée) (**Fig. 1**).

La fragmentation de l'habitat désigne alors le processus par lequel la perte d'habitat entraîne la division de grands habitats contigus en tâches d'habitat plus petites et isolées (Didham 2010). Il convient alors de s'intéresser aux conséquences écologiques attribuables à la diminution de la surface des tâches et à l'augmentation de l'isolement entre tâches.

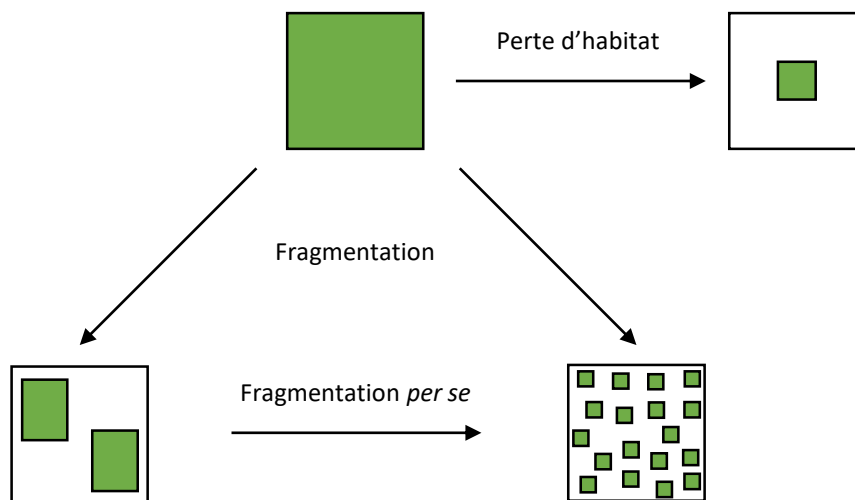


Fig. 1 Illustration des processus (i) de perte d'habitat, (ii) de fragmentation et (ii) de fragmentation *per se* (dans un paysage. D'après Fahrig (2017).

1.2. Fonctionnement des communautés végétales au sein des habitats fragmentés : cadre théorique

La compréhension du fonctionnement des communautés végétales au sein des paysages dont les habitats sont fragmentés peut se réaliser grâce à de multiples cadres théoriques. Au travers de ces différents cadres conceptuels, nous appréhendons comment les processus locaux, les processus de dispersion, mais également l'interaction de ces deux processus régissent les communautés végétales dans les paysages fragmentés.

1.2.1. La théorie de la niche : l'importance des processus locaux opérant au sein des tâches d'habitat

Jusqu'à la seconde moitié du XX^e siècle, l'écologie des communautés considérait, à travers le concept de niche écologique, que seuls les processus locaux déterminaient la distribution des espèces au sein des tâches d'habitat. Le concept de niche écologique a une histoire mouvementée en écologie (Chase & Leibold 2003), formée autour de deux perspectives différentes. Grinnell (1917) définit la niche comme l'ensemble des conditions environnementales, abiotiques et biotiques, nécessaires à l'existence d'une espèce. Une décennie plus tard, Elton (1927) fait évoluer le concept de niche, en proposant la niche comme le rôle fonctionnel d'une espèce dans la chaîne alimentaire et son impact sur l'environnement.

Ainsi, la niche Grinnellienne souligne les effets de l'environnement sur une espèce, tandis la niche Eltonienne souligne les effets d'une espèce sur l'environnement.

Jusqu'ici opposées, ces deux perspectives ont été réunies dans la formalisation du concept de niche par Hutchinson (1957). Hutchinson définit la niche comme un hyper volume, où chaque dimension est une condition abiotique nécessaire à la reproduction et à la survie d'une espèce. En intégrant le principe d'exclusion compétitive de Gause (1934), qui stipule que deux espèces ne peuvent pas coexister indéfiniment lorsqu'elles sont toutes les deux limitées par la même ressource, Hutchinson (1957) distingue la niche fondamentale et la niche réalisée d'une espèce. La niche fondamentale correspond à l'hyper volume à n dimensions en l'absence d'interactions interspécifiques, tandis que la niche réalisée est une sous-partie de la niche fondamentale à laquelle l'espèce est limitée en présence d'interactions interspécifiques. Selon Hutchinson (1957), la niche réalisée d'une espèce est plus petite que sa niche fondamentale, en raison d'interactions interspécifiques négatives, telles que la compétition et, par extrapolation, la prédation et le parasitisme. Toutefois, d'autres auteurs suggèrent que la niche réalisée d'une espèce peut être plus grande que sa niche fondamentale, en raison d'interactions interspécifiques positives (facilitation; Bruno *et al.* 2003) ou d'une dynamique source-puits (colonisation constante d'individus depuis les sources vers les puits qui se trouvent en dehors de leur niche fondamentale; Pulliam 1988, 2000). Hutchinson opère ainsi un changement conceptuel en formalisant la niche comme une propriété de l'espèce plutôt qu'une propriété de l'environnement (Chase & Leibold 2003).

Dans les années 1960, MacArthur & Levins (1967) ont développé l'approche d'Hutchinson, en redéfinissant le concept de niche comme la distribution d'utilisation des ressources. La niche, définie pour une population, revient à la fréquence d'utilisation d'une ressource ordonnée sur une ou plusieurs dimensions et peut être ainsi simplement représentée par un histogramme (Pocheville 2015). MacArthur & Levins (1967) insufflent alors un nouvel élan au concept de niche en écologie, en ouvrant la voie à la quantification des différentes propriétés de la niche (e.g. amplitude de niche, recouvrement de niche) (Vandermeer 1972; Chase & Leibold 2003). Dans ce contexte, les écologistes se concentrent majoritairement sur le rôle de la compétition interspécifique dans la structuration des communautés. En outre, MacArthur & Levins (1967) introduisent le concept de similarité limitante (*limiting similarity*), précisant le seuil maximum de chevauchement de niche entre deux espèces concurrentes qui leur permet de coexister.

Après un déclin de l'utilisation du concept de niche dans les années 1980, Chase & Leibold (2003) ont proposé une nouvelle définition du concept de niche, réunissant ainsi la niche Eltonienne et Hutchinsonienne. La niche est alors définie comme « la description conjointe des conditions environnementales qui permettent à une espèce de satisfaire ses exigences minimales de sorte que le taux de natalité d'une population locale soit égal ou supérieur à son taux de mortalité, ainsi que l'ensemble des effets *per capita* de cette espèce sur ces conditions environnementales ».

Si le concept de la niche écologique permet de définir la tâche d'habitat favorable d'une espèce considérée au temps t , il n'est toutefois pas suffisant pour comprendre les effets de la fragmentation, c'est-à-dire les effets de la surface de la tâche et de l'isolement entre tâches, sur les communautés.

1.2.2. La théorie de la biogéographie insulaire : la reconnaissance de l'importance de la dispersion entre tâches d'habitat

La théorie de la biogéographie insulaire (MacArthur & Wilson 1963, 1967) a été particulièrement influente en écologie des communautés. Elle a reconnu, pour la première fois depuis le début du XX^e siècle, le rôle de la surface des tâches d'habitat et de l'isolement entre celles-ci sur la distribution des espèces. La théorie de la biogéographie insulaire a ainsi fourni un premier cadre théorique pour comprendre les effets de la fragmentation sur les communautés. Dans cette théorie, le paysage est composé d'une source de colonisateurs (« continent »), de tâches d'habitat favorable (« îles continentales ») au sein d'une matrice inhospitalière de non-habitat (« mer »).

Initialement développée pour expliquer la relation aire-espèce au sein des îles, la théorie de la biogéographie des îles prédit que la richesse spécifique (i.e. nombre d'espèces) d'une île est déterminée par un équilibre dynamique entre la colonisation (dispersion) et l'extinction (dérive). Plus particulièrement, elle souligne le rôle de (i) la surface de l'île et (ii) l'isolement de l'île par rapport au continent (i.e. la distance au continent) comme principaux facteurs de la richesse spécifique via leurs effets sur les taux de colonisation et d'extinction. Dans leurs travaux fondateurs, MacArthur & Wilson (1963, 1967) postulent que les îles de petite surface ont un taux d'extinction élevé et que les îles fortement isolées du continent ont un taux de colonisation faible. Les îles de petite surface, en offrant peu de ressources [faible capacité de charge (*carrying capacity*)], abritent des populations de petite taille qui sont particulièrement vulnérables aux événements de stochasticité démographique (plus de

dérive). Les îles fortement isolées, éloignées du continent, reçoivent moins de colonisateurs (moins de dispersion). Ainsi, la théorie prédit que la richesse spécifique est corrélée positivement à la surface de l'île et négativement à l'isolement de l'île.

Cette théorie a été complétée ultérieurement, en intégrant le rôle de la surface de l'île sur les taux de colonisation et le rôle de l'isolement de l'île au continent sur les taux d'extinction. Les îles de petite surface ont un taux de colonisation faible, puisqu'elles retiennent (ou accumulent) moins de colonisateurs que les îles de grande surface par simple hasard [hypothèse d'échantillonnage passif (*passive sampling hypothesis*; Connor & McCoy 1979) ou effet cible (*target effect*; Gilpin & Diamond 1976; Lomolino 1990)]. Les îles fortement isolées sont caractérisées par un taux d'extinction élevé. Les îles éloignées du continent, puisqu'elles ont un taux de colonisation faible, sont privées d'un éventuel effet de sauvetage démographique et génétique (*rescue effect*; Brown & Kodric-Brown 1977).

En omettant les processus locaux, la théorie de la biogéographie insulaire diffère fondamentalement de la théorie de l'assemblage par la niche, pour se rapprocher de la théorie de l'assemblage par la dispersion, ou neutralisme. La théorie de la biogéographie insulaire constitue, en effet, la base de la théorie neutraliste de Hubbell (1997, 2001). La théorie neutraliste diffère de la théorie de la biogéographie des îles en deux points : (i) les processus stochastiques d'extinction et de colonisation à l'échelle des espèces sont transposés à l'échelle individuelle, permettant de prédire les changements aléatoires dans l'abondance relative des espèces dus à la dérive et à la dispersion (ii) le continent est remplacé par une « métacommunauté », dont le nombre d'espèces est déterminé par l'équilibre aléatoire entre l'extinction et la spéciation. Curieusement, les travaux de MacArthur ont apporté une contribution centrale dans le développement de la théorie de la niche et de la théorie neutraliste, bien que diamétralement opposées : c'est le paradoxe de MacArthur (Schoener 1989; Loreau & Mouquet 1999).

1.2.3. La théorie des métapopulations, une version monospécifique de la théorie de la biogéographie insulaire, se différenciant par son réalisme

Dans les années 1990, la théorie des métapopulations a largement remplacé la théorie de la biogéographie insulaire comme paradigme principal pour l'étude des populations en systèmes fragmentés (Merriam 1991; Hanski & Simberloff 1997). Si le concept de métapopulation de Levins (1969, 1970) peut être considéré comme une version monospécifique de la théorie de la biogéographie insulaire, il se différencie principalement par son réalisme, en supposant que

les colonisateurs proviennent d'autres tâches d'habitat occupées, plutôt que d'une source inépuisable de colonisateurs (i.e. le continent).

Introduite par Levins (1969, 1970), le concept de métapopulation se définit comme un réseau de populations locales interconnectées entre elles par la dispersion des organismes (Hanski & Gilpin 1991). La dynamique et la persistance d'une métapopulation sont déterminées par l'équilibre entre les processus de (re-)colonisation et d'extinction. Les populations locales occupent des tâches d'habitat favorable (« îles ») au sein d'une matrice non-habitat (« mer »). Les tâches d'habitat peuvent être occupées ou inoccupées à un moment donné, chaque population locale se caractérisant par une espérance de vie limitée (stochasticité démographique ou environnementale).

Le modèle de métapopulation classique (*classic*) de Levins est simpliste et repose sur les hypothèses suivantes : (i) un nombre infini de tâches d'habitat de même surface et de même qualité, (ii) les tâches d'habitat sont soit occupées, soit inoccupées, ignorant ainsi la dynamique locale des populations (i.e. taille des populations locales) – et (iii) les tâches d'habitat ont la même probabilité de colonisation et d'extinction. En outre, puisque les tâches d'habitat ont la même probabilité de colonisation (i.e. sont également isolées les unes aux autres), le modèle ignore la localisation spatiale des tâches d'habitat : il est ainsi dit spatialement implicite (Hanski 1994a; Hanski & Gilpin 1997). Bien que non réaliste, le modèle de Levins a servi de base pour le développement de modèles intégrant explicitement (i) la dynamique locale des populations (modèles structurés de métapopulation, e.g. Hanski 1985; Hastings 1991) et (ii) les effets de la dispersion sur la dynamique locale des populations et ainsi sur leur risque d'extinction (i.e. effet de sauvetage; e.g. Hanski 1985, 1991).

À la suite de Levins, Boorman & Levitt (1973) élaborent un modèle de métapopulation alternatif appelé îles-continent (*mainland-island*), qui repose sur l'existence d'une grande population source de colonisateurs sans risque d'extinction (« continent ») entourée d'un ensemble de petites populations (« îles ») sujettes à l'extinction. Ce modèle est conceptuellement similaire au modèle « source-puits » (*source-sink*; Pulliam 1988, 2000) qui suppose que les tâches d'habitat diffèrent en qualité. Par la suite, Harrison (1991) élabore un système de classification de structures spatiales de populations, et introduit deux autres modèles : (i) les populations en tâches (*patchy populations*), dans lesquelles le taux de dispersion est si élevé que les « sous-populations » fonctionnent comme une seule et même population, et (ii) le modèle en déséquilibre (*non-equilibrium*), dans lequel la dispersion est trop faible pour la recolonisation, de sorte que les taux d'extinction surpassent les taux de

colonisation. Bien que Hanski (1999) stipule que les populations en tâches ne forment pas des métapopulations, ces quatre modèles sont traditionnellement représentés le long d'un continuum de structures spatiales de populations (Harrison & Taylor 1997; **Fig. 2**).

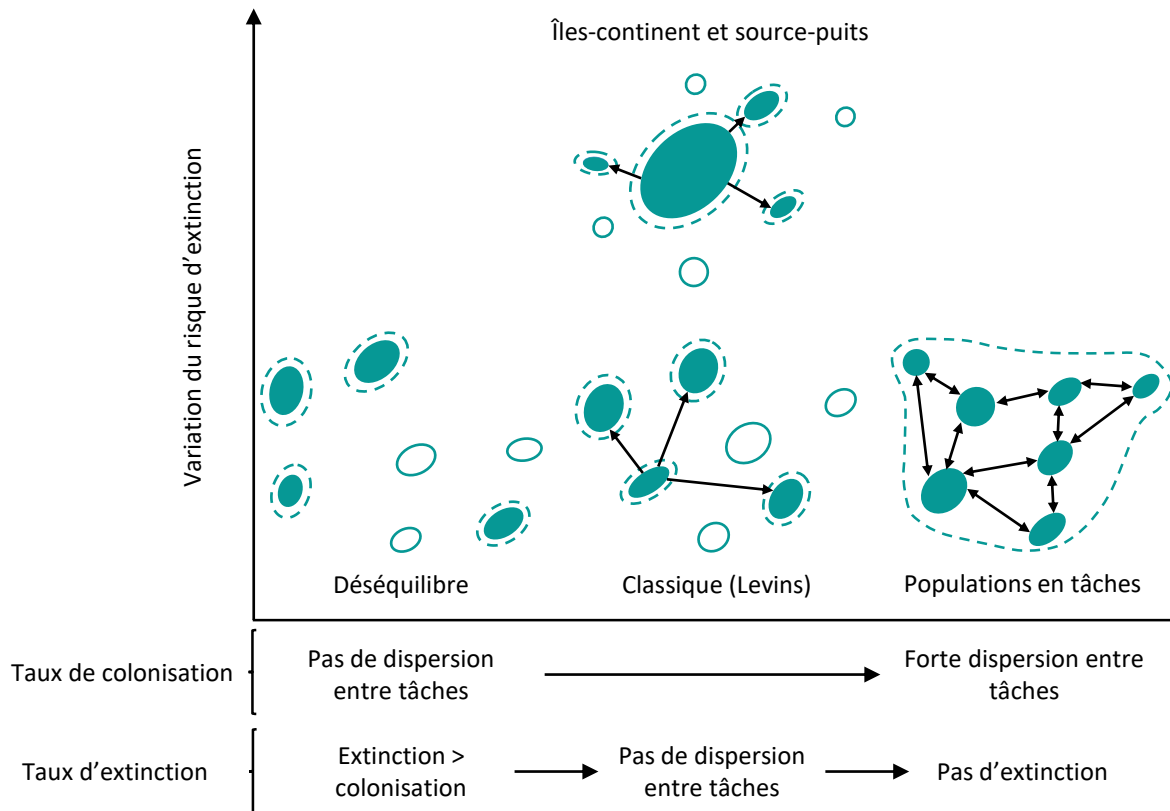


Fig. 2 Illustration des quatre modèles de métapopulations le long d'un continuum de structures spatiales de populations. Ces modèles se distinguent par la variation (i) du risque d'extinction selon la surface et/ou de la qualité des tâches (axe vertical), (ii) la dispersion entre tâches et (iii) le taux d'extinction par rapport au taux de colonisation (axe horizontal). Les cercles pleins et vides représentent les tâches d'habitat occupées et vacantes, respectivement. Les flèches pleines indiquent la dispersion entre tâches d'habitat. Les lignes pointillées indiquent les limites des populations locales. D'après Harrison (1991), Harrison & Taylor (1997) et Driscoll (2007).

Plus récemment, les travaux sur les métapopulations reposent sur des modèles dits spatialement explicites, dans lesquels la localisation spatiale des tâches d'habitat est reconnue, par opposition aux modèles spatialement implicites. Ici, les tâches d'habitat ne sont pas également isolées les unes aux autres : la probabilité de colonisation des tâches dépend, le plus souvent, de la distance à la tâche d'habitat voisine la plus proche. Ces tâches sont représentées par des cellules identiques sur une grille régulière, et seule la présence ou l'absence de l'espèce dans une cellule est prise en compte (Hanski 1994a; Hanski & Gilpin 1997). La modélisation des métapopulations a ensuite progressé vers le développement de modèles spatialement réalistes, incluant des informations supplémentaires concernant les populations locales et les tâches d'habitat qu'elles occupent (e.g. surface, forme, localisation exacte) (Hanski 1994a; Hanski & Gilpin 1997). Parmi ces modèles, le modèle à fonction

d'incidence (IFM; Hanski 1994a, b) est le modèle d'occupation de tâche le plus simple et le plus utilisé. Il représente l'occupation de chaque tâche d'habitat selon une chaîne de Markov avec deux états, occupé et inoccupé, la probabilité de transition entre ces deux états étant déterminée par l'extinction locale et la colonisation. Dans sa forme la plus simple, l'extinction locale est fonction de la surface de la tâche d'habitat, tandis que la probabilité de colonisation dépend de la distance aux tâches d'habitat environnantes et de leur surface (les tâches de grande surface ont une taille de population plus importante, et ainsi une source de nombreux colonisateurs, effet pression de propagules), selon une distance de dispersion donnée spécifique à l'espèce considérée. Le modèle à fonction d'incidence peut inclure l'effet de sauvetage, la probabilité de colonisation réduisant ainsi la probabilité d'extinction locale (Hanski 1994a, b), et/ou l'effet cible, la probabilité de colonisation augmentant avec la surface de la tâche considérée (Moilanen & Hanski 2001; Moilanen & Nieminen 2002).

Les théories de la biogéographie insulaire et des métapopulations ont approfondi notre compréhension de la façon dont la fragmentation affecte les populations et les communautés végétales, en fournissant des modèles de plus en plus réalistes. Cependant, elles omettent toutes deux les processus locaux.

1.2.4. La théorie des métacommunautés : la réunification entre les processus locaux et les processus de dispersion

Le concept de métapopulation a été étendu à l'échelle des communautés sous le concept de métacommunauté (Gilpin & Hanski 1991; Wilson 1992; Leibold *et al.* 2004). En intégrant de multiples espèces en interaction, la théorie des métacommunautés fournit ainsi un cadre conceptuel pour comprendre l'interaction complexe entre les processus locaux (sélection de niche) et la dispersion dans les mécanismes de coexistence au sein des paysages fragmentés.

Une métacommunauté désigne un réseau de communautés locales reliées entre elles par la dispersion de multiples espèces potentiellement en interaction (Leibold *et al.* 2004). Ce concept, en plein essor, a donné lieu à quatre modèles théoriques de coexistence des espèces selon les paradigmes de : (i) la dynamique des tâches (*patch dynamic*), (ii) le tri des espèces (*species sorting*), (iii) l'effet de masse (*mass effect*) et (iv) du neutralisme (*neutral model*). Ces modèles théoriques formulent différentes hypothèses sur l'importance relative de la dispersion, de l'hétérogénéité (abiotique et biotique) des tâches d'habitat, et de l'équivalence entre espèces en matière de niche écologique et de valeur sélective (*fitness*) dans les mécanismes de coexistences des espèces (**Fig. 3**; Leibold *et al.* 2004; Logue *et al.* 2011).

Introduction générale

Dans le paradigme de la dynamique des tâches (Levins & Culver 1971), les tâches d'habitat sont homogènes. Les espèces sont soumises à des extinctions stochastiques et déterministes (en raison de la compétition), ces extinctions étant contrebalancées par la dispersion. Ainsi, le compromis entre capacités de colonisation et de compétition régit la coexistence des espèces. Le long de ce compromis, les espèces à fortes capacités de colonisation ont de faibles capacités de compétition et *vice versa*.

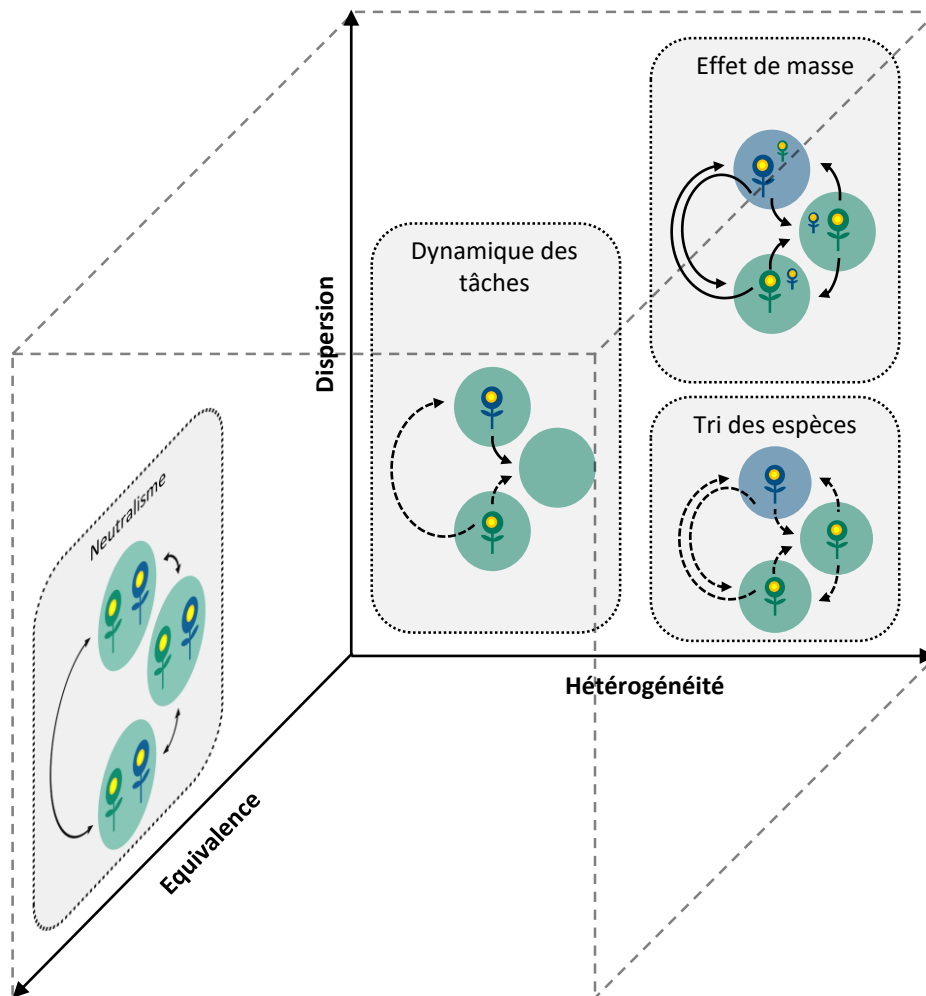


Fig. 3 Illustration des quatre paradigmes associés à la théorie des métacommunautés pour deux espèces A (verte) et B (bleue) concurrentes, replacés selon l'importance relative de la dispersion, de l'hétérogénéité des tâches d'habitat et de l'équivalence entre espèces. Les cercles (vert ou bleu) représentent les tâches d'habitat favorable, selon la niche écologique de l'espèce A ou de l'espèce B (verte ou bleue, excepté au sein du paradigme neutraliste). La concordance entre la couleur de la tâche d'habitat et la couleur de la niche écologique de l'espèce (cercle vert et espèce verte ou cercle bleu et espèce bleue) indique dans quelle mesure l'espèce considérée est une éminente compétitrice dans une tâche d'habitat donnée. La taille de l'espèce indique la taille de la population. Les flèches pleines indiquent une dispersion plus élevée entre tâches que les lignes pointillées. Les flèches simples indiquent une dispersion unidirectionnelle tandis que les flèches doubles indiquent une dispersion bidirectionnelle. D'après Leibold *et al.* (2004) et Logez *et al.* (2011).

Le paradigme de tri des espèces (Chase & Leibold 2003) suppose que les tâches d'habitat sont hétérogènes, et que celles-ci déterminent la survie des espèces et les interactions entre espèces. La dispersion doit être suffisante pour que les espèces puissent « suivre » les tâches d'habitat dans lesquelles les conditions environnementales locales leur sont favorables, par exemple à la suite d'une perturbation. Dans cette perspective, la coexistence repose sur la séparation spatiale de niches, déterminée par des compromis dans la capacité des espèces à faire face à différentes conditions environnementales.

Au sein du paradigme de l'effet de masse, les tâches d'habitat hétérogènes sont étroitement interconnectées par une dispersion continue, de telle sorte que la dispersion entraîne une dynamique « source-puits » entre populations locales. Plus particulièrement, le flux de propagules depuis les populations « sources » aux conditions environnementales favorables vers des populations « puits » aux conditions moins propices permet la persistance de ces dernières (Brown & Kodric-Brown 1977; Shmida & Wilson 1985; Pulliam 1988, 2000). Ainsi, une espèce peut se maintenir, être sauvée de l'exclusion compétitive, dans une communauté où elle est une piètre compétitrice, en immigrant d'une communauté où elle est une éminente compétitrice (Leibold *et al.* 2004).

Le paradigme neutraliste (Hubbell 2001) suppose que les individus – et donc les espèces – sont équivalents. Les individus ne présentent ainsi pas de différences de niches, ni de capacités de dispersion, ni de valeur adaptative (*fitness*). Des processus stochastiques de perte et de gain d'espèces façonnent la coexistence.

Ainsi, la théorie des métacommunautés permet une meilleure compréhension des effets de la fragmentation grâce à l'intégration de l'écologie spatiale, orientée vers les processus d'extinction et de colonisation, et de la vision de l'écologie des communautés, orientée vers la coexistence des espèces. Néanmoins, il est important de souligner que le modèle fondateur de l'écologie spatiale, à savoir, la théorie de la biogéographie insulaire a été remis en question récemment. L'hypothèse de la quantité d'habitat (*habitat amount hypothesis*) réfute le concept de tâche d'habitat, et les effets distincts de la surface des tâches et de l'isolement entre celles-ci sur la richesse spécifique (Fahrig 2013). Elle postule que la richesse spécifique d'un site d'échantillonnage augmente avec la quantité totale d'habitat de son paysage environnant (selon une distance de dispersion donnée). Comme le souligne Martin (2018) dans une première méta-analyse, cette hypothèse est probablement une sur-simplification des processus qui opèrent au sein des paysages; et de nombreuses études empiriques et expérimentales récentes continuent de démontrer des effets (i) de la perte

d'habitat et (ii) de la surface des tâches et de l'isolement entre celles-ci sur la richesse spécifique des communautés (e.g. Haddad *et al.* 2015, 2017; Rybicki *et al.* 2020).

1.2.5. Règles d'assemblages des communautés locales au sein des tâches d'habitat

La compréhension des processus qui façonnent la composition et la diversité des communautés au sein des tâches d'habitat fait l'objet de nombreuses recherches. Introduites par Diamond (1975), les règles d'assemblages conceptualisent le processus d'assemblage comme un ensemble de filtres, qui vont sélectionner, à partir du pool d'espèce régional d'espèces, les espèces végétales susceptibles d'arriver, de s'établir et survivre au sein d'une communauté locale (**Fig. 4**; Zobel 1997; Belyea & Lancaster 1999; Weiher *et al.* 2011; Götzenberger *et al.* 2012; Mittelbach & Schemske 2015).

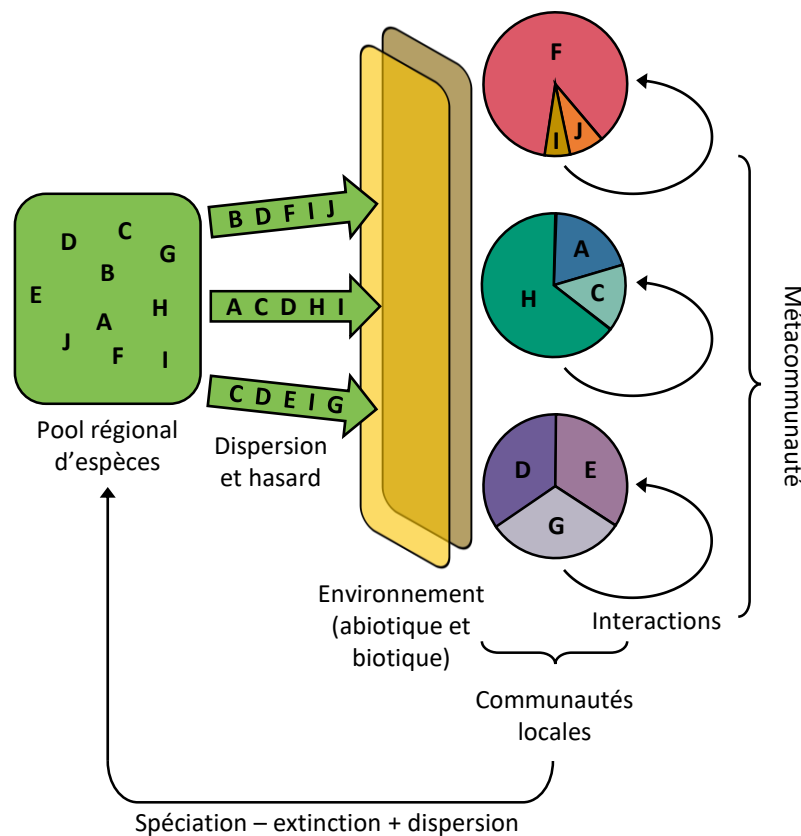


Fig. 4 Illustration des règles d'assemblages des communautés locales. Les communautés locales observées sont composées d'une fraction du pool régional d'espèces qui se sont dispersées (pool local d'espèces) et sont passées à travers les filtres environnementaux abiotiques et biotiques de la tâche d'habitat. Des rétroactions sont désormais reconnues entre les métacommunautés et le pool d'espèces régional au cours des temps écologiques et évolutifs. D'après Mittelbach & Schemske (2015).

Le pool régional d'espèces désigne l'ensemble des espèces présente dans une région particulière qui peuvent potentiellement coloniser une communauté au cours des temps écologiques (Mittelbach & Schemske 2015). Parmi les espèces du pool régional, seules

certaines espèces se dispersent et arrivent au sein d'une tâche d'habitat donnée, constituant ainsi un pool d'espèces local (filtre ou « contraintes » de dispersion). Au sein de cette tâche, les conditions environnementales abiotiques (e.g. stress hydrique, thermique, nutritif, perturbations) déterminent quelles espèces du pool local peuvent germer et s'établir au sein de cette tâche d'habitat (filtre abiotique ou de niche fondamentale). Enfin, les espèces qui survivront et se reproduiront selon les conditions environnementales biotiques de la tâche (e.g. compétition, prédation, maladies, parasitisme, mutualisme) constitueront la communauté végétale locale observée (filtre biotique ou de niche réalisée). Il est également important de noter que des processus historiques, tels que les effets de priorité (*priority effects*), influencent également la communauté végétale locale observée. Les effets de priorité se produisent lorsque les premières espèces qui arrivent au sein d'une tâche d'habitat inhibent ou facilitent l'établissement, la survie et la reproduction des espèces n'arrivant que plus tard (Eriksson & Eriksson 1998; Fukami 2015). La communauté végétale locale observée dépend ainsi de l'identité des espèces ayant colonisé en premier la tâche d'habitat.

Ces différents filtres déterminent si une espèce possède les traits fonctionnels nécessaires pour arriver, s'établir et survivre au sein de la communauté donnée. Les traits fonctionnels désignent les caractéristiques morphologiques, physiologiques ou phénologiques mesurables à l'échelle de l'individu qui impactent sa valeur sélective (*fitness*) (Violle *et al.* 2007). Par conséquent, les traits influençant la probabilité que les propagules soient déposées sur le sol de la tâche d'habitat en dépit des barrières physiques de dispersion (e.g. fort isolement de la tâche d'habitat par rapport à la source de propagules) déterminent quelles espèces constituent le pool d'espèces local. Le filtre de dispersion résulte ainsi d'une interaction complexe entre la structure physique du paysage et les traits déterminant les capacités de production et de dispersion des propagules (cf. introduction, sections 1.3 et 2). Le filtre abiotique exclut les espèces qui ne disposent pas de valeur(s) de traits adaptée(s) aux conditions locales, et qui ne peuvent pas germer et s'établir. Il restreint donc la gamme des valeurs de traits autour d'une (ou plusieurs) valeur(s) optimale(s) au sein de la communauté locale (i.e. convergence des valeurs de traits) (van der Valk 1981; Weiher & Keddy 1995; Laughlin *et al.* 2015). De façon plus complexe, le filtre biotique peut étendre (i.e. divergence des valeurs de traits) ou, au contraire, restreindre la gamme des valeurs de traits. D'après le principe de similarité limitante (*limiting similarity*), les espèces qui ont des valeurs de traits similaires, puisqu'elles occupent les mêmes niches, font l'objet d'une compétition intense (Gause 1934). Ainsi, seules les espèces fonctionnellement différentes peuvent coexister (MacArthur & Levins 1967; Chesson 2000). *A contrario*, le principe de hiérarchie compétitive

prédit que les espèces qui disposent de valeurs de traits leur conférant une forte capacité de compétition excluent les espèces moins compétitives. Seules les espèces qui sont des éminentes compétitrices constitueront ainsi la communauté végétale locale observée (Chesson 2000; Grime 2006; Mayfield & Levine 2010; Herben & Goldberg 2014).

Enfin, une hypothèse largement acceptée en écologie des communautés suggère que les trois filtres sont hiérarchiques, c'est-à-dire qu'ils sélectionnent progressivement les espèces indépendamment, selon l'ordre énuméré ci-dessus. En réalité, la dispersion, les conditions abiotiques et biotiques interagissent simultanément pour assembler les communautés végétales (HilleRisLambers *et al.* 2012; Kraft *et al.* 2015; Cadotte & Tucker 2017). Cependant, l'importance relative de ces trois processus dans l'assemblage des communautés végétales reste inconnue, puisqu'il est difficile – voire impossible – de les dissocier dans le cadre d'études empiriques (HilleRisLambers *et al.* 2012; Kraft *et al.* 2015; Cadotte & Tucker 2017). En outre, ces règles d'assemblages au cours des temps écologiques adoptent une vision indépendante et statique du pool régional d'espèces, négligeant ainsi les rétroactions écologiques et évolutives des métacommunautés locales vers le pool régional d'espèces (Mittelbach & Schemske 2015). La composition et la diversité des espèces du pool d'espèces régional ne seraient pas seulement influencées par la dynamique des métacommunautés au cours des temps écologiques, mais également par la spéciation, l'extinction et la dispersion au cours des temps évolutifs (Mittelbach & Schemske 2015). L'assemblage des communautés, traditionnellement représenté comme un processus descendant (*top-down*), allant du pool d'espèces régional vers les communautés locales) tend désormais à intégrer les rétroactions ascendantes (*bottom-up*) des communautés locales vers le pool d'espèces régional (**Fig. 4**; Spasojevic *et al.* 2014; Mittelbach & Schemske 2015; Myers & LaManna 2016).

Le rôle majeur de la dispersion entre tâches d'habitat pour le maintien des populations et des communautés en paysage fragmenté a été reconnu dans l'ensemble des théories développées depuis les années 1960. Ces théories ont considérablement amélioré notre compréhension des processus impliqués dans la colonisation et l'extinction locale d'espèces au sein des paysages fragmentés. Toutefois, la colonisation et l'extinction locale des espèces ne se produisent pas toujours de façon immédiate.

1.2.6. Le délai de réponse des espèces végétales aux changements paysagers

Les modifications du paysage n'affectent pas nécessairement les communautés végétales au sein des tâches d'habitat de manière instantanée. Un « délai de réponse » de plusieurs années,

décennies, voire de plusieurs siècles, peut être nécessaire à une communauté pour atteindre un nouvel « équilibre » après une modification paysagère (Ovaskainen & Hanski 2002; Kuussaari *et al.* 2009). Dans ce cas, la composition et la diversité des communautés végétales actuelles constituent le reflet du paysage passé (avant modification) plutôt que du paysage actuel (après modification).

A la suite de modifications paysagères « défavorables » (e.g. destruction de tâches d'habitat, diminution de la surface de la tâche, augmentation de l'isolement entre tâches), certaines espèces persistent au sein des tâches d'habitat pendant de longues périodes avant de s'éteindre, même en l'absence de colonisation. Ce délai de réponse, appelé délai de relaxation (*relaxation time*) se traduit par une dette d'extinction (*extinction debt*), c'est-à-dire le nombre d'espèces (ou de populations pour une seule espèce) qui sont vouées à l'extinction dans la tâche d'habitat dès lors que l'équilibre sera atteint (**Fig. 5a**; Kuussaari *et al.* 2009; Cristofoli *et al.* 2010). *A contrario*, à la suite de modifications paysagères « favorables », offrant de nouvelles possibilités de colonisation (e.g. création de nouvelles tâches d'habitat, augmentation de la surface de la tâche, diminution de l'isolement entre tâches), certaines espèces présentent un délai de colonisation (*colonisation* ou *immigration lag*). Ce délai de colonisation conduit à un crédit de colonisation (*colonisation* ou *immigration credit*), qui se définit comme le nombre d'espèces (ou de populations) dont une colonisation est attendue dès lors que l'équilibre sera atteint (**Fig. 5b**; Cristofoli *et al.* 2010; Jackson & Sax 2010).

Théoriquement, une dette d'extinction et un crédit de colonisation peuvent coexister au sein d'une même tâche d'habitat à la suite d'une modification paysagère (Jackson & Sax 2010). Lorsque la dette d'extinction et le crédit à la colonisation sont réalisés, en d'autres termes, lorsque les extinctions et les colonisations se sont produites, les communautés – et donc la richesse spécifique au sein de celle-ci – sont à nouveau à l'équilibre. La dette d'extinction et le crédit de colonisation peuvent se compenser, de sorte que la richesse spécifique de la communauté reste constante. Néanmoins, si la dette d'extinction surpasse le crédit à la colonisation, la communauté à l'équilibre présentera une perte de richesse spécifique et *vice versa*. Qui plus est, les communautés peuvent connaître des périodes transitoires pendant lesquelles la richesse spécifique est excédentaire ou déficitaire, en fonction du « rythme » auquel les extinctions et les colonisations se produisent.

Plusieurs mécanismes ont été proposés pour déterminer la probabilité qu'un délai de réponse se produise à la suite d'une modification paysagère, tels que (i) le temps écoulé depuis la modification paysagère (ii) l'intensité de cette dernière, et (iii) le degré de spécialisation à

l'habitat ou les traits fonctionnels des espèces, y compris végétales (Lira *et al.* 2019). Les délais de réponse seraient ainsi plus susceptibles d'exister dans les paysages où une modification paysagère récente d'intensité intermédiaire s'est produite (Ovaskainen & Hanski 2002; Cousins 2009; Hylander & Ehrlén 2013). Un délai de réponse à la suite de modifications paysagères devrait également être plus répandu chez les espèces spécialistes, à forte longévité et à faible capacité de dispersion (Cousins 2009; Kuussaari *et al.* 2009; Krauss *et al.* 2010; Hylander & Ehrlén 2013).

Dans les régions tempérées, de nombreuses études se sont intéressées à l'existence de délais de réponse aux modifications paysagères chez les espèces végétales (cf. Lira *et al.* 2019 pour une revue) probablement en raison de leur mode de vie sessile. Les plantes présentent en effet toute une série de stratégies pour se disperser entre tâches d'habitat, et ainsi (re-)coloniser et de persister au sein de ces dernières. Ainsi, la compréhension des mécanismes de dispersion des plantes, en particulier des graines, est essentielle.

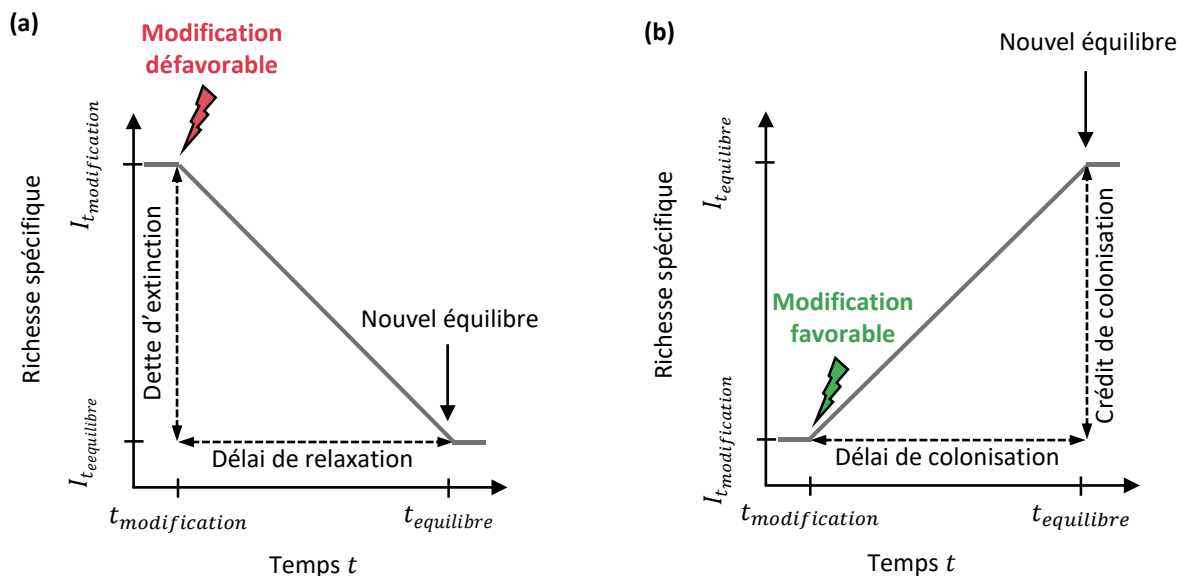


Fig. 5 Illustration des délais de réponse possibles et de leurs effets sur les communautés suite à une modification paysagère (a) « défavorable » ou (b) « favorable » (pour des exemples, cf. texte principal). $t_{modification}$ est le moment où la modification paysagère s'est produite et pour laquelle aucune réponse des espèces (extinction ou colonisation) n'a encore eu lieu. $t_{equilibre}$ est le moment où la réponse des espèces a eu lieu, où un nouvel « équilibre » a été atteint. $S_{t_{changement}}$ et $S_{t_{equilibre}}$ désignent la richesse spécifique aux moments $t_{modification}$ et $t_{equilibre}$, respectivement. D'après Hylander & Ehrlén (2013).

1.3. La dispersion des graines, un mécanisme essentiel au sein des paysages

Chez les plantes, la dispersion (i.e. tout mouvement d'individu ou de propagule ayant un impact potentiel sur les flux de gènes à travers l'espace; Ronce 2007) est un mécanisme passif, impliquant le transfert de propagules depuis la plante mère. La dispersion peut être divisée

en trois phases distinctes comprenant (i) le départ, (ii) le transfert (ou mouvement) et (iii) l'arrivée (Ronce 2007; Bonte *et al.* 2012).

1.3.1. La dispersion par voie sexuée et asexuée

La dispersion des plantes peut se faire par le biais de la reproduction sexuée (pollen et graine), mais aussi – pour de nombreuses espèces en milieu tempéré (jusqu'à 66,5 %; van Groenendael & de Kroon 1990; Klimeš *et al.* 1997) – par le biais de la reproduction asexuée grâce à la multiplication végétative (fragments clonaux). Les fragments clonaux, propagules issues de la reproduction asexuée, désignent les modules (*ramets*) interconnectés d'une plante clonale.

L'existence d'un compromis entre la reproduction sexuée et asexuée a été fréquemment démontrée. Les espèces présentant un fort degré d'investissement dans la reproduction sexuée vont présenter une forte production de graines mais une faible production de fragments clonaux, et *vice versa* (Eriksson 1997; Piquot *et al.* 1998; Stöcklin & Winkler 2004). Outre la production de propagules, ces deux modes de reproduction diffèrent également par leurs distances de dispersion : alors que les graines peuvent être dispersées sur de longues distances, la dispersion des fragments clonaux se réalise le plus souvent sur de courtes distances (Starfinger & Stöcklin 1996; Zobel *et al.* 2010). Par conséquent, seule la dispersion des graines permet la colonisation de nouvelles tâches d'habitat éloignées et non-occupées, aboutissant à l'établissement de nouvelles populations (Cain *et al.* 2000; Stöcklin & Winkler 2004). *A contrario*, la dispersion de fragments clonaux permet la persistance des populations déjà établies et leur expansion grâce à la colonisation rapide de micro-habitats (Winkler & Stöcklin 2002; Stöcklin & Winkler 2004)

La dispersion est dite efficace lorsque le transfert de propagules issues de la reproduction sexuée ou asexuée aboutit à l'établissement d'un nouvel individu (Schupp *et al.* 2010). Si la dispersion du pollen (transport du pollen, fertilisation et développement d'une graine viable; Clobert *et al.* 2012) joue un rôle majeur dans le flux de gènes entre populations (Levin 1981), elle ne permet pas à elle seule – sans la dispersion des graines – l'établissement d'un nouvel individu.

1.3.2. Production, dispersion des graines et recrutement des plantules

Au sein des paysages où les habitats sont fragmentés, la capacité de (re-)colonisation des espèces végétales au sein des tâches d'habitat est ainsi principalement déterminée par la dispersion efficace des graines, c'est-à-dire par (i) la production de graines, (ii) la dispersion

(ou transport) des graines et (iii) le recrutement des plantules (i.e. germination, établissement et survie) (Eriksson 2000).

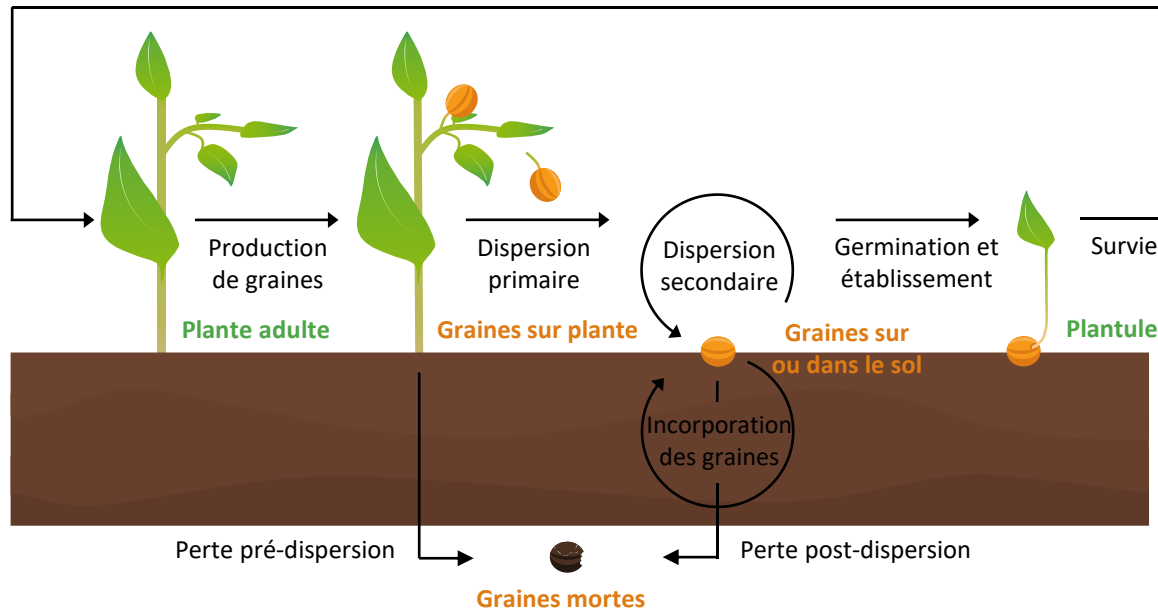


Fig. 6 Diagramme illustrant les devenirs possibles des graines, depuis leur production par la plante mère jusqu'à leur survie au stade plantule. Les flèches représentent les processus impliquant une transition de l'état des graines, de la plantule ou de la plante adulte. D'après Nathan & Muller-Landau (2000) et Vander Wall *et al.* (2005).

La production de graines (**Fig. 6**) varie largement en fonction des espèces (Harper 1977), mais également au sein d'une même espèce en fonction des facteurs environnementaux abiotiques (conditions météorologiques) et biotiques (défoliation, pollinisation des fleurs) (Crawley 2000). Au sein même de la production des graines, il existe un compromis d'allocation des ressources entre le nombre et la taille des graines produites (Jakobsson & Eriksson 2000), déterminant respectivement l'investissement des espèces dans la dispersion et l'établissement (ou compétition) (cf. introduction, section 1.2.4; Westoby *et al.* 1992; Leishman *et al.* 2000; Moles & Westoby 2004). Les espèces produisant beaucoup de petites graines investissent davantage dans la dispersion, alors que les espèces produisant peu de grosses graines investissent davantage dans l'établissement.

A l'issue de la production de graines, les graines non avortées, consommées ou parasitées sont ensuite transférées, le plus souvent de manière successive, avec un premier mouvement depuis la plante mère jusqu'au sol (ou un autre substrat) appelé « dispersion primaire », et un mouvement ultérieur depuis le sol appelé « dispersion secondaire » (Nathan & Muller-Landau 2000; Vander Wall *et al.* 2005) (**Fig. 6**). Les plantes ont développé une large gamme de mode de dispersion, reposant sur différents mécanismes pour disperser leurs

graines avec ou sans l'aide de vecteurs, impliquant le plus souvent les animaux ou le vent (van der Pijl 1972). La distance de dispersion des graines est donc déterminée dans un premier temps par le mode de dispersion des plantes. Chez les espèces autochores (i.e. dispersion des graines sans l'aide de vecteurs de dispersion, ci-après dénommées espèces non-assistées), deux modes de dispersion sont communément distingués : la dispersion barochore (i.e. dispersion des graines par la gravité) et la dispersion balistique (i.e. dispersion des graines par explosion des fruits), qui restreignent le transfert des graines à de très courtes distances. Chez les espèces allochores (i.e. dispersion des graines à l'aide de vecteurs de dispersion), les graines peuvent être dispersées par des vecteurs abiotiques (vent, eau) et biotiques (animaux). Si les graines dispersées par anémochorie (i.e. dispersion des graines par le vent), hydrochorie (i.e. dispersion des graines par l'eau) et zoochorie (i.e. dispersion des graines par les animaux) peuvent atteindre plusieurs kilomètres (Vittoz & Engler 2007), la majorité des graines produites sera déposée à quelques mètres de la plante mère; et ce, indépendamment du mode de dispersion (i.e. distribution leptokurtique de la distance de dispersion; Willson 1993). Qui plus est, la plupart des espèces allochores n'est pas dispersée par un seul vecteur, mais plutôt par une combinaison de vecteurs principaux et secondaires (Berg 1983; Ozinga *et al.* 2004). La distance de dispersion est ainsi déterminée par la succession de l'ensemble des vecteurs de dispersion qui transfèrent les graines depuis la plante mère (Nathan & Muller-Landau 2000). Au sein d'un mode de dispersion, la distance de dispersion peut être très variable selon les combinaisons de valeurs de traits fonctionnels. Par exemple, les espèces anémochores disposant à la fois d'une hauteur de rejet des graines importante et d'une faible vitesse de chute des graines disperseront sur de plus longues distances (Tackenberg 2003).

Une fois arrivées sur le sol [i.e. pluie de graines (*seed rain*)], les graines peuvent germer immédiatement, être incorporées dans la banque de graines du sol et/ou mourir (e.g. prédation, parasitisme) (**Fig. 6**). Les graines peuvent rester dans le sol pendant des mois (i.e. banque de graines transitoire), des années, voire des décennies (i.e. banque de graines persistante), leur permettant « d'attendre » des conditions favorables à la germination. Outre la quantité de graines viables présentes sur et dans le sol [i.e. banque de graines (*seed bank*)], Nathan & Muller-Landau 2000), le recrutement des plantules est influencé par la qualité et/ou la quantité de microsites disponibles (Eriksson & Ehrlén 1992; Nathan & Muller-Landau 2000; Muller-Landau *et al.* 2002). Au sein de ces microsites, les filtres abiotiques et biotiques, en interaction avec les traits fonctionnels des espèces, détermineront la germination des graines, l'établissement des plantules et leur survie jusqu'au stade adulte (Harper 1977).

Si les tâches d'habitat peuvent être (re-)colonisées à la suite d'un recrutement immédiat, la banque de graines est également un processus clé pour la recolonisation des tâches précédemment occupées après une période défavorable (Bakker *et al.* 1996b). Toutefois, la colonisation ne sera possible que si les tâches d'habitat sont suffisamment connectées entre-elles pour faciliter la dispersion (ou transport) des graines (Fahrig & Merriam 1985; Bowne & Bowers 2004).

2. La connectivité, une composante essentielle des paysages déterminant la dispersion entre tâches d'habitat

2.1. La connectivité, un concept aux multiples facettes

La connectivité est définie comme le degré avec lequel le paysage facilite les mouvements des organismes entre tâches d'habitat (Taylor *et al.* 1993). Cette définition souligne l'influence majeure de la structure physique du paysage (i.e. sa composition et sa configuration) sur le mouvement des organismes, et, en définitive, sur la dynamique des populations et la structure des communautés (Taylor *et al.* 2006). Chez les espèces végétales, la connectivité facilite les mouvements de dispersion des organismes, contrairement aux espèces animales où l'ensemble des mouvements sont concernés (e.g. recherche de nourriture, reproduction, migration, dispersion).

Émanant conceptuellement de la théorie de la biogéographie insulaire et de la théorie des métapopulations, l'augmentation de la connectivité a été proposée comme une solution majeure pour enrayer la perte de biodiversité floristique. Une forte connectivité devrait, en effet, en facilitant la dispersion des plantes, favoriser la (re-)colonisation des tâches d'habitat et ainsi, réduire les taux d'extinction au sein des tâches d'habitat (Wilson & Willis 1975; Brown & Kodric-Brown 1977).

2.1.1. Quels éléments paysagers favorisent la connectivité entre tâches d'habitat favorable ?

La connectivité est un concept que l'on retrouve aussi bien dans la théorie de la biogéographie insulaire, de la théorie des métapopulations ou de l'écologie du paysage. De ces différentes origines ont émergé différents modèles théoriques de représentation de la structure physique du paysage (**Fig. 7**).

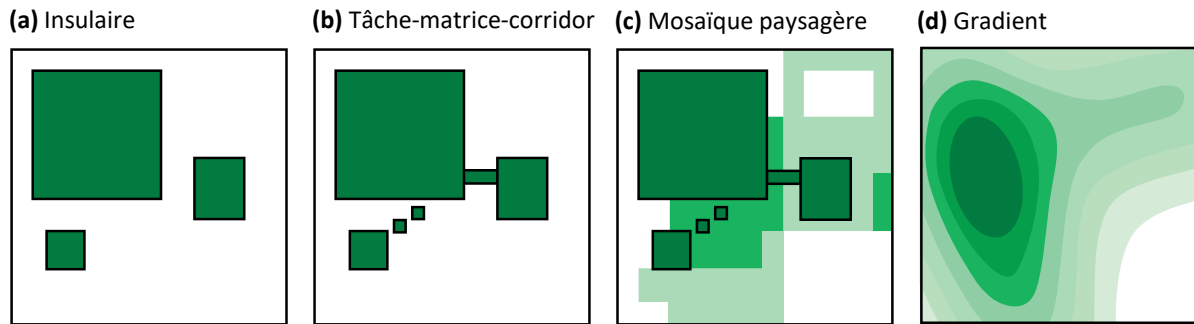


Fig. 7 Illustration des modèles théoriques de représentation de la structure physique du paysage couramment utilisés pour caractériser la connectivité : le modèle (a) insulaire, (b) tâche-matrice-corridor, (c) mosaïque paysagère et de (d) gradient. Les rectangles vert foncé entourés de noir indiquent les tâches d'habitat favorable (a-c), les corridors et les pas japonais (b-c). Les nuances de vert indiquent une perméabilité à la dispersion croissante (blanc – vert) des types d'habitat composant la matrice (a-c) ou de la variable environnementale continue (e.g. densité de la couverture arborée) (d) pour l'organisme considéré. D'après Fletcher & Fortin (2018).

La théorie de la biogéographie insulaire (MacArthur & Wilson 1963, 1967) et la théorie des métapopulations Levins (1969, 1970) reposent sur une vision binaire du paysage, composé de tâches d'habitat favorable (« îles ») au sein d'une matrice inhospitalière de non-habitat (« mer ») (Wiens 1997; Haila 2002; **Fig. 7a**). Ce modèle « insulaire » a été étendu et supplanté par le modèle « tâche-matrice-corridor » (Forman 1995; **Fig. 7b**), qui inclut désormais la présence de corridors et de pas japonais (*stepping-stones*) (i.e. bandes d'habitat linéaires ou petites tâches d'habitat discontinues qui relient des tâches d'habitat autrement isolées) au sein de la structure physique du paysage. Au sein de ces deux modèles théoriques, regroupés communément sous le nom de « tâche-matrice » (Brudvig *et al.* 2017), la connectivité dépend de l'isolement de la tâche d'habitat, ou de l'existence de corridors ou de pas japonais. Cette dichotomie « tâche-matrice », qui ignore la façon dont les organismes interagissent avec le paysage, a été progressivement abandonnée (McGarigal & Cushman 2005; Kuefler *et al.* 2010) au profit du modèle de « mosaïque paysagère » (Wiens 1995).

Le modèle de « mosaïque paysagère » (Wiens 1995; **Fig. 7c**) reconnaît que les paysages ne sont pas simplement des tâches d'habitat intégrées au sein d'une matrice homogène, mais au sein d'une matrice hétérogène composée de tâches de différents types d'habitat, qui varient dans leur perméabilité (ou inversement, dans leur résistance) à la dispersion des organismes (Ricketts 2001) végétaux (Murphy & Lovett-Doust 2004). Au sein de ce modèle, la connectivité dépend de la mesure dans laquelle la dispersion est facilitée par les différents types d'habitat constituant la matrice, et résulte de l'interaction entre les organismes et la structure du paysage (McGarigal & Cushman 2005). Toutefois, les modèles « tâche-matrice » et « mosaïque paysagère » supposent que le paysage est composé de tâches d'habitat homogènes, délimitées par des frontières nettes et arbitraires, et appartenant à différentes

catégories d'habitat (McGarigal & Cushman 2005; Fischer & Lindenmayer 2006; Cushman *et al.* 2010; Lausch *et al.* 2015; Brudvig *et al.* 2017). Plutôt que de restreindre le paysage à des tâches d'habitat homogènes et catégorielles, le modèle de « gradient » (**Fig. 7d**; McGarigal & Cushman 2005; Fischer & Lindenmayer 2006; Cushman *et al.* 2010) représente la structure du paysage sous la forme d'un ensemble de gradients environnementaux continus qui varie dans l'espace selon la distance à laquelle l'organisme perçoit la structure physique du paysage (e.g. densité de la couverture arborée dans un rayon donné; Price *et al.* 2009), résultant en un gradient de perméabilité à la dispersion pour une espèce donnée.

La connectivité est favorisée par l'existence de continuités écologiques qui relient les tâches d'habitat autrement isolées. Initialement défini par la simple existence de corridors ou de pas japonais reliant les tâches d'habitat, le concept de continuité écologique inclut désormais l'ensemble des éléments paysagers qui sont perméables à la dispersion de l'organisme considéré. Dès lors, les modèles théoriques de représentation du paysage se sont progressivement détournés de la simple prise en compte de la structure physique du paysage au profit de l'interaction entre la structure physique du paysage et la dispersion des organismes. Cette évolution suggère que la connectivité doit être appréhendée de par sa nature fonctionnelle plutôt que structurelle.

2.1.2. Connectivité structurelle et fonctionnelle

En dépit d'une définition originelle insistant sur la nature fonctionnelle de la connectivité, soulignant l'interaction entre la dispersion de l'organisme et la structure physique du paysage, l'utilisation commune du concept de connectivité n'a pendant longtemps mis l'accent sur la seule nature structurelle de la connectivité (Taylor *et al.* 2006).

Ainsi, deux composantes de la connectivité se distinguent dans la littérature : la connectivité structurelle et la connectivité fonctionnelle (Tischendorf & Fahrig 2000; Calabrese & Fagan 2004; Taylor *et al.* 2006). La connectivité structurelle dépend des attributs physiques du paysage (i.e. proximité physique entre tâches d'habitat favorable), indépendamment des capacités de dispersion de l'organisme considéré au sein de la matrice paysagère (**Fig. 8a**). Elle ignore ainsi la réponse des organismes à la structure physique du paysage. Outre la présence de corridors, les mesures de connectivité structurelle se concentrent généralement sur la distance Euclidienne entre tâches et/ou sur la surface des tâches [e.g. distance Euclidienne au plus proche voisin; probabilité de colonisation du modèle

à fonction d'incidence (IFM; Hanski 1994a, b)] (Moilanen & Hanski 2001; Moilanen & Nieminen 2002; Kindlmann & Burel 2008).

La connectivité fonctionnelle considère explicitement la réponse des organismes aux attributs physiques du paysage (Tischendorf & Fahrig 2000; Calabrese & Fagan 2004; Taylor *et al.* 2006). Pour cela, la connectivité fonctionnelle intègre des informations sur les capacités potentielles ou observées de dispersion des organismes au sein de la matrice (e.g. taux de dispersion au sein des différents types d'habitat constituant la matrice, mortalité au cours de la dispersion; Tischendorf & Fahrig 2000; Murphy & Lovett-Doust 2004; Taylor *et al.* 2006; Kindlmann & Burel 2008; **Fig. 8b-c**).

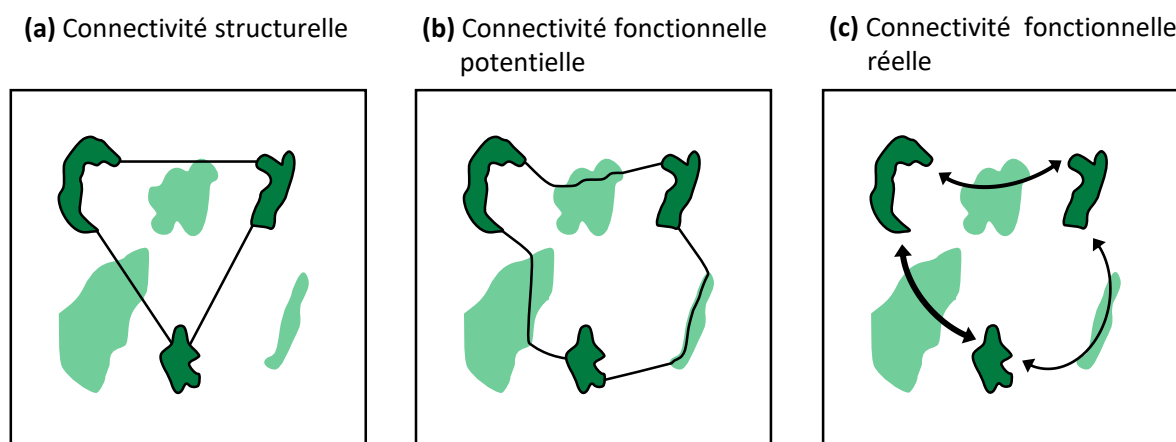


Fig. 8 Illustration des trois composantes de la connectivité : **(a)** la connectivité structurelle, **(b)** la connectivité fonctionnelle potentielle et **(c)** la connectivité fonctionnelle réelle. Les formes vert foncé entourées de noir indiquent les tâches d'habitat. Les nuances de vert indiquent une perméabilité à la dispersion croissante (blanc – vert) des types d'habitat composant la matrice. Les lignes noires représentent les chemins de dispersion potentiels des organismes entre tâches d'habitat, selon (a) les attributs physiques du paysage (b) et les capacités potentielles des organismes à se disperser au sein de la matrice paysagère. L'épaisseur des flèches noires dénotent l'importance des flux d'organismes entre tâches d'habitat, c'est-à-dire leurs capacités réelles à se disperser au sein de la matrice (c). D'après Calabrese & Fagan (2004) et Rayfield *et al.* (2011).

Plus récemment, Calabrese & Fagan (2004) ont proposé de discerner au sein du concept de connectivité fonctionnelle, la connectivité fonctionnelle potentielle et la connectivité réelle. La connectivité potentielle combine les attributs physiques du paysage et des informations limitées, indirectes sur les capacités de dispersion des organismes (**Fig. 8b**). Les mesures de connectivité potentielle reposent sur l'utilisation conjointe de cartes de résistance, traduisant la résistance (i.e. l'inverse de la perméabilité) de la matrice à la dispersion entre deux tâches, et d'algorithmes de connectivité, modélisant les chemins de dispersion potentiels entre deux tâches (Zeller *et al.* 2012, 2018; cf. introduction, section 2.2). La connectivité réelle repose, quant à elle, sur l'observation des mouvements de dispersion des organismes entre tâches (**Fig. 8c**), de façon directe (e.g. télémétrie, observation visuelles, capture-marquage-

recapture) ou indirecte, en utilisant des données génétiques. Chez les plantes, il est possible de mesurer directement le flux de pollen ou de graines (e.g. suivi de la dispersion par fluorescence et piégeage des graines et/ou du pollen, évaluation de la dispersion par piégeage de la pluie de graines, par l'étude de la banque de graines ou des graines contenues dans les excréments d'animaux). Toutefois, ces mesures, chronophages et laborieuses, sont souvent délaissées au profit de la génétique du paysage (Aavik *et al.* 2014; Aavik & Helm 2018).

2.1.3. Connectivité de la tâche et connectivité du paysage : un débat entre écologues finalement résolu ?

Tirant son origine de multiples disciplines de l'écologie, la connectivité a échappé à une définition précise. Plus particulièrement, « l'échelle » à laquelle la connectivité doit-être définie a été l'objet de nombreux débats entre les écologues des métapopulations et les écologues du paysage. D'un côté, les écologues des métapopulations insistaient sur le fait que la connectivité est une propriété au niveau de l'échelle de la tâche d'habitat. De l'autre côté, les écologues du paysage définissaient la connectivité comme une propriété à l'échelle d'un paysage (Tischendorf & Fahrig 2000, 2001; Moilanen & Hanski 2001; Moilanen & Nieminen 2002).

En écologie des métapopulations, la connectivité est définie à l'échelle de la tâche. Plus particulièrement, le taux de colonisation d'une tâche d'habitat inoccupée est fonction de son isolement. L'isolement de la tâche se mesure le plus souvent via la distance Euclidienne à la tâche d'habitat (occupée) la plus proche (distance Euclidienne au plus proche voisin), ou de la surface et la distance Euclidienne des tâches environnantes [probabilité de colonisation du modèle à fonction d'incidence (IFM; Hanski 1994a, b)]. Par conséquent, les mouvements de dispersion entre tâches d'habitat ne dépendent que de la distance entre tâches et de la distance de dispersion de l'organisme. Si l'écologie des métapopulations suppose que la connectivité de la tâche résulte d'un mouvement de dispersion à travers le paysage, ce mouvement n'est toutefois pas explicitement modélisé, la matrice paysagère étant considérée comme homogène et inhospitalière. En écologie du paysage, la connectivité est une propriété du paysage spécifique à une espèce donnée. Elle se réfère donc aux réponses des organismes à la structure physique du paysage. Plus particulièrement, les mouvements de dispersion des organismes entre tâches ne seront pas uniformes à travers le paysage, mais déterminés par l'interaction entre la structure physique du paysage et les capacités de dispersion de l'organisme (e.g. mortalité au cours de la dispersion, taux de dispersion au sein des différents types d'habitat).

Sur la base de ces éléments, Tischendorf & Fahrig (2001) argumentent que la distinction entre connectivité de la tâche et connectivité du paysage ne reposerait pas sur l'échelle à laquelle la connectivité peut être mesurée au travers de métriques (comme précédemment évoqué, e.g. Moilanen & Hanski 2001), mais plutôt sur la distinction entre connectivité structurelle et fonctionnelle. Plus particulièrement, la connectivité de la tâche est seulement basée sur la structure du paysage (i.e. connectivité structurelle) tandis que la connectivité du paysage est basée sur la réponse des organismes à cette structure (i.e. connectivité fonctionnelle). Cependant, de nos jours, la vision de Tischendorf & Fahrig (2001) apparaît trop simpliste, et peut ainsi être remise en cause. Comme le souligne With (2019), la connectivité de la tâche peut être caractérisée d'un point de vue fonctionnel, lorsque la distance entre tâches est pondérée par la perméabilité (ou résistance) de la matrice à la dispersion de l'organisme considéré (Ricketts 2001). Ricketts (2001) étend le principe d'isolement de la tâche (i.e. l'inverse de la connectivité structurelle) à l'isolement efficace de la tâche (*effective isolation*), que nous considérons – par extension – comme l'inverse de la connectivité fonctionnelle potentielle.

A l'issue de ce débat, il n'y a aucune preuve que la connectivité, définie comme le degré avec lequel le paysage facilite les mouvements des individus entre tâches d'habitat, devrait être limitée à une échelle spatiale particulière. La connectivité, sous cette unique définition, peut aussi bien être mesurée à l'échelle de la tâche que du paysage.

2.1.4. La connectivité, un concept dynamique

La connectivité n'est pas un concept statique, mais un « concept dynamique » (*sensu* Taylor et al. 2006) en raison de sa nature imprévisible (Crooks & Sanjayan 2006).

Comme le soulignent (Taylor *et al.* 2006), la connectivité doit être caractérisée dans le contexte du changement d'occupation des sols par l'Homme, aussi bien à court qu'à long terme. Les changements d'occupation du sol opèrent sur des échelles spatiales et temporelles hiérarchiquement imbriquées (O'Neill *et al.* 1986; Allen & Starr 1988), et façonnent ainsi la structure physique du paysage au gré des différentes saisons (e.g. en fonction des pratiques culturelles), des années (e.g. en fonction des rotations culturelles) et des décennies (e.g. en fonction des politiques agricoles). Si ces changements déterminent inévitablement la dynamique temporelle de connectivité structurelle, ils jouent également un rôle crucial sur la dynamique temporelle de connectivité fonctionnelle. En particulier, cette dernière repose sur la capacité de l'espèce à suivre l'évolution de la distribution des tâches d'habitat favorable, à

s'adapter aux modifications de la perméabilité (ou la résistance) de la matrice à leur dispersion, et à persister au sein de ces paysages en constante évolution (Taylor *et al.* 2006).

Différentes méthodes de quantification de la connectivité structurelle et fonctionnelle et donc de sa dynamique temporelle – peuvent être envisagées pour caractériser la connectivité dans l'espace et dans le temps.

2.2. La quantification de la connectivité et de sa dynamique temporelle par la modélisation des graphes paysagers

Deux approches ont largement été adoptées en écologie pour quantifier la connectivité : l'utilisation de (i) mesures dérivées de la théorie des métapopulations quantifiant la connectivité structurelle et (ii) mesures dérivées de la théorie des graphes, quantifiant aussi bien la connectivité structurelle que la connectivité fonctionnelle potentielle. Un grand nombre de ces dernières mesures intègrent les mesures dérivées des métapopulations [distance Euclidienne au plus proche voisin, probabilité de colonisation du modèle à fonction d'incidence (IFM; Hanski 1994a, b)], ou peuvent être considérées comme des équivalents ou des extensions de celles-ci.

Outre le fait qu'elles permettent de caractériser à la fois la connectivité structurelle et potentielle, les mesures dérivées de la théorie des graphes formalisent plusieurs avancées majeures. Notamment, la théorie des graphes est reconnue pour permettre de quantifier la connectivité spatiale à de multiples échelles spatiales, tout en incorporant, par exemple, les tâches d'habitat de type « pas japonais » (Fletcher & Fortin 2018). Elle constitue également un cadre prometteur pour quantifier la dynamique temporelle de connectivité (Fletcher & Fortin 2018). Pour l'ensemble de ces raisons, nous focaliserons dans ce présent manuscrit sur la quantification de la connectivité et de sa dynamique temporelle via l'utilisation de graphes paysagers.

2.2.1. La quantification de la connectivité

Au début des années 2000, Urban & Keitt (2001) introduisent et proposent la théorie des graphes aux écologues du paysage comme un cadre méthodologique commun pour quantifier la connectivité. Dans cette théorie, le paysage est vu comme un graphe (un réseau) composé d'un ensemble de tâches d'habitat favorable, appelées nœuds, qui sont connectées par des liens, représentant les mouvements de dispersion potentiels entre tâches.

Depuis, l'utilisation de cette théorie s'est démocratisée, en particulier pour évaluer la connectivité au sein des paysages où les habitats sont fragmentés en tâches d'habitat discrètes (Fletcher & Fortin 2018; With 2019). La théorie des graphes présente, en effet, l'avantage majeur d'être peu exigeante sur la quantité de données minimales requises pour quantifier la connectivité (localisation des tâches d'habitat et distance de dispersion maximale de l'organisme considéré), tout en permettant d'intégrer des informations supplémentaires sur les tâches d'habitat et sur la perméabilité (ou la résistance) de la matrice à la dispersion de l'organisme pour fournir un meilleur réalisme biologique (Calabrese & Fagan 2004; Urban *et al.* 2009; With 2019).

2.2.1.1. La construction d'un graphe paysager spatial

En dépit de sa simplicité apparente, cette théorie requiert la construction d'un graphe paysager spatial, dans lequel les nœuds et les liens spatiaux doivent être modélisés et définis pour permettre de quantifier la connectivité spatiale (Galpern *et al.* 2011; Foltête *et al.* 2012).

Les nœuds définissent les tâches d'habitat favorable de l'espèce considérée, et peuvent être modélisés sous la forme de points – correspondant généralement aux centroïdes des tâches – ou de polygones – se rapportant à une vision bidimensionnelle des tâches. Outre la localisation et la forme de représentation, les nœuds peuvent être pondérés par des informations supplémentaires (appelés poids ou attributs) telles que la surface ou la qualité intrinsèque de la tâche d'habitat.

La présence d'un lien spatial entre deux nœuds implique que les nœuds sont connectés par les mouvements de dispersion dans l'espace (ci-après dénommée dispersion spatiale). Préalablement à la définition de connexion entre nœuds, il est nécessaire de modéliser les liens potentiels entre nœuds, autrement dit, les chemins de dispersion potentiels des organismes entre tâches. La modélisation des liens spatiaux peut se réaliser au travers de différentes méthodes, dont les plus communément utilisées sont (i) la méthode Euclidienne, (ii) la méthode des chemins de moindre coût (Adriaensen *et al.* 2003) et (iii) la théorie des circuits (McRae 2006; McRae *et al.* 2008). Ces deux dernières méthodes constituent des algorithmes de connectivité (Zeller *et al.* 2012, 2018).

La modélisation Euclidienne des liens spatiaux suppose que les organismes se dispersent le long de lignes droites entre deux nœuds (**Fig. 9a**). *A contrario*, la modélisation des liens spatiaux par le biais des chemins de moindre coût ou de la théorie des circuits reconnaît que les organismes se dispersent selon la perméabilité (ou inversement, la

résistance) de la matrice entre deux nœuds (Ricketts 2001; Murphy & Lovett-Doust 2004). La modélisation des liens spatiaux non linéaires à partir de ces algorithmes de connectivité nécessite la création de carte de résistance (ou de coût), la valeur de résistance reflétant la résistance à la dispersion de l'organisme considéré exercée par les différents types d'habitat (ou le coût écologique de l'organisme à se disperser dans les différents types d'habitat) constituant la matrice paysagère. Plus particulièrement, plus un type d'habitat est perméable à la dispersion de l'organisme considéré, plus la valeur de résistance de ce type d'habitat est faible, et *vice versa* (**Fig. 9b-c**). Si les valeurs de résistances peuvent être estimées à partir de données empiriques (e.g. données de dispersion spatiale ou d'utilisation de l'habitat), elles restent majoritairement estimées à dire d'experts (Rayfield *et al.* 2010; Spear *et al.* 2010; Zeller *et al.* 2012). Outre le fait qu'elles sont le plus souvent subjectives (Spear *et al.* 2010), l'attribution des valeurs de résistances repose sur une hiérarchisation des types d'habitat. Elles priorisent ainsi le rôle que jouent ces derniers pour faciliter (ou entraver) la dispersion des organismes. Une fois que les cartes de résistance sont créées, les liens spatiaux peuvent être modélisés aux travers des algorithmes susmentionnés, chacun d'entre eux se caractérisant par des avantages et des limites. La modélisation par les chemins de moindre coût suppose un chemin de dispersion unique entre deux tâches d'habitat, suggérant que les organismes optent pour un chemin optimal (le chemin disposant du coût cumulé le plus faible) grâce à leur connaissance complète du paysage (i.e. omniscience; **Fig. 9b**; Adriaensen *et al.* 2003; McRae *et al.* 2008). La distance du chemin de moindre coût est exprimée soit en distance métrique, soit en unité de coût (le coût cumulé du chemin le moins coûteux). A l'inverse, la théorie des circuits intègre l'ensemble des chemins de dispersion possibles entre deux tâches d'habitat, en supposant que la dispersion des individus suit une marche aléatoire (i.e. ignorance; **Fig. 9c**; McRae *et al.* 2008). Plus particulièrement, la théorie des circuits tient compte du fait qu'une forte redondance des chemins (ou nombre de chemins) entre tâches favorise la dispersion spatiale (McRae *et al.* 2008; Fletcher *et al.* 2014). La distance du lien (appelé *resistor*, par analogie aux composants électriques qui conduisent le courant) est exprimée en ohm. Bien que ces deux méthodes de modélisation de liens spatiaux soient généralement opposées dans la littérature (dispersion spatiale « optimale » *versus* « aléatoire »), ces deux approches fournissent une modélisation des liens et des distances effectives (ou fonctionnelles) pertinentes et complémentaires (cf. Spear *et al.* 2010) pour plus de détails). En outre, de nouvelles méthodes « hybrides », telles que l'algorithme du chemin aléatoire le plus court (Saerens *et al.* 2009; Kivimäki *et al.* 2014; Panzacchi *et al.* 2016) permettent de réunir ces deux approches.

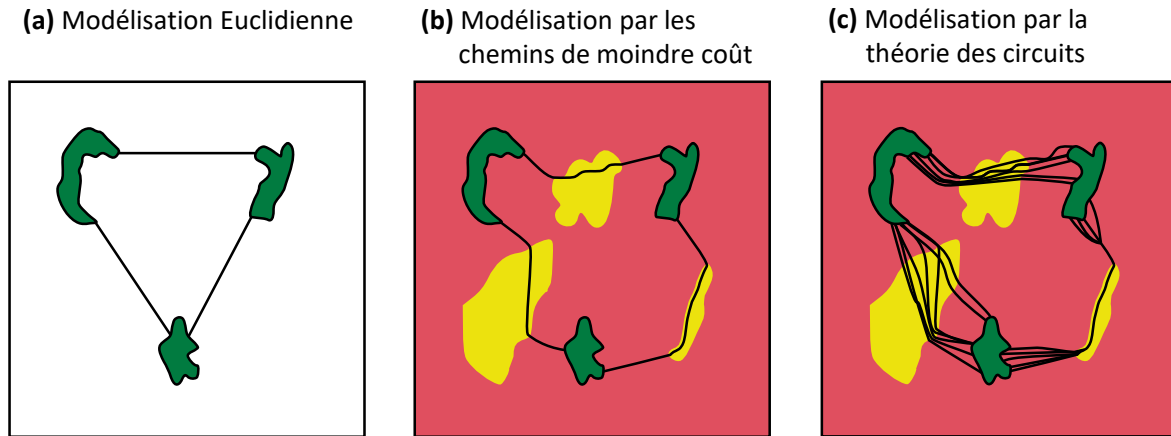


Fig. 9 Illustration des trois méthodes communes de modélisation des liens spatiaux entre nœuds : **(a)** la modélisation Euclidienne, **(b)** la modélisation par les chemins de moindre coût et **(c)** la modélisation par la théorie des circuits. Les formes vert foncé entourées de noir indiquent les nœuds. Les lignes noires représentent les liens spatiaux uniques (a-b) ou multiples (c) entre nœuds. Les liens spatiaux modélisés par le biais des chemins de moindre coût (b) ou de la théorie des circuits (c) reposent sur l'utilisation de cartes de résistance. Le dégradé du vert au rouge (b-c) indique une valeur de résistance à la dispersion croissante des types d'habitat composant la matrice (par analogie avec la perméabilité représenté dans la **Fig. 8**). D'après Rayfield *et al.* (2011).

À l'issue de la modélisation des liens spatiaux, ces derniers peuvent être pondérés (graphe paysager pondéré) ou non (graphe paysager non-pondéré) par l'attribution d'une valeur définissant la force de connexion entre nœuds (e.g. distance Euclidienne, distance effective, probabilité de dispersion distance dépendante). Dans les graphes non-pondérés, la force de connexion est utilisée pour définir la présence (ou l'absence) d'un lien entre nœuds lors de la construction du graphe plutôt qu'en tant qu'attribut du lien. Une façon commune de définir la présence d'un lien entre nœuds lors de la construction d'un graphe non-pondéré est d'utiliser une valeur de seuil, déterminée par la distance de dispersion maximale de l'organisme considéré. Les nœuds seront ainsi connectés par un lien si la distance entre ces derniers (Euclidienne ou effective) est inférieure à la distance de dispersion maximale, et *vice versa* (Urban & Keitt 2001). La présence d'un lien entre nœuds peut également être définie à partir du noyau de dispersion (dispersal kernel) de l'organisme considéré, modélisant la probabilité de dispersion de ce dernier en fonction de la distance entre nœuds (Euclidienne ou effective) pour une distance de dispersion (le plus souvent, médiane ou maximale) donnée (Urban & Keitt 2001). Classiquement ce noyau de dispersion se présente sous la forme d'une fonction exponentielle négative [e.g. probabilité de dispersion du modèle à fonction d'incidence (IFM; Hanski 1994a, b)], telle que : $p_{ij} = e^{-\alpha d_{ij}}$. Ce noyau de dispersion reflète ainsi une décroissance exponentielle (de coefficient α) de la probabilité de dispersion (p_{ij}) entre deux nœuds i et j à mesure que leur distance croît (d_{ij}), comme suit : $p_{ij} = e^{-\alpha d_{ij}}$. Le coefficient de décroissance α est déterminé à partir de la distance de dispersion (d_{ij}) maximale ou

médiane correspondant à une probabilité de dispersion (p_{ij}) faible (e.g. $p_{ij} = 0.05$ ou 0.01) ou médiane ($p_{ij} = 0.5$). Ultérieurement, Saura & Pascual-Hortal (2007) étendent cette approche en introduisant p_{ij}^* , la probabilité maximale du produit de l'ensemble des chemins de dispersion directs ou indirects (chemin de dispersion se réalisant en plusieurs étapes à travers des tâches « pas japonais »). Lors de la construction des graphes pondérés, la présence d'un lien entre nœuds peut également être définie à partir de l'utilisation d'une valeur de seuil [e.g. distance, probabilité (maximale) de dispersion (directe ou indirecte)]. Néanmoins, les graphes pondérés diffèrent des graphes non-pondérés puisqu'ils conservent les informations sur la force de connexion entre nœuds pour mesurer la connectivité à partir du graphe paysager (Galpern *et al.* 2011).

Enfin, les liens spatiaux peuvent également être orientés (liens unidirectionnels, appelés arcs) ou non (liens bidirectionnels). La plupart des graphes paysagers sont, en pratique, non orientés. Néanmoins, la construction de graphes paysagers orientés permet de tenir compte d'une orientation de la dispersion spatiale (e.g. dynamique de population île-continent, source-puits) (Galpern *et al.* 2011; Foltête *et al.* 2012).

2.2.1.2. Mesures du degré de connectivité à partir du graphe paysager

Dans le cadre de la théorie des graphes, un large éventail de métriques a été développé pour quantifier la connectivité spatiale, depuis la connectivité locale, qui mesure la connectivité des éléments composant le graphe paysager (i.e. nœuds et liens), jusqu'à la connectivité globale, qui mesure la connectivité de l'ensemble du graphe paysager (cf. Galpern *et al.* 2011; Laita *et al.* 2011; Rayfield *et al.* 2011 pour des revues). Rayfield *et al.* (2011) ont ainsi proposé une classification de l'ensemble des métriques issues de la théorie des graphes en fonction de (i) l'échelle à laquelle la connectivité est caractérisée et (ii) la propriété de la connectivité considérée. Plus particulièrement, Rayfield *et al.* (2011) distinguent quatre propriétés de la connectivité qui peuvent être mesurées : (i) le flux spécifique au chemin (*route-specific flux*, mesurant la dispersion spatiale entre tâches), (ii) la redondance des chemins (*route redundancy*, mesurant la présence de multiples chemins de dispersion entre tâches) (iii) la vulnérabilité du chemin (*route vulnerability*, mesurant le degré avec lequel le paysage canalise la dispersion spatiale) et (iv) la surface d'habitat connectée (*connected habitat area*, considérant une tâche d'habitat comme un espace où la connectivité existe et mesurant ainsi la surface d'habitat disponible ou atteignable du point de vue de l'espèce en intégrant la quantité d'habitat et la connectivité entre tâches en une même métrique). Si le choix de la

métrique de connectivité se réalise en fonction du contexte de la recherche menée, les choix réalisés en amont (i.e. lors de la construction du graphe), en particulier sur la définition et/ou la pondération des liens spatiaux détermineront la composante de connectivité qui est mesurée (connectivité structurelle *versus* connectivité fonctionnelle potentielle). Plus particulièrement, la caractérisation de la connectivité basée sur la définition et/ou la pondération de liens spatiaux par la distance Euclidienne ne prend en compte que la position spatiale des tâches d'habitat et leurs attributs (i.e. connectivité structurelle; **Fig. 8a** et **Fig. 9a**). A l'inverse, la définition et/ou la pondération des liens spatiaux par une distance effective (distance ou coût cumulé du chemin de moindre coût, distance de résistance) permet de caractériser la connectivité en intégrant la perméabilité de la matrice à la dispersion de l'organisme considéré en plus de la position spatiale et des attributs de tâches (i.e. connectivité fonctionnelle potentielle; **Fig. 8b** et **Fig. 9b-c**).

La théorie des graphes fournit un cadre prometteur pour évaluer la connectivité spatiale, au travers d'une large gamme de métriques qui intègrent explicitement la dispersion spatiale des organismes. Toutefois, comme souligné plus haut, la connectivité varie dans le temps, au gré des changements d'occupation des sols; et toutes les espèces ne réagissent pas instantanément à cette dynamique temporelle de connectivité (cf. introduction, section 1.2.6 et 2.1.4). Lorsqu'elle n'est pas tout simplement négligée, la considération du caractère dynamique de la connectivité dans les études empiriques reste, jusqu'ici, majoritairement implicite. Au cours des deux dernières décennies, la majorité des études s'est concentrée sur les réponses décalées dans le temps des espèces végétales à la connectivité suite aux modifications paysagères, en examinant si les communautés actuelles sont mieux expliquées par la connectivité spatiale passée que par la connectivité actuelle (e.g. Lindborg & Eriksson 2004; Helm *et al.* 2006; Naaf & Kolk 2015). Récemment, plusieurs auteurs ont souligné la nécessité de quantifier explicitement la dynamique temporelle de connectivité, aussi bien à court qu'à long terme, afin d'améliorer notre compréhension des patrons de biodiversité actuels (Kool *et al.* 2013; Zeigler & Fagan 2014; Lira *et al.* 2019).

2.2.2. Quantification de la dynamique temporelle de connectivité

En réponse à cet appel, plusieurs méthodes permettant de quantifier la dynamique temporelle de connectivité ont été développées dans le cadre de la théorie des graphes. Ces méthodes d'évaluation peuvent être divisées en deux approches principales.

La première approche quantifie les changements temporels de connectivité spatiale, c'est-à-dire en ne tenant compte que de la dispersion spatiale des organismes. Elle consiste à évaluer la dynamique temporelle de connectivité spatiale à partir d'une séquence de graphes spatiaux, représentant des « clichés » statiques du paysage à différents moments. La quantification de la dynamique temporelle de connectivité spatiale repose ainsi sur la comparaison des métriques calculées à différents moments.

La seconde approche, récemment développée par Martensen *et al.* (2017), quantifie la connectivité spatio-temporelle. La connectivité spatio-temporelle tient compte à la fois de la dispersion spatiale et de la dispersion temporelle des organismes, c'est-à-dire de leurs mouvements de dispersion dans l'espace et dans le temps. Des avancées récentes dans la théorie des graphes ont conduit au déploiement des graphes spatio-temporels, qui permettent de représenter les nœuds et les liens dans l'espace et dans le temps. Ces développements reposent ainsi sur l'utilisation d'un graphe spatio-temporel représentant un cliché « dynamique », c'est-à-dire avec une épaisseur temporelle, du paysage.

Une revue littéraire visant à synthétiser les méthodes existantes pour évaluer la dynamique temporelle de la connectivité a été réalisée (ARTICLE 1). Cet état de l'art permet de disposer des éléments méthodologiques nécessaires à l'étude et à la compréhension des effets de la dynamique temporelle de la connectivité sur la structuration actuelle des communautés végétales, objet d'étude de cette thèse.

Article 1. How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review

Léa Uroy, Audrey Alignier, Cendrine Mony, Jean-Christophe Foltête, Aude Ernoult.

In major revision, *Landscape Ecology*

Abstract

Context. Landscape connectivity plays a key role in determining the persistence of species inhabiting fragmented habitat patches. In dynamic landscapes, most studies measure connectivity at multiple time steps, but pay less attention to explicitly quantifying its temporal dynamics to gain insights into its role in biodiversity patterns, thereby enabling more effective operational outcomes.

Objectives. This article summarizes existing methods for the assessment of the temporal dynamics of connectivity.

Methods. We reviewed literature on the assessment of the temporal dynamics of connectivity.

Results. We presented two main approaches based on graph theory. The first, widely used approach quantifies temporal changes in spatial connectivity but only accounts for the spatial dispersal of organisms. Based on two or multiple time steps in the time series, this approach enables assessment of the sense and magnitude of the temporal changes in spatial connectivity. The second recently developed approach quantifies spatio-temporal connectivity, thus accounting for both spatial and temporal dispersal. So far, this holistic assessment of spatio-temporal connectivity only covers two time steps.

Conclusion. Existing methods for the assessment of the temporal dynamics of connectivity provide indicators to advance our understanding of biodiversity patterns, and to be able to implement measures to conserve and restore connectivity. We discuss the differences between the two main approaches from their conceptual and operational perspective and propose future research directions.

Introduction

Landscapes are inherently dynamic both in space and over time (Sprugel 1991; Turner 1993). In recent decades, anthropogenic disturbances, particularly urbanisation and agricultural intensification, have led to major changes in the type, use and spatial distribution of land cover (Fahrig *et al.* 2011), thus affecting landscape composition and configuration. These changes in land cover have caused habitat fragmentation (i.e. the breaking apart of the habitat patches, Fahrig 2003) resulting in biodiversity loss (Haddad *et al.* 2015; Fletcher *et al.* 2018).

In landscapes where habitats are fragmented, species are patchily distributed in a set of local populations forming a metapopulation (Opdam 1991; Hanski 1994a) and species assemblages are structured in a set of local communities forming a metacommunity (Wilson 1992; Leibold *et al.* 2004). In this context, dispersal is an important driver of the maintenance of species populations and assemblages, because it enables the exchange of individuals among local populations and communities. Dispersal is affected by landscape connectivity, defined as the degree to which the landscape facilitates the movement of individuals among habitat patches (Taylor *et al.* 2006). However, connectivity varies over time following land cover changes. Because the changes occur over a wide range of hierarchically nested spatial and temporal scales (O'Neill *et al.* 1986; Allen & Starr 1988), the temporal dynamics of connectivity range from short (e.g. inter-seasonal) to long (e.g. from inter-annual to inter-decadal) time scales. Faced with these temporal dynamics of connectivity, some species react immediately whereas others respond with a time-lag (Ovaskainen & Hanski 2002; Kuussaari *et al.* 2009). A time-lagged response of species or assemblages to connectivity loss may reflect a relaxation time, resulting in extinction debt (Diamond 1972; Tilman *et al.* 1994; Kuussaari *et al.* 2009). Conversely, a time-lagged response of species or assemblages to connectivity gain may reflect immigration lag, resulting in immigration credit (Kuussaari *et al.* 2009; Jackson & Sax 2010) (**Fig. 1**). Accounting for the temporal dynamics of connectivity in biodiversity studies is consequently important but is often overlooked.

The first studies to investigate time-lagged responses of biodiversity to connectivity investigated whether past connectivity explains current species distributions better than current connectivity (Lira *et al.* 2019). Past and current connectivity were assessed using a spatial connectivity index that accounts for the spatial dispersal of organisms. This index is calculated from static snapshots of the landscape, often two time steps that represent the landscape before and after the assumed change in connectivity. Using this approach, time-lagged responses to connectivity have been demonstrated, primarily in plants (van

Ruremonde & Kalkhoven 1991; Lindborg & Eriksson 2004; Helm *et al.* 2006; Naaf & Kolk 2015) but also in mammals, birds, amphibians (Metzger *et al.* 2009) and invertebrates (Petit & Burel 1998; Bommarco *et al.* 2014). This approach emphasizes the importance of past connectivity in understanding current biodiversity patterns.

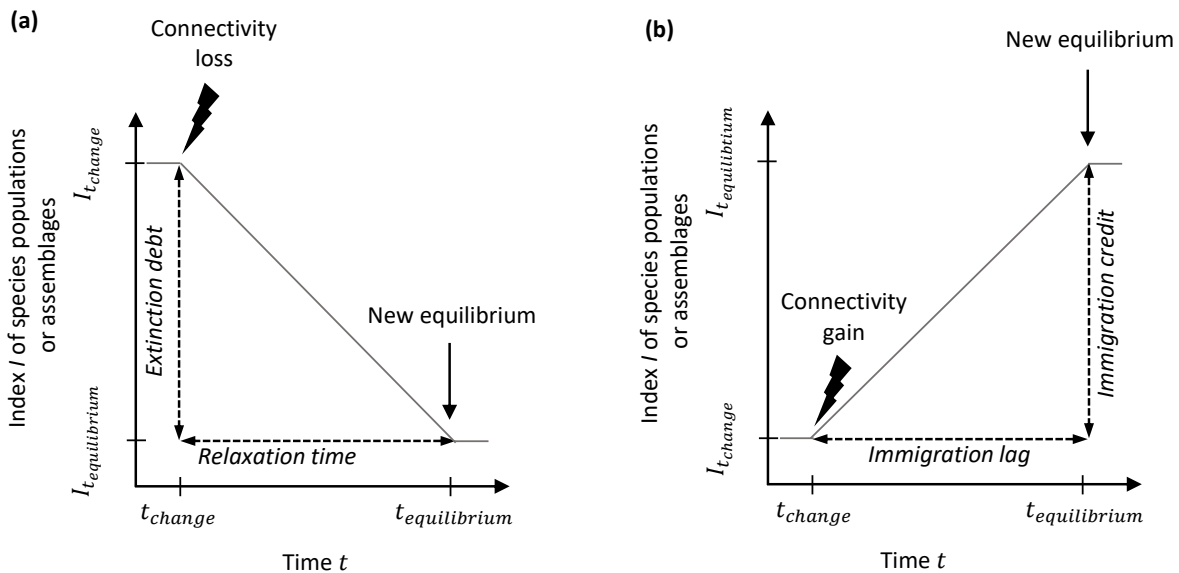


Fig. 1 Illustrations of time-lagged responses and their effects on species populations or assemblages following a (a) loss or (b) gain in landscape connectivity. t_{change} is the time step at which connectivity changed (either loss or gain) and for which no response of species (either extinction or immigration) has yet taken place. $t_{equilibrium}$ is the time step at which species response has occurred and a new equilibrium has been reached. $I_{t_{change}}$ and $I_{t_{equilibrium}}$ are an index I describing either species populations (e.g. presence, density) or assemblages (e.g. species richness, diversity) at t_{change} and $t_{equilibrium}$, respectively. Adapted from (Hylander & Ehrlén 2013).

Next, some authors pointed to the need to measure the temporal dynamics of connectivity more explicitly, either at short or long time scales, to better understand its role in current biodiversity patterns to enable more effective conservation or restoration actions (Kool *et al.* 2013; Zeigler & Fagan 2014; Lira *et al.* 2019). To this end, two main approaches have been developed. The first approach quantifies the temporal changes in spatial connectivity. In contrast to the investigation of time-lagged responses, this approach compares multiple spatial connectivity indices calculated independently from static snapshots of the landscape. It thus only accounts for the spatial dispersal of organisms, ignoring the probability that organisms disperse among habitat patches over time. The second approach, recently developed by Martensen *et al.* (2017), quantifies spatio-temporal connectivity by accounting for both the spatial and temporal dispersal of organisms. Both these approaches are rooted in the same mathematical framework, graph theory. However, they differ considerably in their outputs and in their implications for the ecological understanding of population dynamics and assembly rules.

Here, we review existing methods for the assessment of the temporal dynamics of connectivity, and highlight their usefulness in understanding biodiversity patterns. We briefly describe their theoretical framework, present examples of the application of each method, discuss their advantages and limitations and suggest new research directions to obtain more insights into species assembly rules. Finally, we discuss their divergences from a conceptual and operational perspective.

Theoretical background

Graph theory applied to landscape connectivity

Urban & Keitt (2001) introduced graph theory to landscape ecologists as a modelling framework to assess landscape connectivity. In this framework, the landscape is viewed as a graph composed of a set of nodes corresponding to favourable habitat patches, connected by edges representing potential ecological fluxes (e.g. dispersal) among nodes. The nodes and edges can be weighted by the size or quality of the habitat patches and by the distance between the patches, respectively, to better represent their contribution to connectivity. The edges can be weighted by Euclidean distance, least-cost distance (Adriaensen *et al.* 2003) or resistance distance (McRae 2006). Euclidean distance is rooted in a binary representation of the landscape (i.e. habitat patches vs uniform matrix), which assumes that organisms disperse along straight lines between two nodes (Forman & Godron 1986). By contrast, the distances resulting from least-cost paths or circuit theory acknowledge that matrix heterogeneity is an important factor in determining the dispersal of organisms (Ricketts 2001). In this framework, a wide range of indices has been developed to quantify spatial connectivity at different levels, including local connectivity, which measures the connectivity of the elements comprising the graph (i.e. nodes or edges) and global connectivity, which measures the connectivity of the entire graph (for reviews, see Galpern *et al.* 2011; Laita *et al.* 2011; Rayfield *et al.* 2011).

Graph theory applied to the temporal dynamics of landscape connectivity

The temporal dynamics of landscape connectivity is the result of patch turnover, due to the occurrence of disturbances which lead to changes in habitat patches; leading to changes in the degree of potential dispersal among favourable habitat patches. Landscape graphs are thus the right tool to model landscape dynamics and hence to assess the temporal dynamics of connectivity in prospective or retrospective studies. More specifically, the temporal dynamics of connectivity can be predicted or evaluated by simulating virtual changes under different

scenarios or by analysing real changes to the nodes and/or edges that make up landscape graphs.

The first applications of graph theory to landscape modelling used spatial graphs, which meant only temporal changes in spatial connectivity could be modelled. Recent advances underlined the relevance of spatio-temporal graphs, in which nodes and edges are represented in both space and time in a multiple-layer graph (Dale 2017). This approach combines layers representing the spatial graph at each time step of the time-series studied and the temporal edges between layers. This makes it possible to transpose the spatio-temporal properties of graphs in a landscape perspective that is useful for the assessment of spatio-temporal connectivity (Rayfield 2009; Fletcher & Fortin 2018).

Whatever the type of landscape graph used, the impact of the temporal dynamics of connectivity can be either assumed or tested. This dichotomy is found in all studies of connectivity using landscape graphs (Foltête *et al.* 2020). The first set of studies investigates the temporal dynamics of connectivity without testing their effects on biodiversity. In these studies, the impact of the temporal dynamics of connectivity on biodiversity is assumed, based on the hypothesis that landscape graphs used for connectivity assessment accurately represent the presence and the dispersal movements of the species concerned (see for instance Bishop-Taylor *et al.* 2015; Liu *et al.* 2017; Huang *et al.* 2020). The second set of study goes further thanks to empirical testing (Metzger *et al.* 2009; Bommarco *et al.* 2014; Huber *et al.* 2017; Raatikainen *et al.* 2018; Horváth *et al.* 2019) – and sometimes, to validation (Metzger *et al.* 2009; Bommarco *et al.* 2014; Raatikainen *et al.* 2018; Horváth *et al.* 2019) – of the impact of temporal dynamics of connectivity on biodiversity patterns.

Methods for assessing the temporal dynamics of landscape connectivity

Our review showed that the methods to assess the temporal dynamics of landscape connectivity can be divided into two main approaches: (i) the quantification of temporal changes in spatial connectivity, which only accounts for spatial dispersal and (ii) the quantification of the spatio-temporal connectivity, which account for both spatial and temporal dispersal. Yet, most works on the temporal dynamics of connectivity are based on the first approach. This first approach relies on the comparison of spatial connectivity indices computed from a sequence of spatial landscape graphs representing static snapshots of the landscape at two (**Fig. 2a**) or multiple (**Fig. 2b**) time steps in the time series. The second method quantifies the spatio-temporal connectivity in a spatial-temporal graph representing

a dynamic snapshot (i.e. a snapshot with a temporal thickness) of the landscape. Yet it has only been developed for two time steps to date (Fig. 2c).

Quantification of temporal changes in spatial connectivity using multiple spatial landscape graphs

The quantification of temporal changes in spatial connectivity relies on the comparison of two (Fig. 2a) or more (Fig. 2b) spatial connectivity indices computed from a sequence of spatial landscape graphs, representing static snapshots of the landscape at each time step in the time series.

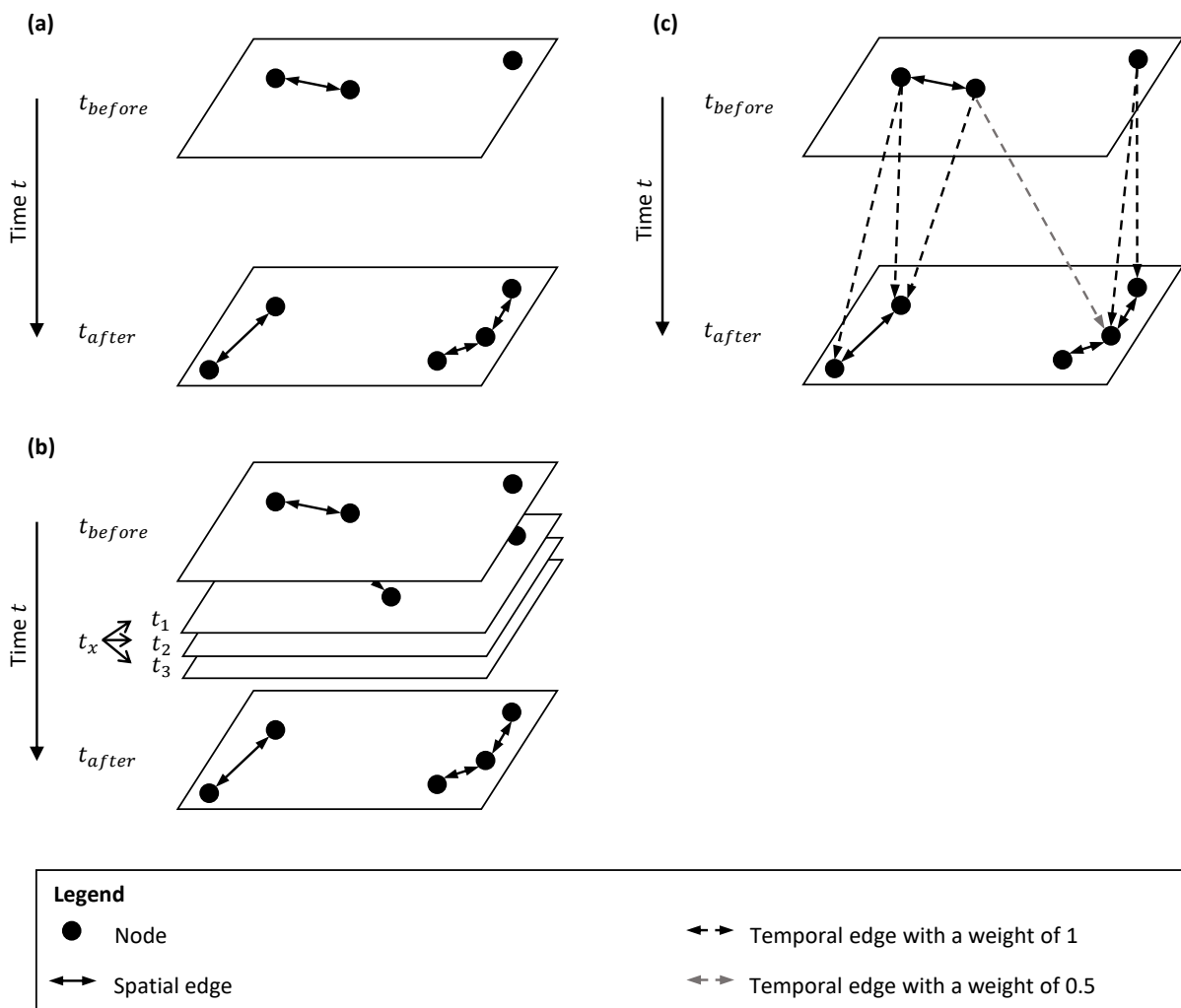


Fig. 2 The temporal dynamics of landscape connectivity can be assessed from spatial landscape graphs (left) either for (a) two time steps of the time series [i.e. before (t_{before}), and after (t_{after})] the change in connectivity or (b) multiple time steps t_x ($t_{before} < t_x < t_{after}$) or from a spatio-temporal landscape graph (right) for (c) two time steps of the time series, that is with temporal edges running between the two spatial landscape graphs. Adapted from Martensen *et al.* (2017).

(1) Two time steps in the time series

A set of studies analysed the temporal changes in spatial connectivity between two time steps: before (t_{before}), and after (t_{after}) the assumed change in connectivity (**Fig. 2a**). The temporal changes were assessed by analysing variations before and after the loss or gain in spatial connectivity (**Fig. 3a**). Originally, this approach was used to assess the relative contribution of a given node or edge to the global connectivity, by computing the loss in connectivity after the removal of the element concerned (e.g. Keitt *et al.* 1997; Rothley & Rae 2005; Matisziw & Murray 2009; Bodin & Saura 2010; Rubio *et al.* 2015; Mui *et al.* 2017). The variation in global connectivity was transposed to a more temporal perspective, for instance to enable conservation or restoration measures to be applied to specific patches (García-Feced *et al.* 2011) or landscapes (Rappaport *et al.* 2015). For instance, Rappaport *et al.* (2015) proposed an “urgency indicator” based on the differences in the amount of habitat and global connectivity between t_{before} and t_{after} to enable prioritisation of the landscapes to be protected or restored. These authors differed markedly in their ranking of forest landscapes to be restored or conserved both in the sense and the magnitude of changes in habitat cover and connectivity taken into account. This suggests that prioritisation of landscapes to be restored or conserved may be hampered by disregarding landscape dynamics.

Variations in spatial connectivity have also been used to understand the effect of land cover changes on the temporal changes in spatial connectivity, often at global scale (Baudry *et al.* 2003; Saura *et al.* 2011, 2019; Mazaris *et al.* 2013; Liu *et al.* 2014, 2017; Mui *et al.* 2017; Sahraoui *et al.* 2017), sometimes coupled with the local scale (Mazaris *et al.* 2013; Mui *et al.* 2017). For instance, Liu *et al.* (2017) tested the effect of forest plantation expansion on global spatial connectivity of natural forests. They reported that connectivity loss varied from 55% to 96% between 1972 and 2012, depending on the degree of forest plantation expansion in three of the four areas they studied, while the gain in connectivity was 2% over the same period in areas where no forests were planted. Other authors, including Horváth *et al.* (2019), went further by testing the effect on biodiversity of the variation in local spatial connectivity between 1957 and 2010. In temporary ponds subject to up to 70% of habitat loss, these authors showed that the greater the loss of local connectivity, the greater the loss of invertebrate zooplankton richness over the period concerned. However, they focused on changes in spatial connectivity between two time steps, without investigating whether the loss or gain in connectivity was significant; e.g. by testing whether the mean value of connectivity differed statistically between t_{before} and t_{after} . By contrast, through the use of the standard error of

the mean and statistical tests, respectively, Bommarco *et al.* (2014) and Huber *et al.* (2017) demonstrated significant losses of local connectivity of grasslands before analysing whether a time-lagged response in biodiversity had taken place.

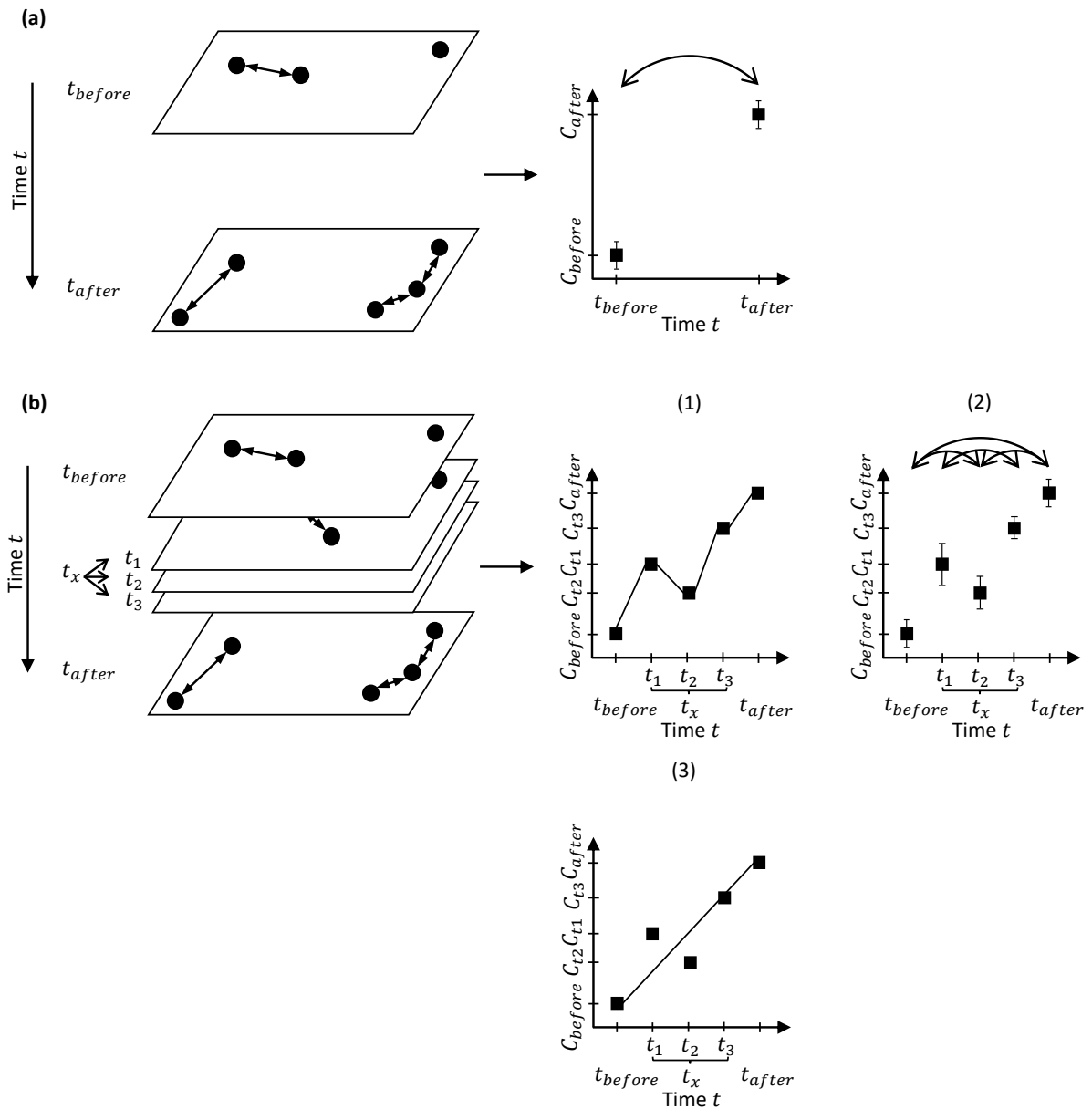


Fig. 3 Overview of possible approaches to assess the temporal changes in spatial connectivity from the comparison of multiple spatial connectivity indices, calculated independently for different time steps in the time series. Such temporal changes can be assessed with **(a)** two time steps in the time series [i.e. before (t_{before}) and after (t_{after}) the change in connectivity] by assessing the variation in spatial connectivity values or **(b)** multiple time steps t_x ($t_{before} < t_x < t_{after}$) by (1) visually examining the curve of spatial connectivity values, (2) assessing the variation in spatial connectivity values or (3) assessing the overall trend of spatial connectivity values using statistical analysis.

Overall, assessing temporal changes in spatial connectivity based on variations in spatial connectivity at two time steps is a simple, time-saving and affordable method to assess whether (significance), how (sense) and to what extent (magnitude) connectivity values have changed or could change over time. Since this variation is based on two time steps, the assessment of temporal changes in spatial connectivity assumes that connectivity changes in a purely linear way over time. However, additional changes in connectivity may occur between the two time steps, particularly during long time series. Studying these changes may provide deeper insights into biodiversity patterns. The use of a higher temporal resolution with multiple time steps t_x over the time series studied ($t_{before} < t_x < t_{after}$) should thus improve the assessment of temporal changes in spatial connectivity.

(2) Multiple time steps t_x in the time series

- Visual examination of the curve representing spatial connectivity values

Among studies based on multiple time steps over the time series (**Fig. 2b**), those focusing on graph robustness (i.e. the number of elements that can be removed without altering global connectivity; Minor & Urban 2008) were probably the first to visually examine the curve of global spatial connectivity over successive deletions of nodes or edges (e.g. Urban & Keitt 2001). Originally used to study the sensitivity of global connectivity to disturbances, this approach has been transposed to a more temporal perspective (**Fig. 3b-1**). For instance, Tulbure *et al.* (2014) investigated how the global connectivity of aquatic habitat patches might change in a warmer climate, assumed to lead to aquatic habitat patch loss. They assessed the robustness of the aquatic landscape by studying the curve of global connectivity with an increasing proportion of sequentially removed aquatic habitat patches. Other authors go further, reporting a visual examination of the temporal changes in spatial connectivity accounting for changes in nodes and/or edges at both global (Bishop-Taylor *et al.* 2015; Saura *et al.* 2019) and local (Rappaport *et al.* 2015; Raatikainen *et al.* 2018) scales. For example, Bishop-Taylor *et al.* (2015) considered global spatial connectivity of surface water habitats under eight flooding scenarios ranging from no flood to a 100-year average recurrence interval in an aquatic landscape. They found that the flooding recurrence interval was positively correlated with global connectivity, suggesting that flooding creates a “transient connectivity window” (Zeigler & Fagan 2014), i.e. a period during which matrix conditions increase the probability of successful individual movement between habitat patches.

Although the use of curves provides a better overview of the temporal changes in spatial connectivity than values measured at successive time steps in the time series, it

remains a purely descriptive indicator quantifying the sense and the magnitude of the temporal changes in spatial connectivity.

- Assessment of variations in spatial connectivity values

Above and beyond visual examination of the curve of spatial connectivity over multiple time steps, it is possible to extend the approach based on the variation of spatial connectivity values before and after an assumed change in connectivity (see section “Two time steps in the time series”) to multiple time steps in the time series (**Fig. 3b-2**). This approach has been used to identify appropriate locations for connectivity measures (Foltête *et al.* 2014; Clauzel *et al.* 2015; Foltête 2018). Foltête *et al.* (2014) investigated the gain in global connectivity over 10 successive additions of wildlife crossings in a pond network for amphibian species as a criterion to identify the location of each new wildlife crossing to be added in order to maximize global connectivity. Nevertheless, the investigation of the variation of connectivity over multiple time steps has mainly been used to study temporal changes in spatial connectivity as changes in land cover occur. For instance, Metzger *et al.* (2009) assessed the changes in local connectivity values in three successive time steps (1962, 1981, 2000). These changes over successive-decades were assessed using two indicators for each habitat patch: the differences in connectivity between 1962 and 1981 and between 1981 and 2000. Interestingly, they provided the first and so far, the only evidence that both past connectivity (1962 and/or 1981) and the successive temporal changes in connectivity (1962-1981 and/or 1981-2000) explain the current diversity patterns of trees, frogs and birds. Similar approaches were applied by Hernández *et al.* (2015) and McIntyre *et al.* (2018), who used variations in global and/or local spatial connectivity over several time steps to assess temporal changes in the spatial connectivity of forest and aquatic habitats over long time periods (1975-2011 and 1945-2000s), respectively. McIntyre *et al.* (2018) averaged connectivity values obtained from numerous short time steps (e.g. intra-decadal) to a few long time steps (e.g. inter-decadal). However, averaging may conceal notable variability of connectivity values over time which could be crucial for aquatic biodiversity, as shown by Tulbure *et al.* (2014) and Bishop-Taylor *et al.* (2018) (see section “Assessment of the overall trend of spatial connectivity values using statistical analysis”).

By contrast, several studies tested for significant differences in local or global connectivity between time steps in the time series. These differences were assessed by comparing the standard error (Rayfield *et al.* 2008; Raatikainen *et al.* 2018) or the 95% confidence interval (Bishop-Taylor *et al.* 2015) around mean connectivity values. Statistical

tests could be also used though already done yet. For instance, Rayfield *et al.* (2008) analysed temporal changes in global spatial connectivity of forest habitat patches in four time steps over a 200-year time series according to five scenarios of protection of the patches. Applying ten replicates of each scenario, they averaged the global connectivity of forest patches for each time step. By reporting the initial connectivity and the average connectivity coupled to its standard error obtained at each time step on a plot, they demonstrated that global connectivity decreased in most of the scenarios investigated.

To go further, especially if many time steps are involved, it is possible to use statistical modelling to identify the sign and the magnitude of the overall trend of connectivity values, while accounting for the variability of connectivity values occurring over the period concerned.

- Assessment of the overall trend of spatial connectivity values using statistical analysis

Although indicators derived from statistical modelling of the relationship between time and connectivity can accurately assess temporal changes in spatial connectivity in multiple time steps, their use remains rare (**Fig. 3b-3**). To our knowledge, only two studies have used trend analysis to assess the temporal changes in spatial connectivity (Tulbure *et al.* 2014; Bishop-Taylor *et al.* 2018). Tulbure *et al.* (2014) analysed global connectivity values of aquatic habitat patches for 278 time steps over a 13-year time series. Using a Mann-Kendall trend test, these authors reported that global connectivity was subject to high seasonal variability while significantly decreasing over the whole period, suggesting potential consequences for species inhabiting these aquatic habitats. Extending the use of statistical analysis to assess the overall trend of spatial connectivity values at multiple time steps is probably the most promising quantitative and precise approach for the assessment of temporal changes in spatial connectivity. The relationship between time and connectivity can be explored, for instance, through linear, logarithmic, exponential polynomial or power functions. Assessing trends in spatial connectivity at multiple time steps makes it possible to determine not only the significance and the sense of the overall temporal changes in spatial connectivity but also the magnitude of the changes.

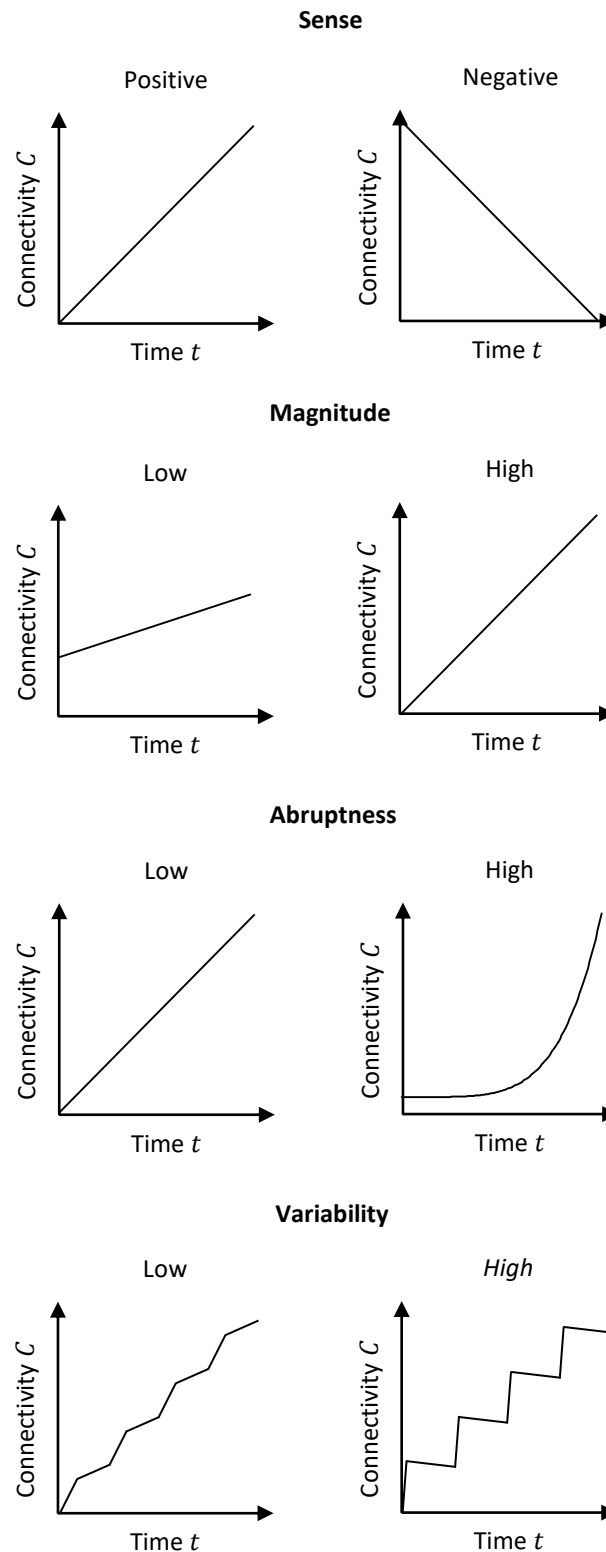


Fig. 4 Overview of the different components of the temporal changes in spatial connectivity that could be provided by statistical modelling of the relationship between time and connectivity (trend analysis).

The use of multiple time steps provides a finer assessment of the temporal changes in spatial connectivity before and after an assumed change, by accounting for the inner connectivity variability between the two time steps. Including the multiple changes in

connectivity that occur within a time series in the assessment of the temporal changes in spatial connectivity is particularly important to reflect the underlying ecological processes as accurately as possible. Besides the sense and magnitude of these temporal changes, their abruptness and their variability can also be assessed (**Fig. 4**). Trend analysis is a powerful but still underexploited tool to make a finer yet broader assessment of the temporal changes in spatial connectivity by means of additional indicators (e.g. variability: standard error of the residuals; abruptness: power value n of a power function fitted to the data). Although the effects of the sense and the magnitude of the temporal changes in spatial connectivity still need to be fed by evidence (but see Metzger *et al.* 2009; Bommarco *et al.* 2014; Huber *et al.* 2017; Raatikainen *et al.* 2018; Horváth *et al.* 2019), we recommend going further by exploring the effects of the variability and the abruptness in connectivity. These two components also likely drive the dispersal movements of organisms, and hence their response to temporal changes in spatial connectivity. Although the recent incorporation in the metacommunity theory of temporal variations in dispersal (Matias *et al.* 2013) that could be related to temporal changes in spatial connectivity may help predict biodiversity patterns, abrupt changes in dispersal processes have yet to be included.

The quantification of the spatio-temporal connectivity using a spatio-temporal landscape graph

The assessment of the temporal dynamics of landscape connectivity based on a sequence of spatial landscape graphs only accounts for spatial dispersal among favourable habitat patches over the time series. It has been challenged, notably by Rayfield (2009), who argued that changes in habitat patches do not only affect spatial dispersal between habitat patches at a given time step, but also the dispersal of organisms between habitat patches between time steps. Rayfield (2009) and more recently Martensen *et al.* (2017) and Fletcher & Fortin (2018) discussed the need to assess connectivity using spatio-temporal landscape graphs, which represent a dynamic snapshot of the landscape over the time series, thereby to a certain extent, integrating temporal thickness, to assess spatio-temporal connectivity. Rayfield (2009) suggested that spatial and temporal edges can be weighted by the spatial distance and the duration of the time series, respectively; but this approach has not yet been explored. Martensen *et al.* (2017) proposed a similar method, in which spatial and temporal edges are weighted based on the probability of spatio-temporal dispersal (**Fig. 2c**). Each node is weighted by its change over the time series, that is, by habitat patch turnover between t_{before} and t_{after} . Specifically, the node can be either gained (node absent in t_{before} but present in

t_{after}), lost (node present in t_{before} but absent in t_{after}) or remain stable (node present in t_{before} and in t_{after}). The weight attributed to the temporal edges between nodes depends on the (possible) simultaneous existence of nodes between the time steps considered (i.e. at t_x , between t_{before} and t_{after}). If the two nodes exist simultaneously at t_x (e.g. if the organism disperses from a node being lost or gained to a stable node between t_{before} and t_{after}), the weight attributed to a temporal edge is 1. If information concerning the simultaneous existence of two nodes at t_x is unknown (e.g. if the organism disperses from a node gained to a node lost between t_{before} and t_{after} , or the opposite), the weight is 0.5. By multiplying the spatial and temporal weight of the edge, the probability of spatio-temporal dispersal between two habitat patches is obtained and hence a spatio-temporal connectivity index is calculated between the two time steps.

To date, only Martensen *et al.* (2017) and Huang *et al.* (2020) have used this framework. Martensen *et al.* (2017) examined the spatio-temporal connectivity before (1990) and after (2001) a hypothesised change in connectivity in a forest landscape. They compared the global connectivity of forest patches obtained from the only-spatial approach based on static snapshots of the landscape at the two time steps studied, with those obtained from the spatio-temporal approach based on a dynamic snapshot of the landscape over these two time steps. Notably, they demonstrated that only-spatial connectivity can lead to an underestimation (on average 30%, but can reach 150%) of the spatio-temporal connectivity, especially in landscapes where the loss of habitat is high. Huang *et al.* (2020) observed similar patterns by simulating hypothetical distributions of 300 species in virtual landscapes under climate change. In particular, the spatial-temporal connectivity was higher than the only-spatial connectivity in 44% of the 300 virtual species, and underestimation occurred when loss of habitat amount, quality and isolation occurred between t_{before} and t_{after} . The authors also investigated how the ability of three “real” species to expand their range under different climate change scenarios affected underestimation of only-spatial connectivity. They found that the difference between future (2030) only-spatial connectivity and the spatio-temporal connectivity measured over the time series [from the present (1970-2018) to future (2030)] declined in species that will probably expand their range, and *vice versa*. These studies emphasise the need to include the consequences of changes in habitat patches in the ability of an organism to reach habitat patches between two time steps to quantify the “real” (i.e. spatio-temporal) connectivity and its potential consequences for biodiversity.

Overall, the inclusion of both the spatial and temporal components of the dispersal processes enabled more precise quantification of connectivity in dynamic landscapes. Nevertheless, this novel approach is, so far, restricted to two time steps (t_{before} and t_{after}) over the time series, which probably justifies the trinary weighting of temporal edges and thus a very simplified view of the process of temporal dispersal. Including multiple time steps t_x will pave the way for possible improvements to accurately fit the dispersal process of organisms, such as the (i) time and the period (e.g. linked to the state of habitat patches) required to disperse among habitat patches and (ii) the temporal scale at which organisms respond to connectivity. This would first require accounting for the duration of the (possible) simultaneous existence of two habitat patches in the spatio-temporal model of connectivity, by weighting the probability of temporal dispersal between two habitat patches as a function of the duration of their simultaneous existence (Rayfield 2009). The duration of temporal edges is indeed likely to drive the magnitude of the dispersal flux (number of individuals) but also the probability of species with low dispersal ability to disperse over time from one favourable habitat patch to another. In addition, weighting the temporal edges according to the simultaneous existence of two habitat patches in a particular state (e.g. flooding) could make it possible to account for the most suitable or required dispersal periods for the organism concerned. Further, the potential legacy effects exerted by connectivity on current biodiversity patterns need to be explicitly accounted for to reach a holistic understanding of how spatio-temporal connectivity affects existing biodiversity patterns. Adequate weighting of the spatio-temporal probability to disperse between two habitat patches between two successive time steps is one way to include the time-lag curves (i.e. the degree to which species respond to connectivity at different time steps of the time series studied) in the spatio-temporal connectivity approach.

Do the temporal dynamics of landscape connectivity need to be assessed from spatial or spatio-temporal graphs? A discussion of their conceptual and operational divergences

Our literature review was rooted in the dichotomy of two main approaches to assess the temporal dynamics of landscape connectivity: the first one quantifies the temporal changes in spatial connectivity from multiple spatial graphs, while the second quantifies spatio-temporal connectivity from a single spatio-temporal graph. Here, we discuss their differences from both a conceptual and an operational viewpoint to guide methodological choices.

While major advances have been made in methods to assess the temporal dynamics of connectivity, it is still not clear if the two main approaches reflect the same ecological processes and answer the same questions. By accounting for spatial dispersal, the quantification of temporal changes in spatial connectivity reflects the patterns of opportunities for the dispersal of organisms at multiple time steps, but not between these time steps. Nonetheless, considering the temporal changes in spatial connectivity is one step forward in our understanding of the persistence of (meta)-populations and (meta-)communities, which so far has only been seen as determined by spatial connectivity [i.e. the degree of spatial connectivity obtained from a single snapshot or an average of multiple static snapshot(s) of the landscape]. The magnitude, the frequency and even the duration of transient changes in spatial connectivity as drivers of the persistence of (meta)-populations and (meta)-communities were overlooked until the recent works of Perry & Lee (2019) and Reigada *et al.* (2015). In dynamic landscapes, habitat patch turnover may outweigh the relationships between spatial connectivity and species occupancy, even if the spatial connectivity shapes colonisation processes (Biedermann 2004; Hodgson *et al.* 2009). Therefore, like habitat loss (Keymer *et al.* 2000), spatial connectivity should be at least as important as its patterns of temporal changes – if not more so – in determining current biodiversity patterns. But patch turnover also provides spatio-temporal connectivity among patches, thereby allowing individuals to disperse among ephemeral patches over time, even though the patches are spatially isolated at any single time step (Keymer *et al.* 2000; Matlack & Monde 2004; Wimberly 2006). Omitting the spatio-temporal connectivity may therefore not only lead to the absence of apparent connectivity effects, but also to underestimating connectivity in dynamic landscapes. Moreover, the spatio-temporal connectivity as modelled by Martensen *et al.* (2017), that is, by weighting the temporal edges as a function of the changes of patches, to a certain extent implies that high patch turnover rates may result in “pulsed” release of dispersers, thereby increasing colonisation rates and occupancy over time (Reigada *et al.* 2015). Overall, spatio-temporal connectivity is a promising avenue towards understanding the “real” relationships between biodiversity and connectivity in dynamic landscapes, although also limiting our predictions about whether and how spatial connectivity varies over time.

Our review also revealed marked differences in how the two main approaches estimate temporal dynamics of connectivity. Although the four components (sense, magnitude, variability, and abruptness) of the temporal changes in spatial connectivity can be properly estimated, spatio-temporal connectivity cannot estimate these components, since they are

intrinsically embedded in the spatio-temporal connectivity itself. Only spatio-temporal connectivity provides a single holistic estimate of connectivity in space and over time and therefore corresponds to a dynamic snapshot of the “real” connectivity in landscapes. However, this promising approach has several limitations. So far, spatio-temporal connectivity cannot be assessed based on multiple time steps t_x in the time series. Although considering a higher temporal resolution would probably only strengthen the patterns observed by Martensen *et al.* (2017) and Huang *et al.* (2020), this needs to be tested. Today, obtaining a finer temporal resolution is easy, especially thanks to the recent development of powerful tools to (i) rapidly and accurately digitise past land cover maps, such as the HistMapR free package (Auffret *et al.* 2017a) and (ii) obtain accurate data at a frequent time resolution to digitise current land cover maps thanks to the recent advances in remote sensing methods, accessible at low cost, coupled with efficient machine-learning algorithms (Rapinel *et al.* 2019). However, considering patch turnover involves particularly high methodological requirements in terms of land cover resolution and classification (i.e. spatial resolutions and classification techniques must be identical and land cover maps completely overlaid over the time series). Therefore, the estimation of the spatio-temporal connectivity may be biased, especially when studying long time series that require the use of land cover maps from decades or centuries ago. In this particular case, the methodological requirements needed to address spatio-temporal connectivity are hard to meet due to changes in the nature of the sensors. Therefore, improving spatio-temporal connectivity estimates with a greater number of spatial and temporal edges will be challenging, and will also require continuing to bridge the gap between spatio-temporal graphs – which can involve long and often complex mathematical calculations – and ecologists. Moreover, the difficulty in disentangling the underlying components of the temporal changes in spatial connectivity can also hamper the choice of actions to be implemented to manage connectivity in dynamic landscapes. Spatio-temporal connectivity may thus be an innovative and powerful tool for land-use planners, but ultimately, it needs to move toward a realistic and feasible indicator for setting conservation and restoration priorities. We believe that - at present - the joint use of the two approaches would allow more precautionary management of connectivity and its impacts on biodiversity.

Our progress in understanding the conceptual and operational advantages and limitations of the two approaches is, so far, slowed down by the lack of confrontation with biological data. To go further, the two approaches need to be compared, their respective effects on biodiversity tested jointly. With that aim in view, future studies should bear in mind that assessing the temporal dynamics of connectivity needs to be adapted to the ecological

processes studied in order to account for the processes underpinning the relationships between connectivity, its temporal dynamics and biodiversity patterns. To this end, the temporal range, that is the duration of time series considered, needs to match the temporal scale of the response of the organisms studied, which is relative to their longevity, turnover rate, and dispersal capacity (Kuussaari *et al.* 2009; Jackson & Sax 2010). Future research should also keep in mind that the temporal scales of response are hierarchically nested (level of organisation), the temporal response at the individual- scale being shorter than that of community scale (Hylander & Ehrlén 2013). Existing works, even those based on multiple intra- and inter-annual time steps (Tulbure *et al.* 2014; Bishop-Taylor *et al.* 2018), investigated the temporal dynamics of connectivity based on the time steps taken independently, hence omitting the short-term (e.g. intra-annual) temporal dynamics of connectivity are indeed nested in long-term (e.g. inter-annual) dynamics. Therefore, considering the hierarchically nested structure of the temporal dynamics of connectivity is a promising way to accurately estimate the conceptual and operational divergences between the temporal changes in spatial connectivity and the spatio-temporal connectivity.

Conclusion

Methods designed for the assessment of the temporal dynamics of landscape connectivity provide insights into the consequences for landscape connectivity of both natural and anthropic disturbances. The methods provide operational indicators to identify which specific areas (from patches to landscapes) have undergone changes in connectivity over time, or not, and to what extent these changes may affect or have affected biodiversity patterns through time-lagged or immediate responses. The approaches reviewed in this article could provide new methods and decision-making tools for land-use planners. They could help prioritize specific areas to be protected or to be used to implement and test connectivity conservation or restoration measures in a dynamic perspective (i.e. “mobile” protected areas, the locations of which change over time; Bull *et al.* 2013). This approach accounts for both immediate and time-lagged responses of biodiversity and can thus provide guidelines on how to maintain, restore and protect biodiversity in a changing world.

Acknowledgements

This work was funded by the Fondation de France (BISCO project). We thank Daphné Goodfellow for the English editing.

3. Effet de la connectivité sur la structure des communautés végétales

Alors qu'un corpus solide de théories écologiques prédit l'importance de la connectivité pour les communautés végétales, l'incorporation de sa dynamique temporelle dans les modèles théoriques reste insuffisante. D'un côté, la théorie souligne l'importance de maintenir ou de restaurer la connectivité pour faciliter la dispersion des plantes entre tâches, permettant ainsi de générer des prédictions sur la structure des communautés végétales. De l'autre côté, la théorie n'intègre qu'implicitement le rôle de la dynamique temporelle de connectivité, en révélant que les gains et les pertes de connectivité peuvent entraîner des délais de réponses au sein des communautés végétales.

De manière générale, la théorie des métacommunautés propose que la connectivité, qu'elle soit présente ou passée, devrait influencer la structure taxonomique des communautés végétales (cf. introduction, section 1.2.4). Plus particulièrement, une forte connectivité pourrait accroître la richesse spécifique des communautés locales, mais également la similarité de composition spécifique entre communautés locales (Mouquet & Loreau 2003).

Cependant, un simple aperçu de la structure taxonomique des communautés végétales, basée sur l'identité des espèces, ne permet pas de révéler les mécanismes impliqués dans l'assemblage des communautés en réponse à la connectivité. La capacité des plantes à se disperser, depuis la plante mère jusqu'à une nouvelle tâche d'habitat, est souvent déterminée par le mode de dispersion des espèces (cf. introduction, section 1.3). Toutefois, au sein d'un même mode de dispersion, elle sera modulée par la possession de valeurs de traits fonctionnels favorisant une forte production de propagules et une forte distance de dispersion (cf. introduction, section 1.3; Johst *et al.* 2002; Nathan 2006; Auffret *et al.* 2017b). Ces traits fonctionnels peuvent ainsi constituer des traits de réponse à la connectivité (*sensu* Lavorel *et al.* 1997; Lavorel & Garnier 2002; Suding *et al.* 2008).

Ainsi, la connectivité devrait influencer la structure fonctionnelle des communautés végétales, définie comme la composition et la diversité fonctionnelle au sein des communautés. Qu'elle soit appréhendée à partir d'un ou de multiples traits fonctionnels, l'étude de la structure fonctionnelle des communautés en réponse à la connectivité peut se réaliser au travers de deux approches, l'une étant basée sur l'utilisation de groupes fonctionnels, l'autre étant basée sur l'utilisation de métriques quantifiant la distribution des valeurs de traits au sein de la communauté.

La première approche consiste à définir des groupes fonctionnels de réponse, c'est-à-dire à regrouper des espèces qui répondent de façon similaire à la connectivité (*sensu* Lavorel *et al.* 1997), de manière indirecte ou directe. La méthode « indirecte » consiste à regrouper *a priori* des espèces fonctionnellement similaires sur la base de groupes prédéfinis ou définis par l'analyse des corrélations entre traits (e.g. analyses multivariées, groupes émergents, *sensu* Lavorel *et al.* 1997), et à tester la réponse de ces différents groupes à la connectivité. La méthode « directe », repose sur un regroupement *a posteriori* des espèces qui répondent de façon similaire à la connectivité, dès lors qu'au moins une relation entre la connectivité et un trait donné a été établie.

La seconde approche consiste à évaluer l'effet de la connectivité sur la structure fonctionnelle des communautés, cette dernière étant quantifiée au travers d'un panel de métriques différentes. Ces métriques définissent (i) la composition fonctionnelle d'un trait et (ii) la diversité fonctionnelle, soit l'ampleur des différences de valeurs de traits, au sein de la communauté (Petchey & Gaston 2002). La composition fonctionnelle d'un trait unique est reflétée par la valeur de trait agrégé à l'échelle de la communauté (i.e. la moyenne des valeurs de trait pondérée par l'abondance des espèces, ou *community weighed mean*; Garnier *et al.* 2004). La diversité fonctionnelle se décrit et se mesure selon ses trois composantes : la richesse, l'équitabilité et la divergence fonctionnelle (cf. Mason *et al.* 2005; Mouchet *et al.* 2010). Initialement développées pour ne tenir compte que d'un trait unique, des avancées plus récentes ont permis d'évaluer les trois composantes de la diversité fonctionnelle à partir de multiples traits (Villéger *et al.* 2008; de Bello *et al.* 2009; Laliberté & Legendre 2010).

Bien que l'influence de la dispersion sur la structuration des communautés locales a été largement soulignée, la théorie des métacommunautés reconnaît également que la coexistence des espèces est déterminée par les conditions abiotiques et biotiques locales (cf. introduction, section 1.2.4; Mouquet & Loreau 2003). En d'autres termes, seule une fraction des espèces dont les graines arrivent au sein d'une tâche grâce à une forte connectivité (i.e. *pool local d'espèces*) constitue la communauté locale observée, à la suite du « filtrage » local (cf. introduction, section 1.2.5). Si la théorie prédit que la connectivité favorise la dispersion des graines, on ignore si les graines seront recrutées depuis le sol sous l'influence des processus locaux, autrement dit, si la dispersion est efficace. L'effet de la connectivité sur les communautés végétales peut, ainsi, être occulté par l'effet des processus locaux (facteurs abiotiques et biotiques). Non sans lien avec le concept de connectivité réelle, il semble ainsi crucial de déterminer l'effet de la connectivité sur le seul processus de dispersion des graines

via l'observation des flux de graines (e.g. pluie de graines ou banque de graines; cf. introduction, section 2.1.2), et ce à l'échelle des communautés. De tels travaux sont nécessaires et complémentaires à l'étude « traditionnelle » de l'effet de la connectivité sur la dispersion efficace des graines via l'observation du couvert végétal.

Sur la base de ce corpus théorique, des efforts considérables ont été déployés pour tester ces hypothèses, si bien que l'effet de la connectivité sur les communautés végétales est devenu un sujet d'étude central en écologie du paysage. Bien qu'il existe un nombre important et croissant d'études empiriques sur le sujet, nous ne savons toujours pas si les prédictions théoriques coïncident avec les preuves empiriques existantes. Dans la suite de cette partie, nous passons en revue la littérature publiée au cours de ces deux dernières décennies, afin de fournir une vue d'ensemble de l'influence de la connectivité sur les communautés végétales (ARTICLE 2). Les connaissances scientifiques existantes sur l'effet de la connectivité sur les communautés végétales ont permis d'identifier les lacunes et les besoins de recherches supplémentaires sur le sujet et de préciser la problématique de cette thèse.

Article 2. Effect of landscape connectivity on plant communities: a review of response patterns

Léa Uroy, Aude Ernoult, Cendrine Mony

Landscape Ecology (2019) 34, 203–225

Abstract

Context. Fragmentation in agricultural landscapes is considered as a major threat to biodiversity. Thus, ecological corridors are deployed at multiple scales to increase connectivity. However, there is limited consensus about their efficiency, especially for plants.

Objectives. We assimilated existing knowledge to assess whether and how landscape connectivity impacts plant communities.

Methods. We reviewed published literature across more than 20 years, providing an overview on the influence of connectivity on plant communities.

Results. We found that landscape connectivity has a varying and complex influence on the composition and diversity of plant communities (i.e. community taxonomic structure), due to the multiplicity of factors that modulate its effect. Our understanding of how of landscape connectivity impacts the dispersal of plants is improved by using biological traits (i.e. community functional structure). Finally, we showed that landscape connectivity promotes actual dispersal between connected communities.

Conclusions. This review emphasises the pertinence of trait-based and actual dispersal approaches to improve our understanding and ability to predict the effect of connectivity loss on plant communities, allowing us to identify new prospects for future research.

Introduction

Anthropogenic activities, including urbanization and agricultural intensification, present major threats to biodiversity, notably through their effects on landscape fragmentation (Stoate *et al.* 2001; Kato *et al.* 2009; Haddad *et al.* 2015). Landscape fragmentation impacts the populations of plants through two distinct effects: habitat loss (i.e. a decrease in habitat area) and connectivity loss (i.e. decreased plant dispersal among remnant patches; Taylor *et al.* 1993) (Fahrig 2003; Fischer & Lindenmayer 2007). Because of their sessile way of life, plants are particularly vulnerable to these effects, and many studies have reported a strong decline in floristic diversity in fragmented agricultural landscapes (Andreasen *et al.* 1996; Kleijn & Verbeek 2000; Luoto *et al.* 2003; Baessler & Klotz 2006; Kleijn *et al.* 2009). The effect of habitat area on plant diversity is well established (e.g. Scanlan 1981; Dzwonko & Loster 1988; Zacharias & Brandes 1990; Honnay *et al.* 1999; Godefroid & Koedam 2003; Gignac & Dale 2007). Small patch size increases extinction risk by reducing carrying capacity. Consequently, populations in smaller habitats are more susceptible to extinction, due to demographic stochasticity (MacArthur & Wilson 1967). Only in the last two decades have studies begun investigating how connectivity loss affects plant diversity and the corresponding mechanisms; consequently, there is a low level of synthesis of existing knowledge.

Depending on the intensity of connectivity loss, the spatial distribution of species might range from a continuous population to a set of isolated populations with a metapopulation structure (i.e. a network of local populations linked by dispersal fluxes, Hanski 1994a) as an intermediate case. More recently, the metapopulation concept has been extended to the community level (i.e. metacommunity concept, Leibold *et al.* 2004). A metacommunity refers to a set of local communities that are linked by the dispersal of multiple potentially interacting species (Wilson 1992). The strong interest in metacommunity theory has given rise to four paradigms to describe metacommunities: (i) species sorting (i.e. habitat patches are environmentally heterogeneous with high enough dispersal to enable species to fill niches within habitat patches because of niche diversification); (ii) mass effects (i.e. habitat patches are environmentally heterogeneous and high dispersal enough override local dynamics); (iii) patch dynamics (i.e. habitat patches are environmentally homogeneous and species differ in their ability to disperse. Along a colonisation–competition trade-off, successful colonisers outcompete poor competitors and *vice versa*); and (iv) neutral models (i.e. species do not differ in their fitness or niche) in the case of ecological drift (Leibold *et al.* 2004; Logue *et al.* 2011). These models formulate different hypotheses on the relative

importance of dispersal, habitat heterogeneity and interactions between species in the structuring mechanisms of local communities (Leibold *et al.* 2004; Logue *et al.* 2011). Plant disperse passively between habitat patches via pollen and/or seeds. However, this process is only successful if habitat patches are sufficiently connected (Fahrig & Merriam 1985; Bowne & Bowers 2004); in other words, plant dispersal among source patches must be facilitated by suitable landscape elements (Taylor *et al.* 1993). Landscape connectivity might be promoted by the occurrence of corridors between favourable patches, such as continuous, relatively narrow, habitat bands connecting two patches (Burel & Baudry 1999). However, connectivity might also include nonlinear or discontinuous landscape features that are permeable to plant dispersal (Beier & Noss 1998; Chetkiewicz *et al.* 2006). Thus, high connectivity between habitat patches might reduce the adverse effects of fragmentation by facilitating genetic fluxes among local populations through plant dispersal (Wilson & Willis 1975), which contrasts with animals for which all movements is concerned.

However, the ability of plants to disperse in fragmented landscapes might depend on their dispersal strategy, with some being more or less able to promote frequent long-distance dispersal events. For instance, if wind-dispersal or water-dispersal is generally achieved over a long distance, depending on the intensity of the wind or current and the adaptations of the seeds, gravity-dispersed plants (i.e. barochory) are dispersed more locally (Nathan *et al.* 2002; Tackenberg 2003; Vittoz & Engler 2007; Pollux *et al.* 2009; Nilsson *et al.* 2010). Animal-dispersed plants are dispersed over short distances of <100 m (e.g. by small animals, such as insects, small mammals and some bird species) to long distances of several kilometres (e.g. by large or migratory animals; Vittoz & Engler 2007). These vectors might be influenced differently by landscape elements and, in turn, might influence plant responses to connectivity loss. Within a certain type of dispersal mode, plant species might represent a large range of capacities to disperse with respect to quantity (i.e. number of potential dispersers) and distance (i.e. dispersal range) (Johst *et al.* 2002; Nathan 2006; Auffret *et al.* 2017b), which might decrease or increase their chance to disperse. These response involve a selection of particular biological traits (i.e. morphological, biochemical, physiological, structural, phonological or behavioural characteristics of organisms that influence performance or fitness, Violle *et al.* 2007). At the plant community scale, analyses of how these traits respond to connectivity might help us to understand the processes that are involved, which would facilitate a more mechanistic analysis of plant assembly in fragmented landscapes.

Because plants are sessile, the effect of connectivity on plant assemblages might be time-dependent, with responses reflecting a relaxation time (i.e. the time taken for a community of species to reach a new equilibrium after an environmental disturbance, (Diamond 1972; Kuussaari *et al.* 2009). By extension, the response of plant to connectivity might also reflect an extinction debt, which is defined as the number or proportion of extant species predicted to become extinct as the species community reaches a new equilibrium after an environmental disturbance (Tilman *et al.* 1994; Ovaskainen & Hanski 2002; Kuussaari *et al.* 2009). The response of plant assemblages to connectivity might also reflect an immigration lag, i.e. the time that has elapsed between an immigration-committing forcing event (e.g. increasing connectivity) and the establishment of an immigrating species (Jackson & Sax 2010). By extension, this phenomenon would lead to immigration credit (Jackson & Sax 2010), which is defined as the number of species committed to eventual immigration following a forcing event (Kuussaari *et al.* 2009). In addition, temporal lags in extinction and immigration are mediated by variation in traits across species under experimental situations (Haddad *et al.* 2015). Thus, considering the role of historical connectivity on the composition and diversity of plant communities and how traits mediate the delayed response of plant might improve our understanding of how plant species respond to connectivity loss.

Metacommunity theory recognizes that established local communities may additionally be driven by stochasticity (which is eventually spatially correlated), local patch conditions and species traits (i.e. colonisation vs. competition trade-offs) (Mouquet & Loreau 2003). As a result, recent studies argued that assessing how connectivity affects established communities in habitat patches is subject to bias. Indeed, once a propagule arrives in a patch, its ability to establish depends on a large range of local factors linked to local habitat quality (e.g. management, land-use history, Brudvig 2016) and biotic interactions (e.g. plant-plant, plant-animal, plant-soil interactions, Pyke & Archer 1991; Fukami & Nakajima 2013). Therefore, it might be difficult to disentangle the effects of landscape connectivity and local filters. In addition, the increase of connectivity might indirectly affect the establishment and coexistence of plants in the community by promoting the displacement of: (i) organisms that might predate on (e.g. herbivores and granivorous species, Orrock *et al.* 2003; Orrock & Damschen 2005; Rossetti *et al.* 2017) or parasitize seeds (e.g. Sullivan *et al.* 2011), or (ii) strong competitors that once, they arrived in a local patch, drive local biotic interactions and outcompete less competitive species (Hanski & Simberloff 1997; Mouquet & Loreau 2003, e.g. exotic invasive plant species, Minor *et al.* 2009; Minor & Gardner 2011). To assess the direct effect of connectivity on seed dispersal, Calabrese & Fagan (2004) proposed the concept of

actual functional connectivity (**Fig. 1** and **Box 1**). This concept is based on the direct assessment of seed fluxes depending on habitat connectivity. This form of direct assessment might reflect the effect of connectivity on the process of dispersal alone, independent of other local factors that are difficult to standardise.

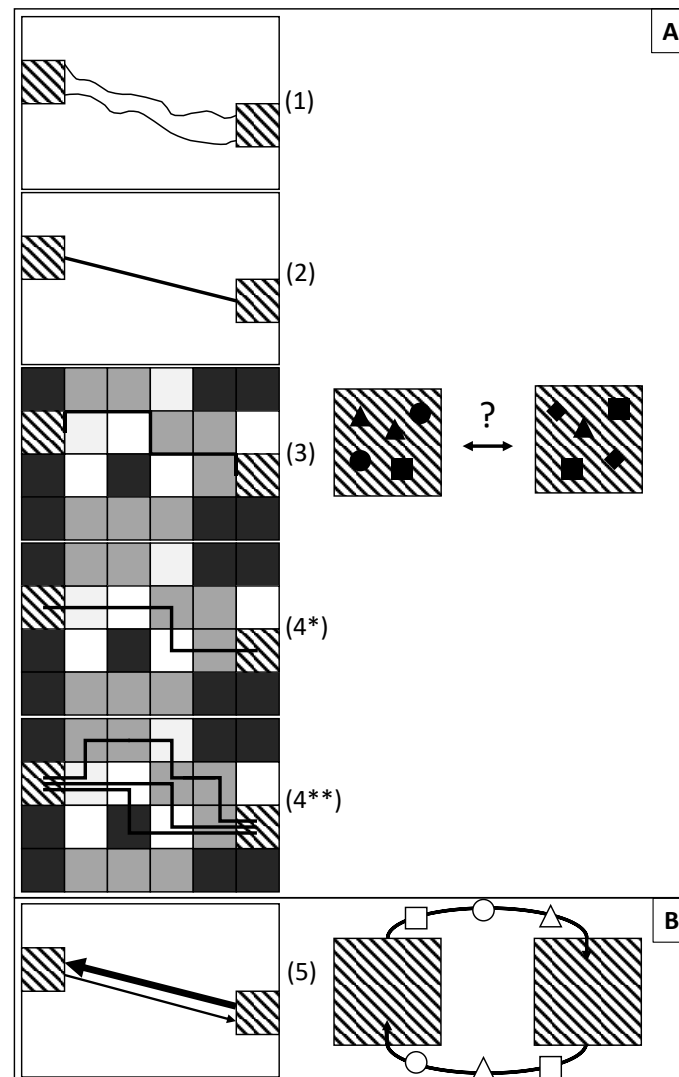


Fig. 1 Methods used to determine how landscape connectivity influences plant dispersal. **(A)** Study of potential dispersal (i.e. results of seed bank expression in habitat patches, integrating hence the local establishment process). White squares with diagonal lines represent focal habitat patches (patches of interest). Solid squares, triangles, circles and rhombus represent different plant species. Four measures of connectivity are employed: (1) Presence/absence of corridors; (2) Euclidian distance; (3) Structural connectivity and (4) Potential functional connectivity. White squares represent landscape elements of the same habitat type than the focal habitat patches. Grey and black squares represent two different types of habitat patches. To determine potential functional connectivity, two different modelling approaches are commonly employed: (4*) least cost path and (4**) circuit theory. Both methods require parameterising resistance surfaces, with cost value reflecting the cost of species to traverse landscape features. In these cases, assigned costs to landscape features increase from white (highly permeable to dispersal) to black (slightly permeable to dispersal). **(B)** Study of actual dispersal (i.e. seed rain) White squares with diagonal lines represent habitat patches. Solid squares, triangles, circles and rhombus represent the seeds of different plant species. One measure of connectivity is employed: (5) Actual functional connectivity. Thicker arrows represent a higher rate of movement (i.e. higher connectivity), while thinner arrows represent a lower rate of movement (i.e. lower connectivity).

The number of studies analysing the influence of landscape connectivity on biodiversity has increased considerably since the early part of the 21st century (Correa Ayram *et al.* 2016). To facilitate the identification of general patterns, reviews have been compiled on how connectivity affects global biodiversity (Murphy & Lovett-Doust 2004; Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016). These reviews have provided evidences of the effect of connectivity at different levels of organization (individuals, populations and communities) essentially through experimental approaches (Haddad & Tewksbury 2006; Haddad *et al.* 2011, 2015) or sometimes coupled with correlatives ones (Murphy & Lovett-Doust 2004; Gilbert-Norton *et al.* 2010; Fletcher *et al.* 2016). However, these reviews mostly focus on animal biodiversity. When these reviews consider existing literature on plants, the response of plants to connectivity is usually often assessed at the population level and under experimental conditions and does not take into account the traits of plant species (Murphy & Lovett-Doust 2004; Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016). As a result, our understanding of the role of connectivity for plants remains limited, especially at the community level. The effect of connectivity on plant communities cannot be predicted from its effect on plant populations and individuals, as communities incorporate distinct properties linked to their dynamics such as priority effects (Fukami 2015) and successional changes in species diversity over time. This lack of knowledge may be particularly problematic for the conservation of plant biodiversity, which aims to go beyond single-species approaches (Groves *et al.* 2002).

In the present review, we aimed to provide a synthesis of existing scientific knowledge on how connectivity loss influences plant communities. To achieve this synthesis, we only considered studies that assessed connectivity and plant species responses at the community level. Connectivity was analysed under experimental approaches through the presence or absence of an experimentally-created corridor between patches (**Fig. 1** and **Box 1**) or under correlative approaches using quantitative indices. Quantitative connectivity assessments were based on isolation metrics such as Euclidean distance, structural connectivity indices (see various examples in the main text), least-cost distance and resistance distance (respectively derived from graph and circuit theory, potential functional connectivity) (**Fig. 1** and **Box 1**). This approach included: (i) analysis of individual species responses across most species of the community and, (ii) aggregated measures across most species of a given community (for more details, see **Appendix S1**).

Specifically, we present how landscape connectivity influences the richness and composition of plant communities (section “Contrasted effect of landscape connectivity on plant community taxonomic structure”). We also review how plants respond to connectivity from a mechanistic perspective (related to dispersal vector mode and plant dispersal traits), to demonstrate that traits may help to define species sensitivity to connectivity loss (section “Effect of landscape connectivity on the functional structure of plant communities”). We also evaluate how time affects plant taxonomic and functional response to connectivity (section “Effect of time on the response of plants to connectivity”). Finally, we review how connectivity drives actual dispersal (“Effect of landscape connectivity on actual seed dispersal”). We conclude that landscape connectivity influences plant communities as a filter for species and traits. We also emphasize that trait-based and actual dispersal approaches are the most relevant for predicting how connectivity loss affects plant communities. We use our findings to suggest further research needs.

Contrasted effect of landscape connectivity on plant community taxonomic structure

Higher connectivity facilitates plant dispersal and thus decreases the probability of local extinction. Thus, high connectivity might influence the taxonomic structure of communities (i.e. the composition and diversity of plant communities), increasing species diversity and similarity in composition between connected patches.

Plant community diversity

How connectivity affects species diversity has been a central question in landscape ecology over the last two decades. Early studies tested this question by comparing pairs of patches that were (or not) connected through a corridor. The effect of the presence/absence of a corridor on plant diversity has been, for instance, addressed through the experimental manipulation of connectivity between habitat patches. One of the most well-known designs is based at Savannah River Site (South Carolina, USA), which supports a range of landscape designs embedded in a forest matrix. In this experimental design, each landscape is composed of a central patch that is connected to one peripheral patch by a corridor, and a peripheral patch that is not connected to the central patch (**Box 2**). In this design, patches connected by a corridor displayed a richness higher than 20% compared to the non-connected patches (Damschen *et al.* 2006). Plant species richness also increases from 10 to 18% in the matrix

surrounding the connected patches by a mass spatial effect (Brudvig *et al.* 2009); thus, the presence of corridors might positively impact adjacent landscape elements.

Another set of studies used connectivity measurements based on the Euclidean distance or on the permeability of the landscape elements to dispersal. In the latter case, these measurements incorporate the physical attributes of the landscape with or without information about the organism of interest (structural or potential functional connectivity) and assess the degree of connectivity for each habitat patch (**Fig. 1** and **Box 1**). Depending on the ecosystem type, landscape connectivity has a contrasting effect on community diversity. For instance, local heathland species richness increases with structural connectivity [measured through the Incidence Function Model index (IFM index)] based on the area and the Euclidean distance to other patches of similar habitat type, Hanski 1994a; Moilanen & Nieminen 2002) (Piessens *et al.* 2004), whereas structural connectivity does not influence the richness and the density of species (i.e. average number of species per square meter) of local plant communities in semi-natural grasslands (Lindborg & Eriksson 2004; Helm *et al.* 2006; Cousins *et al.* 2007). Lindborg & Eriksson (2004) demonstrated that this absence of a relationship with connectivity was maintained at different spatial scales (1 km or 2 km radius). Only one study demonstrated a negative influence of connectivity on local plant community richness in riverine wetlands. Specifically, Bornette *et al.* (1998) reported that high connectivity decreases species richness when assessing structural surficial connectivity between cut-off channels and the river by quantifying the overflows and backflows of rivers into cut-off channels. Under these conditions, high connectivity impedes recruitment due to over-frequent flood scouring or due to nutrient-rich and turbid surficial waters being supplied to the wetland, which reduces species richness.

Most studies investigating how landscape connectivity affects plant species communities measure species richness at the alpha-scale (i.e. local diversity) (Bennett 2003). In comparison, studies carried out at a gamma-scale (i.e. landscape diversity) remain limited. For instance, Favre-Bac *et al.* (2014) reported that the structural connectivity of ditch networks (i.e. number of disconnected network units) decreases species richness of ditch bank communities when analysing 27 square sites of 500 x 500 m. This result might be attributed to the influence of landscape heterogeneity, which might mitigate the negative effects of habitat fragmentation (Tschardtke *et al.* 2012).

Overall, no general pattern has been detected on the positive effect of corridors on plant diversity through correlative approaches, contrary to experimental approaches (Haddad

et al. 2015). Two possible explanations why correlative studies have failed to demonstrate a general pattern are: (i) the too low suitability and number of available habitat patches for plants to colonise and establish, and (ii) the lack of consideration of the quality (e.g. management practice) of the landscape elements. These studies assessed connectivity through the presence and identity of landscape elements to determine their permeability to dispersal, overlooking the potential effect of the quality of these elements on their permeability.

Box 1 Glossary

Structural connectivity: measure of connectivity based on the spatial position of patches independent of the attributes of the organism of interest (Tischendorf & Fahrig 2000; Bennett 2003; Taylor *et al.* 2006).

Potential functional connectivity: measure of connectivity that combines the physical attributes of the landscape with limited information about dispersal ability (Calabrese & Fagan 2004). This measure explicitly considers the behavioural responses of organisms to the physical structure of the landscape (Tischendorf & Fahrig 2000; Bennett 2003; Taylor *et al.* 2006).

Least-cost path: modelling method to determine potential functional connectivity that assumes a unique path between two patches (represented by a solid line in **Fig. 1**), hypothesising that individuals perceive their environment in a way that leads them to “select” the optimal path (Adriaensen *et al.* 2003). The connectivity measure that results from this modelling method is an isolation measure called least-cost distance: the higher the least-cost distance, the lower connectivity.

Circuit theory: modelling method to determine to determine potential functional connectivity that evaluates all possible paths (represented by the three different solid lines in **Fig. 1**), assuming that dispersal follows random walks (McRae *et al.* 2008). The connectivity measure that results from this modelling method is an isolation measure called resistance distance: the higher the resistance distance, the lower connectivity.

Actual functional connectivity: measure of connectivity based on the observation of individuals moving through a landscape (Calabrese & Fagan 2004). This measure explicitly considers the behavioural responses of organisms to the physical structure of the landscape (Tischendorf & Fahrig 2000; Bennett 2003; Taylor *et al.* 2006).

Box 2 Example of the Savannah River Site (SRS) experimental design for connectivity studies.

This experimental design is located in the Savannah River Site, a National Environmental Research Park in South Carolina, USA.

In 2000, eight 50-hectares landscapes were selected. These landscapes were composed of mature (40- to 50-year-old) forest, dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*Pinus palustris*).

Within each landscape, five early-successional habitat patches were created by

cutting and removing all trees, and then burning the cleared areas. The patches included (Fig. 2): one central patch of 1 ha (A) and four peripheral patches (B, C, D, E) that were equal in distance (150 m) from the central patch, but with different structures (see below).

The experiment focused on two corridor functions. First, how a corridor impact connectivity through the following configuration: the central patch is connected to one peripheral patch (B) by a 150 m long and 25 m wide corridor and is not connected to the three other peripheral patches (B, C, D). The three other peripheral patches are equal in area to a patch plus a corridor (1.375 ha). Second, how a corridor impacts patch shape through the following manipulation of peripheral patches: in four landscapes, two of the remaining three peripheral patches were winged (C and D) and one was rectangular (E); in the other four landscapes, two peripheral patches were rectangular and one was winged.

The number of experimental landscapes used varied from six (Damschen *et al.* 2006) to eight (Tewksbury *et al.* 2002; Haddad *et al.* 2003, 2015; Levey *et al.* 2005; Damschen *et al.* 2008; Brudvig *et al.* 2009). This number was not clarified in Haddad *et al.* (2003).

In our review, only the connectivity function of the corridor is discussed; thus, we only refer to connected patches *versus* unconnected patches.

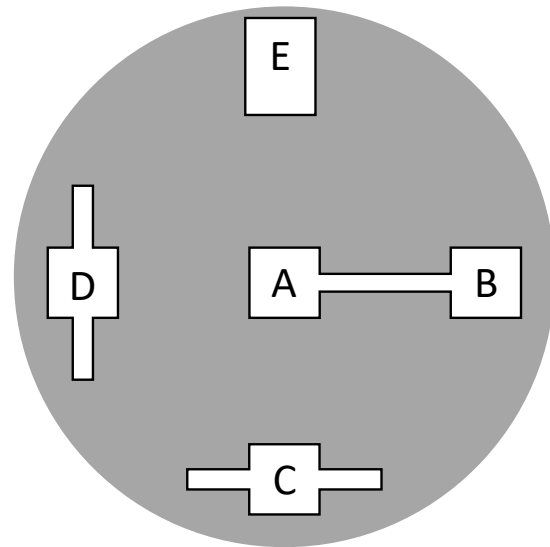


Fig. 2 One of the eight experimental landscapes in the SRS.

Plant community composition

In fragmented landscapes, remnant habitat patches might be highly heterogeneous, causing strong divergence in the composition of local communities (Tscharntke *et al.* 2012). In addition, the amount of dispersal between remnant patches might strongly impact these dynamics (Mouquet & Loreau 2003; Mouquet *et al.* 2006). When isolated, seed limitation is expected to enhance divergence between local communities at the metacommunity scale, further reducing their similarity (Mouquet & Loreau 2003; Tscharntke *et al.* 2012). A particular case of dissimilarity in species composition, the nested subset (i.e. a community in which the species present at species-poor sites constitute subsets of those from species-rich sites, (Patterson & Atmar 1986) was highlighted in heathland communities by Piessens *et al.* (2004). In these systems, dissimilarity increases as structural connectivity decreases. The higher the landscape structural connectivity, the higher the similarity of the community. Similar results were also reported for communities of linear landscape elements, such as field margins, road verges and ditches (Thiele *et al.* 2017). For instance, Thiele *et al.* (2017) tested three types of connectivity metrics (Euclidian distance, potential functional connectivity: least-cost distance and resistance distance, see **Fig. 1** and **Box 1.**), and demonstrated that the results were independent of the way that connectivity was evaluated.

Within local communities, fragmentation theoretically decreases species richness because it acts as a strong ecological filter, selecting for species that are able to disperse and survive in isolated patches. Thus, Haddad & Tewksbury (2006) theorised that specialist species should be more affected by connectivity loss than generalist species, because the latter group might perceive corridors as being of lower quality compared to the surrounding habitats. Isolated patches might contain more generalist than specialist species in plant communities compared to connected patches. In grassland communities, specialist species decrease to a greater extent compared to generalist species in response to the loss of structural connectivity (Adriaens *et al.* 2006; Brückmann *et al.* 2010; Evju *et al.* 2015). Adriaens *et al.* (2006) reported that only specialist species are impacted by a change to the structural connectivity (assessed with the IFM index) of grasslands, with the mean number of species per site decreasing by about 37%. Similar results were obtained by Brückmann *et al.* (2010) and Evju *et al.* (2015). For instance, Brückmann *et al.* (2010) recorded a decrease of 24-37% in the richness of specialist species in grasslands in response to a total loss of structural connectivity (IFM index), whereas generalists were not affected. Therefore, the effect of connectivity on plant species depends on the degree of specialisation. Thus, different types of ecological corridors might interact in

a landscape. For instance, grassland corridors between forest patches might reinforce the effect of forest corridors in connected forest patches only when considering generalist species in forests. These interactions between corridor types might rank from potential complementarity for generalist species to potential antagonism for specialist species, in which one ecological corridor type is favourable while the other constitutes a barrier. Thus, it is important to consider how complementary between the different types of ecological corridors are in studies linking connectivity to plant communities. This consideration could be coupled with the improved modelling of ecological corridor types through the use of SDMs (Species Distribution Models; Guisan & Thuiller 2005), which represent a promising approach to assess the permeability of landscape features to dispersal (e.g. Morato *et al.* 2014), rather than expert knowledge (Rayfield *et al.* 2010; Spear *et al.* 2010; Koen *et al.* 2012; Zeller *et al.* 2012).

Effect of landscape connectivity on the functional structure of plant communities

Because of the contrasting results provided by taxonomic approaches, there is a growing need to predict how plant communities respond to changes in connectivity. Analyses based on the functional structure of communities (i.e. the composition and diversity of traits) might help to improve our understanding of species responses by providing a mechanistic explanation (for a detailed synthesis of these studies, see **Table 1**).

Dispersal vector mode

Studies using trait-based approaches initially focused on how plant dispersal vectors influence their responses to connectivity. Plant dispersal vectors determine plant dispersal distance. For instance, dispersal is close to the parent plant for gravity-dispersed species, and up to several hundred metres or even kilometres for animal-, wind- and water- dispersed species (Sorensen 1986; Nathan *et al.* 2002; Tackenberg 2003; Vittoz & Engler 2007; Pollux *et al.* 2009; Nilsson *et al.* 2010).

Animal-dispersal is oriented, and depends on animal behaviour and movement in the landscape. There is broad consensus that animal movement is facilitated by landscape connectivity (Murphy & Lovett-Doust 2004; Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016); thus, animal-dispersed plant species might be largely dependent on landscape connectivity. It is more difficult to predict how connectivity affects wind-dispersed plants, as this type of dispersal is made at random or occurs in relation to the dominant wind direction. Differences in these two plant dispersal vectors might lead to different responses to connectivity. Damschen *et al.* (2008) surveyed the

species richness of bird-dispersed and wind-dispersed species over a seven-year period in the Savannah River Site (**Box 2**). The authors demonstrated that, for both functional groups, the richness of communities was lower in unconnected *versus* connected patches. However, this difference in richness reached an asymptote for bird-dispersed species after five years, but not for wind-dispersed species. This asymptote is due to the behaviour of birds that regularly visit all patches of the experimental design. As a result, even isolated patches occasionally receive new colonists, reducing the difference in species richness between connected and unconnected patches over time. By contrast, the presence of an open corridor affects wind dynamics by redirecting and promoting airflow and “ejection hotspots” (i.e. locations in which seeds have a relatively high probability of being uplifted) in connected patches. These processes increase the likelihood of seed uplift, and, therefore, the likelihood of seed redirection and bellow among connected patches (Damschen *et al.* 2014). As a result, the difference in species richness between connected and unconnected patches continues to increase over time. Based on the same design, Brudvig *et al.* 2009) showed that the richness of animal-dispersed species increased by 13–19% per 100 m² in the surrounding matrix in response to connectivity, whereas no mass spatial effect was found for wind-dispersed species. This result was due to a barrier effect of the surrounding matrix of dense pine plantations on wind-dispersed species (Damschen *et al.* 2014). In contrast, animals were not restricted to the experimental design, moving in and out of patches to the matrix, resulting in their contributing to the dispersal of plants. When assessed in more correlative approaches, no particular influence of landscape connectivity (Euclidean distance, structural and potential functional connectivity) was demonstrated on animal- (external, internal and by ants) and wind-dispersed species (Piessens *et al.* 2005; Lindborg 2007; Evju *et al.* 2015; Thiele *et al.* 2017) but see contrasting results provided by Verheyen *et al.* 2004 who only considered vertebrate-animal dispersal and wind dispersal), despite their potential for long-distance dispersal. This finding suggests that, in real systems, the effect of connectivity on the functional structure of plant communities is overshadowed by other characteristics of the landscape, such as patch shape, which influences the quantity of the interface with other habitats (e.g. Arellano-Rivas *et al.* 2016) nor the fine-scale structuring of corridors. In turn, this phenomenon influences the degree of permeability for animal- (e.g. animal vector behavioural changes) and wind- (e.g. wind dynamics changes) dispersed species.

Another dispersal mode contributing to long-distance dispersal is hydrochory. Many studies have investigated the role of water dispersal in structuring plant communities, in both flowing and stagnant systems (for a review, see Nilsson *et al.* 2010). However, very few studies

present the effect of connectivity on water-dispersed plant communities. Favre-Bac *et al.* (2014) showed that the richness of water-dispersed species at the landscape scale was independent of ditch network connectivity, regardless of the measures of connectivity considered (i.e. total ditch length, number of culverts, number of intersections and number of disconnected ditch network subunits). However, similarity within local water-dispersed communities decreased with the number of intersections, suggesting that these intersections act as barriers to dispersal and cause a decrease of seed fluxes between communities (Favre-Bac *et al.* 2014). Similar results were obtained by Piessens *et al.* (2005).

Other modes have been less studied, mostly because they were supposed to contribute less to long-distance dispersal and, therefore, to plant sensitivity to connectivity. Nonetheless, several studies have demonstrated a positive response of unassisted species (i.e. species without dispersal structures, mostly gravity-dispersed species) in response to connectivity by both experimental (Damschen *et al.* 2008) and correlative (Kolb & Diekmann 2005; Thiele *et al.* 2017) approaches. Damschen *et al.* (2008) demonstrated that the difference in unassisted species richness between connected and non-connected patches was been six-fold greater after seven years. A similar response was obtained by Thiele *et al.* (2017). The authors obtained a positive relationship between connectivity (Euclidean distance and potential functional connectivity) and similarity for unassisted species communities of linear landscape elements (field margins, ditches, road verges). Despite the increase in unassisted species richness (Damschen *et al.* 2008), the relative proportion of these species does not seem to be influenced by connectivity within communities. When using a correlative approach, Lindborg (2007) reported that the proportion of unassisted species in semi-natural grasslands was independent of structural connectivity (IFM index). These results corroborate the work of Piessens *et al.* (2005), who demonstrated that unassisted species are not sensitive to structural connectivity. However, the dispersal mechanisms explaining the differential responses of unassisted species in terms of richness and relative proportion to landscape connectivity have yet to be clarified. As suggested by Damschen *et al.* (2008), these results challenge the notion that unassisted species are truly unassisted in their dispersal, corroborating evidence from other studies (Higgins *et al.* 2003; Vellend *et al.* 2003).

Table 1 Synthesis of studies dealing with the effect of current and historical landscape connectivity on functional structure of plant communities. See **Fig. 1** for detailed explanations on the connectivity measures.

Approach	Community type	Connectivity measure	Community response variable	Main results	Reference
Experimental	Early successional vegetation of large pine plantations	Connected vs. unconnected patches (during 7 years)	Difference in alpha species richness	↗→ for animal dispersed species ↗ for wind dispersed species ↗ for unassisted species	Damschen <i>et al.</i> (2008)
Correlative	Field margins, road verges & ditches	Euclidian distance Potential connectivity: least-cost and resistance distance	Jaccard similarity	∅ for animal and wind dispersed species ↘ for unassisted species	Thiele <i>et al.</i> (2017)
Correlative	Ditches	Structural connectivity: Total ditch length (TDL) Number of culverts (NoC) Number of intersections (NoI) Number of subunits (NoS)	Gamma richness and similarity Species trait values: Seed mass Seed buoyancy Seed morphology Seed velocity Seed germination	∅ for water-dispersed species ↘ (TDL); ∅ (NoC); ↗ (NoI) ∅ (TDL); ↗ (NoC, NoI) ↗ species with round seeds (TDL); ↗ species with long seeds (NoC, NoI) ↘ (TDL); ∅ (NoC); ↗ (NoI) ↘ (TDL); ∅ (NoC); ↗ (NoI)	Favre-Bac <i>et al.</i> (2014) Favre-Bac <i>et al.</i> (2017a)
			Standard effect size values calculated for Rao's quadratic entropy and gamma scale weighed mean trait values Seed production Seed buoyancy Seed mass	∅ (TDL, NoC); ↘ Convergence toward the production of small seeds (NoI); ↗ Convergence (NoS) toward the production of small seeds ∅ (TDL; NoI; NoS); ↗ Convergence toward a high buoyancy (NoC) ↗ Divergence (TDL); ∅ (NoC, NoI, NoS);	Favre-Bac <i>et al.</i> (2017b)

Correlative	Temperate forests	Structural index)	connectivity	(IFM	Trait values of emergent groups to connectivity loss	Sensitive group:	emergent	Resistant group:	emergent	Kolb & Diekmann (2005)
						Unassisted dispersal		Assisted dispersal		
						Few and heavy seeds		Many and thin seeds		
						High clonality		No or little clonality		
						Short seed bank longevity		Long seed bank longevity		
						Small height		Tall		
Correlative	Grasslands	Structural index)	connectivity	(IFM	Species richness of emergent groups	↗ for perennial rosette				Adriaens <i>et al.</i> (2006)
						∅ for orchids, half-rosette and annuals species				
Correlative	Dry calcareous grasslands	Structural index)	connectivity	(IFM	Probability of occurrence in response to connectivity	↗ for species with low seed number				Evju <i>et al.</i> (2015)
						∅ for species whatever their dispersal mode (wind-dispersal or not), seed mass or seed bank longevity				
						↗ for short-living species				
						∅ for clonal species				
Correlative	Heathlands	Structural index)	connectivity	(IFM	Species richness in the different categories of the seed longevity index	↗ for species with short seed bank longevity				Piessens <i>et al.</i> (2004)
Correlative	Heathlands	Structural index)	connectivity	(IFM	Regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity	↗ for species with short seed bank longevity				Piessens <i>et al.</i> (2005)
						∅ for species whatever their mean plant height, seed mass, dispersal mode, growth form, self-compatibility, clonal growth form and seed number				

Correlative	Temperate forests	Structural connectivity (modified version of IFM index that incorporates patch age)	Regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity	\nearrow for vertebrate and wind-dispersed species \nearrow for species with low seed production \nearrow for species with small height \emptyset for species whatever their life cycle duration	Verheyen <i>et al.</i> (2004)
Correlative	Urban - ruderals	Structural connectivity (IFM index)	Trait values of response groups to connectivity: Terminal velocity Number of seeds Seed mass	Sensitive > resistant species Sensitive < resistant species Sensitive = resistant species	Schleicher <i>et al.</i> (2011)
Correlative	Grasslands	Current (C) and historical (H) structural connectivity (IFM index) 1 km radius 2 km radius	Proportion of species	\emptyset for animal-, wind- dispersed and unassisted species \emptyset for species whatever their seed size \emptyset (C); \searrow (H) for long seed bank persistence species \nearrow (C); \emptyset (H) for annual plants \emptyset (C); \searrow (H) for perennials with or without clonality at 1 km scale. \emptyset (C) for perennials with or without clonal ability at 2 km scale \searrow (H) for perennials without clonal ability at 2 km scale	Lindborg (2007)

Plant dispersal traits

Beyond the dispersal mode, precise combinations of traits might favour the ability of plants to produce a large number of potential dispersers (e.g. seed number, vegetative fragmentation), and to be dispersed over long distances (e.g. seed mass, low terminal velocity, high gut retention), with both characteristics corresponding to the definition of species dispersal ability (Johst *et al.* 2002; Nathan *et al.* 2002; Auffret *et al.* 2017b). Thus, species with traits promoting high dispersal ability might be less sensitive to connectivity loss.

(1) Emergent groups to connectivity

Initially, studies that analysed the dispersal traits of plants in response to connectivity were based on a functional group approach similar to the one proposed by Lavorel *et al.* (1997); namely, emergent groups are groups of species that reflect natural correlation of biological attributes. By coupling changes to plant occurrence or abundance along the gradient of connectivity and trait-data on plant species, these studies analysed the syndrome of traits that characterise plant sensitivity or resistance to connectivity.

One of the very first studies on emergent groups focused on forest communities (Kolb & Diekmann 2005). These authors analysed species biological traits for two groups of plants: one corresponding to sensitive plants (i.e. the occurrence of which decreases with structural connectivity loss, evaluated through IFM index) and one corresponding to resistant plants (i.e. the occurrence of which is not impacted by structural connectivity loss). Sensitive plants were characterised by high clonality, few and heavy seeds and unassisted dispersal. Resistant plants displayed assisted dispersal, no or little clonal growth and produced many and thin seeds. Traits promoting local establishment instead of long-distance dispersal contributed to plant sensitivity to connectivity loss. Using a similar approach, Adriaens *et al.* (2006) classified specialist species from calcareous grasslands, using 16 life-history traits, and detected four different groups. Higher structural landscape connectivity increased species richness in only one of the groups, whereas the other groups were not affected. This group contains species that are characterised by a perennial rosette with no vegetative multiplication and no long-distance dispersal mode (i.e. ballistochory, ant-dispersed seeds, barochory). Such species are more sensitive to connectivity loss, as they are less likely to recolonise and establish in patches after extinction. The three other groups were not impacted by connectivity loss. These groups included orchids (characterised by short flowering, low mass seeds and wind-dispersal), half-rosette species (with fruity dispersules and seeds, with optional vegetative

reproduction mechanisms) and annual species (early and long flowering small autogamous annuals, low mass and no long-distance dispersal mode). However, the use of a large set of many traits, including ecological traits (i.e. linked with species niche), makes it difficult to disentangle the effect of dispersal traits from the other traits when evaluating how species respond to connectivity loss.

(2) Response traits to connectivity

Studies over the last two decades have focused on traits considered individually to define individual response traits (i.e. traits reflecting the response of organisms to a given environmental factor, Lavorel *et al.* 1997) to landscape connectivity. This approach differs from the emergent group approach by analysing one trait at a time to characterise species sensitivity to connectivity. Species that displayed similar trait values in response to connectivity are designed as response groups of plants (i.e. group of species that respond in similar ways to a given environmental factor for a given trait, Lavorel *et al.* 1997)

Verheyen *et al.* (2004) characterised species sensitivity for 17 species of temperate forest communities to connectivity loss through the regression coefficient derived from the regression model, using patch occupancy as the dependent variable and structural connectivity (modified version of IFM index that incorporates patch age, Verheyen *et al.* 2004) as the independent variable. Species characterised by lower numbers of seeds (and thus, a low number of potential dispersers) were sensitive to connectivity loss. In ruderal (brownfields) communities, Schleicher *et al.* (2011) demonstrated that wind-dispersed species sensitive to structural connectivity loss are those characterised by lower seed number and higher terminal velocity (i.e. rate at which a seed can fall in still air). High terminal velocity corresponds to short dispersal range by reducing the probability of dispersal by air uplift, while reduced seed number corresponds to a low number of potential dispersers. Consequently, both trait expressions are indicative of low dispersal ability. Sensitive and resistant plants were the most differentiated using a quotient of the seed number divided by terminal velocity. Moreover, the authors found that the clearest differentiation between the two connectivity response groups was obtained when combining seed number and terminal velocity in a quotient. These results highlight a compensatory relationship between these two traits; high dispersal distance might counterbalance low numbers of dispersers and *vice versa*. Favre-Bac *et al.* (2017a) used traits directly linked to water-dispersal to analyse how ditch communities respond to connectivity loss. The authors demonstrated that water-dispersed species that are highly sensitive to structural connectivity loss are characterised by short and round seeds

with low mass and low buoyancy (Favre-Bac *et al.* 2017a). Low buoyancy does not favour long-distance dispersal in low current systems because species do not tolerate long or frequent retention events when being dispersed. The authors also demonstrated the role of seed form on the probability of being retained by obstacles in stagnant ditches during dispersal events. In this case, long and thin seeds might be better aligned to flow direction, and succeed better in passing obstacles, such as culverts and intersections (De Ryck *et al.* 2012). This type of study advanced our understanding of the factors that induce dispersal in the studied system, providing some predictions on the mechanisms causing species resistance in less connected networks.

Some studies demonstrated that connectivity responses are associated to traits linked with the ability of plants to establish in habitat patches. For instance, Favre-Bac *et al.* (2017a) reported that, in highly branched ditch networks (i.e. where intersections constitute obstacles to dispersal), the most resistant plants had higher seed germination rates. This higher seed germination rate increased their ability to develop when blocked by obstacles during dispersal. Other traits linked to further steps of plant growth, such as competition (for instance, plant height) and duration of growth (life-cycle duration), were also investigated. It was found that species with lower competition capacity and short life-cycles (in temperate forest communities, Verheyen *et al.* 2004, in heathland communities, Piessens *et al.* 2004, 2005; in dry calcareous grasslands communities, Evju *et al.* 2015) are more sensitive to the loss of structural connectivity.

Therefore, it is important to develop approaches that take dispersal traits into account. Such approaches are expected to complement and fill knowledge gaps on existing work based on vector-types. Transposing the conceptual framework of response traits developed by Lavorel *et al.* (1997) to landscape ecology represents a promising avenue towards understanding and predicting plant community responses to changes in connectivity.

Community weighted mean traits and functional diversity

Studies over the last 15 years on community ecology have developed other methods to describe the functional structure of plant communities. These methods include aggregated measures quantifying the community the mean (i.e. community weighted mean traits) and range of trait values (functional diversity, for review, see Mouchet *et al.* 2010). In response to local factors, environmental filtering leads to convergent trait values that are adapted to environmental characteristics (van der Valk 1981; Weiher & Keddy 1995; Grime 2006). In

contrast, biotic filtering can lead to: (i) divergent trait values within communities (limiting similarity theory, MacArthur & Levins 1967; Grime 2006), leading to niche differentiation, or (ii) convergent trait values within communities (competitive hierarchy theory, Herben & Goldberg 2014) due to the competitive exclusion of less competitive species. Transposition of these theories to the landscape scale is a promising research avenue in functional ecology. In response to reduced connectivity, plant communities at the landscape level should be filtered toward trait syndromes that promote high dispersal ability (i.e. low functional diversity and weighted mean trait values converge toward high seed number or traits promoting long-distance dispersal).

Research assessing how the functional structure of communities respond at the gamma scale depending on landscape characteristics is still at an early stage. To our knowledge, only one study has used this highly promising approach (Favre-Bac *et al.* 2017b). The authors demonstrated that lower ditch network connectivity induces convergent trait values toward small seed production and high seed buoyancy. Higher seed buoyancy is particularly favourable for successfully passing culverts, which constitute barriers (Soomers *et al.* 2010), because seeds might persist until water level changes, wind strength or wind direction enables them to continue moving downstream. In comparison, lower seed production indicates that species invest heavily in vegetative growth, consolidating isolated local populations (Stöcklin & Winkler 2004). By contrast, higher connectivity in ditch networks reduces this filtering effect, or, even, leads to divergent trait values in seed mass. Consequently, in widely connected landscapes, several strategies coexist across local communities constituting the metacommunity. Higher seed weight provides more resources to guarantee growth during the early stages of establishment (Cornelissen *et al.* 2003), which mostly depend on competitive interactions with other plants within the local community. This local biotic filter favours the dissimilarity of plant traits involved in harvesting resources through the niche-partitioning effect (limiting similarity, MacArthur & Wilson 1967; Pacala & Tilman 1994). These results demonstrate that, at the gamma scale, reduced connectivity acts as a filter on the dispersal traits of plant species involved in resistance to connectivity loss.

Contribution of functional traits towards improving landscape connectivity models

Trait-based studies provide a better understanding of the mechanisms involved in how plants respond to connectivity. Thus, by integrating plant traits in landscape connectivity modelling, a more accurate prediction of the responses of species to connectivity loss should be obtained.

This approach has been facilitated by the development of potential functional connectivity models (**Fig. 1 and Box 1**) that account for species dispersal distance in addition to the cost of species to cross over landscape features such as those of Pascual-Hortal & Saura (2006, Integral Index of Connectivity, IIC) and Saura & Pascual-Hortal (2007, Probability of Connectivity, PC). The two indices – IIC and PC – are based on different assumptions about the probability of connection between two considered patches (binary or probabilistic, respectively). However, only a few studies have used this type of graph-based connectivity index for plants (see García-Feced *et al.* 2011; Aavik *et al.* 2014). Thus, these approaches need to be generalised.

Effect of time on the response of plants to connectivity

Historical landscape connectivity drives the taxonomic structure of plant communities

Most studies have overlooked the potential effect of relaxation time when analysing the influence of connectivity on plant communities. However, this effect has been detected in grassland communities. For example, Helm *et al.* (2006) showed that the alpha richness of specialist calcareous grasslands is independent of their current structural connectivity, but is dependent on their connectivity 70 years ago (i.e. dependent on the state of the landscape before drastic habitat loss and connectivity loss). These results strongly support the concept that some plant communities are mostly composed of species that have the ability to resist to fragmentation by persisting without completing the whole life cycle (i.e. with no sexual reproduction stages, Eriksson 1996). Grassland plant communities are indeed mostly composed of perennial plants with long-lived vegetative life-cycle, and may then survive for decades after environmental changes (Eriksson 1996). Lindborg & Eriksson (2004) also detected a response of alpha diversity (richness and density) to landscape structural connectivity older than 50 years and 100 years ago in semi natural grasslands. The authors demonstrated an interactive effect between time and spatial resolution. A positive effect of connectivity 50 years ago was only detected for alpha diversity at the smaller scale (1 km radius); however, a positive effect of connectivity 100 years ago was detected at both scales considered (1 km radius and 2 km radius). The presence of a relaxation time following an environmental perturbation might have indirect consequences on the biological scale of the response. For instance, Cousins & Vanhoenacker (2011) demonstrated that the gamma diversity of semi-grassland ecosystems decreases more slowly after a decline in grasslands abundance in the landscape compared to alpha diversity. Although no study has yet investigated the difference in the response of alpha and gamma diversity on historical

connectivity, we assume that such results could be transposed to connectivity loss. The time required to establish an equilibrium between spatial connectivity and species richness or diversity is longer at larger spatial and biological scales compared to smaller scales (O'Neill *et al.* 1986; Allen & Starr 1988); thus, the relaxation time of plant assemblages occurs at different spatial scales.

To our knowledge, only Naaf & Kolk (2015) and Haddad *et al.* (2015) have investigated how connectivity affects the magnitude of immigration credit. By studying newly-established forest patches, Naaf & Kolk (2015) found that the magnitude of immigration credit mainly depends on the structural connectivity of forests (IFM index). In connected forest patches, immigration lag affected five forest specialist species compared to nine species in highly isolated forest patches. Haddad *et al.* (2015) obtained similar results by studying successional vegetation of pine plantations over a decade in the Savannah River Site experimental design (**Box 2**). More specifically, immigration lags resulted in 15% fewer species after a decade in unconnected patches compared to connected patches. Future studies should investigate this effect in other community types.

Dispersal traits promoting time-dependent responses to connectivity

Because plants might respond to connectivity time-dependently (either with relaxation time or with immigration credit), some biological traits might promote such effects. For instance, the life duration of species or seed-bank persistence might contribute to the delayed response to changes in connectivity. The work of Lindborg (2007) supported this assumption, demonstrating that the proportion of short-lived plant species is influenced by current structural connectivity, whereas that of clonal long-lived and long seed-bank persistence species is influenced by historical structural connectivity (**Table 1**). Conversely, some traits might influence the effect of immigration lag. For instance, species with poor dispersal abilities might contribute strongly to immigration credit. This assumption was verified by Naaf & Kolk (2015). The authors demonstrated that immigration credit is higher in species that are characterised by low seed production and dispersal potential (*sensu* Vittoz & Engler 2007) compared to species with high seed production and dispersal potential in forest specialist communities. However, few studies have used trait-based approaches to determine how connectivity changes over time.

Effect of landscape connectivity on actual seed dispersal

Studies assessing actual dispersal (**Fig. 1**) in response to connectivity have developed over the last 15 years, but remain limited. Many papers have assessed seed fluxes at the community level, particularly for water-dispersed species (e.g. Andersson & Nilsson 2002; Boedeltje *et al.* 2003, 2004; Moggridge *et al.* 2009), but very few studies have considered the effect of connectivity on these seed fluxes. Only a few studies have taken connectivity into account, with the response of plants being almost exclusively assessed at the species level, which are presented in the next section.

Number of dispersed seeds

The effect of connectivity on the abundance of dispersed seeds has mostly been investigated under experimental conditions, focusing on particular species that were selected for their abundance or representativeness of the community process. Seed fluxes for three plant species dispersed by birds were assessed in connected and unconnected patches using the Savannah River Site experimental design. Seeds were trapped in peripheral (i.e. receiver) patches, of which just one was connected to the central patch and the others were not (**Box 2**). To provide confidence that all seeds or fruits found in seed traps were exclusively derived from the central patch, two methods were carried out, depending on the abundance of the species considered: (i) the removal of all naturally occurring individuals from the peripheral patches, and (ii) the use of marked seeds or fruits in the central patch by fluorescence. Based on this approach, Tewksbury *et al.* (2002) reported that twice the number of *Ilex vomitoria* seeds was trapped in connected patches compared to unconnected patches. The authors also reported that a greater proportion (an increase of 18%) of *Myrica cerifera* were present in faecal samples collected in connected patches that contained fluorescent powder compared to unconnected patches. Similar results were obtained by Haddad *et al.* (2003) for both *Myrica cerifera* and *Rhus copallina*, with five and two times more seeds, respectively, being transported from the central patch in connected compared to unconnected patches. Using an individual-based model, Levey *et al.* (2005) demonstrated that the distribution of *Myrica cerifera* is explained by the movement of birds that were 31% more likely to be found in connected patches compared to unconnected patches. Thus, it is important that future studies extend these analyses to consider other modes of dispersal.

Seed flux composition

Studies analysing the seed communities of plants that actually disperse in response to landscape connectivity remain scarce. To our knowledge, only one study investigated this type of relationship (Suárez-Esteban *et al.* 2013). The authors assumed that unpaved roads act as corridors, and analysed actual dispersal along unpaved roads in comparison to adjacent scrubland, which was not considered to be a corridor. By analysing the seeds of all fleshy-fruit shrubs that were contained in the faecal samples of frugivorous mammals, the authors demonstrated that the composition of seed communities in unpaved roads differed to that observed in scrublands, due to the effect of corridors on animal behaviour. However, this finding was dependent on the animal-vector being considered (rabbit, carnivore or ungulate). Such studies analysing actual dispersal are expected to improve the accuracy of assessing current seed dispersal, allowing us to determine how connectivity influences dispersal *per se*.

New prospects for future research

Analysing the response of the plant community to connectivity loss has not been as extensively studied as for animal guilds, despite the dispersal specificity of plants. Through our review, we demonstrated that: (i) landscape connectivity does promote the actual dispersal of plants between communities (section “Effect of landscape connectivity on actual seed dispersal”), but (ii) its influence on community taxonomic structure does not follow a general pattern due to the many factors that modulate its effect (sections “Contrasted effect of landscape connectivity on plant community taxonomic structure” and “Effect of time on the response of plants to connectivity”). We also found that: (iii) the use of functional traits provides a better understanding of the mechanisms involved in plant responses to connectivity (sections “Effect of landscape connectivity on the functional structure of plant communities” and “Effect of time on the response of plants to connectivity”).

These three key-findings should be considered in light of several limitations related to the studies selected for this review. First, this review did not compare the relative role of landscape connectivity vs. other landscape factors (e.g. habitat size or habitat amount) in structuring plant communities. Thus, it is beyond the scope of this review to shed light on the SLOSS (Single Large Or Several Small) debate, derived from island biogeography or to discuss on the relative importance between SLOSS and the Habitat Amount Hypothesis (Fahrig 2013) (but see Lindgren & Cousins 2017). Secondly, the dark diversity (i.e. all species that are absent from a habitat patch but that could disperse to and establish there, Pärtel *et al.* 2011) may

result from dispersal limitation (Riibak *et al.* 2015). However, the reviewed studies investigated the role of landscape connectivity on expressed plant communities (i.e. potential dispersal, **Fig. 1**), rather than on the absence of species, neglecting the role of landscape connectivity on dark diversity. Third, the consideration of traits in the response to connectivity raises a question for some authors (see for example Haddad *et al.* 2015). These authors suggest that plant dispersal might be better described by statistical probabilities and stochastic factors rather than traits. Within these limitations, we identified research prospects from the three key-findings identified here:

- (1) Landscape connectivity promotes actual dispersal between connected communities. Because of the scarcity and the animal-dispersed species focus of the studies on this topic, we can only encourage more studies to use this approach, particularly for other dispersal modes.
- (2) The influence of landscape connectivity on plant taxonomic structure do not follow a general pattern because of the multiplicity of factors that modulate its effect. To better disentangle the effect of landscape connectivity from the other factors, explicit consideration of both spatial and temporal scales is necessary to define a relevant resolution of the landscape. An assessment of landscape connectivity at different spatial scales should be developed to detect the dispersal range at which plant species respond to changes in connectivity. Because some species exhibit a time lag in their response to connectivity changes, efforts to incorporate historical data to model historical connectivity are necessary. In addition, the presence of a corridor *per se* is not sufficient to connect habitats. Indeed, the quality of the corridors (or landscape elements) should be considered and determined by their management practice. For instance, in hedgerows, the corridor quality is determined by the vegetation structure and vertical organisation at a fine scale. The assessment of connectivity might account for these fine-scale characteristics by using recent remote sensing techniques (Betbeder *et al.* 2014). 2014) to better predict species abundance such as for carabids (Betbeder *et al.* 2015). Future studies should investigate this new methodology for plants. Connectivity might be evaluated while considering the potential interaction between habitats, to better account for the degree of ecological specialisation of species. Complementarity between the different ecological corridor types (i.e. provided by different habitat types) might explain the lowest sensitivity of generalist species to connectivity loss. In contrast, antagonistic effects might occur for specialist

species. The deployment of such multi-habitat landscape connectivity models (which independently consider different ecological corridor types) could enhance our understanding of the responses of plant species to connectivity at a community scale.

- (3) Using functional traits provides a better understanding of the mechanisms involved in plant responses to connectivity. Some trait syndromes characterise species that are highly sensitive to connectivity loss. Determining trait combinations that might predict, at best, plant responses in time and space to changes in connectivity is a key challenge of forthcoming research. Using such functional indicators would allow these species to be detected in a manner that is reproducible and independent of ecosystems and regional pools (Lavorel *et al.* 1997). This approach is promising for defining general functional indicators of sensitivity. Such indicators may, for instance, help to identify species that are less likely to colonise and establish in patches after connectivity loss. In addition, the use of functional connectivity indices, which considers the dispersal distance of species, should be generalized in studies investigating plants, especially at the community level. The dispersal traits that promote time-dependent responses to connectivity that we have identified should be integrated in these indices to provide an adequate understanding of connections between plant communities over time.

Beyond highlighting needs for future research, this synthesis provides information of use for land-use planning (green and blue infrastructure implementation, for instance, Sandström 2002; Tzoulas *et al.* 2007). Such information could provide new methods and decision-making tools to promote the operational establishment of ecological corridors, taking plant communities into account.

Acknowledgements

This work was funded by the Fondation de France (BISCO project). We thank the two anonymous referees for their constructive work and remarks on the manuscript

Appendix S1 Methods

We systematically reviewed articles to assess whether and how landscape connectivity affects the assembly of plant communities. Using Web of Science and Google Scholar to gather publications using the following keywords: landscape connectivity, habitat isolation, corridors and plants. Because ecosystem functioning is completely different in tropical systems, we excluded these studies, only considering studies conducted in temperate systems. We also excluded studies that focus on fragmentation (i.e. that are conducted in a fragmented landscape context); that is, when it is not possible to disentangle the effects of decreased connectivity (variable of interest) and decreased habitat area. We only considered studies that: (i) manipulated connectivity through the presence (or absence) of an experimentally-created corridor between two habitat patches for experimental approaches, and (ii) measured connectivity in a quantitative manner (via the use of indices) for correlative approaches. Quantitative connectivity assessments were based on isolation metrics such as Euclidean distance, structural connectivity indices (see various examples in the main text), least-cost distance or resistance distance. We selected studies that focused on how landscape connectivity affected plants at the community level. Within this framework, we included studies with taxonomic approaches (i.e. looking at the composition and diversity of plant communities) and trait-based approaches (i.e. looking at the composition and diversity of traits). These studies assessed plant community response through: (i) analysis of individual species responses across most species at the community level, and (ii) aggregated measures across most species of a community. More specifically, only the following measures were extracted from articles that provided: (i) taxonomic and (ii) trait-based approaches:

- (i) Taxonomic approaches: alpha diversity (species richness, species density or species abundance), beta diversity (Jaccard similarity index) and gamma diversity (gamma species richness)
- (ii) Trait-based approaches:
 - a. Dispersal mode approach: analyses similar to the taxonomic approach but per dispersal mode, proportion of species per dispersal mode and indicators for species sensitivity to connectivity (probability of occurrence in response to connectivity, regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity)

- b. Emergent groups approach: trait values of emergent groups and species richness of emergent groups
- c. Response traits approach: indicators for species sensitivity to connectivity (probability of occurrence in response to connectivity, regression coefficient resulting from the logistic regression between patch occupancy for each species as explained by connectivity intensity), species richness in the different categories of the seed longevity index, proportion of species characterised by a trait, trait value of response groups to connectivity and species trait values
- d. Community weighted mean traits and functional diversity approach: functional gamma diversity (standard effect size values calculated for Rao's quadratic entropy traducing functional divergence or convergence) and gamma aggregated mean trait values (gamma scale weighed mean trait values, indicating the mean value towards which traits converged)

Concerning actual dispersal approaches, we included studies at the species level because very few studies have assessed the actual dispersal of communities in relation to connectivity.

4. Problématique et organisation de la thèse

Le maintien et la restauration de la connectivité entre tâches d'habitat ont été proposés comme une stratégie fondamentale à l'échelle des paysages pour atténuer la perte de biodiversité végétale au sein des paysages fragmentés.

Afin de déterminer l'efficacité de cette stratégie, de nombreuses études empiriques se sont intéressées à l'effet de la connectivité sur la structuration des communautés végétales. Jusqu'à présent, les études réalisées *in situ* ont produit des résultats contradictoires, aboutissant à une absence de consensus scientifique quant à l'effet de cette stratégie pour les plantes (ARTICLE 2). Cette absence de consensus peut probablement s'expliquer par le fait que ces études (i) sous-estiment l'effet des différents types d'habitat contribuant à la connectivité et (ii) sous-explorent l'effet de la dynamique temporelle de connectivité sur la structuration des communautés végétales.

L'objectif général de cette thèse est de déterminer l'effet de la connectivité fournie par les différents types d'habitat et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales. L'approche fonctionnelle vise à évaluer si, et dans quelle mesure, les traits de colonisation – et en particulier de dispersion – déterminent la réponse des espèces végétales à la connectivité et à sa dynamique temporelle. Afin d'accroître la portée des résultats issus de cette thèse au sein des paysages agricoles, cette thématique sera étudiée sur les trois types d'habitats dominants de ces paysages agricoles : les bois, les prairies et les cultures de céréales.

Pour se faire, nous avons cherché à caractériser la connectivité fournie par les différents types d'habitat et la dynamique temporelle de connectivité dans le cadre de la théorie des graphes (chemins de moindre coût, théorie des circuits). D'un côté, les méthodes « traditionnelles » de caractérisation de la connectivité (cf. introduction, section 2.2.1) ont été améliorées afin de s'affranchir de la priorisation du rôle exercé par les différents types d'habitat sur la connectivité (ARTICLES 3 et 4). D'un autre côté, une revue littéraire synthétisant les méthodes existantes de caractérisation de la dynamique temporelle de connectivité a été réalisée (cf. introduction, section 2.2.2; ARTICLE 1). Cette revue nous a permis de développer, ultérieurement, des métriques innovantes pour mesurer, outre le degré de connectivité, l'intensité ou encore la variabilité des changements temporels de connectivité spatiale (ARTICLE 5).

A la suite de cette introduction générale, la **Première Partie** de cette thèse s'intéresse aux éléments méthodologiques supplémentaires mis en œuvre *in situ* pour répondre à l'objectif susmentionné. Elle comprend plus particulièrement une description de la zone d'étude, de la sélection des tâches d'habitat (bois, prairies et cultures céréalières) et des méthodes d'échantillonnage des communautés végétales.

La **Deuxième Partie** a pour objectif d'évaluer l'influence de la connectivité fournie par les habitats boisés, prairiaux et cultivés sur la structuration taxonomique et la composition fonctionnelle des communautés végétales. Au sein d'un **Premier Chapitre** (ARTICLE 3), nous cherchons à déterminer l'influence de la connectivité fournie par les différents types d'habitat sur la similarité de composition des communautés et ce, en fonction, du mode de dispersion des espèces (zoochores, anémochores et non-assistées). L'étude a porté sur les communautés végétales boisées, prairiales et adventices (i.e. espèces sauvages non cultivées cohabitant avec les cultures). Au sein d'un **Second Chapitre** (ARTICLE 4), nous nous focalisons sur les communautés adventices, particulièrement intéressantes en raison de leur double rôle au sein des paysages agricoles (support de fonctions écosystémiques vs. compétition vis-à-vis de l'espèce semée). Nous testons les effets de la quantité d'habitat et de la connectivité, toutes deux fournies par les différents types d'habitat, sur la diversité spécifique (richesse et équitabilité) et l'abondance totale des espèces au sein de ces communautés, celles-ci constituant des proxys de la résistance de la culture céréalière à la colonisation par les adventices. En particulier, nous évaluons si, et comment, ces effets sont déterminés par la composition fonctionnelle des communautés adventices.

L'objectif de la **Troisième Partie** est de déterminer l'influence de la dynamique temporelle de connectivité (i.e. degré de connectivité, intensité et variabilité des changements temporels de connectivité) sur la structuration taxonomique et fonctionnelle des communautés végétales. Dans ce **Troisième Chapitre** (ARTICLE 5), nous explorons, pour l'une des toutes premières fois, les effets cumulés de sept décennies de changements de connectivité spatiale sur les communautés végétales actuelles. Pour se faire, nous nous concentrons sur les communautés végétales boisées, particulièrement reconnues pour leurs réponses décalées de longue durée. Plus particulièrement, nous déterminons si la dynamique temporelle de connectivité affecte la diversité spécifique et la structure (composition et diversité) fonctionnelle des communautés végétales boisées actuelles au sein de tâches d'habitat boisé ayant été soumises à des tendances ascendantes (i.e. gain de connectivité au

cours du temps) et descendantes (i.e. perte de connectivité au cours du temps) de connectivité sur les 70 dernières années.

Enfin, dans la **Quatrième Partie (discussion générale)**, nous discutons de l'ensemble de ces résultats au regard des cadres théoriques et méthodologiques mobilisés, et ouvrons des perspectives de recherches tant fondamentales qu'opérationnelles

Partie I

Elements méthodologiques

1. Le site agricole « de Pleine-Fougères » de la Zone Atelier Armorique, un site d'étude à l'histoire paysagère mouvementé
2. Sélection des tâches d'habitat
3. Echantillonnage des communautés végétales

1. Le site agricole « de Pleine-Fougères » de la Zone Atelier Armorique, un site d'étude à l'histoire paysagère mouvementé

Cette thèse a été réalisée au sein du site agricole « bocage », dit de Pleine-Fougères, site atelier de recherche socio-écologique à long terme (Long Term Socio-Ecological Research, LTSER) de la « Zone Atelier Armorique » (ZAAR).

1.1. Caractéristiques du site d'étude : contexte géographique, physique et paysager

Localisé en France, au nord-est du département de l'Ille-et-Vilaine et au sud de la Baie du Mont-Saint-Michel (48°36'N, 1°32'W), le site agricole de Pleine-Fougères s'étend sur une superficie de 130 km² (**Fig. 1a**). La topographie est plate, le sol repose sur des roches granitiques, gréseuses et schisteuses, et le climat est tempéré océanique (température annuelle moyenne de 12°C, précipitations annuelles moyennes de 700mm; Joly *et al.* 2010). Ce site d'étude se caractérise par un paysage bocager, dominé par des systèmes agricoles de type polyculture-élevage, en particulier bovin laitier. Le paysage se compose principalement de céréales d'hiver (majoritairement du blé et de l'orge), de maïs ensilage et de prairies temporaires [en grande partie semées à partir de Ray-grass anglais (*Lolium perenne*)], séparés par un vaste réseau de haies et entrecoupés par des bois. Il comprend également une grande forêt ancienne dans le sud. La plupart de ces bois sont dominés par le Châtaignier commun (*Castanea sativa*), le Hêtre commun (*Fagus sylvatica*) et/ou le Chêne pédonculé (*Quercus robur*), en raison de la composition initiale de leurs plantations et de leurs successions spontanées. Les haies sont composées majoritairement de Chêne pédonculé et/ou de Châtaignier commun, les arbres étant généralement plantés sur un talus de terre (Burel *et al.* 1998).

1.2. Un site d'étude dont le paysage bocager fit l'objet de profondes transformations au cours des années 1950

Comme dans la plupart des territoires du nord-ouest de l'Europe, le paysage bocager du site agricole de Pleine-Fougères a subi de profondes modifications depuis le milieu des années 1950 jusqu'à nos jours (**Fig. 1b**), du fait de politiques successives, notamment la politique agricole commune (PAC).

Caractérisé par la présence d'un large réseau de haies, le paysage bocager de Pleine-Fougères se composait majoritairement de prairies permanentes, et de cultures fourragères, minoritaires, céréalières ou sarclées (racines et tubercules) (Flatrès 1979; Burel & Baudry 1999; Baudry *et al.* 2000).

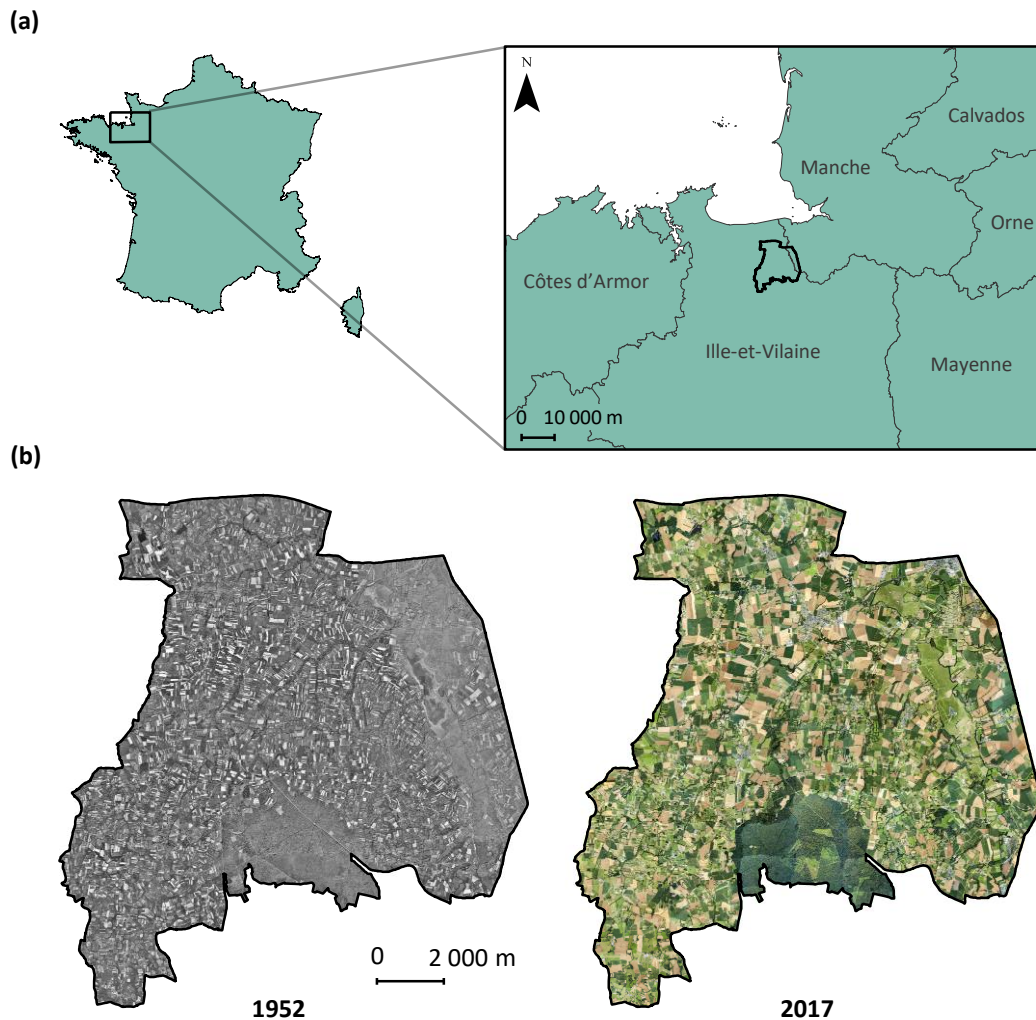


Fig. 1 (a) Localisation et (b) images aériennes, datant de 1952 et de 2017, du site agricole de Pleine-Fougères (Zone Atelier Armorique).

Après la Seconde Guerre Mondiale, la promulgation d'un décret Français en 1955 introduisant la politique de « remembrement », suivie par la mise en place de la PAC en 1962, ont initié les modifications radicales de ces paysages (Meynier & Deniel 1965; Flatrès 1979; Burel & Baudry 1999; Baudry & Papy 2001). Lancées en faveur de l'intensification agricole, ces politiques ont entraîné la destruction des haies et l'abandon des prairies permanentes (grâce au drainage) et des cultures de racines et de tubercules fourragères au profit de prairies temporaires et de cultures de maïs (Burel & Baudry 1999; Huyghe 2009).

Au terme d'une période de surproduction, une prise de conscience des impacts de l'intensification de l'agriculture sur la perte de la biodiversité s'est progressivement opérée et développée à partir des années 1990. Face à ce constat, les accords internationaux (e.g. Convention « de Rio » sur la diversité biologique, 1992), les directives européennes (e.g. réformes successives de la PAC), les lois nationales (e.g. lois Grenelle I, 2009 et II, 2010) et des programmes régionaux soulignent la nécessité de concilier productivité et protection de la biodiversité au sein des paysages agricoles (Baudry & Papy 2001; Huyghe 2009). Plusieurs programmes, mesures et outils incitatifs en faveur de la protection, du maintien et/ou de l'établissement d'éléments semi-naturels au sein des paysages (e.g. haies, bois, prairies permanentes, bandes enherbées) ont été ainsi instaurés à diverses échelles (mesures de verdissement de la PAC à l'échelle européenne, création de la Trame Verte et Bleue à l'échelle nationale).

Les conséquences de ces politiques successives sur (i) le pourcentage de superficie totale et (ii) la surface moyenne des habitats boisés (bois et haies), des prairies et des cultures depuis les années 1950 peuvent être retracées grâce aux cartes paysagères couvrant le site agricole de Pleine-Fougères (**Fig. 2**). Les cartes d'occupation du sol (base de données vectorielles de la ZAAr) et les cartes des habitats boisés (base de données raster Kermap) ont été établies à partir d'images aériennes d'une résolution de 5 m. Les cartes d'occupation du sol ont été réalisées à partir de six catégories d'occupation du sol : bois, prairies, cultures, voiries, zones bâties et plans d'eau; des sous-catégories étant disponibles pour les quatre premières catégories au sein des cartes les plus récentes. Les cartes des habitats boisés comprennent les bois et les haies; mais aussi les arbres isolés et vergers complantés (i.e. disséminés au sein des cultures) pour les cartes les plus anciennes. A partir de ces bases de données, six dates ont été sélectionnées (**Fig. 2a**), selon les différentes politiques mises en œuvre susmentionnées et les images aériennes disponibles : 1952 (image aérienne disponible la plus ancienne), 1974, 1985, 2000, 2006 et 2017 (image aérienne la plus récente à ce jour).

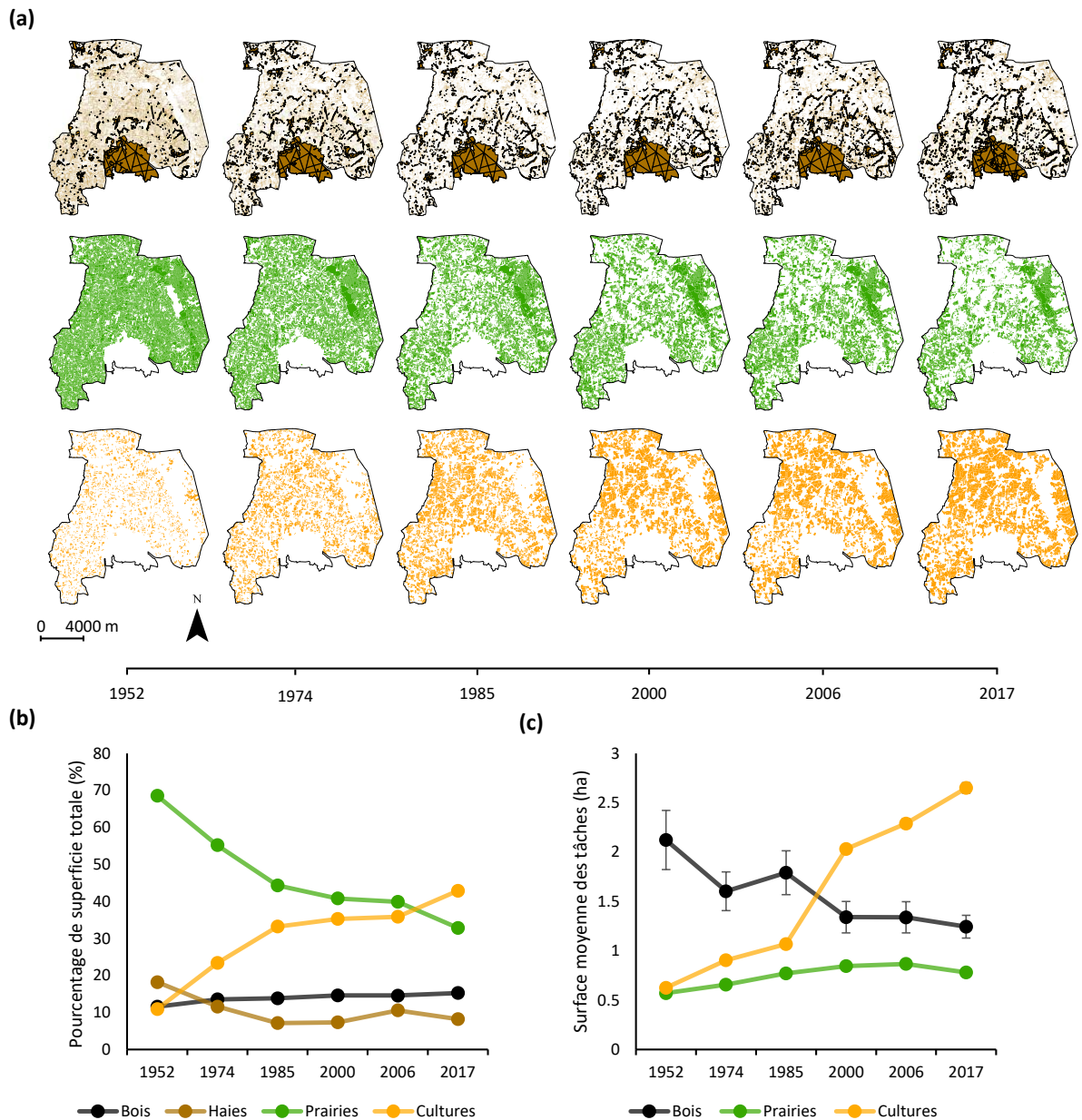


Fig. 2 (a) Cartes du site agricole de Pleine-Fougères illustrant l'évolution des habitats boisés (en haut), comprenant les bois (entités marron foncé entourées de noir) et les haies (entités marron clair), des prairies (entités vertes, au milieu), et des cultures (entités jaunes, en bas) entre 1952 et 2017. Graphiques linéaires représentant **(b)** le pourcentage de superficie totale des bois, des haies, des prairies et des cultures et **(c)** la surface moyenne \pm erreur standard (indiquée par des barres verticales) des tâches de bois, de prairie et de culture.

Dans l'ensemble, ces différentes politiques ont entraîné une forte diminution (ca. 61 %) de la superficie totale recouverte par les haies entre 1952 et 1985, suivie d'une légère augmentation (ca. 15 %) entre 1985 et 2017. Sur l'ensemble de la période, la superficie totale recouverte par les prairies a également fortement diminué (ca. 52 %), tandis que celle recouverte par les bois et les cultures ont, respectivement, légèrement (ca. 32 %) et considérablement (ca. 294 %) augmenté (**Fig. 2b**). La surface moyenne des tâches a diminué

pour les bois (ca. 41 %) au cours de cette même période, tandis qu'elle a augmenté pour les prairies (ca. 37 %) et les cultures (ca. 324 %) (**Fig. 2c**).

2. Sélection des tâches d'habitat

Dans le cadre de cette thèse, trois types d'habitat représentant près de 70 % du paysage actuel (2017) du site agricole de Pleine-Fougères ont été étudiés : les bois (14%, en excluant les friches), les prairies (33%, en excluant les bandes enherbées) et les cultures de céréales (20%, les cultures de maïs ayant une proportion équivalente).

Les résultats présentés dans le cadre du premier chapitre de ce manuscrit (ARTICLE 3) sont issus d'études de terrain réalisées en amont de cette thèse. Les résultats présentés ultérieurement (ARTICLES 4 et 5) s'appuient sur une étude de terrain propre à cette thèse, celle-ci s'inscrivant dans une démarche très similaire aux études précédentes. Seule l'étude de terrain réalisée dans le cadre de cette thèse est présentée ci-dessous.

Table 1 Caractéristiques des tâches d'habitat de bois, de prairie temporaire et de culture céréalière sélectionnées pour l'étude des communautés (i) du couvert végétal (abréviation : CV) et (i) de la banque de graines (abréviation : BDG)

	Bois		Prairie		Culture		
	CV	BDG	CV	BDG	CV	BDG	
Nombre	50	25	48	25	27	25	
Surface (ha)	Moyenne	1,11	0,61	0,92	0,94	1,81	1,85
	Min - Max	0,16 – 5,78	0,26 – 1,77	0,19 – 2,33	0,39 – 2,32	0,55 – 4,38	0,55 – 4,38
Composition initiale du semis ou de plantation*	Châtaigner commun, Hêtre commun et/ou Chêne pédonculé		Ray-grass anglais		Blé ou Orge		
Âge	Continuellement boisé depuis 1952		Continuellement en prairie suite au retournement d'une culture en : 2010, 11, 12 ou 13 2012 ou 13		Continuellement en cultures suite au retournement d'une prairie en 2013, 2014 ou 2015		
Pratique de gestion	Extensif		Pâturage et/ou fauche, avec possibilité d'amendements		Conventionnel (labour, amendements et herbicides)		

* la composition initiale des espèces plantées au sein des bois a été estimée à partir de la composition des espèces arborées dominantes, en supposant qu'elle reflète la composition initiale plantée, celle-ci n'étant pas disponible

Au total, 50 tâches de bois, 48 tâches de prairie temporaire et 27 tâches de culture céréalière (blé ou orge) réparties au sein du site d'étude ont été sélectionnées pour l'étude des communautés du couvert végétal (ou communautés réalisées), avec une distance d'au moins 150 m entre deux bordures de tâches pour chaque type d'habitat. Leur surface, leur composition initiale (dominante) de semis ou de plantation, leur âge (i.e. nombre d'années successives sans changement d'occupation du sol) et leur pratique de gestion ont été standardisées, en fonction des caractéristiques typiques de ces trois types d'habitat dans le site agricole de Pleine-Fougères. Parmi ces tâches d'habitat, 25 tâches de bois, prairie temporaire et de culture céréalière ont été sous-sélectionnées pour l'étude des communautés de la banque de graines (ou communautés potentielles; **Table 1 et Fig. 3**).

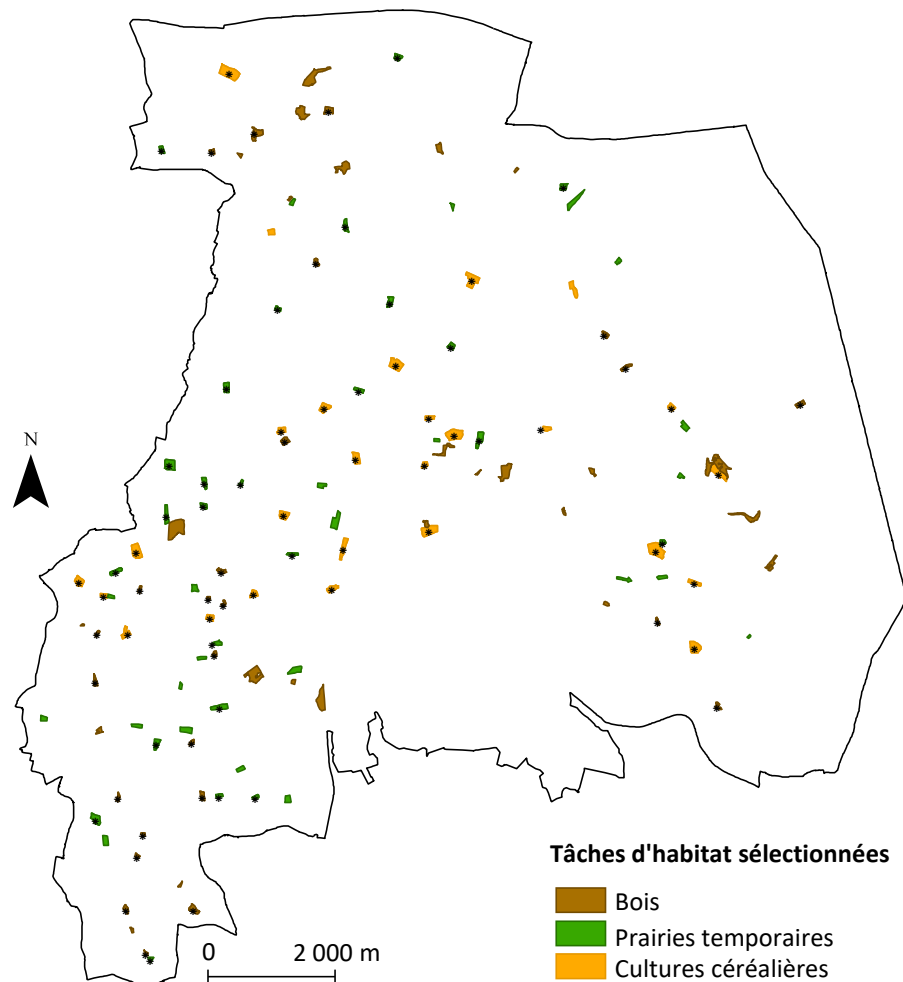


Fig. 3. Distribution des 50, 48 et 27 tâches de bois, de prairie temporaire et de culture céréalière respectivement sélectionnées pour l'échantillonnage du couvert végétal sur l'ensemble du site d'étude, le site agricole de Pleine-Fougères (LTSER Zone Atelier Armorique). Les 25 tâches de bois, de prairie temporaire et de culture céréalière sous-sélectionnées pour l'échantillonnage de la banque de graines sont indiquées par un astérisque (*).

L'ensemble de cette sélection a été réalisée à partir des cartes d'occupation du sol couvrant le site agricole de Pleine-Fougères et d'enquêtes réalisés auprès d'une centaine d'agriculteurs.

3. Echantillonnage des communautés végétales

Au sein de ces multiples tâches de bois, de prairie temporaire et de culture céréalière, nous avons réalisé un échantillonnage des communautés (i) du couvert végétal et de (ii) la banque de graines.

Seuls les résultats issus de l'échantillonnage du couvert végétal pour les cultures et les bois sont présentés dans ce manuscrit (ARTICLES 4 et 5). L'ensemble des données acquises, provenant de ces deux campagnes d'échantillonnage, est actuellement en cours d'exploration afin de répondre aux perspectives dégagées à l'issue de ces travaux de thèse (cf. discussion).

3.1. Echantillonnage du couvert végétal

Un échantillonnage du couvert végétal a été effectué au sein des 50 tâches de bois, 48 tâches de prairie temporaire et 27 tâches de culture céréalière entre avril et juillet 2018.

L'identité et l'abondance (en pourcentage de recouvrement au sol) de chaque espèce ont été déterminées au sein de huit quadrats de 10 m × 5 m dans les bois, dix quadrats de 2 m × 2 m dans les prairies temporaires et dix quadrats de 2 × 2 m dans les cultures céréalières, dont la surface totale correspond à la surface minimale d'échantillonnage recommandée pour chaque type d'habitat (Mueller-Dombois & Ellenberg 1974). Les quadrats ont été uniformément répartis au sein de chaque tâche d'habitat, et à au moins 5 m (bois et prairies) ou 10 m du bord (cultures). Il est à noter qu'au sein des trois plus petites tâches de bois, seuls six quadrats sur huit ont pu être réalisés. La composition et l'abondance spécifique ont été obtenues pour chaque tâche d'habitat de bois, de prairie temporaire et de culture céréalière, en regroupant les données collectées dans les différents quadrats.

3.2. Echantillonnage de la banque de graines du sol

Entre février et mars 2019, la banque de graines du sol a été échantillonnée au sein de 25 tâches de bois, 25 tâches de prairie temporaire et 25 tâches de culture céréalière.

Au sein de chaque quadrat préalablement utilisé, cinq, deux et deux carottes de sol de 3,8 cm de diamètre et de 20 cm de profondeur ont été respectivement prélevées dans les bois, les prairies et les cultures. Au total, 40 (ca. 9 L), 20 (ca. 4.5 L) et 20 (ca. 4.5 L) carottes de sol ont été respectivement réalisées dans chaque tâche de bois, de prairies et de cultures, dont le volume correspond au volume minimal d'échantillonnage recommandé pour chaque type d'habitat (Hutchings 1986; Thompson *et al.* 1997). Après avoir retiré la litière, les échantillons de banque de graines ont été divisés en trois sous-échantillons de 0 – 5 cm, 5 – 10 cm et 10 –

20 cm. Cette division en sous-échantillons a été réalisée pour les bois et les prairies, afin de conserver la stratification verticale de la banque de graine du sol, liée à la dynamique de dépôt des graines (Bakker *et al.* 1996a; Grandin & Rydin 1998; Fenner & Thompson 2005). Elle n'a, en revanche, pas été menée pour les cultures, celles-ci étant régulièrement retournées. Tous les (sous-) échantillons d'une même tâche d'habitat ont été ensuite regroupés, avant d'être stockés à 4°C dans l'obscurité pendant a minima trois semaines afin d'être déshydratés et de lever la dormance des graines contenues (Vanesse 1997; Decocq *et al.* 2004). Les (sous-) échantillons ont ensuite été concentrés selon la méthode proposée par Ter Heerdt *et al.* (1996), c'est-à-dire lavés à travers un tamis de 4 mm, puis de 0.2 mm afin de retirer cailloux, fragments végétatifs, mais également de réduire le volume de sol. Les (sous-) échantillons concentrés ont ensuite été étalés en une fine couche sur du sable au sein de barquettes polystyrènes (20,2 cm x 15,2 cm x 6,2 cm) préalablement remplies de terreau et de stable stérilisés (Ter Heerdt *et al.* 1996). L'ensemble des barquettes a été disposé aléatoirement au sein d'une serre expérimentale à température contrôlée (20°C jour – 18°C nuit) sans éclairage artificiel, et a été arrosé quotidiennement. Quinze barquettes témoins ont également été utilisées afin de déceler une éventuelle contamination par des graines possiblement présentes dans la serre. Les plantules émergentes ont été identifiées, comptées et retirées. Les plantules non identifiées ont été transplantées dans des godets individuels, jusqu'à ce qu'une identification soit possible. Lorsqu'aucune émergence des graines n'a été relevée pendant deux semaines consécutives au sein d'une barquette, la fine couche de sol concentré a été ameublie afin d'exposer les graines enterrées à la lumière. Le suivi de l'émergence des plantules issues des échantillons de banque de graine du sol a été réalisé jusqu'en janvier 2020, date à laquelle la germination a été jugée terminée. Au total, 12060, 13566 et 16679 plantules ont émergé pour les échantillons issus des bois, des prairies et des cultures.

Que ce soit pour l'échantillonnage de la végétation du couvert ou de la banque de graines, seules les espèces herbacées ont été considérées pour les analyses ultérieures. Les espèces ligneuses recensées étaient, en effet, exclusivement associées à la plantation initiale et aux pratiques de gestion des bois, ou des haies bordant les prairies temporaires et les cultures céréalières.

Partie II

Connectivité fournie par les différents types d'habitat et communautés végétales

Chapitre 1 : Effet de la connectivité fournie par les différents types d'habitat sur la similarité de composition des communautés végétales

Chapitre 2 : Effets de la quantité d'habitat et de la connectivité sur la diversité spécifique et l'abondance totale des espèces adventices au sein des cultures céréalières : une approche taxonomique et fonctionnelle

1. Contexte scientifique

A l'issue de l'introduction générale, il ressort que la priorisation du rôle respectif des différents types d'habitat sur la dispersion des espèces végétales dans la caractérisation de la connectivité peut expliquer la difficulté des études empiriques à dégager un patron général quant à l'effet de la connectivité sur la structuration des communautés végétales. Dès lors, nous devons déterminer si, et de quelle façon, les différents types d'habitat contribuant indépendamment à la connectivité agissent, de manière respective, dans l'assemblage des communautés végétales. En ce sens, cette deuxième partie vise à étudier les effets additifs de la connectivité fournie par les habitats boisés, prairiaux et cultivés – autrement dit, les trois types habitats qui prédominent au sein de la matrice des paysages agricoles – sur la structuration des communautés végétales.

D'un point de vue taxonomique, une forte connectivité fournie par les différents types d'habitat devrait augmenter la dispersion entre communautés locales, et ainsi accroître la diversité spécifique (richesse et équitabilité) et l'abondance totale des espèces au sein des communautés locales, tout comme la similarité de composition spécifique entre celles-ci (Mouquet & Loreau 2003).

D'un point de vue fonctionnel, la connectivité fournie par les différents types d'habitat devrait également influencer la colonisation de certaines espèces, en fonction de leur mode de dispersion, ou d'une combinaison de valeur de traits fonctionnels définissant plus finement leur capacité de colonisation. Concernant le mode de dispersion des espèces, il existe un certain consensus démontrant l'efficacité de la connectivité sur les mouvements des animaux au sein d'un large panel d'habitats (Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016). Dès lors, il est aisé de prédire que la présence des espèces zoochores devrait être favorisée par une forte connectivité, et ce, quel que soit le type d'habitat contribuant à la connectivité. *A contrario*, il est plus difficile de dégager des prédictions quant au rôle des différents types d'habitat contribuant à la connectivité vis-à-vis des espèces anémochores ou non-assistées.

Au-delà du mode de dispersion, une forte connectivité devrait favoriser la colonisation des espèces qui possèdent des valeurs de traits leur conférant de faibles capacités de dispersion et d'établissement (Johst *et al.* 2002; Nathan *et al.* 2002; Auffret *et al.* 2017b), impactant ainsi la composition fonctionnelle au sein des communautés. Comme le souligne notre revue littéraire (ARTICLE 2), ces prédictions ont d'ores et déjà été explorées par les écologues du

paysage afin de définir des traits de réponse à la connectivité. Si ces prédictions théoriques ont été confirmées, notamment au sein des communautés boisées et prairiales, elles n'ont jamais été évaluées pour les communautés adventices.

Récemment, les malherbologues se sont détournés de la simple étude des communautés adventices en lien avec les pratiques agricoles locales pour intégrer progressivement le contexte paysager. L'effet de la quantité d'habitat boisé, prairial ou encore cultivé sur la diversité spécifique et l'abondance totale des adventices au sein des cultures est désormais largement reconnu (Petit *et al.* 2013) *A contrario*, l'effet de la connectivité n'a reçu aucune attention, et peu d'études en malherbologie ont tenté de définir les traits de réponse au paysage (mais cf. Alignier *et al.* 2012; Fried *et al.* 2018). Pourtant, les preuves empiriques issues de l'écologie du paysage peuvent être mobilisées pour émettre, mais également appuyer, des prédictions quant à l'effet de la quantité d'habitat, mais aussi de la connectivité sur la structuration taxonomique et fonctionnelle des communautés adventices. D'un autre côté, les cultures constituent un habitat particulier, en raison de l'intensité et de la fréquence des perturbations auquel elles sont soumises (e.g. travail du sol, application d'herbicide). En raison de cette spécificité, seule une faible fraction des espèces dont les graines arrivent et s'établissent au sein de la culture grâce à un contexte paysager favorable (i.e. forte quantité d'habitat et connectivité) devrait parvenir à constituer la communauté locale. Ainsi, les cultures qui reçoivent des espèces possédant des valeurs de traits maximisant l'établissement et le développement des plantules en dépit de ces perturbations devraient être caractérisées par une forte diversité et abondance totale. Les traits d'établissement et de compétition constitueraient, de ce fait, des traits d'effet (i.e. les traits fonctionnels traduisant l'effet des plantes sur le fonctionnement de l'écosystème; *sensu* Lavorel *et al.* 1997; Lavorel & Garnier 2002; Suding *et al.* 2008) reflétant la diversité spécifique et l'abondance totale des adventices au sein des cultures. Cependant, nous ignorons si les changements dans la composition de valeurs de traits fonctionnels induits par le contexte paysager (trait de réponse) peuvent impacter, à leur tour, la résistance des agroécosystèmes à la colonisation des adventices (trait d'effet).

2. Objectifs

Cette partie a pour objectif de décrire l'influence de la connectivité fournie par les différents types d'habitat (habitats boisés, prairiaux et cultivés) sur la structuration taxonomique et la composition fonctionnelle des communautés végétales. Nous avons plus particulièrement cherché à répondre aux questions suivantes :

- (1) **Chapitre 1.** Quels sont les effets respectifs des différents types d'habitat contribuant de manière indépendante à la connectivité sur la similarité de composition spécifique des communautés végétales ? Dépendent-ils du mode de dispersion considéré ? (ARTICLE 3)
- (2) **Chapitre 2.** Quels sont les effets de la connectivité et de la quantité d'habitat fournie par les différents types d'habitat sur la diversité spécifique et l'abondance totale des adventices ? Ces effets sont-ils médiés par la composition fonctionnelle des communautés adventices ? (ARTICLE 4)

3. Démarches mises en œuvre

Pour répondre à ces deux questions, plusieurs tâches d'habitat de bois, de prairie temporaire (ARTICLE 3) et de culture céréalière (ARTICLES 3 et 4) ont été sélectionnées pour l'échantillonnage du couvert végétal (cf. partie I, sections 2 et 3.1). Nous avons mesuré la connectivité (ARTICLES 3 et 4) et la quantité d'habitat (ARTICLE 4) fournies indépendamment par les habitats boisés, prairiaux et cultivés. Plus particulièrement, la mesure de la connectivité a été basée sur l'utilisation conjointe d'une carte de résistance et d'une modélisation des chemins de dispersion potentiels entre tâches [chemins de moindre coût (ARTICLE 4) et théorie des circuits (ARTICLE 3)] pour chaque type d'habitat considéré. Pour le premier chapitre, la similarité de composition spécifique des communautés boisées, prairiales et adventices a été évaluée pour chaque mode de dispersion principal des espèces (espèces zoochores, anémochores et non-assistées; ARTICLE 3). Pour le second chapitre, la composition fonctionnelle des communautés adventices a été mesurée par la valeur agrégée de cinq traits potentiels de réponse et d'effet, ceux-ci étant liés aux capacités de dispersion, d'établissement et de compétition des espèces (nombre de graines, type de reproduction, masse des graines, hauteur des plantes et taux de germination; ARTICLE 4). La diversité spécifique (richesse et équitabilité) et l'abondance totale des adventices (recouvrement de l'ensemble des espèces au sol) ont également été mesurées comme proxys de la résistance de la culture céréalière à la colonisation des adventices (ARTICLE 4).

4. Principaux résultats

Les résultats confirment l'importance de la connectivité dans les mécanismes d'assemblages des communautés végétales. Ces deux chapitres soulignent que les différents types d'habitat (contribuant à la connectivité) agissent sur les traits fonctionnels (y compris leur mode de dispersion) des espèces pour déterminer l'assemblage des communautés végétales au sein des

trois habitats dominant les paysages agricoles. Une forte connectivité peut favoriser ou entraver la colonisation des espèces, selon (i) le type d'habitat contribuant à la connectivité et (ii) le mode de dispersion ou la possession de certaines valeurs de traits qui les caractérisent, au sein des tâches d'habitat.

Les résultats issus du premier chapitre (ARTICLE 3) montrent que la similarité de composition des communautés végétales zoochores des tâches de bois et de prairie temporaire dépend de la connectivité, contrairement à celle des tâches de culture céréalière. La similarité des communautés zoochores au sein des bois est accrue par une forte connectivité fournie par les habitats boisés, tandis qu'elle est réduite par une forte connectivité fournie par les habitats cultivés. *A contrario*, la similarité des communautés zoochores au sein des prairies temporaires est accrue par une forte connectivité fournie par les habitats cultivés.

En s'appuyant simultanément sur une approche taxonomique et fonctionnelle, les résultats du second chapitre (ARTICLE 4) permettent de révéler les effets de la connectivité au sein de tâches de culture céréalière. L'approche taxonomique ne démontre pas d'effet du paysage, à la différence de l'approche fonctionnelle. La connectivité et, dans une moindre mesure la quantité d'habitat, toutes deux fournies par les habitats prairiaux, affectent la composition fonctionnelle des communautés adventices. Une forte quantité d'habitats prairiaux favorise les espèces produisant de nombreuses graines. Une forte connectivité fournie par les habitats prairiaux favorise les espèces produisant peu de graines, ayant un fort investissement dans la reproduction végétative et un fort taux de germination. A son tour, un fort taux de germination réduit l'abondance totale des adventices au sein des cultures céréalières. Ainsi, une forte connectivité fournie par les habitats prairiaux réduit l'abondance totale des adventices en favorisant leur taux de germination, probablement en raison d'une faible dormance des graines (Colbach *et al.* 2006; Baskin & Baskin 2014, cf. discussion, section 1.4).

Dans leur ensemble, ces résultats améliorent, d'une part, notre compréhension du rôle de la connectivité dans les règles d'assemblage des communautés végétales, via son effet sur le mode de dispersion, ou plus largement, sur les traits fonctionnels, des espèces. D'autre part, ces résultats approfondissent notre aptitude à prédire l'effet du paysage sur le fonctionnement des écosystèmes (e.g. résistance de la culture céréalière à la colonisation des adventices les plus abondantes) en élargissant le cadre théorique « trait de réponse – trait d'effet » aux mécanismes d'assemblage des communautés opérant à l'échelle du paysage.

Chapitre 1

Effet de la connectivité fournie par les différents types
d'habitat sur la similarité de composition des communautés
végétales

Article 3. Additive effects of connectivity provided by different habitat types drive plant assembly

Léa Uroy, Cendrine Mony, Aude Ernoult.

Scientific Reports (2019) 9, 13952

Abstract

How connectivity affects plant assemblages is a central issue in landscape ecology. So far, empirical studies have produced contradictory results, possibly because studies: (1) inaccurately assess connectivity by prioritizing the respective effect of the type of habitat on plant assemblages and (2) omit the range of possible plant responses to connectivity depending on dispersal vectors. We focused on three dominant habitat types in agricultural landscapes (woodland, grassland and cropland), and analysed the effect of connectivity on herbaceous plant assemblage similarity for three primary dispersal modes (animal-dispersed, wind-dispersed and unassisted). Using circuit theory, we measured connectivity provided by woodland, grassland and cropland habitats independently. The similarity of plant assemblages was evaluated relative to the random expectation based on the regional pool. Overall, plant assemblage similarity in woodlands and temporary grasslands was dependent on connectivity, but not in wheat croplands. Only animal-dispersed species responded to connectivity. The similarity of animal-dispersed assemblages in woodlands was increased by the connectivity provided by woodland habitats, but was reduced by cropland habitats, whereas in temporary grasslands, similarity was increased by the connectivity provided by cropland habitats. Our results suggest that animal-dispersed species supplement their dispersal pathways, thus improving our knowledge of plant assembly rules in fragmented landscapes.

Introduction

Habitat isolation is a major cause of loss of plant diversity in agricultural landscapes (Luoto *et al.* 2003; Hooftman *et al.* 2016). In such heterogeneous landscapes, plant species are distributed across a set of local communities linked through dispersal, which ensures their persistence as a metacommunity in the landscape (Wilson 1992; Leibold *et al.* 2004). Dispersal between communities is enhanced by landscape connectivity (Fahrig & Merriam 1985). High connectivity enhances plant dispersal and increases genetic fluxes among local populations, thereby reducing the adverse effects of isolation. Therefore, high connectivity should enhance plant coexistence in multi-species assemblages. In experimental landscapes, connected patches have been shown to have higher species richness than unconnected patches (Haddad *et al.* 2015). This pattern is less clear in empirical studies where the relationship between connectivity and species richness and/or similarity in composition has been shown to be positive (Piessens *et al.* 2004; Thiele *et al.* 2017, 2018a), negative (Bornette *et al.* 1998), or absent (Lindborg & Eriksson 2004; Cousins *et al.* 2007).

Inaccurate assessments of landscape connectivity may explain why empirical studies fail to demonstrate a common pattern. Assessing connectivity *in situ* is difficult and different approaches have been attempted. Some authors estimated connectivity through a binary landscape representation (Ricketts 2001; Watling *et al.* 2011) using the abundance and spatial configuration of patches of a given habitat (i.e. structural connectivity; Calabrese & Fagan 2004). For example, the connectivity of a woodland fragment is calculated as a combination of the sizes of nearby woodland fragments and the Euclidean distance to those fragments [incidence function model index (IFM; Hanski 1994a; Moilanen & Nieminen 2002), e.g. Lindborg & Eriksson 2004; Piessens *et al.* 2004; Cousins *et al.* 2007]. Other studies improved these estimates of connectivity by using functional indices [e.g. integral index of connectivity (IIC; Pascual-Hortal & Saura 2006) and probability of connectivity (PC; Saura & Pascual-Hortal 2007)]. Both IIC and PC indices incorporate dispersal and plant habitat specificities in addition to the abundance and spatial configuration of patches (i.e. potential functional connectivity; Calabrese & Fagan 2004) and are based on graph theory (least-cost path distance; Adriaensen *et al.* 2003) or circuit theory (resistance distance; McRae 2006; McRae *et al.* 2008). Initially developed for animals, these indices are now increasingly used for plants although not yet widely at the plant community scale (but see Thiele *et al.* 2017, 2018a, b; Mony *et al.* 2018). These functional indices still consider that species which co-exist in plant communities may occupy different ecological niches and rely on different habitats to disperse (Chesson

1991). Functional landscape connectivity is indeed calculated using resistance maps. These maps include all the landscape patches with associated resistance values per habitat type (i.e. the higher the type of habitat suitable to plant dispersal, the lower the habitat type resistance value), hence including the heterogeneity of the landscape matrix (Ricketts 2001; Bender & Fahrig 2005; Ziólkowska *et al.* 2014). However, one limitation to using such indices is assigning resistance values, which is based on expert knowledge (i.e. subjective) (Rayfield *et al.* 2010; Spear *et al.* 2010; Koen *et al.* 2012; Zeller *et al.* 2012) and assumes a role hierarchy exerted by the various types of habitat on the connectivity among habitat patches. Understanding how the different habitat types between patches are independently involved in connectivity may thus improve our understanding of their effects on plant biodiversity. For example, a patch of a given habitat type can be connected to other patches of the same type by woodland, grassland and cropland habitat patches, even though their respective effect may differ. Improved understanding of the influence of landscape connectivity on species assemblages can be achieved by evaluating the additive influences of each type of habitat (the resulting effect, computed as the sum of the independent individual effect of the connectivity provided by each habitat type) on plant composition.

Considering each habitat type separately when assessing landscape connectivity is even more important in the case of plants. Plant seeds are dispersed in a landscape by a wide variety of vectors, whose response to connectivity is likely to differ depending on the type of habitat. In the case of animal-dispersed plant species, there is a broad consensus that animal movements are promoted by landscape connectivity in a wide range of habitats (Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016). Therefore, all habitat types should facilitate dispersal of plants by animal species [e.g. by forest birds and mammals through woodland habitats (Gelling *et al.* 2007; Martensen *et al.* 2012; Gil-Tena *et al.* 2013) and by amphibians through aquatic habitats (Watts *et al.* 2015)]. However, for other modes of dispersal, plant dispersal is likely to depend on the type of habitat on which connectivity was based. For example, wind dispersal depends on prevailing winds. Open habitats (e.g. grasslands, grassy strips and croplands) affect wind dynamics (redirection and promotion of airflow) thereby increasing the likelihood of wind-dispersed seed uplift. In contrast, closed habitats (e.g. forests, woodlands and hedgerows) are known to impede wind dispersal (Greene & Johnson 1996; Schurr *et al.* 2008; Damschen *et al.* 2014). Therefore, connectivity provided by open habitat patches should promote the dispersal of wind-dispersed species, while that provided by woodland habitats should impede their dispersal. In unassisted species (i.e. plant that are not dispersed by vectors), dispersal occurs

step-by-step from the parent plant over successive generations because their seeds are not adapted for dispersal (Willson *et al.* 1990). Because annual dispersal occurs over such short distances in unassisted species and because their progenies require a similar habitat to that of their parents, dispersal should be enhanced only by the connectivity provided by the focal habitat (habitat of interest) and inhibited by others. Accounting for the influence of connectivity provided by each habitat type according to the dispersal mode of plant species may provide insight into plant community assembly.

The aim of this study was to test the effect of landscape connectivity on herbaceous plant assemblages according to their dispersal mode. Our analysis focused on three habitat types typical of agricultural landscapes: woodland, grassland, and cropland. In these three habitat types, we assessed the response of plant assemblages to connectivity. Connectivity was measured as the addition of the independent effects of connectivity provided by the patches of each habitat type.

We calculated connectivity using the resistance distance for each habitat type. For a given habitat type, the effect of connectivity on plant assemblage similarity was tested with respect to each mode of dispersal (animal-dispersed, wind-dispersed and unassisted dispersal). Plant response was evaluated relative to the random similarity expected based on the regional species pool. In the three habitats, we specifically tested the following assumptions:

H1: Similarity between plant assemblage pairs for a given focal habitat is better predicted by simultaneously accounting for the contribution of the various habitat types to connectivity rather than by only examining only the focal habitat type.

H2: The independent effect of the connectivity provided by the different habitat types depends on the dispersal mode considered.

H2.1: The similarity among animal-dispersed species assemblages is increased by connectivity provided by any habitat type.

H2.2: The similarity among wind-dispersed species assemblages is increased by connectivity provided by open habitats (e.g. grassland and cropland) and reduced by closed habitats (e.g. woodland), because of their barrier effect

H2.3: Due to the short dispersal distances of unassisted species, the similarity among such species assemblages is increased by connectivity provided by habitats of the same type and is reduced by others.

Methods

Study area and selected sites

This study was carried out in the LTSER site “Zone Atelier Armorique” (ZAAr, ca. 13,000 ha) located in Brittany, western France (48° 36′ N, 1° 32′ W). The study area is characterised by a *bocage* landscape dominated by multicrop-livestock farming systems, determined by similar physical constraints. The topology is flat, the soil is on granitic and sandstone bedrocks and the climate is temperate oceanic. The landscape in this study area has been changing since 1955 as a result of successive agricultural policies (Meynier & Deniel 1965). Changes included a decrease in the length and the connectivity of the hedgerow network (Burel & Baudry 1999), abandonment of (i) permanent grasslands and (ii) of root and tuber croplands in favour of (i) temporary grasslands (i.e. regularly ploughed) and (ii) maize fields (Huyghe 2009) resulting in an increase in the size of grassland and cropland patches.

We analysed the effect of connectivity on plant assemblages in three habitat types that represent 90% of the landscape: cropland (44%), grassland (31%) and woodland (15%) (for more details about changes over time in the study area, see **Supplementary Fig. S1**). We assessed the effect of connectivity provided by cropland, grassland and woodland habitats on plant assemblage similarity for each habitat type. For each habitat type studied (wheat croplands, temporary grasslands and woodlands), we selected 25 patches scattered throughout the landscape with a distance of at least 150 m between any two patches to reduce spatial autocorrelation. Patch selection was based on land-cover maps in the ZAAr database. The maps were constructed using aerial imagery based on ten land-cover categories: woodland, grassland, grassy strip, fallow land, maize, cereal cropland, other cropland, built up area, road, and aquatic habitat. The hedgerow network was obtained from the 2016 Kermap (geographic raster) database for woodland habitats. We selected patches of similar size (about 2 ha for woodland, 1 ha for temporary grassland and 2.5 ha for wheat cropland), based on the average patch size of these three habitat types in the study area. We interviewed farmers to determine and standardize patch age, the management regime and previous land cover (i.e. the habitat type on which the patch was established) for woodland, temporary grassland and wheat cropland, and initial species sowing composition for temporary grassland and wheat cropland. Since the initial species composition was not available for planted woodlands, we selected woodland patches with similar dominant tree species composition, assuming they reflect the initial planting composition (**Table 1**). We checked that patches did not originate from the fragmentation of an initially single habitat patch (up to 1952, which is the oldest

land-cover map available in the study area, for woodlands and to previous land cover for temporary grassland and wheat croplands).

Table 1 Habitat patches characteristics of woodland, temporary grassland, and wheat cropland habitats.

		Woodlands	Temporary grasslands	Wheat croplands
Size (ha)	Median	2	1	2.5
	Range	1.06–8.00	0.44–2.48	1.95–3.12
Age		> 64	6 – 7	1
Initial sowing composition			<i>Trifolium repens</i> and <i>Lolium perenne</i>	<i>Triticum sp.</i>
Dominant tree species composition	tree	<i>Fagus sylvatica</i> , <i>Quercus robur</i> and <i>Castanea sativa</i>		
Management regime		Very extensive or absence of management	Grazing with occasional mowing and an occasional use of a soil enrichment product	Intensive crop management
Previous land cover		Cropland or grassland	Cropland	Cropland (<i>Zea mays</i>)

Assessment of similarity among plant assemblages

We performed floristic surveys in the 25 patches of woodland, temporary grassland and wheat cropland selected for the study. Floristic surveys were conducted in six 14 × 5 m quadrats in woodlands, ten 5 × 5 m quadrats in temporary grasslands and five 5 × 5 m quadrats in wheat croplands, i.e. the minimum recommended sampling area for each cover type (Mueller-Dombois & Ellenberg 1974). These quadrats were located equidistantly from each other in the patch and at least 20m from the edge of the patch. In each quadrat, we identified species composition and measured species abundance (in percentage cover). Only herbaceous plant species were considered, since ligneous species recorded were related to local management practices linked to tree plantations (i.e. dominant tree species composition of woodlands or dominant tree and shrub species composition of hedgerows surrounding habitat patches). We sampled plant assemblages in woodlands in 2013 (some of these data are already published in Mony *et al.* 2018) and in temporary grasslands and wheat croplands in 2016.

The effect of connectivity on similarity among species assemblages was analysed for each primary dispersal mode. We assessed the primary dispersal mode for each species using the *Baseflor* database (Julve 1998) with the following typology: animal-dispersed, wind-dispersed, unassisted (i.e. gravity-dispersed and autochorous species) and water-dispersed species (referred as “other” in Fig. 1, since they were not included in this study). The main animal species in our study area which could be involved in plant dispersal are mostly small species (e.g. insects, small mammals and granivorous birds), following the disappearance of most large wild species due to the low carrying capacities of the remaining natural areas (Groupe Mammalogique Breton 2015). We focused on the primary dispersal mode for each species, although most species have the ability to be dispersed by more than one vector (2.15 on average (Ozinga *et al.* 2004), owing to the absence of data on these secondary (or other) dispersal modes in the existing databases. Data on the primary mode of dispersal were available for all the species identified. Plant species in a few genera (e.g. *Carex*, *Epilobium*, *Leotodon*, *Taxaracum* and *Oxalis* sp.) could not be determined to species level (5.3% of plants in woodlands, 7.8% in temporary grasslands and 6.4% in wheat croplands). In these particular cases, we assigned the primary dispersal mode of close relatives by assuming phylogenetic conservatism (Baeten *et al.* 2015).

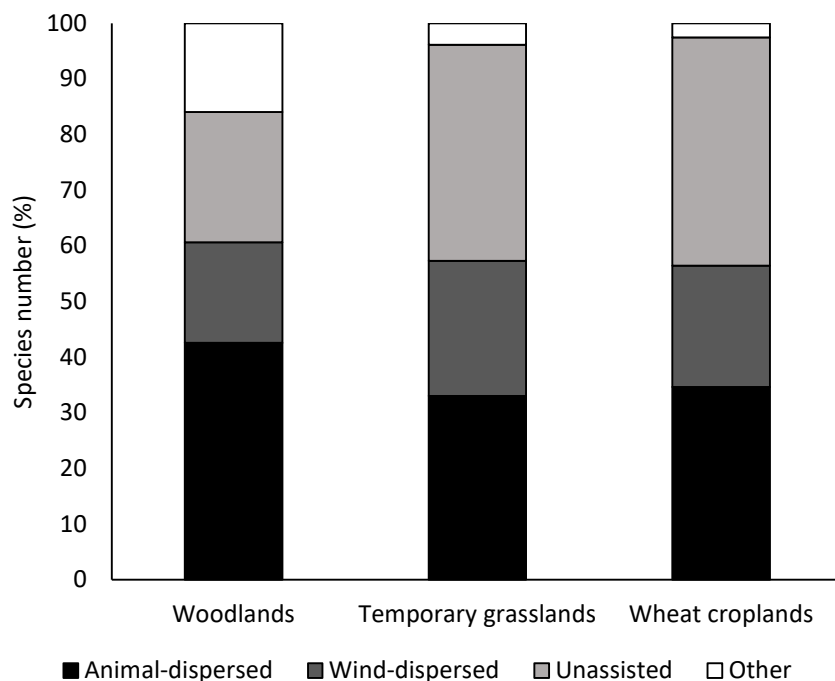


Fig. 1 Number of herbaceous species (in percentage), by mode of dispersal and habitat type (woodland, temporary grassland, and wheat cropland). “Other” refers to water-dispersed species that were not included in this study.

For each habitat type, we assessed similarity in plant composition for each pair of habitat patches as a proxy of dispersal (Thiele *et al.* 2017, 2018b). Thanks to the standardisation of habitat patches mentioned above, we assumed that similarity in plant composition could substitute the most reliable proxy of dispersal, i.e. genetic similarity, which is restricted to the population level (Baguette *et al.* 2013). For each pair of habitat patches, we separately calculated the Sørensen similarity index $S_{Sør}$ for assemblages of animal-dispersed, wind-dispersed and unassisted species. This index was calculated using the *ade4* package (Dray & Dufour 2007). The higher the similarity index ($S_{Sør}$), the higher the similarity between a given pair of habitat patches.

Assessment of landscape connectivity between habitat patches

For each habitat type (see **Fig. 2** for the example of sampled woodland habitats), we assessed the landscape connectivity provided by three types of habitat: woodland, grassland and cropland. We considered woodland habitats as forests, woodlots, and hedgerows; grassland habitats as grasslands, grassy strips and fallow lands and cropland habitats as maize, cereal cropland and other cropland types and grouped these land-cover types accordingly based on our land-cover maps (**Fig. 2a**). The landscape connectivity provided by each habitat type (woodland, grassland and cropland) was measured for all pairs of habitat patches in each habitat type (i.e. 25 habitat patches is equivalent to 300 pairs of habitat patches for each habitat type).

We used circuit theory (McRae 2006; McRae *et al.* 2008) to model connectivity between patches. This modelling method depends on random walk theory and incorporates the contributions of all dispersal pathways to evaluate the degree of connectivity between patches. These contributions depend on the resistance to movement between habitats. The connectivity value that results from this modelling method is a measure of the degree of isolation, called resistance distance: the higher the resistance distance, the lower the connectivity.

(1) Creating resistance maps

This modelling method requires the creation of resistance maps. Resistance maps were created using sliding (moving) window analysis, which makes it possible to assign a resistance value to each focal pixel of the landscape, the value being calculated and mediated by the neighbouring pixel values (McGarigal & Cushman 2005). Based on the gradient (or continuum) model (McGarigal & Cushman 2005; Fischer & Lindenmayer 2006), this method

avoids assigning resistance values based on a discrete representation of the landscape matrix (McGarigal & Cushman 2005; Fischer & Lindenmayer 2006; Cushman *et al.* 2010; Lausch *et al.* 2015; Brudvig *et al.* 2017). For each habitat type, resistance values were calculated as one hundred and one minus the proportion of the habitat type in a given landscape window, here simulated as a sliding circular window of a given diameter. A focal pixel for which the proportion of the habitat type over the window (i.e. focal neighbourhood) is 100% was assigned a resistance value of 1 (i.e. highly suitable to dispersal). Conversely, a focal pixel for which the proportion of the habitat type is 0% was assigned a resistance value of 101 (i.e. slightly suitable to dispersal) (see **Supplementary Fig. S2**). The creation of resistance maps based on the proportion of woodland, grassland and cropland habitat for each habitat type reduced subjectivity (i.e. expert knowledge) and avoided hierarchisation of habitat types when assigning resistance values. The proportion of woodland, grassland and cropland habitats was calculated from the number of pixels in the circular sliding window with a displacement and interpolation values of one pixel (i.e. 5 m). We tested sliding windows of different diameters of 5 (25 m), 11 (55 m), 21 (105 m) and 41 (205 m) pixels – closely linked to the range of local dispersal distances of plants (Nathan 2006; Schurr *et al.* 2008) – to test the sensitivity of the connectivity indices to continuous landscape representation (**Fig. 2b**). These resistance maps were produced using Chloé2012 software (Boussard & Baudry 2014).

(2) Landscape connectivity assessment

We calculated landscape connectivity using resistance distance. For each pair of habitat patches, we calculated the resistance distance based on the resistance maps using Circuitscape software (McRae *et al.* 2008) (**Fig. 2c**). Graphab 3.0.2 software (Foltête *et al.* 2012) was used to generate Euclidean links between each pair of habitat patches for each type of habitat. Pairs of habitat patches located at the boundary of the study area, for which Euclidean links were outside the study area, were excluded from subsequent analyses. We used Pearson correlations to examine relationships among the different resistance distances we calculated for the various diameters (5–205 m) of the sliding windows. Resistance distances obtained from habitats of the same habitat type for the different sliding window sizes were strongly correlated ($r \geq 0.95$, $p < 0.001$). We then selected resistance distances obtained from the intermediate-diameter sliding window (11 pixels, i.e. 55 m).

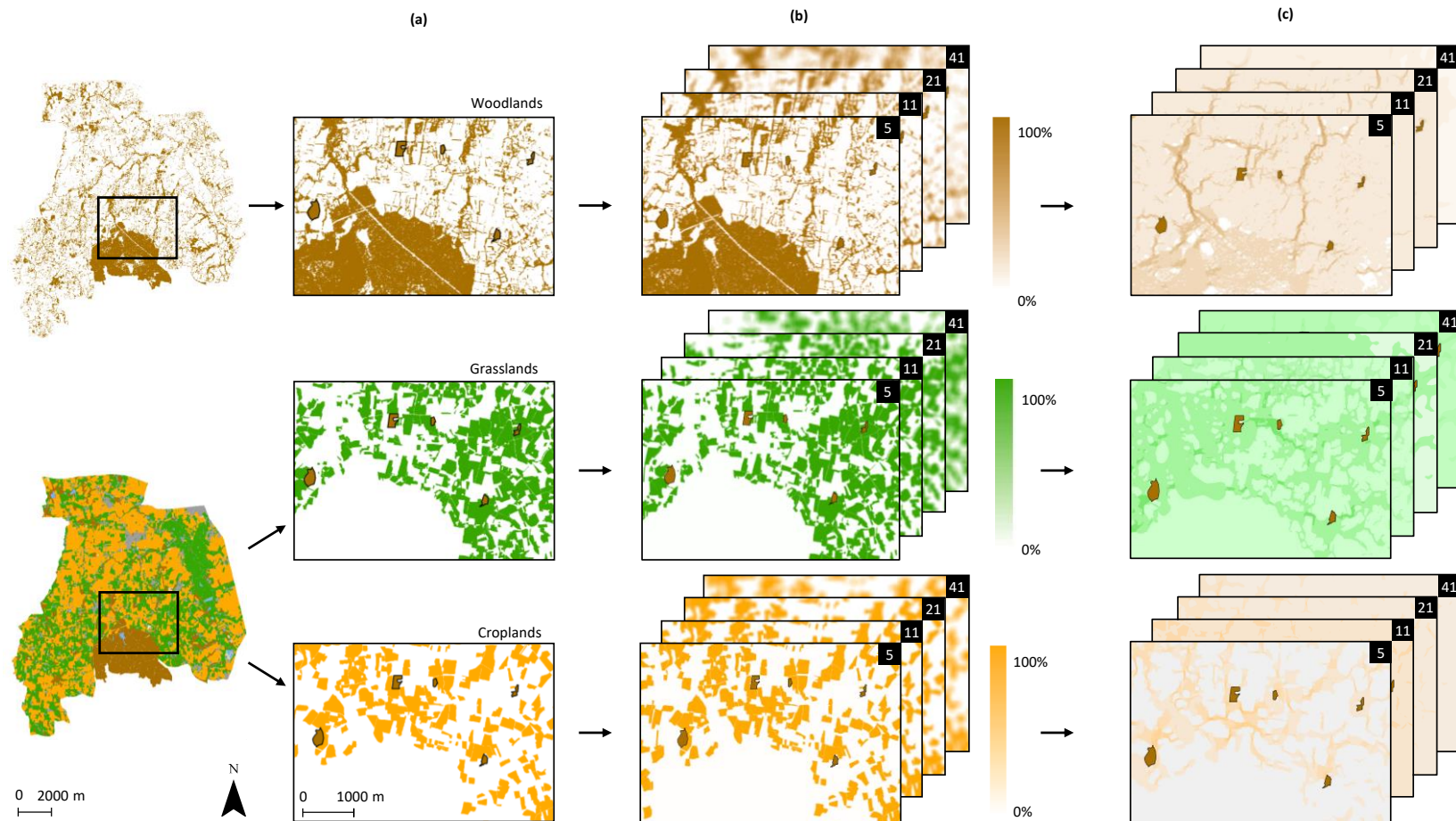


Fig. 2 Illustration of the method used to model connectivity as provided by woodland, grassland and cropland habitats. Example of sampled woodland habitats. Sampled woodlands are indicated in brown and surrounded with a black edge on all maps. **(a)** Extraction of woodland, (top), grassland (middle) and cropland (bottom) habitats derived from (i) the Kemap geographic raster database for woodland habitats and (ii) the land-cover map of the study area. **(b)** Calculation of the proportion of woodland, grassland and cropland habitat derived from the number of pixels in circular sliding windows of 5-, 11-, 21- and 41-diameter pixels. **(c)** Electric current fluxes based on circuit theory between woodlands, based on woodland, grassland and cropland habitats. For a given habitat type, a focal pixel for which the proportion of the habitat over the window (i.e. focal neighbourhood) is 100% was assigned a resistance value of 1 (i.e. highly suitable to dispersal), whereas a focal pixel for which the habitat proportion is 0% was assigned a resistance value of 100 (i.e. slightly suitable to dispersal).

Statistical analysis

(1) Detection of non-random response patterns using a null model

To focus on non-stochastic processes, we assessed the effect of connectivity on the similarity between pairs of assemblages (observed $S_{s\theta r}$ -similarity) according to the distribution of the similarity index based on the calculation of random assemblages (expected $S_{s\theta r}$ -similarity) using a null model. This random similarity reflected random dispersal of seeds (i.e. a lack of a dispersal filter). The null distribution was calculated from data on assemblages derived from a random sampling of species from the regional species pool (Mason *et al.* 2008). Random assemblages had similar species richness to the corresponding observed assemblage. The probability of each species being selected in the random assemblages was weighted by the occurrence of the species within the regional species pool considered (i.e. all recorded observed species). This process was repeated for each primary dispersal mode and for each type of habitat.

An effect size (ES) was calculated based on the probability that the observed value $S_{s\theta r}$ was lower than the value expected under the null hypothesis (i.e. the quantile of the null distribution for which the observed value was derived Kelt *et al.* 1995; Chase *et al.* 2011), see **Supplementary Methods** for calculation). ES of similarity values vary between -1 and 1 . In our study, when the ES was close to zero, the observed similarity value between each pair of assemblages was considered to be random. Due to the non-normality of ES values, we used a Wilcoxon test, which is routinely used to test whether ES values were significantly overall different from zero (Kraft *et al.* 2008; Swenson & Enquist 2009; Bernard-Verdier *et al.* 2012; Favre-Bac *et al.* 2017b), and thus for the significance of non-random plant assemblage similarities between pairs of habitat patches. When the Wilcoxon test was significant, negative ES values indicated that observed similarity values between each pair of assemblages were lower than expected by chance under the null hypothesis (i.e. dispersal barrier effect). In contrast, positive ES values revealed that the observed similarity values were higher than expected under the null hypothesis (i.e. dispersal enhancing effect).

(2) Influence of landscape connectivity on similarity between plant assemblages

We used linear mixed models to assess the influence of landscape connectivity on the similarity of plant assemblages using the ES of similarity value for each pair of assemblages and primary dispersal mode as the dependent variable and the resistance distances obtained between each pair of habitat patches as independent variables for: (1) woodland, (2) grassland

and (3) cropland. To account for the partial dependence of the data on matrices of ES values, the two habitat patches comprising each pair of assemblages analysed were considered as the two random effects (Clarke *et al.* 2002; Van Strien *et al.* 2012; Thiele *et al.* 2018b). In order to ensure unbiased (i) estimates of fixed effects and (ii) model selection procedures (Verbeke & Molenberghs 2000; Orelie & Edwards 2008; Bolker *et al.* 2009; Zuur *et al.* 2009; Faraway 2016; Row *et al.* 2017), these linear mixed models were fitted using the maximum likelihood (ML) estimation of the variance components. Resistance distances were centered and scaled to ensure the regression coefficients were comparable among models. Each model was performed using a model-averaging method, which takes model selection uncertainty into account (Burnham & Anderson 2002). We built all possible models based on all additive combinations of explanatory variables and ranked them using the Akaike information criterion corrected for small sample sizes (AICc). We then generated full-model averaged estimates of each independent variable across the most parsimonious models (Burnham & Anderson 2002) ($\Delta\text{AICc} < 4$, **Supplementary Table S1**). We considered independent variables to be significant if their 95% confidence intervals did not overlap with zero (Burnham & Anderson 2002). Finally, we calculated the proportion of variance explained by fixed effects (marginal R^2) and by fixed and random effects (conditional R^2) of the most parsimonious model (Nakagawa & Schielzeth 2013).

We also checked whether the effect of connectivity on plant assemblage similarity was not indirectly due to the patches having similar local environmental conditions. To this end, we used the similarity of Ellenberg's indicator values between each pair of assemblages (moisture, nutrient availability and pH), in addition to using resistance distances to explain ES similarity values (see **Supplementary Methods**). The results of the averaged models obtained from these preliminary analyses were consistent with the averaged models, which included only the resistances distances as fixed effects (**Supplementary Table S2**). This confirmed that the relationships we demonstrated between resistance distance and plant assemblage similarity were robust.

All statistical analyses were performed using R.3.5.1 (R Core Team). Linear mixed models, model averaging and associated marginal and conditional R^2 were calculated using `lmerTest` (Kuznetsova *et al.* 2017), `MuMIn` (Barton 2018) and `piecewiseSEM` (Lefcheck 2016) packages.

Results

Characteristics of the plant assemblages studied

The regional species pools of woodlands, temporary grasslands and wheat croplands contained 94, 103 and 78 herbaceous species, respectively. Similarity values between species pools using Sørensen indices were: 0.26 between woodlands and temporary grasslands, 0.23 between woodlands and wheat croplands and 0.53 between temporary grasslands and wheat croplands, revealing marked differences between plant assemblages in the three habitat types. Total herbaceous species richness according to habitat type and mode of dispersal were as follows: (1) woodland: 40 animal-dispersed, 17 wind-dispersed and 22 unassisted species, (2) temporary grassland: 34 animal-dispersed, 25 wind-dispersed and 40 unassisted species and (3) wheat cropland: 27 animal-dispersed, 17 wind-dispersed and 32 unassisted species. No exotic species were recorded in plant assemblages in woodlands, temporary grasslands or wheat croplands, based on the *List of invasive vascular plants in Brittany* (Quééré & Geslin 2016). Characteristics of the plant assemblages for woodlands, temporary grasslands and wheat croplands are summarized in **Table 2** and **Fig. 1**.

Table 2 Characteristics of herbaceous species assemblages (species richness and Sørensen similarity index) for woodland, grassland and cropland habitats. Plant assemblages were sampled 25 patches of woodlands [sampling area = 6 × (14 × 5 m) quadrats = 420 m²], temporary grasslands [sampling area = 10 × (5 × 5 m) quadrats = 250 m²] and wheat croplands [sampling area = 5 × (5 × 5 m) quadrats = 125 m²] selected for the study. SD= standard deviation.

	Woodlands		Temporary grasslands		Wheat croplands	
	Mean (SD)	Min-Max	Mean (SD)	Min-Max	Mean (SD)	Min-Max
Whole plant assemblages						
Richness	15.8 (8.3)	2–36	26.9 (8.4)	17–51	13.6 (6.9)	3–36
Similarity	0.29 (0.15)	0–0.67	0.59 (0.07)	0.41–0.75	0.29 (0.14)	0–0.67
Animal-dispersed assemblages						
Richness	8.7 (3.6)	2–17	8.80 (2.9)	4–14	4.3 (2.2)	0–10
Similarity	0.37 (0.17)	0–0.80	0.62 (0.12)	0.35–0.92	0.22 (0.21)	0–0.89
Wind-dispersed assemblages						
Richness	1.6 (1.4)	0–5	6.6 (2.8)	3–15	2.5 (2.0)	0–8
Similarity	0.09 (0.20)	0–1	0.57 (0.14)	0.17–0.91	0.21 (0.24)	0–0.80
Unassisted assemblages						
Richness	3.7 (2.8)	0–12	11.1 (3.7)	6–22	6.6 (3.6)	1–19
Similarity	0.20 (0.22)	0–0.80	0.60 (0.11)	0.35–0.90	0.36 (0.17)	0–0.86

Effect of connectivity on assemblage similarity

We demonstrated a non-random pattern of plant similarity between patches for all assemblages, except for three models (**Fig. 3**): wind-dispersed and unassisted plant

assemblages in woodlands and animal-dispersed plant assemblages in wheat croplands. For the non-random patterns, effect size (ES) of similarity values were best explained by models that included resistance distance (distR) of the various habitat types than by models that included only distR of the same habitat type (**Supplementary Table S1**). In most cases, the probability of the distR of the other habitat types to appear in the best model explaining ES values was at least equal to the probability of the distR of the same habitat type, as indicated by their relative importance (**Table 3**).

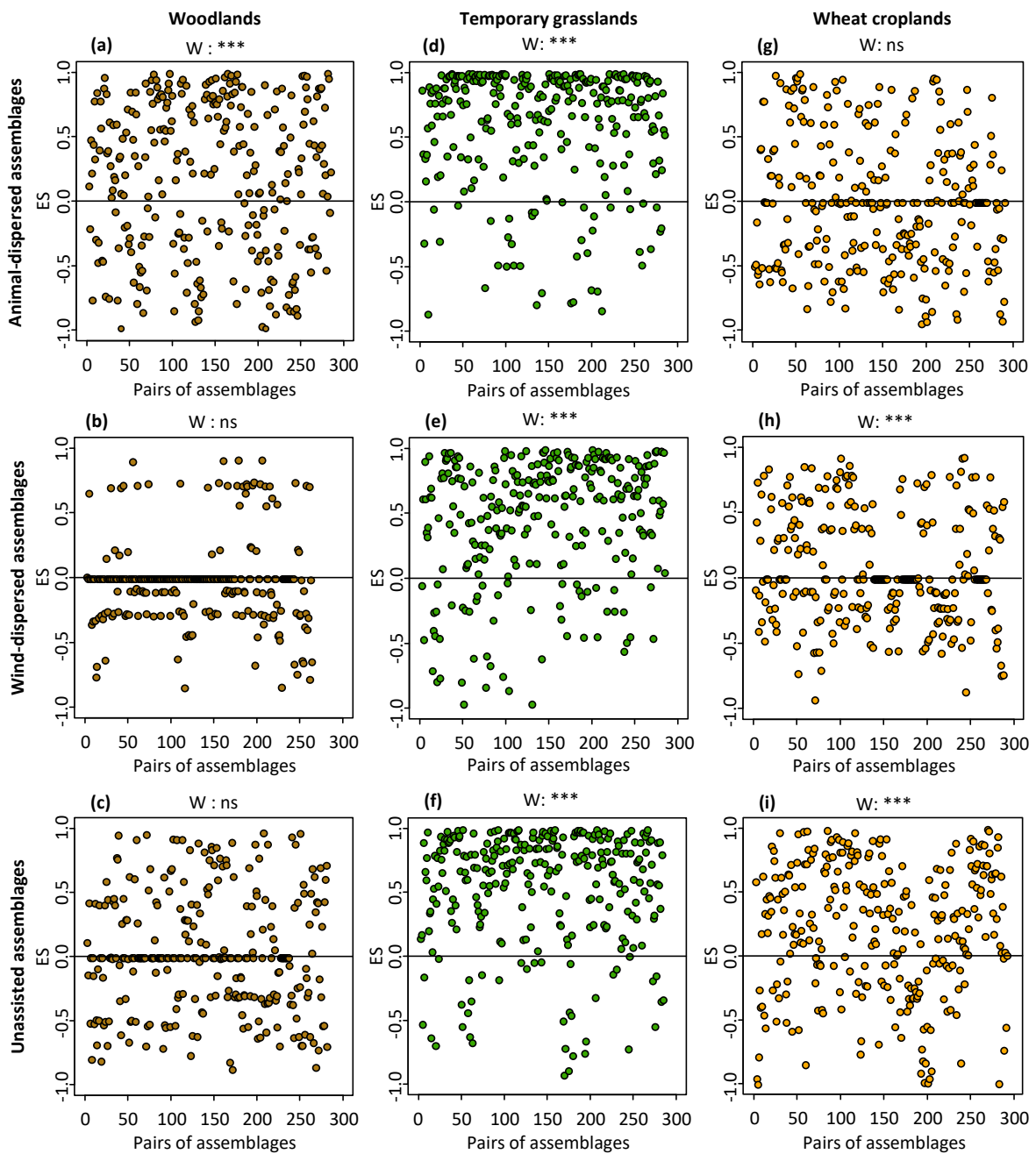


Fig. 3 Effect size (ES) of similarity values for all pairs of animal-dispersed, wind-dispersed, and unassisted assemblages in habitats of woodland (brown dots), temporary grassland (green dots) and wheat cropland (yellow dots). P-values for the Wilcoxon tests (W) are on each graph. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns (not significant): $p > 0.05$.

Table 3 Summary of the model-averaged estimates, relative importance (RI) and 95% confidence interval (CI) of the independent variable(s) according to the AICc framework. Full models included three independent variables, resistance distance of woodlands (DistR woodlands), grasslands (DistR grasslands), and croplands (DistR crops), and one dependent variable, the effect size (ES) of similarity values. Models were done for animal-, wind-dispersed and unassisted assemblages for woodland, temporary grassland and wheat cropland habitats. Abbreviation: "-" [a random similarity pattern (ES not different from zero)]. Models were not done in this latter case. Confidence interval that did not encompass zero are in bold.

	Models			Intercept	DistR woodlands			DistR grasslands			DistR croplands		
	N	R ² m	R ² c		Estimate	RI	CI	Estimate	RI	CI	Estimate	RI	CI
Woodlands													
Animal-dispersed assemblages													
ES	283	0.09	0.48	0.20	-0.32	1.00	(-0.53, -0.10)	0.06	0.44	(-0.12, 0.23)	0.21	1.00	(0.07, 0.34)
Wind-dispersed assemblages													
ES	-	-	-	-	-	-	-	-	-	-	-	-	-
Unassisted assemblages													
ES	-	-	-	-	-	-	-	-	-	-	-	-	-
Temporary grasslands													
Animal-dispersed assemblages													
ES	283	0.09	0.56	0.62	0.01	0.37	(-0.06, 0.09)	0.03	0.49	(-0.05, 0.10)	-0.13	1.00	(-0.22, -0.04)
Wind-dispersed assemblages													
ES	283	0.00	0.62	0.50	-0.01	0.32	(-0.06, 0.05)	-0.01	0.36	(-0.06, 0.04)	-0.00	0.26	(-0.05, 0.04)
Unassisted assemblages													
ES	283	0.04	0.45	0.59	-0.07	0.74	(-0.19, 0.05)	-0.02	0.45	(-0.11, 0.07)	0.03	0.45	(-0.06, 0.11)
Wheat croplands													
Animal-dispersed assemblages													
ES	-	-	-	-	-	-	-	-	-	-	-	-	-
Wind-dispersed assemblages													
ES	287	0.02	0.20	0.07	-0.01	0.38	(-0.08, 0.06)	-0.05	0.73	(-0.13, 0.03)	-0.01	0.28	(-0.04, 0.06)
Unassisted assemblages													
ES	290	0.00	0.34	0.22	0.00	0.21	(-0.04, 0.04)	-0.01	0.28	(-0.05, 0.04)	-0.00	0.21	(-0.04, 0.04)

(1) Woodland assemblages

Animal-dispersed plant assemblages were more similar than expected when the connectivity provided by woodland habitats increased (dispersal enhancing effect) and when the connectivity provided by cropland habitats decreased (dispersal barrier effect) (**Table 3** and **Fig. 4a-b**). The observed similarity values between wind-dispersed and unassisted plant assemblages did not differ from random distributions.

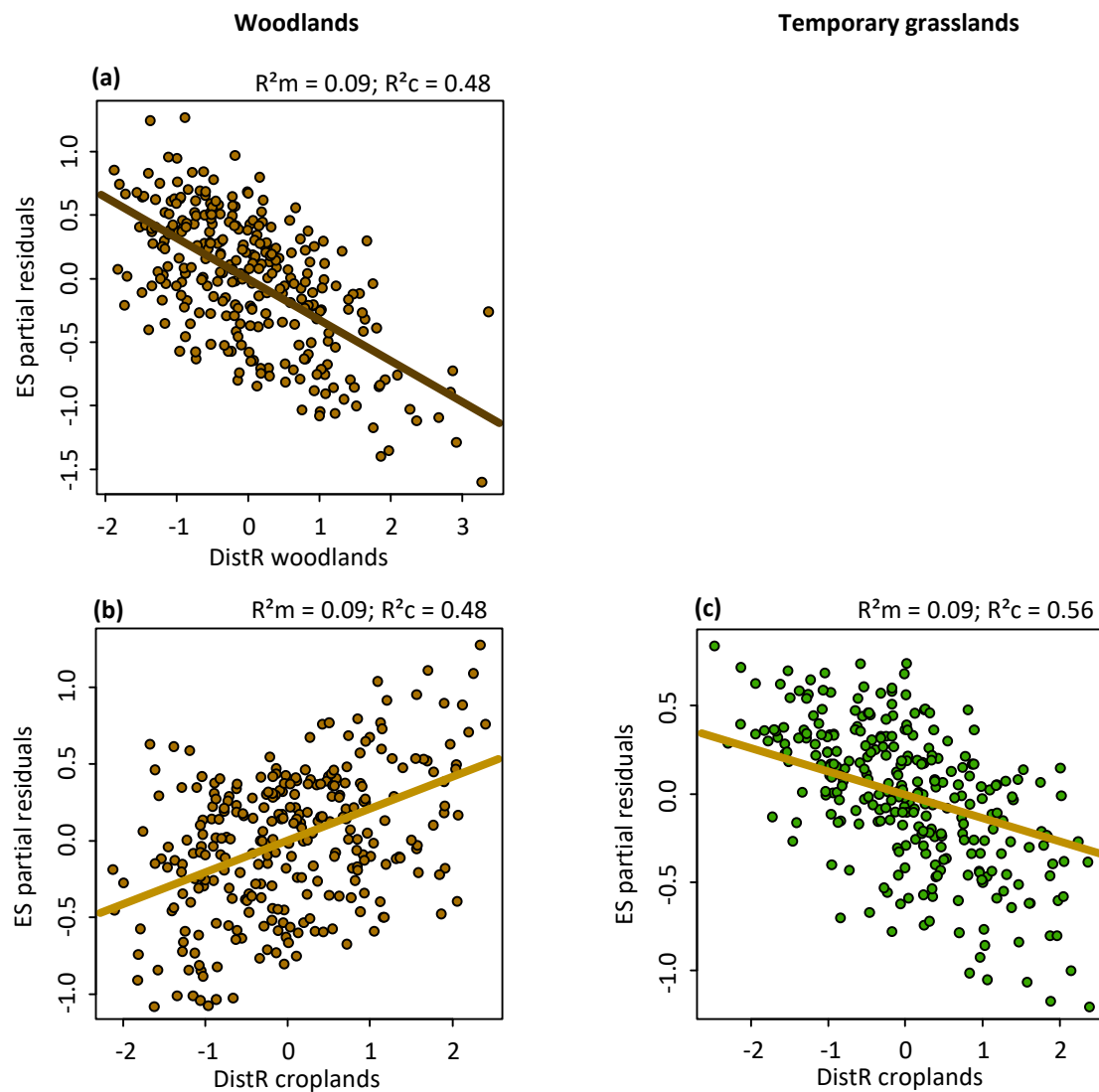


Fig. 4 Partial residual plots denoting the significant impact of the resistance distance (distR) of woodlands (brown lines) and croplands (yellow lines) on the effect size (ES) of similarity values for animal-dispersed assemblages in woodlands (left, brown dots) and temporary grasslands (right, green dots). These plots show the effects of a given independent variable when all other independent variables are statistically fixed. The marginal (R^2_m) and conditional (R^2_c) R^2 of the model are on each plot.

(2) Temporary grassland assemblages

Animal-dispersed plant assemblages were more similar than expected by chance when connectivity provided by cropland habitats increased (dispersal enhancing effect) (**Fig. 4c**), whereas wind-dispersed and unassisted assemblages were independent of connectivity regardless of habitat type on which connectivity was based on (**Table 3**).

(3) Wheat cropland assemblages

Observed similarity values for animal-dispersed assemblages did not differ from random distributions. ES values for wind-dispersed and unassisted assemblages were independent of connectivity (**Table 3**).

Discussion

Regardless of habitat type and of the primary dispersal mode, most plant assemblages displayed non-random dispersal patterns, suggesting a dispersal limitation. The three assemblages showing a random dispersal pattern – wind-dispersed and unassisted assemblages of woodlands and animal-dispersed assemblages of wheat croplands – were characterised by low species richness and a restricted regional species pool. These characteristics may explain why observed similarity values were statistically similar to expected similarity values.

Plant assemblages in temporary grasslands and woodlands were dependent on landscape connectivity but wheat cropland assemblages were not. By taking the influences of woodland, grassland and cropland habitats into account simultaneously, we improved our ability to predict species response to changes in connectivity in accordance with our first hypothesis (H1). This suggests that the dispersal of plant species is affected by the connectivity provided by various habitat types simultaneously. As a common pattern for woodland and temporary grasslands, the connectivity provided by grassland habitats had no effect on the similarity of plant assemblages between habitat patches. The absence of any effect has been demonstrated for grassland assemblages (Lindborg & Eriksson 2004; Helm *et al.* 2006; Cousins *et al.* 2007; Gil-Tena *et al.* 2013) and is extended here to woodland assemblages. Plant dispersal in grassland habitats is mainly achieved by anthropogenic vectors, such as livestock and agricultural machinery (Strykstra *et al.* 1997; Couvreur *et al.* 2004; Cosyns *et al.* 2005). Dispersal in grasslands might thus be more dependent on farm logistics than on connectivity. However, the absence of effect here could also be due to our inability to map narrow, linear, herbaceous-dominated habitats, such as grassy strips along

the edges of croplands, road and railway verges, even though they are all likely to play an important role in the dispersal of grassland plant species (Tikka *et al.* 2001; Thiele *et al.* 2017). The absence of a landscape connectivity effect in wheat cropland plant assemblages may be explained by two non-exclusive hypotheses: (1) the high proportion (>30%) of croplands in the landscape may be more important to seed dispersal than the role of connectivity, which is in agreement with the fragmentation threshold hypothesis (Andr en 1994) and (2) the dominance of generalist species (which occupy broad ecological niches) in wheat cropland assemblages, due to the high disturbance rate and environmental variability of cropland habitat. Such generalist species display high dispersal abilities and are not restricted to any specific habitat type (Fischer & St ocklin 1997; Honnay *et al.* 1999), which implying that generally, they may not be affected by connectivity (Adriaens *et al.* 2006; Br uckmann *et al.* 2010).

In woodland and temporary grassland assemblages, we detected common patterns of response to the connectivity provided by grassland habitats for woodlands and temporary grasslands. However, we did not find any general pattern for the connectivity provided by woodland and cropland habitats. The ability of woodland and cropland habitats to provide connectivity appeared to be dependent on the primary dispersal mode of plant species, in agreement with our second hypothesis (H2).

We partially validated our first sub-hypothesis (H2.1), since the dispersal of animal-dispersed plants (i.e. similarity between assemblages) was enhanced by the connectivity provided by certain types of habitat. However, their dispersal was also reduced or not affected by others. For example, the dispersal of animal-dispersed plant species inhabiting woodland habitats was enhanced by the connectivity provided by woodland habitats but inhibited by the connectivity provided by cropland habitats. This may be explained by two processes. Movement of animal species is indeed known to preferentially occur through woodland habitats (Pardini *et al.* 2005). In contrast, wood-dwelling animal species, such as mammals (Rosalino *et al.* 2011; Wereszczuk & Zalewski 2015) or birds (Lima & Dill 1990; Rodr iguez *et al.* 2001; Turcotte & Desrochers 2003) may avoid open habitats due to the higher risk of predation. We found that in temporary grassland assemblages, dispersal of animal-dispersed plant species was enhanced by the connectivity provided by cropland habitats, but was not affected by other types. We hypothesise that seeds are transferred by animal vectors (i.e. granivorous animal species) from croplands to grasslands during periods of seed dispersal in grasslands. This may occur after cereals have been harvested, when seed resources in

croplands are low and animals switch their foraging focus to wild grass seeds. A change to from a cropland to a grassland habitat for foraging has already been shown to occur in carabid species (French *et al.* 2001; Madeira *et al.* 2016). Our results suggest an expansion of this concept to the landscape scale.

In contrast to our second sub-hypothesis (H2.2), we found that wind dispersal was not affected by landscape connectivity even though wind can disperse seeds over long distances (Nathan *et al.* 2002; Tackenberg 2003). Specifically, for these species, we were unable to demonstrate either a dispersal barrier effect of woodland habitats or a enhancing dispersal effect of open habitats (i.e. grassland and cropland habitats), even though such effects have already been demonstrated in simplified experimental conditions (Greene & Johnson 1996; Schurr *et al.* 2008; Damschen *et al.* 2014). One possible explanation for our results is that fine-scale habitat structure may be more important in enhancing or inhibiting seed dispersal than the simple presence or absence of woodland or open habitats. For example, hedgerows vary in height, width, vertical stratification and frequency of gaps, all of which affect small-scale wind patterns and hence, drive wind-dispersal patterns. Similarly, crops vary in height, density and cover depending on the type of management practices applied. Betbeder *et al.* (2015) used new remote sensing techniques to quantify fine-scale landscape structure to improve animal species distribution models at the landscape scale. A similar approach should be used to examine plant distribution. Such studies could be coupled with large-scale wind dynamics data, which could be used to determine the distance, direction, frequency and intensity of seed dispersal patterns (Nathan *et al.* 2002, 2011; Tackenberg 2003; Tackenberg *et al.* 2003).

Unassisted dispersal was independent of landscape connectivity for all assemblage types (temporary grassland and wheat cropland assemblages), thus contradicting our third sub-hypothesis (H2.3). Despite the fact unassisted species only disperse over a short distance (a minimum of 5 m y^{-1} ; van Dorp *et al.* 1997), these species did not depend on the connectivity provided by their own habitats. Our results suggests that the ploughing up of grassland (every 5 years) and cropland (every 1 year) habitats on average in our study area is probably too frequent for unassisted plant species to disperse from one habitat patch to another. In such intensively managed habitats, connectivity depends on time, which would require incorporating past land-cover maps (Lindborg & Eriksson 2004; Cousins *et al.* 2007) in the assessment of connectivity effects (Williams *et al.* 2013; Zeigler & Fagan 2014).

Taking into account the additive effects of the connectivity provided by the three types of habitats shed light on the mechanisms of plant dispersal.

We found opposite effects on dispersal of the connectivity provided by habitats of the same type (dispersal enhancing effect) and by the other habitat types (dispersal barrier effect) (e.g. woodland animal-dispersed assemblages). Both enhancement and inhibition may partly compensate for one another. We also found that the connectivity provided by habitat of the same type does not affect plant assemblages of the same habitat, but that provided by other habitat types enhance dispersal (e.g. grassland animal-dispersed assemblages). Such positive effects of other habitat types have been demonstrated at the local scale for animals of a given habitat type [e.g. for birds (Whitcomb *et al.* 1977) and for beetles (Campbell & Meinke 2006)], leading to the concept of landscape supplementation (Dunning *et al.* 1992). Organisms supplement their resource intake by using resources in nearby patches of the same habitat or by using a substitutable resource in nearby patches of a different habitat type (Dunning *et al.* 1992). In agreement with Dunning *et al.* (1992), our results suggest that plant species could also supplement their “natural” dispersal pathway (i.e. habitats of the same type) by using other types of habitats. The supplementation of dispersal pathways for animal-dispersed plant species may be indirectly linked to habitat supplementation by animal species. The validation of this concept in animal-dispersed plant species – and its possible extension to wind-dispersed and unassisted species – is an interesting perspective and could be achieved by analysing the genetic similarity of some representative species of each primary dispersal mode. Using a combination of dispersal pathways would increase a plant’s effective dispersal and improve population fitness, especially in intensified agricultural landscapes where habitats are extremely fragmented.

Data availability

All data and scripts used to perform the main analyses are available on Figshare (doi: 10.6084/m9.figshare.7321268).

Acknowledgements

We are grateful to Jeremie Guy and Juliette Abadie for assistance in the field, Maxime Dahirel for help with the statistical analyses and Hugues Boussard for help with Chloe2012 software. This work was funded by the French Ministry of Agriculture (DIVA – Agriconnect project) and the Fondation de France (BISCO project) and was supported by landscape databases

collected in the LTSER site “Zone Atelier Armorique”. Land-cover maps were established by Jean Nabucet (LETG-Rennes-Costel) and Kermap.

Authors contributions

C.M. and A.E. conceived the idea of the project and all authors contributed to the methodology of the study; all authors collected the data; L.U. analysed the data and wrote the manuscript. All authors contributed critically to interpretations of results and to the drafts and gave final approval for publication.

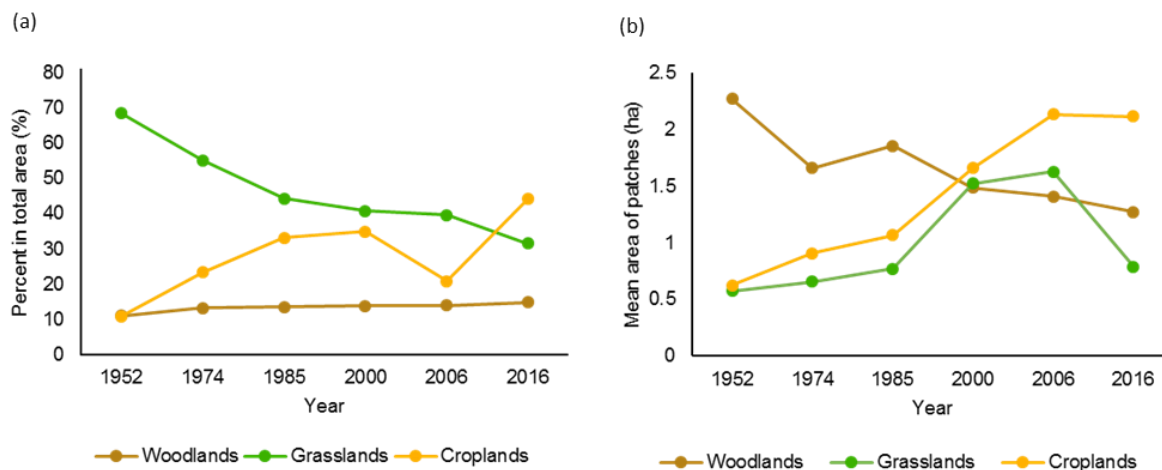
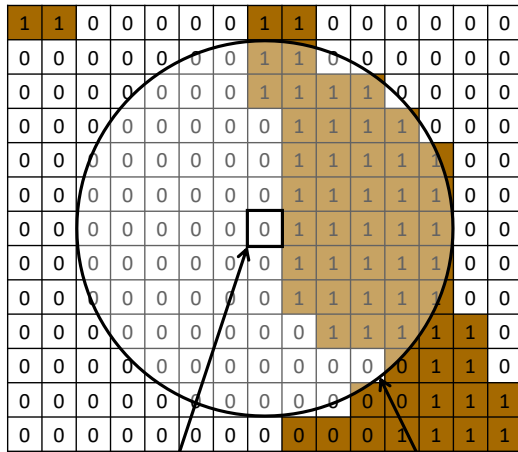


Fig. S1 (a) Percentage of total area and **(b)** mean area of patches in the study area over time (1952 – 2016) for each habitat type. These metrics have been measured from land-cover maps in the ZAAr database.

Raster map of the presence-absence of woodland habitats



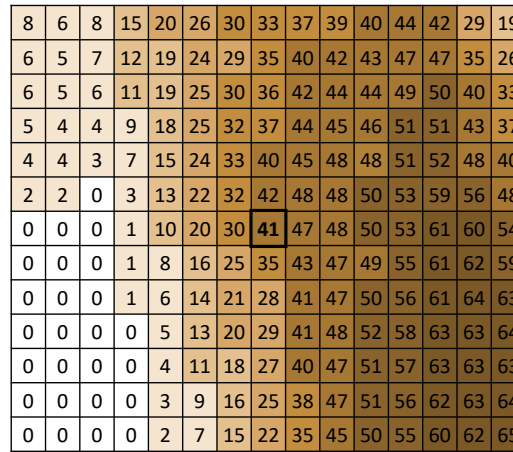
Focal pixel

Focal neighborhood
Diameter = 11 pixel

Proportion



Raster map of the proportion of woodland habitats



Resistance



Raster map of the resistance of woodlands habitats

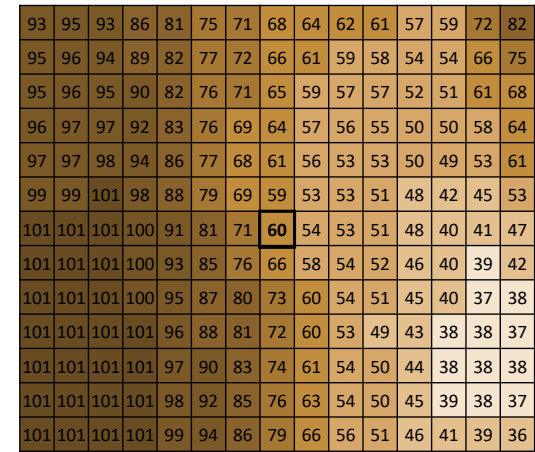


Fig. S2 Schematic representation of the sliding (moving) circular window analysis used to create resistance maps for each habitat type. Example of woodlands habitats in a sliding circular window of 11 pixels (55 meters). Resistance values were calculated as one hundred and one minus the proportion of woodland habitats in a given landscape window, here simulated as a sliding circular window of a given diameter. A focal pixel for which the proportion of the habitat type over the window (i.e. focal neighbourhood) is 100% was assigned a resistance value of 1 (i.e. highly suitable to dispersal). Conversely, a focal pixel for which the proportion of the habitat type is 0% was assigned a resistance value of 101 (i.e. slightly suitable to dispersal).

Supplementary Methods

Detection of non-random response patterns using a null model

Each observed value $S_{s\theta r}$ was compared to its null distribution by calculating the one-tailed probability P that the observed value $S_{s\theta r}$ was lower than the value expected under the null hypothesis. That is, the quantile of the null distribution for which the observed value was derived as follows (Kelt *et al.* 1995; Chase *et al.* 2011): $P = \frac{\sum S_{s\theta r}(null < obs) + \frac{\sum S_{s\theta r}(null = obs)}{2}}{1000}$, where $S_{s\theta r}(null < obs)$ = number of times in which the expected value $S_{s\theta r}$ was lower than the observed value and $S_{s\theta r}(null = obs)$ = number of times in which the expected value $S_{s\theta r}$ was equal to the observed value. This one-tailed probability was then used to compute an effect size (ES) of similarity as follows: $ES = (P - 0.5) \times 2$ (Kelt *et al.* 1995; Chase *et al.* 2011). This calculation of effect size was preferred to the Standardized Effect Size (SES) due to the asymmetry and non-Gaussian shape of the majority of null distributions we found with our data (Bernard-Verdier *et al.* 2012).

Influence of landscape connectivity on similarity between plant assemblages

We checked whether the effect of landscape connectivity on plant assemblage similarity was not indirectly due to the patches having similar local environmental conditions. The similarity of Ellenberg's indicator values $S_{E_{ij}}$ between each pair of assemblages [moisture, nutrient availability and pH, extracted from the Baseflor database] was used as a proxy of the similarity of environmental conditions. These similarities of Ellenberg's indicator values were calculated as $S_{E_{ij}} = |\bar{E}_i - \bar{E}_j|$, where \bar{E}_i and \bar{E}_j are the mean of Ellenberg's indicator values of species recorded in the i and j assemblages from habitat patches. We thus tested the effect of both i) resistance distance between pairs of habitat patches and ii) similarity of Ellenberg's indicator values for the same pairs on ES similarity values. These relationships were investigated using linear mixed models, using both resistance distances and the similarity of Ellenberg's indicator values for the same pairs as a fixed effect and the two habitat patches constituting the pair of assemblages as the two random effects. We then performed a model-averaging method following the same procedure as the main analyses of the manuscript.

Table S1 Summary of the most parsimonious regression models according to the AICc framework used for model averaging. Full models included three independent variables, resistance distance of woodlands (DistR woodlands), grasslands (DistR grasslands), and croplands (DistR crops), and one dependent variable, the effect size (ES) of similarity values. Models were done for animal-, wind-dispersed and unassisted assemblages for woodland, temporary grassland and wheat cropland habitats. Abbreviations: “x” [the independent variable(s) included in non-significant models] and “-” [a random similarity pattern (ES not different from zero)]. Models were not done in this latter case. The significance of each model was assessed by comparing the defined and null models [i.e. model without any independent variable(s)] using a likelihood ratio test (Pinheiro & Bates 2000; Bolker *et al.* 2009). The significance of each independent variable in each model was assessed with ANOVA, based on type II sums of squares. Models in bold are significant. ***: $p < 0.001$. **: $p < 0.01$; *: $p < 0.05$; ns: $p > 0.05$.

	N	Models			p	Intercept	DistR woodlands			DistR grasslands			DistR croplands		
		AICc	R ² m	R ² c			Estimate	χ^2	p	Estimate	χ^2	p	Estimate	χ^2	p
Woodlands															
Animal-dispersed assemblages															
ES	283	425.0	0.09	0.463	***	0.20	-0.26	16.74	***				0.20	8.68	**
	283	425.5	0.10	0.503	***	0.21	-0.39	11.40	***	0.13	1.77	ns	0.21	9.29	**
Wind-dispersed assemblages															
ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unassisted assemblages															
ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Temporary grasslands															
Animal-dispersed assemblages															
ES	283	222.2	0.09	0.56	**	0.62				0.05	2.67	ns	-0.14	11.53	***
	283	222.9	0.05	0.54	**	0.62							-0.10	9.38	**
	283	222.3	0.08	0.56	**	0.62	0.05	1.78	ns				-0.14	9.89	**
	283	224.5	0.09	0.57	**	0.62	-0.00	0.00	ns	0.05	0.86	ns	-0.14	10.28	**
Wind-dispersed assemblages															
ES	283	226.5	0.00	0.62	ns										
	283	227.0	0.00	0.63	ns					x	x	x			
	283	227.3	0.00	0.62	ns		x	x	x						
	283	228.1	0.00	0.63	ns								x	x	x
	283	229.0	0.01	0.63	ns					x	x	x	x	x	x
	283	229.1	0.00	0.63	ns		x	x	x	x	x	x			
	283	229.4	0.01	0.62	ns		x	x	x				x	x	x

Unassisted assemblages

ES	283	278.1	0.04	0.45	**	0.59	-0.09	8.00	**						
	283	278.3	0.06	0.46	**	0.60	-0.12	9.53	**				0.06	1.93	ns
	283	279.3	0.02	0.44	**	0.59				-0.07	6.77	**			
	283	280.2	0.03	0.45	*	0.59	-0.08	1.18	ns	-0.01	0.03	ns			
	283	280.3	0.04	0.45	*	0.59				-0.09	7.31	**	0.04	1.02	ns
	283	280.4	0.06	0.46	*	0.59	-0.11	2.12	ns	-0.02	0.07	ns	0.06	1.97	ns

Wheat croplands

Animal-dispersed assemblages

ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
----	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

Wind-dispersed assemblages

ES	287	289.9	0.02	0.20	*	0.07				-0.06	5.12	*			
	287	291.5	0.03	0.20	ns					x	x	x	x	x	x
	287	291.9	0.02	0.20	ns		x	x	x	x	x	x			
	287	292.0	0.01	0.19	ns		x	x	x						
	287	292.8	0.00	0.17	ns										
	287	293.4	0.03	0.20	ns										
	287	293.5	0.02	0.18	ns		x	x	x				x	x	x

Unassisted assemblages

ES	290	388.7	0.00	0.34	ns										
	290	390.6	0.00	0.34	ns					x	x	x			
	290	390.7	0.00	0.34	ns								x	x	x
	290	390.7	0.00	0.34	ns		x	x	x	x	x	x			
	290	392.5	0.00	0.34	ns										
	290	392.6	0.00	0.34	ns								x	x	x

Table S2 Summary of the model-averaged estimates, relative importance (RI) and 95% confidence interval (CI) of the independent variable(s) according to the AICc framework. Full models included six independent variables, resistance distance of woodlands (DistR woodlands), grasslands (DistR grasslands), and croplands (DistR crops) and similarity edaphic indicator values of nutrient availability (S_{Eij} Nutrient), moisture (S_{Eij} Moisture) and pH (S_{Eij} pH) and one dependent variable, the effect size (ES) of similarity values. Negative ES values indicate a lower similarity value than expected, due to a dispersal (if a significant effect of one or several distR variables is detected) and/or local environmental conditions (if a significant effect of one or several variables S_{Eij} is detected) effect(s). Positive ES values indicate a higher similarity than expected, due to a dispersal (if a significant effect of one or several distR variables is detected) and/or local environmental conditions (if a significant effect of one or several variables S_{Eij} is detected) effect(s). Models were done for animal-, wind-dispersed and unassisted assemblages for woodland, temporary grassland and wheat cropland habitats. Abbreviations: "-" [a random similarity pattern (ES not different from zero)]. Models were not done in this latter case. Confidence interval that did not encompass zero are in bold.

Models			Intercept	DistR woodlands			DistR grasslands			DistR crops			S_{Eij} Nutrient			S_{Eij} Moisture			S_{Eij} pH			
N	R ² m	R ² c		Estimate	RI	CI	Estimate	RI	CI	Estimate	RI	CI	Estimate	RI	CI	Estimate	RI	CI	Estimate	RI	CI	
Woodlands																						
Animal-dispersed assemblages																						
ES	283	0.23	0.55	0.19	-0.30	1.00	(-0.51, -0.08)	0.06	0.49	(-0.11, 0.24)	0.16	1.00	(0.04, 0.29)	-0.01	0.31	(-0.07, 0.05)	-0.15	1.00	(-0.21, -0.09)	-0.17	1.00	(-0.25, -0.10)
Wind-dispersed assemblages																						
ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Unassisted assemblages																						
ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Temporary grasslands																						
Animal-dispersed assemblages																						
ES	283	0.08	0.58	0.63	0.02	0.37	(-0.06, 0.09)	0.02	0.38	(-0.05, 0.08)	-0.10	0.97	(-0.20, -0.01)	0.01	0.29	(-0.03, 0.04)	-0.00	0.24	(-0.03, 0.02)	-0.09	1.00	(-0.14, -0.05)
Wind-dispersed assemblages																						
ES	283	0.00	0.62	0.50	-0.01	0.27	(-0.06, 0.04)	-0.01	0.35	(-0.06, 0.04)	-0.00	0.20	(-0.04, 0.04)	-0.01	0.35	(-0.05, 0.03)	-0.01	0.27	(-0.04, 0.03)	-0.00	0.19	(-0.02, 0.02)
Unassisted assemblages																						
ES	283	0.0	0.45	0.59	-0.08	0.77	(-0.20, 0.04)	-0.02	0.38	(-0.10, 0.06)	0.03	0.47	(-0.06, 0.12)	-0.01	0.31	(-0.05, 0.03)	-0.01	0.32	(-0.05, 0.03)	0.00	0.17	(-0.02, 0.02)
Wheat croplands																						
Animal-dispersed assemblages																						
ES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Wind-dispersed assemblages																						
ES	287	0.07	0.22	0.07	-0.01	0.32	(-0.06, 0.05)	-0.06	0.88	(-0.14, 0.02)	0.01	0.25	(-0.04, 0.05)	0.05	0.75	(-0.03, 0.12)	-0.03	0.61	(-0.09, 0.03)	-0.07	1.00	(-0.12, -0.02)
Unassisted assemblages																						
ES	290	0.04	0.33	0.22	-0.00	0.15	(-0.03, 0.03)	-0.01	0.24	(-0.05, 0.04)	-0.00	0.15	(-0.03, 0.03)	0.04	0.63	(-0.05, 0.13)	-0.05	0.75	(-0.14, 0.03)	0.00	0.14	(-0.03, 0.03)

Chapitre 2

Effets de la quantité d'habitat et de la connectivité sur la diversité spécifique et l'abondance totale des espèces adventices au sein des cultures céréalières : une approche taxonomique et fonctionnelle

Article 4. Using the response-effect trait framework reveals that high habitat connectivity reduces weed abundance in winter cereals

Léa Uroy, Cendrine Mony, Aude Ernoult, Audrey Alignier

Rejected after major revision in *Applied Vegetation Science*, to be resubmitted

Abstract

Questions. While studies have explored how habitat amount drives the taxonomic diversity and abundance of weed assemblages in agroecosystems, knowledge remains limited on the effects of habitat connectivity. The response-effect trait framework provides insights on the mechanisms underpinning the relationship between landscape structure and the taxonomic diversity and abundance of weed assemblages. How habitat connectivity and habitat amount affect weed diversity and abundance in winter cereal fields? Are these effects driven by the functional composition of weed assemblages?

Location. Long-Term Socio-Ecological Research (LSTER) “Zone Atelier Armorique” site, Brittany (northwestern France)

Methods. We measured habitat connectivity and habitat amount provided by wooded, grassland, and cropland elements. We selected five traits related to the dispersal, establishment, and competitive abilities of weed species that were potentially both response and effect traits. The functional composition of weed assemblages was assessed using community weighed mean trait values. The taxonomic diversity (total species richness and evenness) and abundance (mean total cover) of weeds assemblages were also assessed.

Results. The taxonomic approach did not reveal any effect of habitat connectivity and habitat amount on weed diversity and abundance in crops. Only the grassland elements that contributed to habitat connectivity, and to a lesser extent habitat amount, drove the functional composition of weed assemblages. High habitat amount favoured species with many seeds, while high habitat connectivity favoured species with fewer seeds, a higher ability to reproduce vegetatively, and higher seed germination rates. In turn, higher seed germination rates in weed assemblages reduced weed abundance in winter cereals.

Conclusion. We demonstrated that high connectivity reduces weed abundance by shaping weed functional composition. Our study advances our ability to predict how landscape-scale processes affect ecosystem functions, such as weed diversity and abundance, by distinguishing solely response traits from those that are both response and effect traits.

Introduction

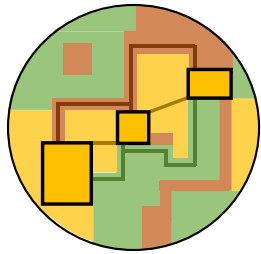
Over the last half-century, agricultural intensification has transformed heterogeneous agricultural landscapes into homogeneous ones (Robinson & Sutherland 2002), leading to biodiversity loss, particularly for arable weed species (Andreasen *et al.* 1996). Because weeds compete with crops, they have long been considered a major problem for farmers, yet they also support important ecosystem functions (e.g. the maintenance of pollination, limiting soil erosion, and providing food and shelter for biodiversity) in agricultural landscapes (Pimentel *et al.* 1995; Marshall *et al.* 2003; Bretagnolle & Gaba 2015).

Weeds assemblages have been for a long time assumed to be driven only by agricultural practices. More recently, studies demonstrated the effect of landscape structure on weed diversity and abundance (Petit *et al.* 2013), and hence on agroecosystem resistance to weed colonization (Dainese *et al.* 2017). Landscape elements surrounding crop fields (e.g. wooded, grassland, and cropland elements) often act as both refugia and sources of dispersers for weeds (Petit *et al.* 2013). While the habitat amount of these landscape elements is widely used as a surrogate of landscape structure in weed studies (see references therein Petit *et al.* 2013); our understanding of how habitat connectivity affects weeds remains limited. Yet, landscape ecologists have demonstrated that connectivity is of key importance in structuring plant assemblages (Haddad *et al.* 2015; Damschen *et al.* 2019). Thus, it is important to determine whether these landscape elements drive the diversity and abundance of weeds by contributing to the connectivity of crop fields. High connectivity increases seed dispersal, decreasing the probability of local extinction in fragmented agricultural landscapes (Wilson & Willis 1975; Taylor *et al.* 1993). Thus, high habitat connectivity and high habitat amount provided by different landscape elements might increase the likelihood of many weed species to disperse and to establish in new crop fields (i.e. mass effect, Shmida & Wilson 1985) and hence, might increase weed diversity and abundance in crops (**Fig. 1a**, hypothesis H1).

The response-effect trait framework proposes to relate plant assemblage responses to the environmental changes and their effect on ecosystem functions based on species traits (Lavorel *et al.* 1997). The effect of environmental changes (at both the field and landscape scale) on plant responses is predicted by response traits, while the effect of these changes on ecosystem functions is predicted by effect traits. This framework has been applied to weeds so far at the field scale (Gaba *et al.* 2017; Bàrberi *et al.* 2018) but should also provide insights on the ecological mechanisms between landscape structure and the diversity and abundance of weeds in crops. However, few studies have attempted to define either weed response traits

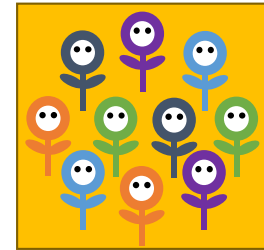
(Alignier *et al.* 2012; Fried *et al.* 2018) either both response and effect traits to landscape structure (Solé-Senan *et al.* 2017; Robleño *et al.* 2018).

(a) Taxonomic approach



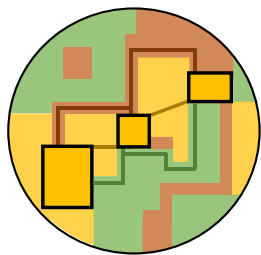
High habitat connectivity and habitat amount

H1 →



High weed diversity and abundance in the crop field

(b) Functional approach



High habitat connectivity and habitat amount

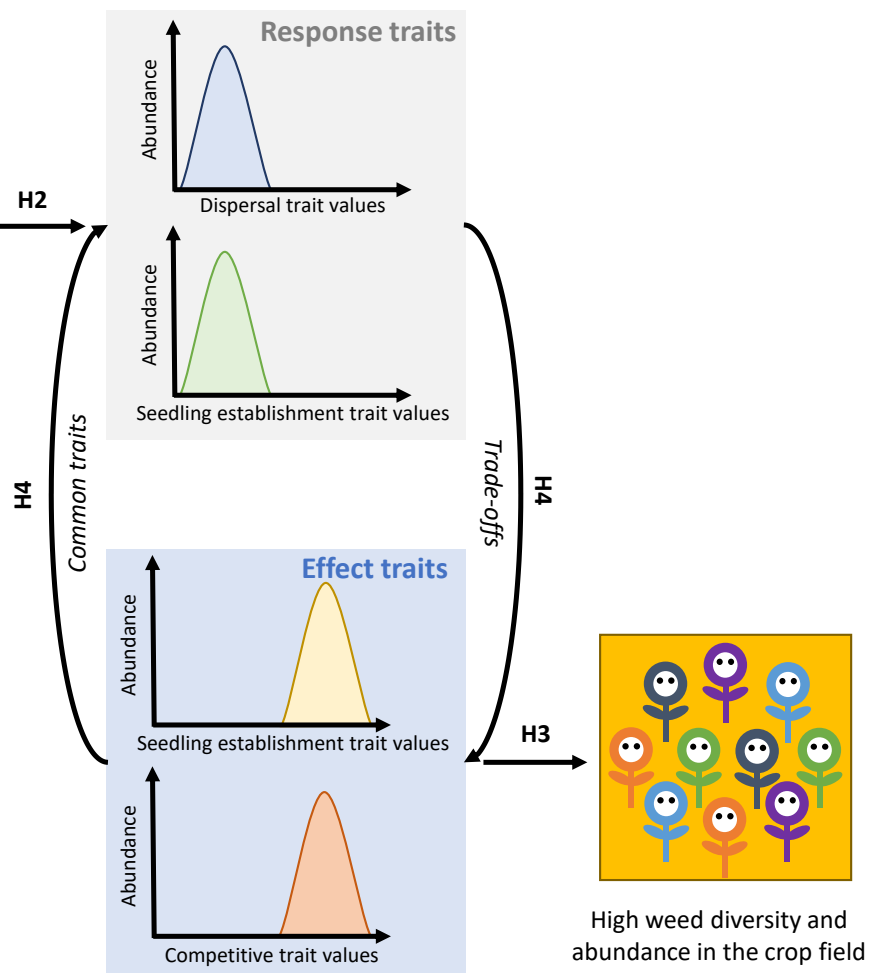


Fig. 1 Illustration of our four hypotheses (H1, H2, H3 and H4) on how habitat connectivity and habitat amount influence weed diversity and abundance in the crop fields based on (a) taxonomic and (b) functional approaches.

Depending on their ability to disperse and to establish seedlings in crop fields, weed species are likely to exhibit different responses to habitat connectivity and habitat amount provided by different landscape elements. Certain species have trait values leading to low

dispersal abilities in space – that is a production of low number of potential dispersers (e.g. low seed number) and / or a short dispersal distance (e.g. high seed mass, high vegetative reproduction, low plant height). If such species also have a low ability for seedlings to establish (e.g. low germination rates, low seed mass), they might be more likely to be favoured by high habitat connectivity and a high habitat amount. Such assumptions have been confirmed in other habitat types, resulting in the dispersal and seedling establishment traits being defined as response traits to habitat connectivity and habitat amount (Zambrano *et al.* 2019). Thus, high habitat connectivity and habitat amount provided by different landscape elements might enhance the occurrence of species with low dispersal and low seedling establishment traits values (i.e. decreased aggregated values of dispersal and establishment traits) within weed assemblages (**Fig. 1b**, hypothesis H2).

The ability of weeds to colonize the available space in the crop field efficiently is dependent the establishment and competitive abilities of the seedlings. The ability for seedlings to establish and develop despite frequent disturbances (e.g. tillage, herbicide application) may be promoted by high germination rates, important vegetative reproduction (Bond & Midgley 2001; Klimešová & Klimeš 2003; Gross *et al.* 2007) and high plant height (Violle *et al.* 2009). High aggregated values of these traits might increase weed diversity and abundance in crops, therefore constituting effect traits (**Fig. 1b**, hypothesis H3).

However, it is not known whether shifts in the functional composition of weed assemblages induced by habitat connectivity and habitat amount provided by different landscape elements changes might have subsequent impacts on weed diversity and abundance in crops. This relationship can be, either direct, due to common traits involved in dispersal, establishment and competitive abilities of the seedlings or indirect, due to the inevitable trade-offs between species traits (e.g. competition-colonization trade-off, Levins & Culver 1971). As a result, the response traits to habitat connectivity and habitat amount might also be effect traits regarding the weed diversity and abundance in crops (**Fig. 1b**, hypothesis H4).

This study investigated how habitat connectivity and habitat amount affect the diversity (total species richness and evenness) and abundance (mean total cover) of weed assemblages in winter cereal fields at three spatial scales (250, 500 and 750 m). Specifically, we tested whether these effects were driven by the functional composition of weed assemblages, based on aggregated values of traits that are assumed to be potentially both response and effect traits. Within this framework, we tested the following hypotheses. First, high habitat connectivity and habitat amount increase weed diversity and abundance in crop

fields (**Fig. 1a**; hypothesis H1). Second, high habitat connectivity and habitat amount decrease the aggregated values of dispersal and seedling establishment traits of weed assemblages. Thus, both dispersal and seedling establishment traits reflect the response of weeds to habitat connectivity and habitat amount (i.e. response traits) (**Fig. 1b**, hypothesis H2). Third, high aggregated values of seedling establishment and competitive traits of weed assemblages increase weed diversity and abundance in crop fields. Thus, establishment and competitive traits reflect the effect of weeds in shaping their colonization ability (i.e. effect traits) (**Fig. 1b**, hypothesis H3). Fourth, the response traits to habitat connectivity and habitat amount are also effect traits regarding the diversity and abundance of weeds in crops. Thus, habitat connectivity and habitat amount shape the aggregated values of dispersal, establishment, and competitive traits of weed assemblages that, in turn, drive their effect in colonizing space in winter cereal fields efficiently (**Fig. 1b**, hypothesis H4).

Material and methods

Study area and field selection

This study was conducted in the LTSER “Zone Atelier Armorique” (ZAAR) site (130 km²), which is located in Brittany, northwestern France (48° 36′ N, 1° 32′ W). This study site is a hedgerow network (*bocage*) landscape characterized by mixed dairy farming and cereal production.

We selected 27 winter cereal fields (wheat or barley) distributed across the study site, with at least 250 m between any two cereal field edges (**Fig. 2**, left). The selected fields were of similar area (mean: 1.81 ha, range: 0.55–4.38 ha), similar crop succession (crops following the ploughing of a grassland in 2013, 2014 or 2015), and similar conventional farming practices (i.e. tillage, fertilizer and herbicide inputs). This standardization was based on interviews with farmers and land-cover maps of the ZAAR database.

Assessment of habitat connectivity and habitat amount

Land-cover maps of the ZAAR raster database were constructed at a high resolution (5 m × 5 m) from aerial imagery based on nine categories: grassland, grass strip, maize, cereal, other crops (e.g. rapeseed), forest or woodland, built area, road, and water. We obtained the complete wooded network (i.e. hedgerows, forest, and woodland), from the Kermap raster database (5 m × 5 m resolution).

We used habitat connectivity and habitat amount as two proxies of the landscape structure. We assessed habitat connectivity and habitat amount as provided by wooded elements (forests, woodlands, and hedgerows; 2016 Kermap database), grassland elements (grasslands and grass strips; 2017 ZAAr database), and cropland elements (maize, cereal, and other crops; 2017 ZAAr database) around the centroid of each winter cereal field at three spatial scales: 250 m (i.e. local scale), 500 m (i.e. intermediate scale), and 750 m (i.e. large scale) (Fig. 2, right). These three spatial scales were relative to the range of spatial scales at which weed species are affected by landscape changes (Gaba *et al.* 2010).

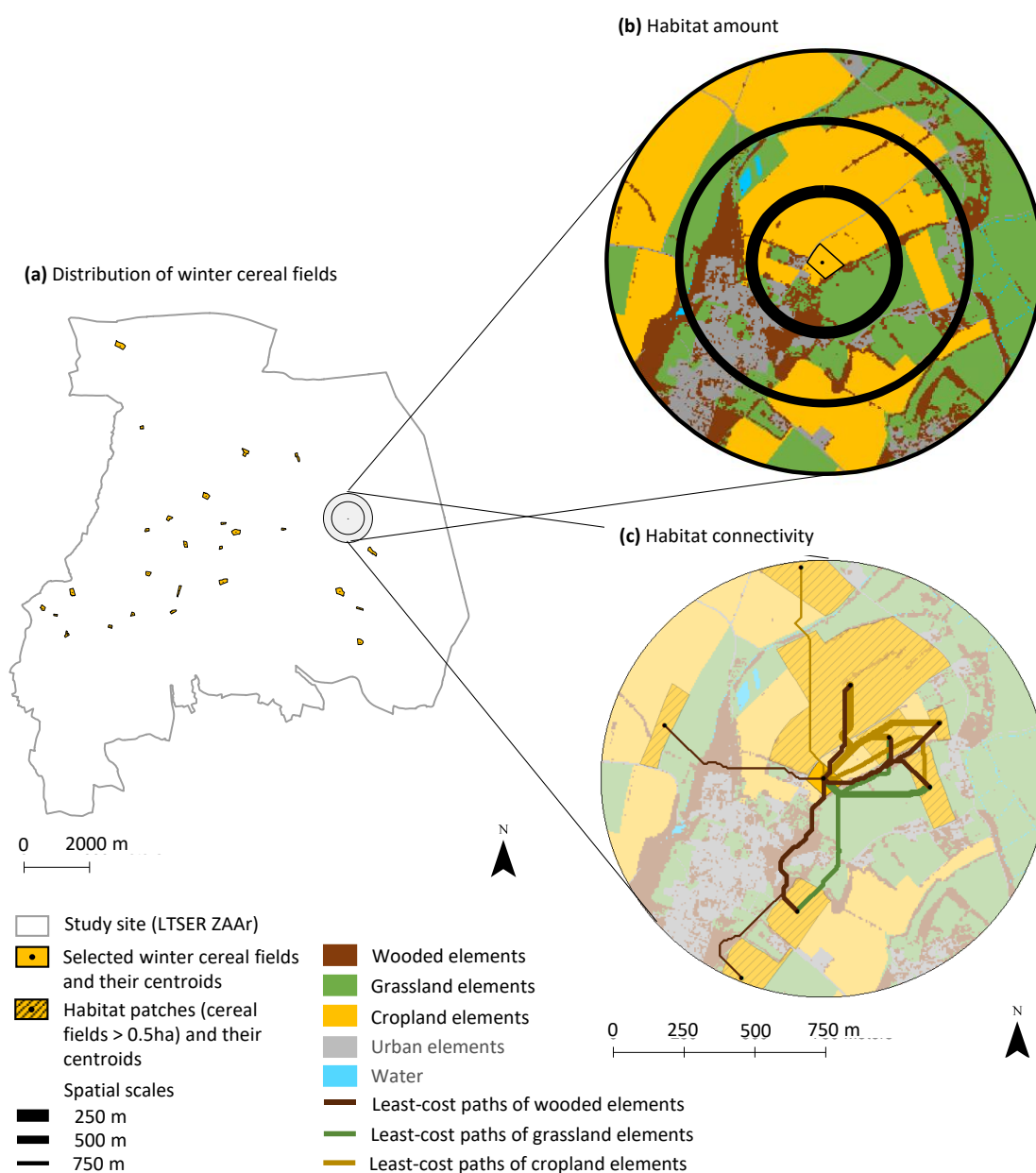


Fig. 2 Illustration of (a) the 27 winter cereal fields distributed throughout the study site, the LTSEr “Zone Atelier Armorique” and the three spatial scales (250 m, 500 m, and 750 m) used to assess of (b) habitat amount and (c) habitat connectivity provided by wooded, grassland and cropland elements (see map symbols). The shaded map symbols (urban elements and water) correspond to the elements that were not considered.

(1) Habitat connectivity

Habitat connectivity was calculated using graph theory-based habitat reachability metrics (Saura & Pascual-Hortal 2007). The graph theory modelling method was based on least-cost paths analyses (Adriaensen *et al.* 2003) that identify the potential dispersal path of plant individuals between two habitat patches. This path depends on the resistance to dispersal between habitat patches.

We considered all cereal fields in 2017 with an area > 0.5 ha as habitat patches, with adjoining cereal fields belonging to the same patch (n = 564 habitat patches, including the selected winter cereal fields). We considered the inter-patch dispersal distances as a function of the proportion of wooded, grassland, and cropland elements; thus, we created resistance maps for each landscape element type (three resistance maps, in total). Resistance values were calculated as the reverse of the proportion of the considered landscape element type in a moving circular window (see **Appendix S1** and **Supplementary Fig. S1** for more details). Then, we calculated the inter-patch distance between each pair of habitat patches from each resistance map as the cumulative cost of the least-cost path using the Graphab 2.2.6 software (Foltête *et al.* 2012). The “proportion of total potential dispersal flux in the landscape” connectivity index (Saura & Rubio 2010) of each selected winter cereal field was calculated for each type of inter-patch distance (i.e. woodland, grassland and cropland elements) and for each spatial scale considered using Conefor 2.6 (Saura & Torné 2009) (see **Appendix S2** for calculations).

(2) Habitat amount

Habitat amount was evaluated using the proportion of each type of landscape element surrounding each selected winter cereal field within 250 m, 500 m, and 750 m radius circular buffers using FRAGSTATS v4 (McGarigal *et al.* 2012).

The distribution of habitat connectivity and habitat amount provided by each landscape element for each spatial scale are summarized in **Appendix S3**. Their correlations are summarized in **Appendix S4**.

Weed data

Weed sampling

We performed weed surveys in the 27 winter cereal fields during June and July 2018. The percent cover of each herbaceous species was recorded using ten plots of 2 m x 2 m, the total

area of which corresponding to the minimal recommended sampling area for weed assemblages (Mueller-Dombois & Ellenberg 1974; Hanzlik & Gerowitt 2016). Plots were evenly distributed within the field, with at least 10 m from each other to account for the spatial heterogeneity of weeds in fields (Cardina *et al.* 1997). The outermost plots were at least 10 m from the field border to avoid edge effects. Nomenclature followed the French taxonomic register TAXREF v12.0 (available at: <https://inpn.mnhn.fr/programme/referentiel-taxonomique-taxref>).

Functional composition of weed assemblages

We selected five functional traits from the TRY (Kattge *et al.* 2011) and Biolflor (Kühn *et al.* 2004) databases: seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH) and seed germination rate (SGR). These traits were chosen as both potential response traits to habitat amount and habitat connectivity and as effect traits regarding the weed diversity and abundance in winter cereal fields. These traits were linked to (i) dispersal, (ii) establishment and (iii) competition (**Table 1** and **Appendix S5**). Concerning continuous traits, several trait values for a given trait and for a given species could be available. Thus, trait values were averaged per trait and per species (see **Appendix S6** for more details on the processing of continuous trait values dataset) Trait distributions are summarized in **Table 1**. The correlations between the five selected traits were either non-significant or low ($-0.34 \leq rho \leq 0.28$, **Appendix S7**). Continuous traits were then either log- or logit-transformed to correct for skewness. The functional composition of weed assemblages was assessed at the field scale (i.e. accounting for all species recorded in the ten plots) using the community-weighted mean (CWM) trait value. The CWM is defined as the mean trait value weighed by the relative abundance of each species (i.e. aggregated values of a given trait). We calculated the CWM trait value for each trait and for each winter cereal field using the “FD” R package.

Taxonomic diversity and abundance of weed assemblages in winter cereal fields

For each winter cereal field, we assessed the diversity and the abundance of weed assemblages at the field scale (i.e. accounting for all species recorded in the ten plots). We assessed diversity using total species richness and Piélou’s total evenness and abundance using the mean total cover. Total species richness and Piélou’s total evenness were calculated using the “vegan” R package. The selected metrics were not correlated or not overly correlated ($rho \leq |0.66|$, **Appendix S8**). The mean total cover was logit- transformed to correct for skewness. None of

Partie II

the selected metrics were spatially auto-correlated (Moran's I test, $p > 0.05$). The similarity in weed composition between each pair of winter cereal fields was also measured with the Sørensen index ($S_{S\text{ør}}$) using the "ade4" R package to obtain additional information on the taxonomic characteristics of weed assemblages. Because the "ade4" R package computes dissimilarity (d) as $\sqrt{1 - S_{S\text{ør}}}$, we applied the following transformation: $S_{S\text{ør}} = (-d^2 + 1)$ to convert dissimilarity (d) into a similarity index. The higher the Sørensen index ($S_{S\text{ør}}$), the higher the similarity between a given pair of winter cereal field.

Table 1 Overview of the five functional traits selected for this study. SE = standard error of the mean. *semi-quantitative trait, (1) log-transformed trait, (2) logit-transformed trait.

Processes	Functional traits	Availability (%)	Description and (units)	Distribution of functional traits before any transformation	
				Mean \pm SE	Min - Max
Dispersal	Seed number per plant ⁽¹⁾	88	(1/plant)	4661.52 \pm 981.32	10.00 – 56536.00
Dispersal, establishment and competition	Type of reproduction*	100	Allocation to vegetative reproduction 1: by seed; 2: mostly by seed, rarely vegetative; 3: by seed and vegetative; 4: mostly vegetative, rarely by seed	1.81 \pm 0.11	1.00 – 4.00
Dispersal and establishment	Seed dry mass ⁽¹⁾	98	(mg)	2.00 \pm 0.51	0.02 – 28.54
Dispersal and competition	Plant vegetative height ⁽¹⁾	100	Maximum vegetative height (m)	0.40 \pm 0.03	0.08 – 1.68
Establishment	Seed germination rate ⁽²⁾	85	Germination efficiency (%)	93.04 \pm 0.92	65.25 – 100

Statistical analyses

Before the statistical analyses, all variables were centered and scaled to allow for comparisons of regression coefficients among and within models.

First, we used multiple ordinary least square (OLS) regression models to assess the effect of habitat connectivity and habitat amount provided by different landscape elements (i.e. woodland, grassland and cropland elements) as independent variables on weed diversity (total species richness and Pielou's total evenness) and abundance (mean total cover) in winter cereal fields as the dependent variable for the three spatial scales considered (250 m, 500 m, and 750 m) (hypothesis H1). Second, we used multiple OLS regression models to assess the effect of habitat connectivity and habitat amount provided by different landscape elements as independent variables on the functional composition of weed assemblages for each trait as the dependent variable (SNPP, ToR, SDM, PVH and SGR CWMs) for the three spatial scales

(hypothesis H2). Third, we used multiple OLS regression models to assess the effect of the functional composition of weed assemblages for each trait considered as independent variables on weed diversity (total species richness and Piélou's total evenness) and abundance (mean total cover) in winter cereal fields as the dependent variable (hypothesis H3). This procedure allows the aggregated trait values that were significantly influenced by habitat connectivity and/or habitat amount to be identified that significantly influenced weed diversity (total species richness and Piélou's total evenness) and abundance (mean total cover) in winter cereal fields. In other words, the traits that were both response and effect traits were identified (hypothesis H4). We then performed a path analysis (Wright 1934) to calculate how habitat connectivity and/or habitat amount affected the weed diversity and abundance in winter cereal fields via the functional composition. We calculated a compound path by multiplying (i) the standardized regression coefficient of the model relating habitat connectivity and habitat amount to functional composition with (ii) the standardized regression coefficient of the model relating functional composition to weed diversity and abundance in winter cereal fields. Compound paths indicate the functional composition-mediated influence (sign and magnitude) of habitat connectivity and/or habitat amount on weed diversity and abundance in winter cereal fields.

All of these models were performed using model-averaging methodology to account for uncertainty in the model selection process (Burnham & Anderson 2002). Full models were tested for multicollinearity; however, none of the independent variables showed a variance inflation factor indicative of overly multicollinearity (i.e. exceeding 10, Hair *et al.* 2014). Due to our small sample size ($N = 27$), we built all possible linear models based on all additive combinations of up to three candidate independent variables. Models were ranked by the Akaike's information criterion corrected for small sample sizes (AICc). We generated the full model-averaged estimates of the independent variables using the 95% confidence set weighed by Akaike weights (Burnham & Anderson 2002). Homoscedasticity and normality of residuals for each models were graphically explored. We considered independent variables significant if the 95% confidence intervals did not overlap with zero. Finally, we calculated the percentage of explained variance for the most parsimonious model (i.e. with the smallest AICc) of the confidence set. All statistical analyses were performed in R. 3.5.1. Model averaging was performed using the "MuMIn" R package.

Results

Characteristics of weed assemblages

In total, 80 herbaceous species were recorded. The most common species were *Juncus bufonius* L., *Poa trivialis* L. (both present in 81.5% of fields), *Poa annua* L. (70.4%), *Senecio vulgaris* L., and *Stellaria media* (L.) Vill. (51.9%) (**Appendix S9**). The similarity between weed assemblages using Sørensen index was 0.32 ± 0.01 (mean \pm SE), and ranged from 0 to 0.68. The taxonomic and functional characteristics of weed assemblages are provided in **Table 2**.

Effect of habitat connectivity and habitat amount on weed diversity and abundance in winter cereal fields

Overall, habitat connectivity and habitat amount did not directly influence total species richness, Piélou's total evenness, and mean total cover. This phenomenon was observed regardless of the spatial scale considered (**Fig. 3** and **Appendix S10**).

Table 2 Taxonomic (total species richness, Piélou's total evenness, and mean total cover) and functional (community weighed means [CWMs] for each trait considered) characteristics of weed assemblages. These metrics were calculated at the field scale, accounting for all species recorded in the ten plots (N = 27). SE = standard error of the mean. ⁽¹⁾ logit-transformed metric. ⁽²⁾ log-transformed trait based metric, ⁽³⁾ logit-transformed trait based metric.

	Distribution of metrics before transformation	
	Mean \pm SE	Min – Max
Taxonomic diversity and abundance		
Total species richness	15.33 \pm 1.56	3.00 – 33.00
Piélou's total evenness	0.59 \pm 0.04	0.10 – 0.92
Mean total cover ⁽¹⁾	19.94 \pm 3.68	0.80 – 78.75
Functional composition (CWMs)		
Seed number per plant ⁽²⁾	8.22 \pm 0.23	6.22 – 10.31
Type of reproduction	1.59 \pm 0.08	1.02 – 2.64
Seed dry mass ⁽²⁾	-1.80 \pm 0.21	-3.72 – 0.23
Plant vegetative height ⁽²⁾	-1.34 \pm 0.05	-1.67 – -0.81
Seed germination rate ⁽³⁾	2.02 \pm 0.12	1.15 – 3.48

Effect of habitat connectivity and habitat amount on the functional composition of weed assemblages

Only habitat connectivity and habitat amount provided by grassland elements significantly affected the functional composition of weed assemblages. Specifically, only the community weighed means (CWMs) of three traits were related to the connectivity provided by grassland elements: seed number per plant (SNPP), type of reproduction (ToR), and seed germination rate (SGR) (**Fig. 3** and **Appendix S11**). The CWMs of SNPP decreased when connectivity increased, whereas the CWMs of ToR increased when connectivity increased, regardless of spatial scale. The CWMs of SGR increased when connectivity increased, but only at 750 m. Only the CWMs of SNPP were positively related to the habitat amount provided by grassland elements at the 500 m scale.

Effect of the functional composition of weed assemblages on weed diversity and abundance in winter cereal fields

None of the CWMs trait values influenced total species richness and Pielou's total evenness of weed assemblages (**Fig. 3** and **Appendix S12**). The CWMs of SGR strongly affected the mean total cover of weed assemblages; the mean total cover of weed assemblages decreased when the CWMs of SGR increased.

Effect of habitat connectivity and habitat amount on weed diversity and abundance in winter cereal fields via the functional composition

As the CWMs of SGR (i) were driven by the habitat connectivity provided by grassland elements at 750 m and (ii) affected the mean total cover of weed assemblages, we obtained a trait-mediated effect of habitat connectivity on the mean total cover of weeds in crop fields. Specifically, habitat connectivity provided by grassland elements at 750 m caused the mean total cover of weeds to decline [-0.45, *i.e.* (0.50 × -0.90)] (**Fig. 3**, **Appendix S11** and **S12**).

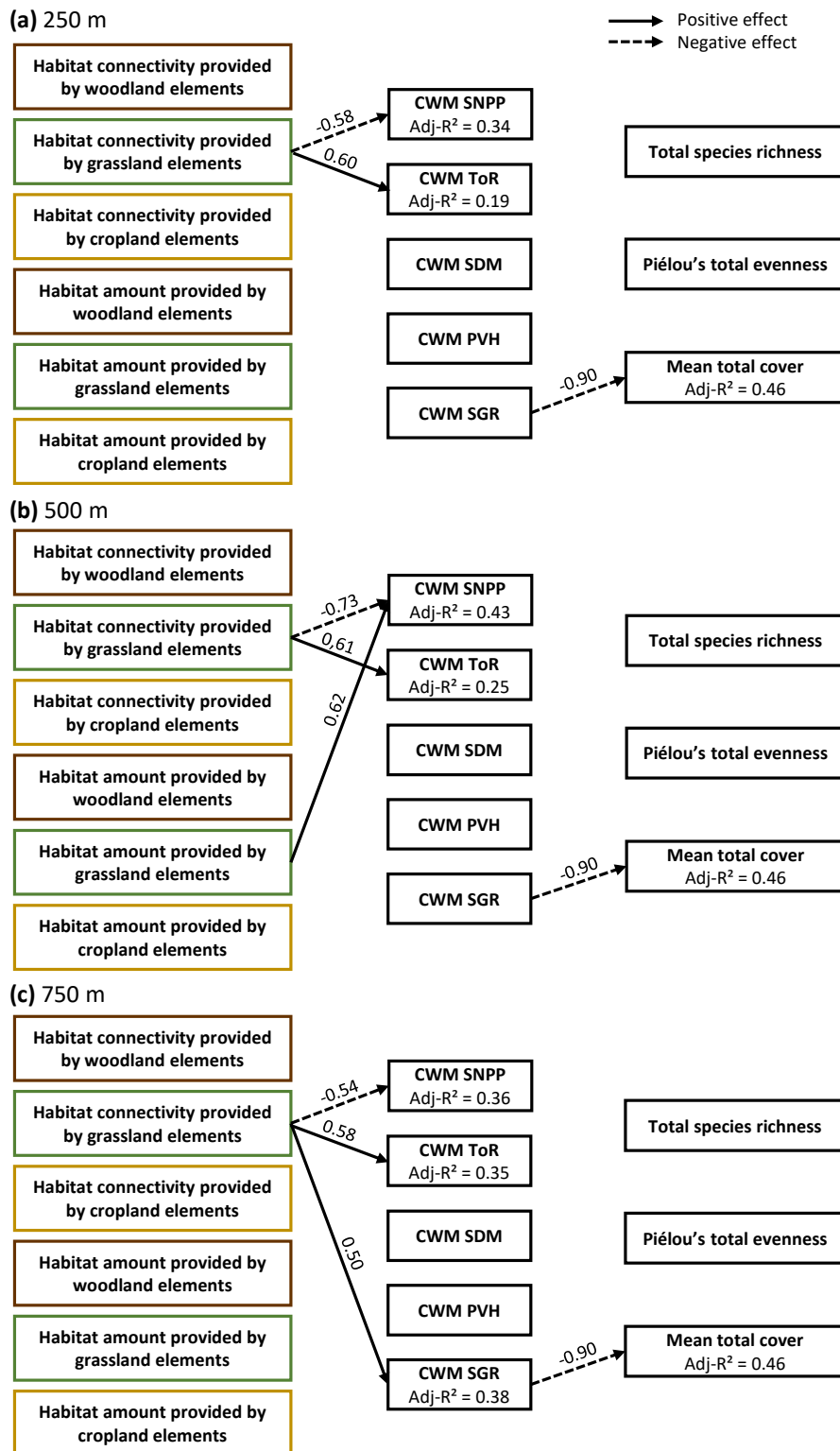


Fig. 3 Overview of the significant effects of (i) habitat connectivity and habitat amount at **(a)** 250 m, **(b)** 500 m, and **(c)** 750 m on the community weighed mean (CWM) trait values for five traits: seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH), and seed germination rate (SGR) (right) and (ii) CWM trait values on total species richness, Piélou's total evenness, and mean total cover of weeds (left). Both dependent and independent variables were calculated at the field scale (N = 27). Effects are indicated as the standardized regression coefficients of the significant model; namely, the sign and magnitude of the effect. Explained variance (Adj-R²) is indicated in the box of each dependent variable for significant models. See details in **Appendix S10, S11, and S12**.

Discussion

Grassland elements drive the functional composition of weed assemblages

Contrary to what we expected, habitat connectivity and habitat amount provided by woodland and cropland elements did not influence the functional composition of weed assemblages, but grassland did. The absence of effect of cropland elements was probably due to the high amount of croplands elements in the landscape surrounding winter cereal fields (between 44.5 and 48.5% on average, depending on the spatial scale considered; **Appendix S3**) to detect their effect on connectivity (“Fragmentation threshold hypothesis”; Andrén 1994). Moreover, the amount of croplands elements might also not be sufficiently limiting (being always greater than 14.9 – 22.6%, depending on the spatial scale considered; **Appendix S3**) to impact the functional composition of weed assemblages. By studying the respective effects of semi-natural elements (i.e. wooded and grassland elements) rather than their combined effects (e.g. Liira *et al.* 2008), we demonstrated that only grassland elements influence the functional composition of weed assemblages. These results contrast with the common perception of hedgerows as weed refugia and source of dispersers (Boutin *et al.* 2008), but might have been obtained because we also included forests and woodlands into wooded elements. Given the high affinity of weeds for nutrient-rich, sunny, and dry habitats (Bourgeois *et al.* 2019), forests and woodlands are less likely to provide refuges or suitable corridors for the dispersal of weeds between cereal fields than grasslands. Similarly, wood-dwelling plant species are less likely to disperse into winter cereal fields compared to grasslands-dwelling ones, given their differing ecological requirements. For instance, wood-dwelling plant species are less nutrient and light demanding and less tolerant to anthropogenic disturbances than grassland-dwelling ones (Löhmus *et al.* 2014).

Surprisingly, among traits related to dispersal and establishment, only one trait influenced how weeds responded to habitat amount, giving only little support to our second hypothesis (H2). A high habitat amount of grassland favoured species with high seed production, probably because grasslands harbour species that produce many seeds. In our study, *Juncus bufonius* L. notably dominated such weed assemblages. This species has an abundant and persistent seedbank and primarily establishes in trampled microsites of grasslands (Matějková *et al.* 2003). Thus, the huge seed production of *Juncus bufonius* L. (more than 50 000 seeds per plant, Kattge *et al.* 2011) that can lie dormant in soils for up to 100 years (Thompson *et al.* 1997) might facilitate its ability to reach winter cereal fields through mass effect.

Conversely, several traits linked to dispersal and seedling establishment were involved in the response of weeds to habitat connectivity. Thus, habitat connectivity might override habitat amount in shaping the functional composition of weed assemblages, minimally supporting the Habitat Amount Hypothesis (Fahrig 2013). Specifically, high habitat connectivity provided by grasslands favoured species that produced few seeds, but also species that had a higher ability to reproduce vegetatively and that had high seed germination rates. The sensitivity of species producing a few number of seeds (i.e. being disfavoured) to connectivity loss is well recognized for forests and grassland plants (e.g. Verheyen *et al.* 2004; Evju *et al.* 2015), with our study demonstrating that this phenomenon extends to weed species. However, the response of clonal plants to connectivity loss does not appear to be straightforward: our findings are in line with the study of Kolb & Diekmann (2005), but also contradict previous studies showing that clonal plants are resistant (i.e. being unaffected or being favoured) to connectivity loss (Piessens *et al.* 2005; Lindborg 2007). Vegetative reproduction is considered as an alternative life cycle that allows the persistence of local species without sexual reproduction (Eriksson 1996), particularly if a population has been isolated (Eriksson & Ehrlén 2001). Vegetative reproduction alone without any traits ensuring long-term persistence (e.g. persistent seed bank) leads to a certain risk of local extinction (Honnay & Bossuyt 2005). Yet, 100% of three species that reproduce mostly vegetatively and 92% of 24 species that reproduce either vegetatively or sexually had a transient or short-term persistent seed bank in our study (LEDA database, Kleyer *et al.* 2008). Our findings also contrast with previous studies demonstrating that plants resistant to connectivity loss display high seed germination rates (Favre-Bac *et al.* 2017a). Habitat connectivity did not affect seed mass nor plant height in our study. However, detecting the effect of habitat connectivity on seed mass and plant height is difficult (Piessens *et al.* 2005; Schleicher *et al.* 2011; Evju *et al.* 2015), especially as their relative roles in dispersal distance are still subject to debate (Thomson *et al.* 2011), and as they are also involved in further stages of plant development before efficient colonization (establishment, competition). Overall, our results demonstrated that traits promoting seedling establishment and/or local persistence, rather than high dispersal abilities, contributed to the sensitivity of plants to connectivity loss.

Interestingly, our findings suggest that studying the local or intermediate landscape surrounding winter cereal fields is less relevant than studying the landscape at a large scale to understand how landscape structure affects the functional composition of weed assemblages. The greater the extent of landscape, the stronger the ability to detect the processes involved in weed responses to landscape structure. These results provide new

insights on the scale of effect (i.e. the spatial extent at which landscape structure best predicts assemblage responses, Jackson & Fahrig 2012) of weed species, contradicting one previous study, which showed that the local landscape best predicts taxonomic responses (Gaba *et al.* 2010).

Germination of weeds reduces their abundance in winter cereal fields

None of the functional traits linked to seedling establishment and competition were related to weed diversity (i.e. richness, evenness) in winter cereal fields, giving only partial support to our third hypothesis (H3). Thus, weed diversity might not be explained by the aggregated trait values of weed assemblages (measured through CWMs). Understanding the mechanisms linked to patterns in diversity requires an explicit insight of niche differentiation through both interspecific and intraspecific trait variation (Silvertown 2004; Clark *et al.* 2011).

Weed abundance in winter cereal fields was driven by a trait related to seedling establishment; namely, seed germination rates. Thus, seed germination rates drive how weeds impact the functioning of this ecosystem. Of note, we found that low seed germination rates increase the abundance of weeds in winter cereal fields. As low germination rates are indicative of high weed seed dormancy (Colbach *et al.* 2006), this effect might cause high seed dormancy of weeds, which is used to synchronize germination (Baskin & Baskin 2014) when crops are sown. Weed species that maximize seedling establishment within winter crops germinate and emerge at around the time that the crop is sown (i.e. between October and November in our study area) (Gunton *et al.* 2011). Despite the ability to maximize seedling establishment and to resist to competitive pressure (by resprouting and spreading laterally), allocation to vegetative reproduction did not predict weed abundance. This result was unexpected, because, in many habitats, greater vegetative reproduction (i.e. both vegetative growth in cultivation and greater lateral expansion) was correlated with higher abundance at both the local and regional scales (Herben *et al.* 2014). Using a combination of clonal traits is more appropriate to describe the clonal strategies accurately, and elucidate the effect of vegetative reproduction on weed abundance. For instance, the presence of an underground vegetative bud bank protected from damage would better reflect seedling establishment (by resprouting after disturbance; Klimešová & Klimeš 2003). In addition, clonal expansion through stolons or the growth of rhizomes should contribute to plants spreading over space (Ross & Harper 1972). Plant height did not influence weed abundance, possibly due to the overriding effect of the winter cereal canopy, which limits the height to which weeds grow (Borgy *et al.* 2016), increasing hence the abundance of small weeds (Perronne *et al.* 2014)

Despite the trade-off between competition and colonization (dispersal) (Levins & Culver 1971), none of the traits involved in dispersal and seedling establishment (i.e. seed number, seed mass) influenced weed abundance. Although seed rain does influence the taxonomic characteristics of assemblages in many habitats (Mouquet *et al.* 2004; Myers & Harms 2009), the disturbances and the competition imposed by farming practices in winter cereal fields might override dispersal processes.

Using the response-effect trait framework for a better understanding of weed diversity and abundance due to habitat connectivity

In contrast to our first hypothesis (H1), the taxonomic approach did not reveal any effect of habitat connectivity and habitat amount on the diversity and abundance of weed assemblages in winter cereal fields. Interestingly, when using the functional approach (response-effect trait framework), we demonstrated that enhancing habitat connectivity provided by grassland elements at a large scale (750 m) could increase the germination success of weeds and, thus, reduce their abundance. This result provides support to our fourth hypothesis (H4) for this particular trait. The negative effect of habitat connectivity on weed abundance mediated by seed germination is probably offset by a positive effect mediated by traits that we did not consider. We also showed that habitat amount did not affect weed abundance. Thus, land-use planning policies that enhance the connectivity provided by grassland elements could benefit farmers through their role in weed abundance. Therefore, farmers might profit from a reduction of weed abundance without compromising the allocation of fields to crop or livestock production (i.e. pasture or hay).

Overall, this study presents a new approach to predict the effect of landscape-scale processes on ecosystem functioning, by expanding the response-effect trait framework to these large-scale assembly processes. The expansion of the response-effect trait framework allows traits that are only response traits to landscape-scale processes to be distinguished from the traits that are both response and effect traits regarding ecosystem functions.

Acknowledgements

We thank Léo Broudic and Mathieu Bijou for assistance in the field and Maxime Dahirel for assistance with the statistical analyses. We also thank the farmers who gave permission for weed surveys to be performed in their fields. This work used landscape databases collected in the LTSER site “Zone Atelier Armorique” and plant traits from the TRY database (<http://www.try-db.org>). Land-cover and hedgerow network maps were established by Jean

Nabucet (LETG-Rennes-Costel) and Kermap. The TRY database is hosted, developed and maintained by J. Kattge and G. Boenisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by Future Earth/bioDISCOVERY and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

Data availability statement

Data and R script used for this study will be made available on Figshare on acceptance (doi: known on acceptance). Land-cover and hedgerow network maps are available on Osuris (<https://accueil.osuris.fr/>).

Appendix S1 Development of resistance maps.

We developed resistance maps for each element type (i.e. wooded, grassland, and cropland elements) using a moving window analysis. This method enables to assign a resistance value to each focal pixel of the landscape, the value being calculated and mediated by the neighbouring pixel values (McGarigal & Cushman 2005). This method avoids assigning resistance values based on a discrete representation of the landscape matrix (i.e. patch-matrix model) in favour of a continuous representation of the landscape matrix (i.e. continuum model) (McGarigal & Cushman 2005; Fischer & Lindenmayer 2006; Cushman *et al.* 2010; Lausch *et al.* 2015; Brudvig *et al.* 2017). Resistance values were calculated as the reverse of the proportion of the considered landscape element type (i.e. 101 minus the proportion of the considered landscape element type) in a given landscape window, which were simulated as a sliding circular window. The proportion of the considered landscape element type was calculated from the number of pixels in a circular moving window of 55 m in diameter, with displacement and interpolation value of 5m. A focal pixel for which the proportion of the landscape element type over the window (i.e. its focal neighbourhood) is 100% was assigned a resistance value of 1 (i.e. highly permeable to dispersal). Conversely, a focal pixel for which the proportion of the landscape element type is 0% was assigned a resistance value of 101 (i.e. slightly permeable to dispersal) (**Fig. S1**). The calculation of three resistance maps, respectively based on the proportion of woodland, grassland and cropland elements reduced subjectivity (i.e. expert knowledge) and avoided hierarchisation of habitat types when assigning resistance values. The three resistance maps were produced using Chloe v4 software (Boussard & Baudry 2014).

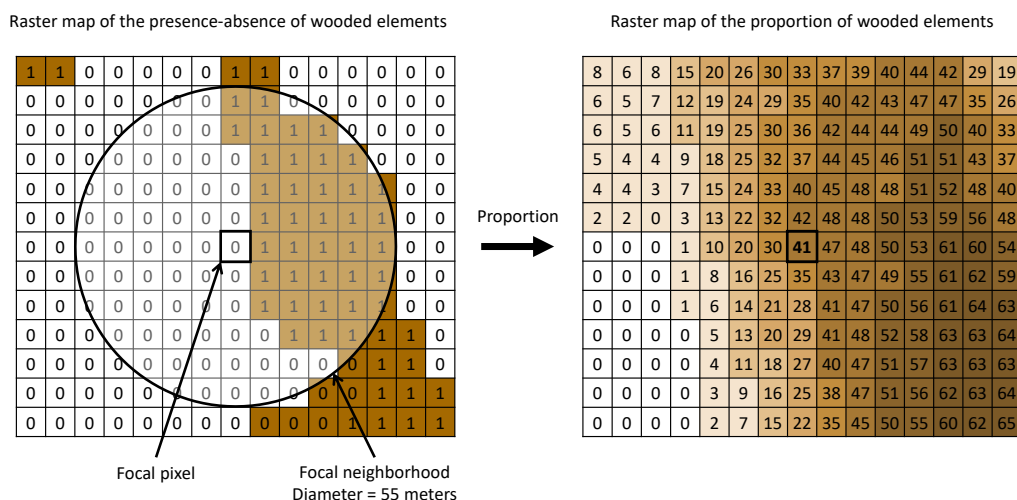


Fig. S1 Schematic representation of the circular moving window analysis used to create resistance maps for each landscape element type. Example of wooded elements.

Appendix S2 Calculation of the “proportion of total potential dispersal flux in the landscape” connectivity index.

For each selected winter cereal field, we computed the “proportion of total potential dispersal flux in the landscape” index (dF_k^* ; Saura & Rubio 2010) as:

$$dF_k^* = \frac{\sum_{i=1, i \neq k}^{n-1} p_{ik}^*}{\sum_{i=1}^n \sum_{j=1, i \neq j}^n p_{ij}^*} \times 100$$

where p_{ij}^* is the maximum product probability of all possible least-cost paths between pairs of habitat patches, i and j , in the landscape, including direct and non-direct (facilitated by other intermediate patches functioning as stepping-stones) dispersal between pairs of habitat patches (Saura & Pascual-Hortal 2007). The probability of direct dispersal (p_{ij}) between pairs of habitat patches was modelled as a negative exponential function of the effective dispersal distance between habitat patches (Bunn *et al.* 2000; Urban & Keitt 2001; Saura & Pascual-Hortal 2007; Gurrutxaga *et al.* 2011). The dF_k^* index was calculated using three potential maximal dispersal distances: 250 m, 500 m, and 750 m (i.e. corresponding to the three spatial scales tested). These potential maximal dispersal distances were converted to accumulated cost for each landscape element using the transformation (Foltête *et al.* 2012): $Dist = e^{intercept + slope \cdot \log(DistM)}$, where $Dist$ is the cumulative cost of the least-cost path between each pair of habitat patches and $DistM$ is the Euclidean distance between each pair of habitat patches. Each “converted” potential maximal dispersal distance was used to set the decay rate of the negative exponential function at $p_{ij} = 0.01$.

Partie II

Appendix S3 Distribution of habitat connectivity and habitat amount provided by each landscape element for 250 m, 500 m and 750 m.

	250m		500m		750m	
	Mean \pm SE	Min – Max	Mean \pm SE	Min – Max	Mean \pm SE	Min – Max
Habitat connectivity provided by:						
Wooded elements	0.45 \pm 0.08	0.01 – 1.69	0.48 \pm 0.07	0.07 – 1.48	0.48 \pm 0.07	0.13 – 1.47
Grassland elements	0.42 \pm 0.15	0.00 – 3.54	0.45 \pm 0.13	0.00 – 2.97	0.45 \pm 0.11	0.00 – 2.55
Cropland elements	0.52 \pm 0.11	0.00 – 2.27	0.39 \pm 0.08	0.00 – 1.50	0.35 \pm 0.07	0.00 – 1.24
Habitat amount provided by:						
Wooded elements	19.36 \pm 2.05	5.52 – 44.71	18.99 \pm 1.41	4.12 – 32.16	19.18 \pm 0.97	10.49 – 29.67
Grassland elements	30.99 \pm 3.29	2.19 – 66.35	35.55 \pm 2.54	14.38 – 57.84	35.83 \pm 1.96	18.86 – 53.17
Cropland elements	48.46 \pm 3.94	14.91 – 85.20	44.55 \pm 2.77	21.00 – 70.95	44.48 \pm 2.09	22.58 – 64.34

Appendix S4 Spearman's correlation (*rho*) between habitat connectivity and habitat amount provided by each landscape element for **(a)** 250 m, **(b)** 500 m and **(c)** 750 m. Significant correlations ($P < 0.05$) are in bold.

(a) 250m	Habitat connectivity provided by woodlands	Habitat connectivity provided by grasslands	Habitat connectivity provided by croplands	Habitat amount provided by woodlands	Habitat amount provided by grasslands	Habitat amount provided by croplands
Habitat connectivity provided by woodlands						
Habitat connectivity provided by grasslands	-0.02					
Habitat connectivity provided by croplands	0.10	-0.16				
Habitat amount provided by woodlands	0.27	-0.08	-0.47			
Habitat amount provided by grasslands	-0.07	0.80	-0.44	0.13		
Habitat amount provided by croplands	-0.12	-0.50	0.52	-0.57	-0.75	
(b) 500m	Habitat connectivity provided by woodlands	Habitat connectivity provided by grasslands	Habitat connectivity provided by croplands	Habitat amount provided by woodlands	Habitat amount provided by grasslands	Habitat amount provided by croplands
Habitat connectivity provided by woodlands						
Habitat connectivity provided by grasslands	-0.13					
Habitat connectivity provided by croplands	0.07	-0.31				
Habitat amount provided by woodlands	0.57	-0.08	-0.35			
Habitat amount provided by grasslands	-0.16	0.70	-0.43	-0.13		
Habitat amount provided by croplands	-0.13	-0.39	0.45	-0.32	-0.71	
(c) 750m	Habitat connectivity provided by woodlands	Habitat connectivity provided by grasslands	Habitat connectivity provided by croplands	Habitat amount provided by woodlands	Habitat amount provided by grasslands	Habitat amount provided by croplands
Habitat connectivity provided by woodlands						
Habitat connectivity provided by grasslands	-0.22					
Habitat connectivity provided by croplands	0.11	-0.35				
Habitat amount provided by woodlands	0.67	-0.04	-0.31			
Habitat amount provided by grasslands	-0.30	0.54	-0.60	0.08		
Habitat amount provided by croplands	0.05	-0.34	0.64	-0.40	-0.76	

Appendix S5 Overview of the mechanisms involved in dispersal, establishment and competition processes for the five functional traits selected for this study.

	Functional traits									
	Seed number per plant		Type of reproduction		Seed dry mass		Plant vegetative height		Seed germination rate	
	Low	High	Low	High	Low	High	Low	High	Low	High
Dispersal										
Mechanism	Number of dispersers		Dispersal distance		Dispersal distance		Dispersal distance			
Sense of variation	Low	High	High	Low	High	Low	Low	High		
Establishment										
Mechanism			Resprouting		Amount of metabolic reserve in the seed		Successful germination from the seed bank			
Sense of variation			Low	High	Low	High	Low		High	
Competition										
Mechanism			Resource acquisition via lateral spread				Resource acquisition via growth in height			
Sense of variation			Low	High			Low	High		

Appendix S6 Processing of the continuous trait values dataset.

Several n continuous trait values for a given trait and for a given species could be available from trait databases. Thus, all n trait values that fell outside the 95% of the normal distribution of the n trait values distribution (if $n \geq 2$) for a given trait and for a given species were considered as outliers and were removed (4.81% of continuous trait values dataset). Then, trait values were averaged per trait and per species. Missing continuous trait values were estimated using Multivariate Imputation by Chained Equation (MICE), which is a procedure that accurately predicts mean matching from functional trait values (Penone *et al.* 2014; Taugourdeau *et al.* 2014). This procedure was performed by setting the family of each species as nested blocks assuming phylogenetic conservatism (Baeten *et al.* 2015), using the “mice” R package.

Partie II

Appendix S7 Spearman's correlation (*rho*) between the five functional traits selected for this study before any transformation. Significant correlations ($P < 0.05$) in bold. *semi-quantitative trait, ⁽¹⁾ log-transformed traits, ⁽²⁾ logit-transformed trait

Functional traits	Seed number per plant ⁽¹⁾	Type of reproduction*	Seed dry mass ⁽¹⁾	Plant t vegetative height ⁽¹⁾	Seed germination rate ⁽²⁾
Seed number per plant ⁽¹⁾					
Type of reproduction*	-0.12				
Seed dry mass ⁽¹⁾	-0.34	-0.14			
Plant vegetative height ⁽¹⁾	0.07	0.14	0.28		
Seed germination rate ⁽²⁾	0.03	0.10	0.15	0.22	

Appendix S8 Spearman's correlation (r) between the three different metrics used to assess the diversity (total species richness, Piélou's total evenness) and abundance (mean total cover) of weed assemblages in winter cereal fields before any transformation. These metrics were calculated at the field scale, accounting for all species recorded in the ten plots ($N = 27$). Significant correlations ($P < 0.05$) are in bold. ⁽¹⁾logit-transformed metrics.

Metrics	Total species richness	Piélou's total evenness	Mean total cover ⁽¹⁾
Total species richness			
Piélou's total evenness	-0.09		
Mean total cover ⁽¹⁾	0.55	-0.66	

Partie II

Appendix S9 Number of occurrences (calculated as the number of fields where the species is present) and total abundance (calculated as the sum of cover values in the ten plots) of the 80 herbaceous species recorded in fields. Nomenclature: TAXREF v12.0, the French taxonomic register (available at: <https://inpn.mnhn.fr/programme/referentiel-taxonomique-taxref>)

Name	Occurrence	Total abundance
<i>Juncus bufonius</i> L., 1753	22.00	1815.50
<i>Poa trivialis</i> L., 1753	22.00	135.50
<i>Poa annua</i> L., 1753	19.00	1143.00
<i>Stellaria media</i> (L.) Vill., 1789	14.00	109.00
<i>Senecio vulgaris</i> L., 1753	14.00	65.00
<i>Rumex obtusifolius</i> L., 1753	13.00	88.50
<i>Hypericum humifusum</i> L., 1753	13.00	88.00
<i>Polygonum aviculare</i> L., 1753	13.00	29.00
<i>Trifolium repens</i> L., 1753	12.00	14.00
<i>Persicaria maculosa</i> Gray, 1821	11.00	44.00
<i>Taraxacum officinale</i> F.H.Wigg., 1780	11.00	18.50
<i>Agrostis stolonifera</i> L., 1753	10.00	209.00
<i>Cerastium fontanum</i> Baumg., 1816	10.00	73.00
<i>Plantago major</i> L., 1753	10.00	27.50
<i>Calystegia sepium</i> (L.) R.Br., 1810	9.00	98.00
<i>Lamium hybridum</i> Vill., 1786	9.00	23.50
<i>Veronica arvensis</i> L., 1753	8.00	123.50
<i>Lysimachia arvensis</i> (L.) U.Manns & Anderb., 2009	8.00	65.50
<i>Lolium multiflorum</i> Lam., 1779	8.00	59.00
<i>Mercurialis annua</i> L., 1753	8.00	41.50
<i>Kickxia elatine</i> (L.) Dumort., 1827	8.00	21.50
<i>Lamium purpureum</i> L., 1753	7.00	27.50
<i>Viola arvensis</i> Murray, 1770	6.00	419.00
<i>Epilobium tetragonum</i> L., 1753	6.00	35.00
<i>Aphanes arvensis</i> L., 1753	6.00	24.00
<i>Fumaria muralis</i> Sond. ex W.D.J.Koch, 1845	6.00	14.00
<i>Fallopia convolvulus</i> (L.) Á.Löve, 1970	6.00	10.50
<i>Dactylis glomerata</i> L., 1753	6.00	6.50
<i>Solanum nigrum</i> L., 1753	6.00	6.50
<i>Tripleurospermum inodorum</i> (L.) Sch.Bip., 1844	5.00	59.00
<i>Convolvulus arvensis</i> L., 1753	5.00	31.00
<i>Ranunculus repens</i> L., 1753	5.00	19.00
<i>Cirsium arvense</i> (L.) Scop., 1772	5.00	18.00
<i>Galium aparine</i> L., 1753	5.00	10.00
<i>Lipandra polysperma</i> (L.) S.Fuentes, Uotila & Borsch, 2012	5.00	6.00
<i>Oxalis fontana</i> Bunge, 1835	4.00	7.50
<i>Veronica chamaedrys</i> L., 1753	4.00	4.00
<i>Rumex crispus</i> L., 1753	3.00	29.50
<i>Rumex acetosella</i> L., 1753	3.00	23.50

<i>Veronica persica</i> Poir., 1808	3.00	20.00
<i>Elytrigia repens</i> (L.) Desv. ex Nevski, 1934	3.00	13.00
<i>Holcus lanatus</i> L., 1753	3.00	12.00
<i>Cerastium glomeratum</i> Thuill., 1799	3.00	10.50
<i>Ranunculus sardous</i> Crantz, 1763	3.00	7.50
<i>Bromopsis erecta</i> (Huds.) Fourr., 1869	3.00	4.50
<i>Chenopodium album</i> L., 1753	3.00	4.00
<i>Cardamine hirsuta</i> L., 1753	3.00	2.50
<i>Holcus mollis</i> L., 1759	3.00	2.50
<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl & C.Presl, 1819	2.00	25.00
<i>Agrostis capillaris</i> L., 1753	2.00	15.00
<i>Panicum dichotomiflorum</i> Michx., 1803	2.00	11.50
<i>Ervilia hirsuta</i> (L.) Opiz, 1852	2.00	9.00
<i>Gnaphalium uliginosum</i> L., 1753	2.00	6.00
<i>Vicia sativa</i> L., 1753	2.00	4.00
<i>Geranium dissectum</i> L., 1755	2.00	2.00
<i>Geranium molle</i> L., 1753	2.00	2.00
<i>Daucus carota</i> L., 1753	2.00	1.50
<i>Veronica serpyllifolia</i> L., 1753	2.00	1.00
<i>Agrostis gigantea</i> Roth, 1788	1.00	99.50
<i>Mentha arvensis</i> L., 1753	1.00	25.50
<i>Ceratochloa cathartica</i> (Vahl) Herter, 1940	1.00	16.00
<i>Echinochloa crus-galli</i> (L.) P.Beauv., 1812	1.00	7.50
<i>Aethusa cynapium</i> L., 1753	1.00	7.00
<i>Medicago sativa</i> L., 1753	1.00	4.50
<i>Plantago lanceolata</i> L., 1753	1.00	4.50
<i>Capsella bursa-pastoris</i> (L.) Medik., 1792	1.00	3.50
<i>Veronica hederifolia</i> L., 1753	1.00	3.50
<i>Digitaria sanguinalis</i> (L.) Scop., 1771	1.00	3.00
<i>Hypochaeris radicata</i> L., 1753	1.00	2.00
<i>Lolium perenne</i> L., 1753	1.00	2.00
<i>Sherardia arvensis</i> L., 1753	1.00	2.00
<i>Sonchus asper</i> (L.) Hill, 1769	1.00	2.00
<i>Lapsana communis</i> L., 1753	1.00	1.50
<i>Matricaria chamomilla</i> L., 1753	1.00	1.00
<i>Poa pratensis</i> L., 1753	1.00	1.00
<i>Silene latifolia</i> Poir., 1789	1.00	1.00
<i>Euphorbia helioscopia</i> L., 1753	1.00	0.50
<i>Oxalis corniculata</i> L., 1753	1.00	0.50
<i>Trifolium pratense</i> L., 1753	1.00	0.50
<i>Urtica dioica</i> L., 1753	1.00	0.50

Appendix S10 Summary of the model-averaged estimates [\pm 95% confidence intervals (CI)] and relative importance (RI) of the habitat connectivity and habitat amount provided by (i) woodland, (ii) grassland and (iii) cropland elements for each spatial scale considered (250m, 500m and 750m) to explain weed diversity and abundance in winter cereal fields [diversity: total species richness and Piélou's total evenness; abundance: mean total cover]. Both dependent and independent variables were calculated at the field scale (N = 27). All confidence intervals did encompass zero meaning that the effect of variables was not significant.

	Adj-R ²	Intercept	Habitat connectivity provided by:						Habitat amount provided by:					
			Woodland elements		Grassland elements		Cropland elements		Woodland elements		Grassland elements		Cropland elements	
			Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI
250 m														
Total species richness	0.09	0.00	0.01 \pm 0.17	0.17	-0.15 \pm 0.43	0.45	0.00 \pm 0.18	0.16	0.00 \pm 0.20	0.16	-0.08 \pm 0.37	0.31	0.06 \pm 0.33	0.26
Piélou's total evenness	0.27	0.00	0.20 \pm 0.46	0.55	0.00 \pm 0.15	0.13	0.11 \pm 0.39	0.35	-0.37 \pm 0.54	0.77	-0.02 \pm 0.20	0.14	0.02 \pm 0.26	0.17
Mean cover	0.00	0.00	-0.09 \pm 0.34	0.35	-0.13 \pm 0.41	0.40	-0.10 \pm 0.38	0.36	0.05 \pm 0.30	0.22	-0.03 \pm 0.27	0.20	0.07 \pm 0.35	0.25
500 m														
Total species richness	0.11	0.00	0.01 \pm 0.17	0.15	-0.08 \pm 0.35	0.32	0.01 \pm 0.18	0.16	0.04 \pm 0.24	0.23	-0.21 \pm 0.52	0.55	0.01 \pm 0.31	0.22
Piélou's total evenness	0.13	0.00	0.10 \pm 0.37	0.36	0.03 \pm 0.23	0.18	0.23 \pm 0.48	0.60	0.00 \pm 0.20	0.16	-0.13 \pm 0.43	0.39	-0.01 \pm 0.24	0.16
Mean cover	0.00	0.00	-0.13 \pm 0.40	0.42	-0.12 \pm 0.39	0.40	-0.04 \pm 0.26	0.23	0.00 \pm 0.19	0.15	0.01 \pm 0.25	0.16	0.08 \pm 0.35	0.30
750 m														
Total species richness	0.00	0.00	0.02 \pm 0.21	0.18	-0.10 \pm 0.36	0.37	0.02 \pm 0.20	0.17	0.04 \pm 0.25	0.24	-0.09 \pm 0.37	0.33	0.01 \pm 0.25	0.18
Piélou's total evenness	0.13	0.00	0.12 \pm 0.40	0.41	0.02 \pm 0.20	0.17	0.17 \pm 0.46	0.49	0.01 \pm 0.19	0.16	-0.15 \pm 0.47	0.42	-0.01 \pm 0.26	0.18
Mean total cover	0.00	0.00	-0.12 \pm 0.39	0.40	-0.11 \pm 0.37	0.39	-0.02 \pm 0.22	0.19	0.00 \pm 0.20	0.17	0.02 \pm 0.26	0.17	0.04 \pm 0.27	0.21

Appendix S11 Summary of the model-averaged estimates [\pm 95% confidence intervals (CI)] and relative importance (RI) of the habitat connectivity and habitat amount provided by (i) woodland, (ii) grassland and (iii) cropland elements for each spatial scale considered (250m, 500m and 750m) to explain the community weighed mean (CWM) trait values [Seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH) and seed germination rate (SGR)]. Both dependent and independent variables were calculated at the field scale (N = 27). Confidence intervals that did not encompass zero are in bold.

Adj-R ²	Intercept	Habitat connectivity provided by:						Habitat amount provided by:						
		Woodland elements		Grassland elements		Cropland elements		Woodland elements		Grassland elements		Cropland elements		
		Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	
250 m														
CWM SNPP	0.34	0.00	-0.13 \pm 0.37	0.41	-0.58 \pm 0.53	0.95	-0.03 \pm 0.21	0.14	0.02 \pm 0.20	0.15	0.11 \pm 0.49	0.24	-0.37 \pm 0.61	0.66
CWM ToR	0.19	0.00	0.03 \pm 0.21	0.21	0.60 \pm 0.51	0.98	0.01 \pm 0.17	0.15	0.02 \pm 0.24	0.17	-0.12 \pm 0.45	0.33	0.08 \pm 0.39	0.28
CWM SDM	0.14	0.00	0.03 \pm 0.22	0.19	0.13 \pm 0.44	0.38	0.03 \pm 0.22	0.18	-0.06 \pm 0.34	0.27	-0.04 \pm 0.40	0.24	0.31 \pm 0.60	0.65
CWM PVH	0.16	0.00	0.05 \pm 0.26	0.24	0.38 \pm 0.61	0.75	0.00 \pm 0.15	0.12	-0.02 \pm 0.26	0.20	-0.08 \pm 0.45	0.26	0.15 \pm 0.49	0.40
CWM SGR	0.20	0.00	0.04 \pm 0.24	0.21	0.47 \pm 0.62	0.85	0.07 \pm 0.30	0.26	-0.05 \pm 0.27	0.22	-0.15 \pm 0.53	0.35	0.08 \pm 0.37	0.26
500 m														
CWM SNPP	0.43	0.00	-0.04 \pm 0.23	0.19	-0.73 \pm 0.38	1.00	-0.08 \pm 0.31	0.31	-0.03 \pm 0.24	0.14	0.62 \pm 0.46	0.97	0.01 \pm 0.21	0.10
CWM ToR	0.25	0.00	0.05 \pm 0.25	0.22	0.61 \pm 0.40	1.00	0.03 \pm 0.20	0.16	0.10 \pm 0.34	0.39	-0.11 \pm 0.40	0.35	0.01 \pm 0.23	0.17
CWM SDM	0.15	0.00	0.03 \pm 0.22	0.18	0.11 \pm 0.41	0.35	0.15 \pm 0.43	0.46	0.07 \pm 0.32	0.28	-0.21 \pm 0.55	0.51	0.02 \pm 0.26	0.17
CWM PVH	0.07	0.00	0.06 \pm 0.29	0.27	0.25 \pm 0.51	0.64	0.02 \pm 0.19	0.16	0.06 \pm 0.29	0.27	-0.07 \pm 0.37	0.26	0.01 \pm 0.21	0.15
CWM SGR	0.33	0.00	0.03 \pm 0.20	0.12	0.52 \pm 0.54	0.91	0.07 \pm 0.32	0.23	0.05 \pm 0.26	0.18	-0.46 \pm 0.86	0.67	-0.22 \pm 0.63	0.42
750 m														
CWM SNPP	0.36	0.00	-0.08 \pm 0.33	0.27	-0.54 \pm 0.41	0.98	-0.07 \pm 0.31	0.21	-0.08 \pm 0.30	0.28	0.40 \pm 0.62	0.75	0.03 \pm 0.34	0.17
CWM ToR	0.35	0.00	0.08 \pm 0.32	0.32	0.58 \pm 0.35	1.00	0.03 \pm 0.19	0.17	0.16 \pm 0.39	0.52	-0.02 \pm 0.16	0.14	0.01 \pm 0.15	0.13
CWM SDM	0.20	0.00	0.03 \pm 0.25	0.17	0.05 \pm 0.27	0.24	0.17 \pm 0.45	0.48	0.20 \pm 0.46	0.56	-0.15 \pm 0.50	0.41	-0.01 \pm 0.32	0.17
CWM PVH	0.16	0.00	0.04 \pm 0.26	0.21	0.20 \pm 0.46	0.57	0.01 \pm 0.17	0.14	0.22 \pm 0.47	0.60	-0.05 \pm 0.31	0.22	0.00 \pm 0.24	0.17
CWM SGR	0.38	0.00	0.02 \pm 0.16	0.07	0.50 \pm 0.48	0.92	0.03 \pm 0.21	0.10	0.06 \pm 0.31	0.19	-0.68 \pm 0.94	0.79	-0.45 \pm 0.79	0.64

Appendix S12 Summary of the model-averaged estimates [\pm 95% confidence intervals (CI)] and relative importance (RI) of the community weighed mean trait values [Seed number per plant (SNPP), type of reproduction (ToR), seed dry mass (SDM), plant vegetative height (PVH) and seed germination rate (SGR)] to explain weed diversity and abundance in winter cereal fields [diversity: total species richness and Pielou's total evenness; abundance: mean total cover]. Both dependent and independent variables were calculated at the field scale (N = 27). Confidence intervals that did not encompass zero are in bold.

		Adj-R ²	Incerpt	CWM SNPP		CWM ToR		CWM SDM		CWM PVH		CWM SGR	
				Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI
Total richness	species	0.21	0.00	-0.01 \pm 0.28	0.14	0.18 \pm 0.52	0.46	0.30 \pm 0.67	0.59	-0.10 \pm 0.49	0.27	-0.29 \pm 0.73	0.52
Pielou's evenness	total	0.51	0.00	0.01 \pm 0.25	0.18	-0.01 \pm 0.16	0.15	0.25 \pm 0.54	0.59	-0.01 \pm 0.25	0.18	0.52 \pm 0.60	0.87
Mean total cover		0.46	0.00	0.16 \pm 0.47	0.43	0.14 \pm 0.39	0.47	0.06 \pm 0.31	0.25	0.01 \pm 0.24	0.12	-0.90 \pm 0.51	1.00

Partie III

Dynamique temporelle de connectivité et communautés végétales

Chapitre 3 : Effet de la dynamique temporelle de connectivité opérée au cours des sept dernières décennies sur la diversité spécifique et la structure fonctionnelle des communautés végétales boisées actuelles

1. Contexte scientifique

Au-delà de la connectivité spatiale, la nature dynamique de la connectivité doit être également explorée pour comprendre pleinement le rôle de la connectivité dans les mécanismes d'assemblage des communautés végétales. Cette deuxième partie vise à étudier les effets de la dynamique temporelle de la connectivité sur la structuration tant taxonomique que fonctionnelle des communautés végétales.

Un nombre croissant d'études empiriques souligne que les communautés végétales actuelles sont façonnées par la dynamique temporelle de connectivité, mais de manière implicite. En effet, ces travaux ont montré que les modifications de connectivité n'affectent pas forcément les processus de (re-)colonisation et d'extinction des espèces instantanément (pour des références, cf. ARTICLES 1 et 2). Dans la mesure où ces études se sont seulement focalisées sur le degré de connectivité à un ou à différents moments, les effets cumulés des changements temporels de connectivité sur les communautés végétales actuelles demeurent méconnus. Pourtant, Perry & Lee (2019) ont récemment montré qu'outre le degré de connectivité, l'intensité et la variabilité de ses changements temporels (ARTICLE 2) déterminaient le ratio entre les taux de colonisation et d'extinction des espèces. Sur la base de ce modèle récent de métapopulation, la théorie des métacommunautés (cf. introduction, section 1.2.4) permet de générer des prédictions nouvelles quant à l'effet de l'intensité et la variabilité des changements temporels de connectivité sur ces communautés.

Les prédictions, bien établies et préalablement développées, de l'effet du degré de la connectivité sur la diversité spécifique sont relativement connues, un fort degré de connectivité devant accroître la diversité spécifique (Mouquet & Loreau 2003). L'effet de l'intensité des changements temporels de connectivité est, quant à lui, susceptible de varier selon le type de tendance de connectivité auxquelles les tâches d'habitat sont soumises, cette tendance pouvant être ascendante ou descendante (i.e. perte ou gain de connectivité au cours du temps). Dans les tâches subissant une tendance ascendante, une forte intensité des changements temporels de connectivité augmente le ratio entre les taux de colonisation et d'extinction (Perry & Lee 2019), de sorte que la diversité spécifique devrait accroître. A l'opposé, une forte intensité des changements temporels de connectivité devrait décroître la diversité spécifique au sein des tâches subissant une tendance descendante de connectivité, en diminuant le ratio entre les taux de colonisation et d'extinction. Quant à l'effet de la variabilité des changements temporels de connectivité, il reste également peu étudié. Plus les périodes de très faible connectivité sont fréquentes, plus le ratio entre les taux de colonisation

et d'extinction diminue (Perry & Lee, 2019), ce qui devrait ainsi réduire la diversité spécifique au sein des tâches (Matias *et al.* 2013; Valanko *et al.* 2015; Stier *et al.* 2019).

Sur le plan fonctionnel, la théorie prédit qu'un fort degré de connectivité devrait favoriser les espèces possédant des valeurs de traits conférant une faible capacité de colonisation (Johst *et al.* 2002; Nathan 2006; Auffret *et al.* 2017b). Sur la base de ce postulat, un fort degré de connectivité devrait non seulement affecter la composition (i.e. valeur de trait agrégée; cf. ARTICLE 4), mais aussi accroître la diversité des valeurs de traits définissant les capacités de colonisation des espèces au sein des communautés (Zambrano *et al.* 2019). En transposant les effets taxonomiques précédemment évoqués, nous faisons l'hypothèse que l'intensité et la variabilité temporelle des changements temporels de connectivité agissent sur les valeurs des traits impliqués dans la colonisation des espèces au sein des communautés.

2. Objectifs

Cette troisième partie (**Chapitre 3**, ARTICLE 5) a pour objectif de déterminer l'influence de la dynamique temporelle de connectivité (i.e. le degré de connectivité, l'intensité et la variabilité des changements temporels de connectivité) sur la diversité spécifique et la structure taxonomique des communautés végétales.

Pour atteindre cet objectif, nous nous sommes intéressés à une dynamique de connectivité à long terme, les réponses décalées des communautés végétales étant jusqu'à présent essentiellement démontrées à l'échelle de plusieurs décennies (cf. ARTICLES 1 et 2 et références incluses). Nous nous sommes focalisés sur les communautés boisées qui constituent des candidates idéales pour notre étude, puisque nous avons démontré qu'elles sont particulièrement sensibles à la connectivité (e.g. ARTICLE 3) en plus d'être reconnues pour présenter de longs délais de réponse aux modifications paysagères, ceux-ci pouvant dépasser le siècle (e.g. Vellend *et al.* 2006; Naaf & Kolk 2015).

Nous souhaitons alors répondre aux questions suivantes : Quels sont les effets (i) du degré de connectivité, (ii) de l'intensité et (iii) de la variabilité des changements temporels de connectivité sur la diversité spécifique et la structure (composition et diversité) fonctionnelle des communautés végétales boisées actuelles ? Les effets de l'intensité des changements temporels de connectivité diffèrent-ils selon le type de tendance de connectivité (ascendante ou descendante) auxquelles les tâches d'habitat ont été soumises ?

3. Démarche mise en œuvre

Pour répondre à ces questions, nous avons détecté les « anciennes » tâches de bois qui subsistent dans le site agricole de Pleine-Fougères (i.e. établies antérieurement à 1952). Pour l'ensemble de ces tâches, nous avons, à partir de six dates (de 1952 à nos jours), mesuré la dynamique temporelle de connectivité par le biais de métriques nouvellement développés et dérivés de la théorie des circuits, mais également identifié leur type de tendance (ascendante ou descendante). Ensuite, 50 tâches ont été sélectionnées pour l'échantillonnage du couvert végétal, ces dernières présentant des tendances de connectivité ascendantes ou descendantes (cf. aussi partie I sections 2 et 3.1). Outre les mesures usuelles de diversité spécifique (richesse et équitabilité), la structure fonctionnelle des communautés boisées a été mesurée par la valeur agrégée et la diversité des valeurs de quatre traits liés aux capacités de colonisation des espèces (nombre de graines, type de reproduction, masse des graines et taux de germination).

4. Principaux résultats

Ce dernier chapitre réaffirme que la connectivité et les traits fonctionnels des espèces interagissent pour déterminer l'assemblage des communautés végétales. Nos résultats soulignent que seules l'intensité et la variabilité des changements temporels de connectivité (et non le degré) déterminent la structure des communautés boisées actuelles.

En l'absence de tout effet sur la diversité spécifique, nos résultats suggèrent que l'intensité et la variabilité des changements temporels de connectivité façonnent la composition en espèces, en agissant sur la structure fonctionnelle des communautés actuelles. La réponse fonctionnelle est modulée par le type de tendance de connectivité auxquelles les tâches ont été soumises. Dans les tâches subissant une tendance de connectivité ascendante, une forte intensité des changements temporels favorise les espèces possédant un fort investissement dans la reproduction sexuée, tandis que la variabilité n'a aucun effet. Dans les tâches subissant une tendance de connectivité descendante, la diversité des valeurs de masse des graines augmente avec une forte intensité et une faible variabilité des changements temporels de connectivité.

Cette partie fournit l'une des premières preuves que les effets cumulés de sept décennies de changements de connectivité, en favorisant ou en entravant la colonisation d'espèces selon la valeur de leurs traits, affectent l'assemblage des communautés végétales boisées actuelles. Dans des paysages où les communautés végétales actuelles sont toujours « hantées » par de tels effets, l'intégration de la dynamique temporelle de connectivité, au-

delà du simple degré de connectivité, est cruciale pour comprendre le rôle de la connectivité sur la biodiversité, aussi bien dans les études empiriques que dans les plans de conservation ou de restauration.

Chapitre 3

Effet de la dynamique temporelle de connectivité opérée au cours des sept dernières décennies sur la diversité spécifique et la structure fonctionnelle des communautés végétales boisées actuelles

Article 5. Unveiling the ghosts of landscapes past: changes in landscape connectivity over the last decades are still shaping current woodland plant assemblages

Léa Uroy, Aude Ernoult, Audrey Alignier, Cendrine Mony

Rejected after reviewing in *Ecography*, to be resubmitted

Abstract

In ever-changing landscapes, there is increasing evidence that current plant assemblages are shaped by the temporal dynamics of landscape connectivity. So far, attempts to take the temporal dynamics of connectivity into account have only focused on the degree of connectivity at moments in time, but neglected the cumulative effects of temporal changes in connectivity. Here, we investigated the effects of the temporal dynamics of landscape connectivity (i.e. the degree of connectivity, the magnitude and the variability of its temporal changes) over the last seven decades on current woodland plant herbaceous assemblages. The assemblages were described using a taxonomic approach combined with a functional approach based on four traits linked to the colonisation capacity of plant species. Our results showed that the degree of connectivity has not affected current woodland assemblages. The taxonomic diversity of current woodland assemblages did not respond to the magnitude and the variability of temporal changes, but the mean and/or the diversity of trait values linked to their colonisation capacity did. Responses were modulated by the type of connectivity trend experienced by woodlands. In woodlands experiencing an upward connectivity trend, high magnitude of temporal changes in connectivity favoured species which invest in sexual reproduction at the expense of vegetative multiplication whereas variability had no effect. In woodlands experiencing a downward connectivity trend, the diversity of seed mass values increased with high magnitude and low variability of temporal changes. Overall, we show that by selecting for particular traits values in species, the cumulative effects of decades of changes in connectivity shape woodland plant community assembly. This study opens new perspectives for integrating the temporal dynamics of landscape connectivity in the theoretical framework of plant assembly rules. It should also be considered in the development of operational strategies to restore and maintain connectivity.

Introduction

Habitat fragmentation is increasing rapidly over time, causing global biodiversity loss (Haddad *et al.* 2015; Fletcher *et al.* 2018) especially for plant species that are sessile and therefore strongly dispersal-limited (Ibáñez *et al.* 2014). Species inhabiting fragmented habitat patches are structured in metacommunities, i.e. a set of local communities linked by the dispersal of multiple potentially interacting species (Leibold *et al.* 2004). Species coexistence within these local communities is driven by the relative importance of dispersal fluxes, niche selection and drift across ecological time scales (Vellend 2010). Fluxes of dispersers are modulated by landscape connectivity, i.e. the degree to which the landscape elements facilitate the dispersal of plant species (Taylor *et al.* 2006). Therefore, improving connectivity among habitat patches should promote plant diversity in habitat patches by increasing (re-)colonisation thereby also reducing extinction rates (Damschen *et al.* 2019).

In a world of ever-changing landscapes, landscape connectivity is likely to vary over time. Despite calls for landscape connectivity research to go further in taking temporal dynamics into account (Kool *et al.* 2013; Zeigler & Fagan 2014), the use of time-varying connectivity in metacommunity models has been poorly explored. Indeed, gains or losses of landscape connectivity do not necessarily instantaneously affect plant assemblages in habitat patches but rather entail time-lagged responses (e.g. Lindborg & Eriksson 2004; Helm *et al.* 2006; Bommarco *et al.* 2014; Bagaria *et al.* 2019). Because previous studies have focused on how the degree of connectivity at a single or at several moments in time explains current plant assemblages, little is known about the cumulative effects of temporal changes in connectivity even though these may operate over years or even decades. In addition to the degree of connectivity itself (i.e. the connectivity value of the patch at a given moment in time), the magnitude (i.e. the strength at which the connectivity of the patch changes over time) and the variability (i.e. alternation of periods with the patch being highly connected and periods with the patch being only slightly connected) (**Fig. 1**) of its temporal changes have recently been shown to determine the ratio between the colonisation and extinction rates of species (Perry & Lee 2019). For instance, in patches experiencing an upward trend in connectivity, a high magnitude of temporal changes in connectivity is likely to increase the ratio between the colonisation and extinction rates of species, hence promoting species richness inversely to those experiencing a downward trend in connectivity. Predicting the effect of the variability of temporal changes in landscape connectivity is less straightforward. The ratio between colonisation and extinction rates has been shown to decrease as low

connectivity periods become more frequent and severe due to the increasing probability of extinction (Perry & Lee 2019), thereby reducing species diversity in patches (Matias *et al.* 2013; Valanko *et al.* 2015; Stier *et al.* 2019). The ecological processes underlying the responses of plant assemblages to the temporal dynamics of connectivity are not yet known but may be analysed using a functional approach.

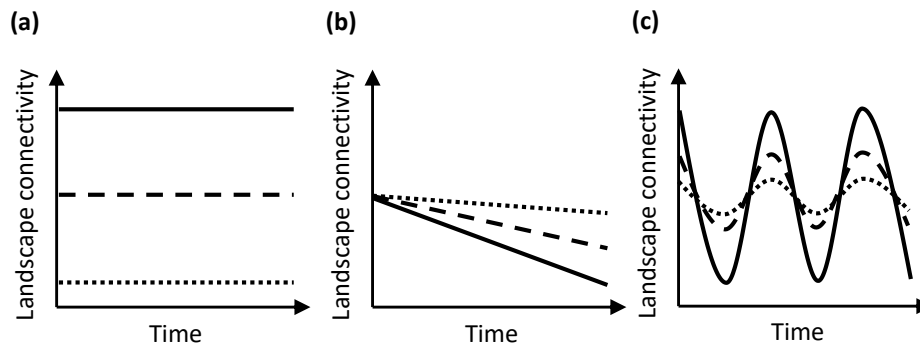


Fig. 1 Schematic plots illustrating each of the three components and their varying levels describing the temporal dynamics of landscape connectivity when all other components are fixed: **(a)** degree of connectivity (i.e. the connectivity value of the patch at a given moment in time), **(b)** magnitude (i.e. the strength at which the connectivity of the patch changes over time) and **(c)** variability (i.e. alternation of periods with the patch being highly connected and periods with the patch being only slightly connected) of the temporal changes in landscape connectivity. The magnitude of the temporal changes in landscape connectivity is represented for a patch experiencing a downward trend in connectivity. Solid, dashed and dotted lines represent their high, medium and low levels, respectively.

A shift away from a taxonomic to a functional lens is thus needed to obtain new insights into the processes involved in how current plant assemblages respond to the temporal dynamics of connectivity. For plants, seed production, dispersal and establishment are key processes in shaping their colonisation capacity (Eriksson 2000). Higher species' sensitivity to changes in connectivity can be related to a set of functional trait values which characterise low colonisation capacity (Zambrano *et al.* 2019). It might thus result from a high investment in vegetative reproduction rather than in sexual reproduction (Kolb & Diekmann 2005), seeds being the only type of propagule that enables long-distance dispersal (Starfinger & Stöcklin 1996). Higher species' sensitivity may also result from the low production of dispersers (fewer seeds, Verheyen *et al.* 2004), their big size which influences their ability to be dispersed over long distances (heavier seeds, Lindborg *et al.* 2012) and their limited success in germinating when they arrive in a patch (low seed germination rate, Favre-Bac *et al.* 2017a). Thus, a general hypothesis is that reduced connectivity disadvantages species with a particular set of traits values which in turn, reduces the colonisation capacity of plant species, affecting the mean and reducing the diversity of trait values (Zambrano *et al.* 2019). Transposing taxonomic

effects, the magnitude and the temporal variability of the temporal changes in connectivity might then also affect trait values related to colonisation capacities in species assemblages.

Here, we evaluated the effects of the temporal dynamics of landscape connectivity (i.e. the degree of connectivity, the magnitude and the variability of the temporal changes in connectivity) on the taxonomic diversity and on the functional structure of current woodland herbaceous assemblages. Woodland herbaceous assemblages are known to display long-lasting lagged responses to landscape changes (Vellend *et al.* 2006; Naaf & Kolk 2015), which makes them good candidate species to test our predictions. We analysed the effect of connectivity dynamics using landscape datasets in six time steps (1952 to the present) to examine these relationships in woodlands experiencing upward or downward trends of connectivity. The functional structure of woodland plant assemblages was evaluated using the mean and the diversity of trait values for four traits related to the colonisation capacity of plant species. We specifically tested the following hypotheses:

H1: The taxonomic diversity and the functional structure of current plant assemblages are better explained by simultaneously considering the degree of connectivity, the magnitude and the variability of the temporal changes in connectivity rather than by only considering the degree of connectivity.

H2: A high degree of connectivity, a high/low (upward/downward trend) magnitude and low variability of temporal changes in connectivity increase the taxonomic diversity of current plant assemblages.

H3: A high degree of connectivity, a high/low (upward/downward trend) magnitude and low variability of temporal changes in connectivity affect the mean and increase the diversity of trait values by favouring species with trait values that confer low colonisation capacity.

Methods

Study area and history of wooded habitats

This study was conducted in the Long-Term Socio-Ecological Research (LTSER) site of “Zone Atelier Armorique” (ZAAR, ca. 130km²) in Brittany, France (48°36′N, 1°32′W). The topology is flat, the soil is underlain by granitic and sandstone bedrocks and the climate is temperate oceanic. The study site is an agriculture-dominated landscape, interspersed with woodlands and a dense network of hedgerows. It also includes a large ancient forest in the south. Most of these woodlands are dominated by *Castanea sativa*, *Fagus sylvatica* and *Quercus Robur*

originating both from their original planting composition and their spontaneous succession. Hedgerows are composed of trees including *Quercus robur* or *Castanea sativa* generally planted on an earthen bank (Burel *et al.* 1998).

The landscape of the study site has undergone major modifications since the mid-late 1950s because of successive policies, particularly the European common agricultural policy (CAP). The consequence of these policies, which were designed to accommodate agricultural intensification (e.g. cutting of hedgerows due to reparation) and progressively accompanied by greening measures (e.g. the planting of post-agricultural woodlands and, to a lesser extent, hedgerows), on the land cover and area of woodlands and hedgerows can be traced back in landscape maps in databases covering our study area. Land cover maps (ZAAr vector database) and the wooded habitat cover maps (Kermap raster database) were established from aerial images with a resolution of 5 m. Land cover maps were classified in seven categories: grasslands, crops, woodlands, paved roads, paths, built-up areas and water bodies. The wooded habitat cover maps comprised woodlands and hedgerows. From these databases, we selected six time steps (**Supplementary Fig. S1a**), related to the different policies implemented and available aerial imagery: 1952 (the oldest available map, hereafter referred to as the initial state of the landscape), 1974, 1985, 2000, 2006 and 2016 (the most recent available map, hereafter referred to as the current state of the landscape). Overall, these different policies resulted in a sharp decrease (ca. 61%) in hedgerow cover between 1952 and 1985, followed by a slight increase (ca. 15%) between 1985 and 2016. Over the whole period, woodland cover increased slightly (ca. 31%), whereas the mean area of woodland cover patches decreased (ca. 42%) (**Supplementary Fig. S1b-c**).

Assessment of the temporal dynamics of landscape connectivity

(1) Landscape connectivity

We used the circuit theory (McRae *et al.* 2008) to assess the landscape connectivity of the remaining “old” woodland patches (i.e. established before 1952) for each time step (i.e. 1952, 1974, 1985, 2000, 2006 and 2016). This modelling method is based on inter-patch distances. It assumes that dispersal follows random walks and includes all possible dispersal pathways between two habitat patches, depending on the resistance (i.e. ecological cost) of the landscape elements to dispersal.

We detected the remaining “old” woodland patches on land cover maps. For each time step, woodland patches located at a distance of less than 20 m from each other – i.e. the short-

distance dispersal distance of plants (Howe & Smallwood 1982) – were considered as belonging to the same patch, except patches crossed by a paved road. The geographical union of these woodland patches from all the time steps was computed to construct a detailed history of woodland continuity. We selected all woodland patches that have been continuously wooded since 1952 comprising an area > 0.1 ha, this area covering, on average, at least one-tenth of the area of the woodland patch at each time step studied. A total of 255 woodland patches that fulfilled these criteria were detected at our study site (Fig. 2a).

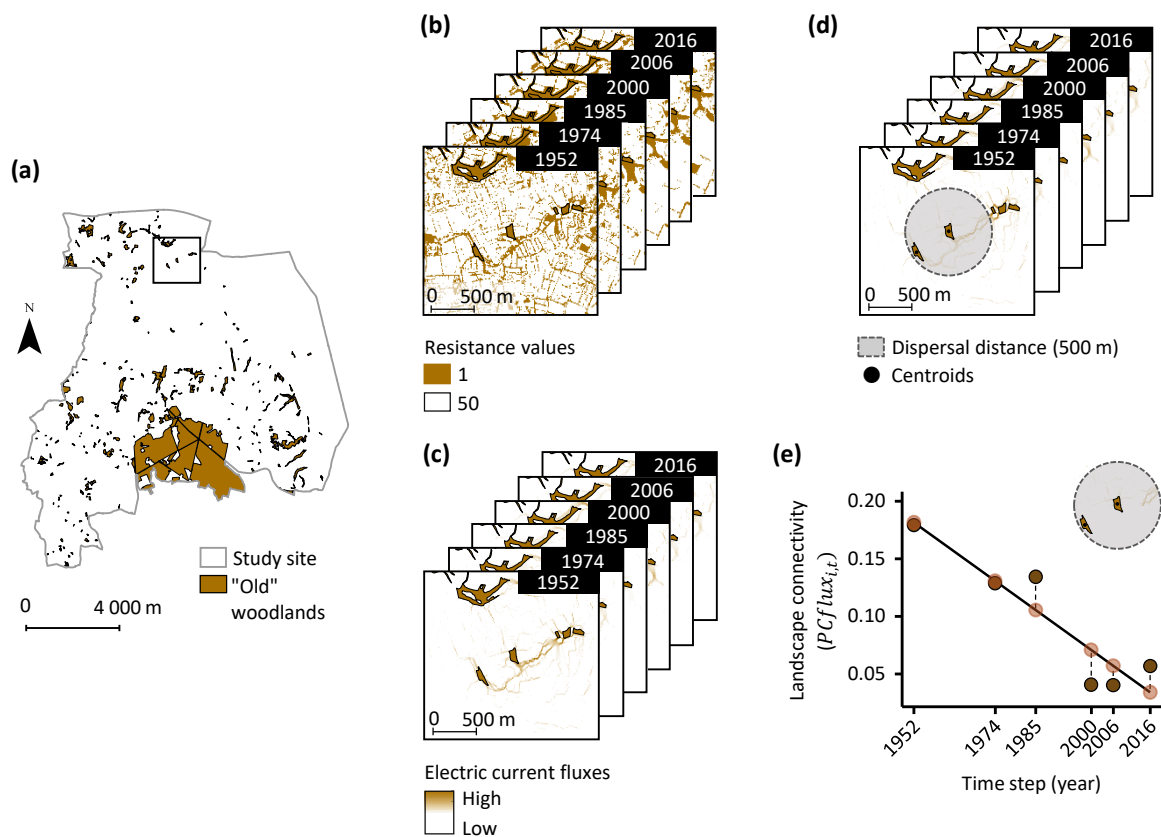


Fig. 2 Illustration of the method used to model landscape connectivity and its temporal dynamics in the remaining “old” woodland patches. **(a)** Detection of the “old” woodland patches in our study site. **(b)** Design of the resistance maps for each time step t (1952, 1974, 1985, 2000, 2006 and 2016). Wooded habitats obtained a minimum resistance value of 1, whereas other types of habitats obtained a maximum resistance value of 50. **(c)** Calculation of the resistance distance between pairs of woodland patches for each time step t from the circuit theory, here graphically represented by the cumulative electric current fluxes using the Circuitscape 4.0.5 software (McRae *et al.* 2008). For a given woodland i : **(d)** Assessment of the landscape connectivity using the potential dispersal flux ($PCflux_{i,t}$) index for each time step t . For a dispersal distance of 500 m around the given woodland i , only resistance distance(s) between woodland patches annotated by their respective centroids were included; **(e)** Assignment of the initial state of landscape connectivity ($PCflux_{i,1952}$), the slope ($|slope_i|$) and the residual standard error (RSE_i) – the two latter derived from the single ordinary least squares regression model – as the degree of landscape connectivity, the magnitude and the variability of the temporal changes in landscape connectivity, respectively.

We assessed the dispersal distance between pairs of “old” woodland patches as a function of the presence of suitable habitats for the dispersal of woodland plant species, that is, wooded habitats (i.e. woodlands and hedgerows). We then calculated resistance maps based on wooded habitat cover maps for each time step (giving a total of six resistance maps), by classifying wooded habitats with a minimum resistance value of 1 (i.e. highly suitable for dispersal) and other habitat types with a maximum resistance value of 50 (i.e. hardly suitable for dispersal) (**Fig. 2b**). The distance between pairs of patches was then assessed from each resistance map as the resistance distance using the R package “gdistance” (van Etten 2017) (**Fig. 2c**).

For each time step t studied, the connectivity of each “old” woodland patch i ($n = 255$) was assessed using the “Potential Dispersal Flux” index ($PCflux_{i,t}$, Saura & Rubio 2010). This index corresponds to the dispersal flux (Urban & Keitt 2001) through the connections of a given woodland patch i with all other patches in the landscapes for a time step t . It is given by: $PCflux_{i,t} = \sum_{j=1, j \neq i}^{n-1} p_{ij,t}^*$, where $p_{ij,t}^*$ is the maximum product probability of all potential paths between pairs of woodland patches, i and j , in the landscape for a time step t (Saura & Pascual-Hortal 2007). The probability of dispersal ($p_{ij,t}$) between pairs of woodland patches at a given time step t was modelled as a negative exponential function of the dispersal distance between woodland patches (Saura & Pascual-Hortal 2007). We calculated the $PCflux_{i,t}$ index using a potential maximum dispersal distance of 500 m (**Fig. 2d**), as it is often considered to be the spatial extent at which landscape processes best predict herbaceous woodland plant species (i.e. the “scale of effect”, Jackson & Fahrig 2015) (e.g. van Ruremonde & Kalkhoven 1991; Usher *et al.* 1992; Petit *et al.* 2004; Bagaria *et al.* 2019; Vanneste *et al.* 2019). The potential maximum dispersal distance of 500 m was converted into resistance distance using the maximum resistance distance observed over the whole period (i.e. all time steps combined) between two habitat patches separated by a Euclidean distance smaller than 500 m. This “converted” potential maximum dispersal distance was then used to set the decay rate of the negative exponential function at $p_{ij} = 0.01$. These calculations were made using Conefor 2.6 software (Saura & Torné 2009). $PCflux_{i,t}$ index obtained was overly correlated between each time step (Pearson correlations, $0.82 \leq r \leq 0.98$)

(2) Temporal dynamics of connectivity

The temporal dynamics of landscape connectivity of each “old” woodland patch over the whole study period were assessed using the connectivity indices obtained for each individual

time step. In particular, the temporal dynamics of landscape connectivity was described using three components: (i) the degree of connectivity (ii) the magnitude and (iii) the variability of the temporal changes in connectivity (**Fig. 2e**). First, the degree of connectivity of each woodland patch i was evaluated by the initial state of landscape connectivity using the “Potential Dispersal Flux” index obtained for the first time step, 1952 ($PCflux_{i,1952}$). Since $PCflux_{i,1952}$ were overly correlated with the $PCflux_{i,t}$ of other time steps t (see above), we assumed it reflects the degree of connectivity of a given woodland patch i . Second, the magnitude and the variability of the temporal changes in the connectivity of each woodland patch i were quantified by performing an ordinary least squares (OLS) regression model for each woodland patch i , with $PCflux_{i,t}$ as the dependent variable and time step t (1952, 1974, 1985, 2000, 2006 and 2016) as the independent variable. We then used the absolute value of the slope ($|slope_i|$) and the residual standard error (RSE_i) of each OLS regression model as proxies of the magnitude and the variability of the temporal changes in the connectivity of each woodland patch i , respectively. The higher the (i) $PCflux_{i,1952}$, (ii) $|slope_i|$ and (iii) RSE_i , the higher (i) the degree of connectivity (ii) the magnitude and (iii) the variability of the temporal changes in the connectivity of the woodland patch i . The sign of the slope of each OLS regression model was also extracted to obtain information about the trend of connectivity values (i.e. upward or downward) to select the “old” woodland patches to be sampled.

Sampling design

To compare the effect of the temporal dynamics of the landscape connectivity on woodland assemblages between upward and downward temporal trends, we selected a total of 50 woodlands to be sampled out of the 255 “old” woodlands in our study site. We specifically selected 20 and 24 woodlands characterised by upward and downward connectivity trends, respectively. Six woodlands were also selected as controls since they remained completely isolated during the study period ($PCflux_{i,t} = 0$) and were characterised by a null trend ($PCflux_{i,1952} = 0$, $PCflux_{i,t} = 0$, $|slope_i| = 0$ and $RSE_i = 0$). Further details about the trend of connectivity experienced by each selected woodland are given in **Supplementary Fig. S2**.

The 50 selected woodlands were distributed across the study site, with a distance of at least 200 m between woodland edges. Their area (mean: 1.11 ha, range: 0.16–5.78), their dominant tree species composition, and their management regime (i.e. extensively managed) were also standardised according to the typical characteristics of these woodlands in our

study site. We also checked that the distribution of values of the three components of the temporal dynamics of landscape connectivity of the selected woodlands was consistent with that observed for all the "old" woodlands detected in our study area (**Supplementary Fig. S3**).

Floristic surveys were conducted in the 50 woodlands from late-May to mid-June 2019. We identified each vascular herbaceous species and estimated its abundance (as percentage cover) using eight 10 m x 8 m quadrats, following the minimum recommended sampling area for woodland assemblages (Mueller-Dombois & Ellenberg 1974). These quadrats were evenly distributed within the woodland at least 5 m from the edge. In the three smallest woodlands, only six quadrats were performed following this distribution. The species composition and species abundance were pooled at the woodland level from the six or eight quadrats. We then weighted the total abundance of each species by the number of quadrats, to account for the disequilibrium in subsequent analyses. Woody species were not recorded due to their dependence on the initial planting composition and management regime of the woodland.

Taxonomic diversity of woodland plant assemblages

The taxonomic diversity of each "old" woodland assemblage was assessed using total species richness and Pielou's evenness, using the "vegan" R package (Oksanen *et al.* 2019). These metrics were not correlated (Pearson correlation, $r = 0.14$, $p = 0.35$) nor spatially auto-correlated (Moran's I test, $p > 0.05$). Sørensen's similarity index between each pair of woodlands was also estimated using the "ade4" R package (Dray & Dufour 2007) to obtain additional information on taxonomic similarity in woodland composition.

Functional structure of woodland plant assemblages

Four functional traits related to colonisation capacity were chosen: the number of seeds per plant, seed dry mass, seed germination rate, and type of reproduction (**Table 1**). We did not consider seed bank persistence nor life-span, as most woodland plant species are long-lived perennials (84.4% of the species recorded in our study according to the Bioflor database, Kühn *et al.* 2004) and have a transient seed bank (80.9% of the species recorded according to the LEDA database, Kleyer *et al.* 2008). Continuous traits (number of seeds per plant, seed dry mass and seed germination rate) were obtained from the TRY global plant trait database (Kattge *et al.* 2011). Trait values with an error risk < 4 (cf. Kattge *et al.* 2011) were averaged per trait and per species, following an outlier detection and removal procedure assuming normal distribution of values per trait and per species (4.4% of the continuous trait values

dataset). The ordinal trait (type of reproduction, describing the investment in vegetative reproduction) was obtained from the BiolFlor database (Kühn *et al.* 2004). We estimated missing trait values using multivariate imputation with the chained equation procedure (Penone *et al.* 2014; Taugourdeau *et al.* 2014), using the family of each species as nested blocks assuming phylogenetic conservatism (Baeten *et al.* 2015). This procedure was performed with the “mice” R package (van Buuren & Groothuis-Oudshoorn 2011). Continuous traits were transformed before analysis to achieve normality (**Table 1**). The selected traits were not overly correlated (Pearson correlations, $-0.39 \leq r \leq 0.15$).

Table 1 Overview of the functional traits investigated. The distribution of traits [mean \pm SE (standard error of the mean); min-max] are indicated before the transformation of any continuous trait. Availability denotes the percentage of species for which the trait value was available in plant trait databases before multivariate imputation using the chained equation (MICE) procedure. See the Methods section for more details.

Trait	Type	Transformation	Unit	Mean \pm SE	Min – Max	Availability (%)
Number of seeds per plant	Continuous	Log	1/plant	4844.9 \pm 1313.1	10.0 – 70250.0	87.6
Seed dry mass	Continuous	Log	mg	2.8 \pm 0.7	0.0 – 47.6	97.8
Seed germination rate	Continuous	Logit	%	91.7 \pm 1.0	55.0 – 100.0	82.0
Type of reproduction	Ordinal	–	1: by seed; 2: mostly by seed, rarely vegetatively; 3: by seed and vegetatively; 4: mostly vegetatively, rarely by seed	2.6 \pm 0.1	1 – 4	97.8

To assess the functional structure of each “old” woodland assemblage, we quantified the mean and the diversity of the trait values using community-weighted mean (CWM; Garnier *et al.* 2004) and Rao’s quadratic entropy (RaoQ; Rao 1982). CWM expresses the mean trait value in the community weighted by the relative abundances of the species. RaoQ combines both functional richness (i.e. the range of trait values) and divergence (i.e. the position of dominant species relative to the centre of the trait range) (Mason *et al.* 2005; Botta-Dukát & Czucz 2016) by quantifying the sum of pairwise distances between species weighted by their relative abundance. CWM and RaoQ were calculated for each trait and each woodland assemblage using the R package “FD” (Laliberté *et al.* 2014). The CWM and RaoQ of seed dry mass were correlated with those of the number of seeds per plant (Pearson correlations, CWM: $r = -0.58$, $p < 0.001$ and RaoQ: $r = 0.31$, $p < 0.05$). The CWM of the number of seeds per plant was also correlated with the CWM of the type of reproduction (Pearson correlations, CWM: $r = -0.33$, $p < 0.05$).

Statistical analysis

We investigated the effects of the temporal dynamics on the taxonomic diversity and the functional structure of woodland plant assemblages for each type of connectivity trend: upward (N = 20) and downward (N = 24). All the controls (i.e. woodlands characterised by a null trend) (N = 6) were included in both datasets for subsequent analysis.

First, we investigated the effects of the temporal dynamics of connectivity (degree of landscape connectivity, magnitude and variability of its temporal changes) on the taxonomic diversity of woodland plant assemblages. We used a (i) binomial generalised linear model with a logit link-function and (ii) a multiple ordinary least squares (OLS) regression model to assess the effects of the temporal dynamics of connectivity on species richness and Pielou's evenness, respectively. Second, we used multiple OLS regression models to assess the effects of the temporal dynamics of connectivity on the functional structure of woodland plant assemblages (CWM and RaoQ of the number of seeds per plant, seed dry mass, seed germination rate and type of reproduction).

Prior to model optimisation, collinearity between independent variables was tested using the variance inflation factor (VIF). The independent variables had VIF values < 5 , indicating negligible collinearity (O'Brien 2007; Hair *et al.* 2014). All the models were optimised using a multi-model inference based on the bias-corrected Akaike information criterion (AICc). In this way, we built all possible candidate models based on all additive combinations of independent variables and assigned them Akaike weights. We retained as the most parsimonious, models with a $\Delta AICc < 2$ according to Burnham & Anderson (2002). When more than one model was retained, we used a model averaging approach to account for uncertainty in the selection process (Burnham & Anderson 2002). The full-model averaged estimates and 95% confidence intervals of each independent variable were generated across the most parsimonious models. Independent variables were considered significant if their 95% confidence intervals did not overlap zero. Model averaging was performed using "MuMIn" R package (Barton 2018). All statistical analyses were conducted in R version 3.5.1.

Results

A total of 89 herbaceous plant species were recorded. Woodland plant assemblages contained from zero to 28 herbaceous plant species, with 9.3 ± 0.9 (mean \pm SE) species on average. The Pielou's evenness of woodland assemblages ranged from zero to 0.98 (mean \pm SE: 0.66 ± 0.03). Sørensen's similarity between woodland assemblages ranged from zero to 0.76 (mean \pm SE: 0.22 ± 0.01). The distributions of the mean (CWM) and the diversity (RaoQ) of the trait values for the four traits studied are summarized in **Table 2**.

Table 2 Functional characteristics of woodland plant assemblages. The distribution of each community-weighted mean (CWM) and Rao's quadratic entropy (RaoQ) are given for each trait studied (number of seeds per plant, seed dry mass, seed germination rate and type of reproduction). ⁽¹⁾ and ⁽²⁾ indicates traits that were (1) log- and (2) logit-transformed beforehand to meet normality. SE = standard error of the mean

Trait	CWMs		RaoQ	
	Mean \pm SE	Min – Max	Mean \pm SE	Min – Max
Number of seeds per plant ⁽¹⁾	5.86 ± 0.13	4.47 – 8.29	0.44 ± 0.07	0.00 – 2.31
Seed dry mass ⁽¹⁾	0.36 ± 0.11	-1.84 – 2.12	0.53 ± 0.06	0.00 – 2.08
Seed germination rate ⁽²⁾	2.08 ± 0.09	0.98 – 3.66	0.75 ± 0.07	0.00 – 1.75
Type of reproduction	3.15 ± 0.07	2.08 – 3.97	0.68 ± 0.09	0.00 – 2.43

Effects of the temporal dynamics of landscape connectivity on the taxonomic diversity of woodland plant assemblages

The degree of landscape connectivity, the magnitude and the variability of the temporal changes in landscape connectivity did not affect species richness nor Pielou's evenness of plant assemblages whatever the connectivity trend (upward or downward) (**Table 3**).

Effects of the temporal dynamics of landscape connectivity on the functional structure of woodland plant assemblages

Two traits were significantly related to the magnitude and/or the variability of the temporal changes in landscape connectivity: the type of reproduction in woodlands experiencing an upward connectivity trend and seed dry mass in woodlands experiencing a downward connectivity trend. In woodlands experiencing upward connectivity trends, the CWM of type of reproduction was negatively related to the magnitude of the temporal changes in landscape connectivity. In woodlands experiencing downward connectivity trends, the RaoQ of seed dry mass was positively related to the magnitude and negatively related to the variability of the temporal changes in landscape connectivity (**Table 3, Fig. 3**).

Table 3 Summary of the model-averaged estimates \pm 95% confidence interval (CI) and relative importance (RI) of the effects of the temporal dynamics of landscape connectivity [the degree of landscape connectivity ($PCflux_{i,1952}$), magnitude ($|slope_i|$) and variability (RSE_i) of the temporal changes in landscape connectivity] on the taxonomic (species richness, Piélou’s evenness) and functional structure [community-weighted mean (CWM) and Rao’s quadratic entropy (RaoQ) of the number of seeds per plant, seed dry mass, seed germination rate and type of reproduction] of woodland plant assemblages. Models were performed for each type of woodland experiencing either an upward (upward woodlands) or a downward (downward woodlands) trend of connectivity. Models with only intercept values indicate a null model (i.e. a model with no independent variables). 95% confidence intervals that did not encompass zero are in bold.

	Model	Intercept	$PCflux_{i,1952}$		$ slope_i $		RSE_i	
	N		Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI	Estimate \pm 95% CI	RI
Taxonomic structure								
<i>Upward trending woodlands</i>								
Species richness	26	2.35			19.75 \pm 89.54	0.32		
Piélou’s evenness	26	0.66	0.02 \pm 0.12	0.28				
<i>Downward trending woodlands</i>								
Species richness	30	2.10	-0.09 \pm 0.30	0.38			-0.41 \pm 1.52	0.31
Piélou’s evenness	28	0.69	0.04 \pm 0.13	0.37	6.63 \pm 19.50	0.44	-0.88 \pm 1.10	0.88
Functional structure								
<i>Upward trending woodlands</i>								
CWM								
Number of seeds per plant	26	5.79						
Seed dry mass	26	0.48			-15.75 \pm 83.14	0.25	-0.65 \pm 3.28	0.26
Seed germination rate	26	2.15			20.06 \pm 83.55	0.35		
Type of reproduction	26	3.22	0.14 \pm 0.50	0.30	-124.17 \pm 106.98	1	1.60 \pm 4.39	0.44
RaoQ								
Number of seeds per plant	26	0.56					-0.97 \pm 3.21	0.42
Seed dry mass	26	0.47	0.04 \pm 0.26	0.28				
Seed germination rate	26	0.89			20.53 \pm 92.52	0.24	-1.90 \pm 4.71	0.57
Type of reproduction	26	0.65			39.41 \pm 107.97	0.46	0.36 \pm 2.28	0.18
<i>Downward trending woodlands</i>								
CWM								
Number of seeds per plant	28	5.86	0.04 \pm 0.25	0.22			0.19 \pm 1.43	0.21
Seed dry mass	28	0.46	-0.06 \pm 0.30	0.26			-0.22 \pm 1.48	0.21
Seed germination rate	28	1.91	0.03 \pm 0.18	0.16	25.03 \pm 64.41	0.53	-0.75 \pm 2.72	0.30
Type of reproduction	28	3.14	0.02 \pm 0.12	0.21			0.17 \pm 0.89	0.26
RaoQ								
Number of seeds per plant	28	0.43						
Seed dry mass	28	0.40	0.16 \pm 0.33	0.63	53.19 \pm 39.71	1	-2.29 \pm 1.68	1
Seed germination rate	28	0.93	-0.16 \pm 0.28	0.70			-0.34 \pm 1.25	0.30
Type of reproduction	28	0.58						

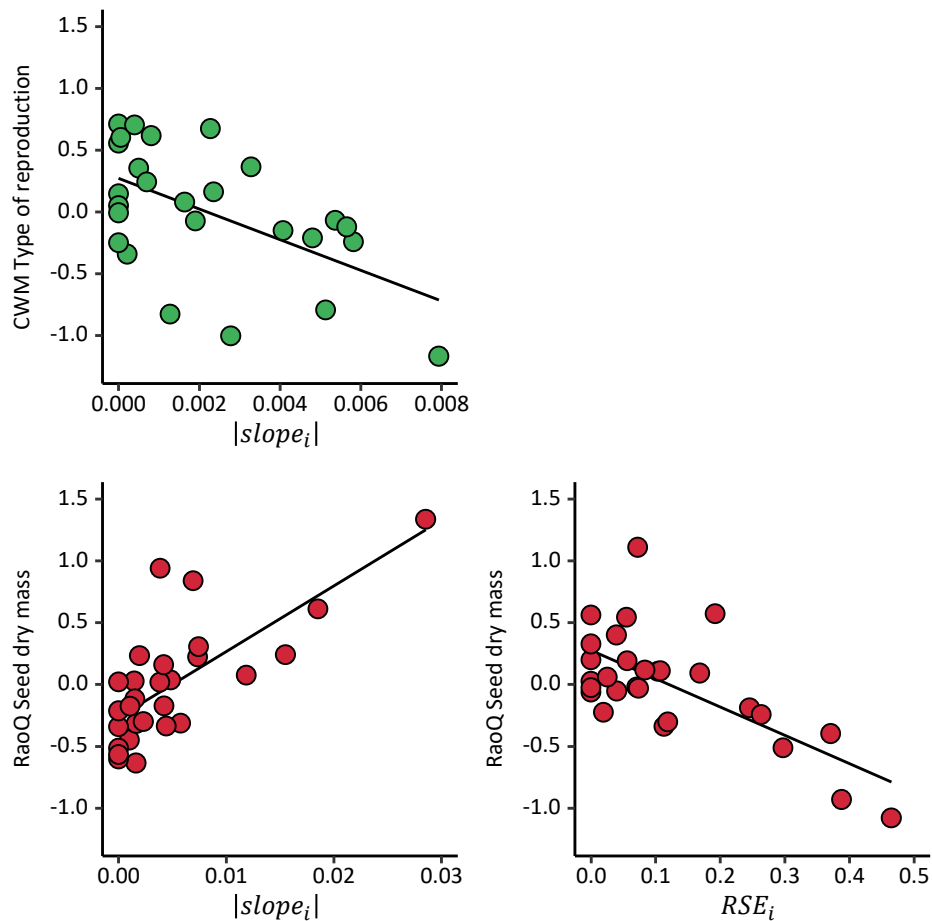


Fig. 3 Partial residual plots showing the significant effects of the temporal dynamics of landscape connectivity on woodland plant assemblages for woodlands characterised by an upward (green dots) and a downward (red dots) trend of connectivity. CWM = community weighed mean. RaoQ = Rao's quadratic entropy. $|slope_i|$ = the magnitude of temporal changes in landscape connectivity. RSE_i = the variability of temporal changes in landscape connectivity.

Discussion

The magnitude and the variability of temporal changes in connectivity drive current woodland plant assemblages

In agreement with our first hypothesis (H1), accounting for the independent effects of the degree of connectivity, the magnitude and the variability of temporal changes in connectivity improved our ability to predict current plant assemblages' response to the temporal dynamics of connectivity. It is worth noting that only the magnitude and the variability of temporal changes (not the degree) in connectivity drive current woodland plant assemblages. These findings support previous theoretical (Keymer *et al.* 2000) and empirical evidence in other wooded ecosystems (Metzger *et al.* 2009) underlying the overriding effect of the magnitude of temporal changes in landscape-scale processes. Our findings suggest that these statements extend to the temporal changes in landscape connectivity (i.e. its magnitude and variability)

and woodland plant species assembly, probably due to their long life cycle and poor dispersal capacity (Ehrlén & Lehtilä 2002; Hermy & Verheyen 2007).

Plant functional response to temporal changes in connectivity is modulated by the type of connectivity trend

Contrary to what we expected (H2), the taxonomic diversity of current woodland plant assemblages did not respond to either the magnitude or the variability of temporal changes in connectivity. Our results suggest that temporal changes in landscape connectivity did not promote species coexistence in woodland patches but rather drove a shift in species composition. This shift may be driven by particular trait values related to the colonisation capacity of plant species, hence warranting further investigation into the functional structure of woodland plant assemblages.

The magnitude of the temporal changes in connectivity did not have the same effect on the functional structure of current plant assemblages, depending on whether the woodlands experienced upward or downward connectivity trends, supporting our third hypothesis (H3) for this particular effect. Specifically, in woodland assemblages experiencing upward connectivity trends, we demonstrated that a high magnitude of the temporal changes in connectivity did not affect the diversity of trait values for any given trait, but favoured species investing mostly in sexual reproduction at the expense of vegetative reproduction. This suggests that by promoting long dispersal distance events, a higher investment in sexual reproduction in woodland herbaceous species (Starfinger & Stöcklin 1996) may favour faster colonisation of woodland patches (Brunet *et al.* 2012). Species that reproduce sexually may thus benefit most from a marked increase in connectivity over time (Naaf & Kolk 2015). Besides, by arriving first in woodland patches, these species may have a competitive numerical advantage over others (i.e. priority effects, Drake 1991), that could be the slow and hence late-arriving colonists, characterised by their higher investment in vegetative reproduction. This would have resulted in the shift of composition actually observed in the woodland.

In woodland assemblages experiencing downward connectivity trends, a high magnitude of temporal changes in connectivity increased the diversity of seed mass values but without affecting the mean value. The marked decrease in dispersal fluxes, and hence in the colonisation rates in the woodland patch increased the importance of local-scale factors (i.e. niche differences) in shaping woodland community assembly (Leibold *et al.* 2004). As seed

mass displays competitive ability during establishment (Leishman *et al.* 2000), higher diversity in trait values may indicate that limiting similarity (MacArthur & Levins 1967) shapes current woodland species assembly due to competitive interactions among species. Moreover, the functional structure of current woodland assemblages experiencing a downward connectivity trend depended on the variability of the temporal changes in connectivity, while those experiencing an upward connectivity trend did not. This finding suggests that by reducing dispersal fluxes thereby increasing extinction rates, periods of low connectivity have a stronger effect on assemblages that are becoming increasingly isolated than on assemblages that are becoming increasingly connected. In particular, in woodlands experiencing downward connectivity trends, current woodland assemblages displayed a reduced diversity of seed mass values in response to the high variability of the temporal changes in landscape connectivity, with no change in the associated mean values. This finding suggests that species with extreme seed mass values, either the lowest or the highest of the regional species pool of woodlands, were less able to colonise these woodlands. Two non-mutually exclusive hypotheses could explain this observation. First, species with light seeds generally disperse over long distances (Muller-Landau *et al.* 2008) but an increasing proportion of their seeds is lost in the inhospitable matrix among patches in low connectivity periods (Ouborg *et al.* 2006). Because light seeds do not survive long during the early stage of seedling establishment (Moles & Westoby 2004), the probability of their successful establishment along the dispersal pathway may decrease, preventing them from pursuing their dispersal in a context of ever-changing connectivity where only some periods are favourable for dispersal. Second, species with heavy seeds may also experience increased difficulty dispersing as connectivity declines over time, especially during low connectivity periods, due to their short-distance dispersal (Muller-Landau *et al.* 2008). The limited persistence of heavy seeds in the soil (Leishman *et al.* 2000) combined with the increased risk of predation (Orrock *et al.* 2003) or parasitism (Sullivan *et al.* 2011) of seeds immobilized along the dispersal pathways during low connectivity periods means they cannot postpone a new dispersal event until the occurrence of high connectivity period.

Lastly, we found no evidence that the number and germination of seeds played a role in the strategies used by woodland species to overcome the magnitude and/or the variability of the temporal changes in landscape connectivity. This finding suggests that two processes that influence the colonisation capacity of plant species, i.e. the production of dispersers and the successful germination of dispersers once they arrive, are not among the strategies used by woodland community assemblages facing decades of connectivity changes.

Current plant assemblages are haunted by the cumulative effects of decades of connectivity changes

This study provides some of the very first evidence that the cumulative effects of decades of connectivity changes exert a strong influence in shaping woodland plant community assembly, by favouring or disadvantaging species with particular trait values involved in the colonisation process. In particular, the magnitude and the variability of these changes drive functional traits values in the community. Overall, our findings underline the need to better integrate landscape connectivity temporal dynamics in metacommunity theory, as its role in driving the temporal intensity and the fluctuation dispersal fluxes over time and subsequently in shaping community assembly has not yet been incorporated. This study also opens up new perspectives for connectivity research and application. It underlines the need to use a new method which simultaneously accounts for the different components of the temporal dynamics of landscape connectivity to reveal the real dispersal processes of plants. Strategies to conserve and restore landscape connectivity, which are often based on moments in time, should go further by including the cumulative effect on biodiversity of past changes in connectivity.

Acknowledgements

We thank L. Broudic, M. Bijou for their contribution to fieldwork, M. Dahirel for advice on statistics, J-C. Foltête for feedback on resistance distance conversion, L. Morel, L. Lecoq for stimulating discussions on the processing of trait values and D. Goodfellow for English editing. This work used landscape databases (available at <https://accueil.osuris.fr/>) collected in the LTSER site “Zone Atelier Armorique” and plant traits from the TRY initiative (<http://www.try-db.org>). Land cover and wooded habitat cover maps were established by J. Nabucet, T. Alcalá Jimenez and C. Brabant (LETG-Rennes-Costel) and Kermap. The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Boenisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by Future Earth/bioDISCOVERY and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

Funding

This work was funded by the Fondation de France (BISCO project), BiodivERsA (Woodnet project) and by European Regional Development Fund (ERDF) under the umbrella of INTERREG Atlantic Area (ALICE project, EAPA_261/2016).

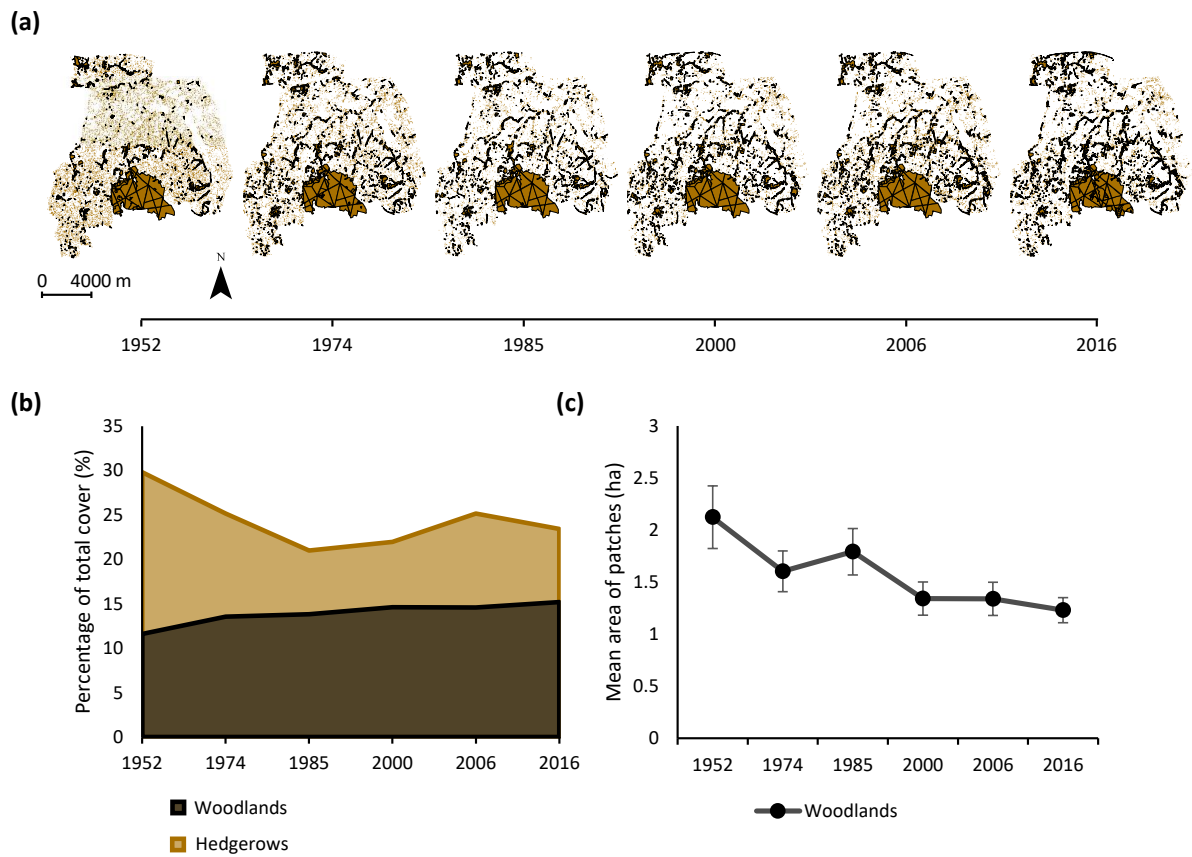


Fig. S1 (a) Maps showing woodland cover (indicated by dark-brown features outlined in black) and hedgerow cover (indicated by light-brown features) for each of the six time steps selected. **(b)** Stacked area graph representing the percentage of total cover for woodlands (in total area) and hedgerows (in total number of pixels) for each time step selected. **(c)** The line represents the mean area \pm standard error of the mean (indicated by vertical bars) of woodland patches for each time layer selected.

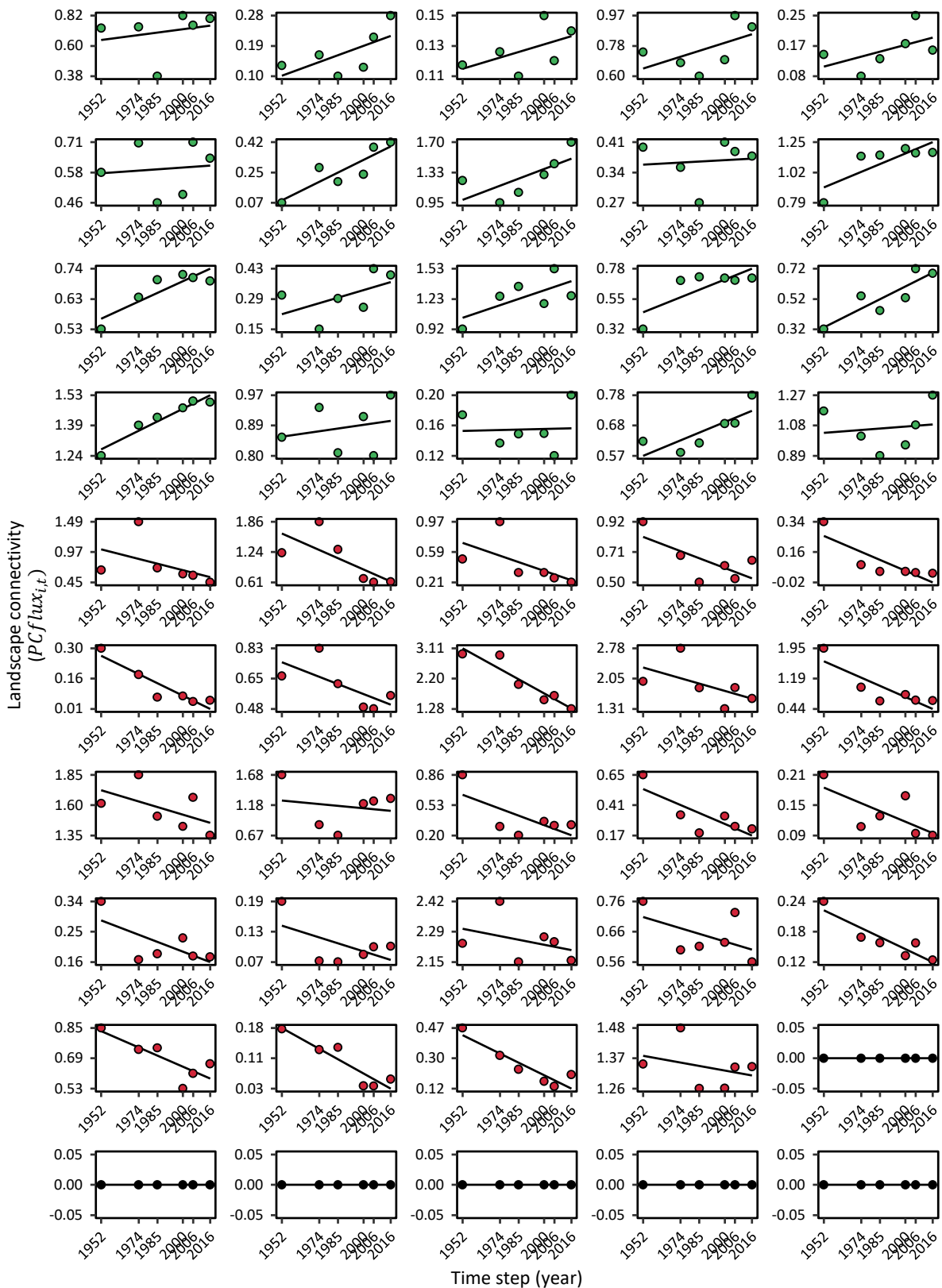


Fig. S2 Overview of the single ordinary least squares regression models performed for each selected woodland i. Green dots mean the woodland experienced an upward trend, red dots a downward trend, and black dots, no trend.

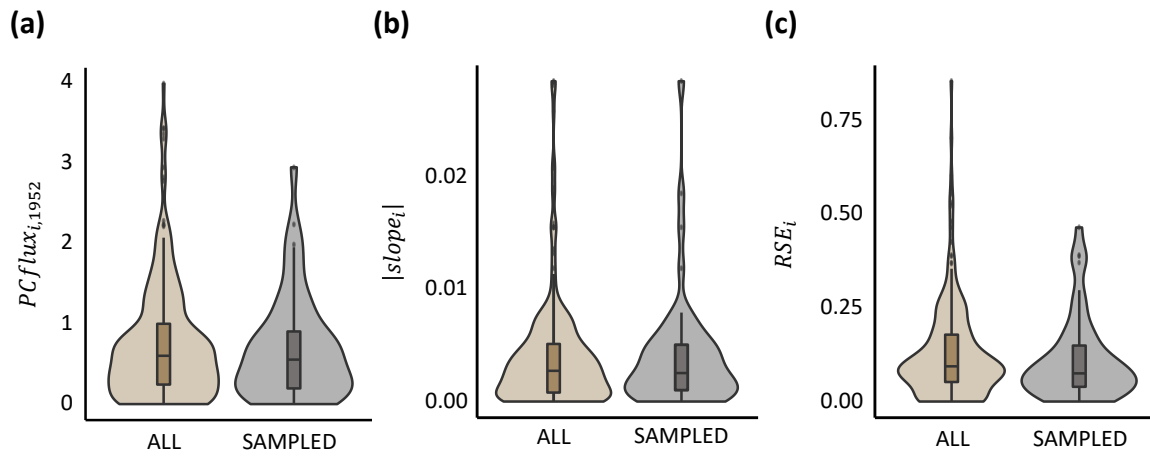


Fig. S3 Violin plots showing variations in the distribution of the three components used to describe the temporal dynamics of connectivity: **(a)** the degree of landscape connectivity ($PCflux_{i,1952}$), **(b)** the magnitude ($|slope_i|$) and **(c)** the variability (RSE_i) of temporal changes in landscape connectivity for all (N=255, “ALL” acronym, in brown) and sampled (N=50, “SAMPLED” acronym, in grey) woodland i.

Partie IV

Discussion générale

1. La connectivité, un phénomène complexe agissant dans l'espace et dans le temps, pour déterminer l'assemblage des communautés végétales
2. La considération conjointe des différents types d'habitat et de la dynamique temporelle, une voie vers une méthodologie pertinente de l'évaluation de la connectivité pour les communautés végétales
3. Implications pour la conservation de la biodiversité floristique au sein des paysages agricoles
4. Conclusion

En dépit d'une attention grandissante, le rôle de la connectivité sur les plantes, en particulier à l'échelle des communautés, est relativement méconnu (ARTICLE 2). Ancrée dans ce contexte, cette thèse démontre que l'amélioration de la compréhension du rôle la connectivité sur la structuration des communautés végétales doit considérer, de manière conjointe, (i) les différents types d'habitat contribuant à la connectivité et (ii) la dynamique temporelle de la connectivité. Conformément à nos attentes, ce travail de thèse alimente le corpus de connaissances quant à l'effet de la connectivité sur les communautés végétales non seulement décrites d'un point de vue taxonomique, mais également fonctionnel (section 1), grâce à l'intégration de ces multiples aspects dans l'évaluation de la connectivité (section 2). Ce travail offre ainsi de multiples implications pour la conservation de la biodiversité floristique au sein des paysages bocagers, en fournissant des éléments de connaissance pour une mise en place opérationnelle pertinente des stratégies de restauration de la connectivité, et en particulier de la Trame Verte et Bleue (TVB) (section 3). Il présente également l'intérêt d'adopter une approche pluri-habitat au sein d'un même paysage, ouvrant ainsi la voie à une certaine généralisation des résultats obtenus.

1. La connectivité, un phénomène complexe agissant dans l'espace et dans le temps, pour déterminer l'assemblage des communautés végétales

En premier lieu, nos travaux soulignent que la connectivité spatiale et sa dynamique temporelle (intensité et variabilité des changements temporels, uniquement) affectent seulement la similarité de composition spécifique, et non la diversité spécifique (richesse et équitabilité) ou l'abondance totale des espèces au sein des communautés végétales (ARTICLES 3 à 5). La connectivité influence ainsi la composition spécifique des communautés, c'est-à-dire l'identité des espèces, en agissant sur les traits fonctionnels liés à la colonisation et ce, dans l'espace et dans le temps (ARTICLES 3 à 5). Ces modifications au sein des communautés végétales entraînent des conséquences potentielles sur le fonctionnement des écosystèmes (ARTICLE 4).

1.1. La connectivité spatiale et sa dynamique temporelle n'influencent pas la diversité spécifique ni l'abondance totale des espèces, mais affectent plutôt la composition spécifique des communautés

Nous avons démontré qu'une forte connectivité fournie par les différents habitats affecte la similarité de composition spécifique entre les communautés zoochores au sein des tâches de bois et de prairie temporaire, mais pas au sein des tâches de culture céréalière (ARTICLE 3). A

contrario, la connectivité et/ou la dynamique temporelle de connectivité n'influençaient ni la diversité spécifique au sein des tâches de bois (ARTICLE 5) et de culture céréalière (ARTICLE 4), ni même l'abondance totale des adventices au sein de ce dernier habitat (ARTICLE 4). Nos résultats concernant la similarité de composition spécifique confirment nos prédictions théoriques (Mouquet & Loreau 2003), à l'exception des cultures. Cependant, nos résultats concernant la diversité spécifique et l'abondance totale en espèces sont contraires à nos attentes. Nos résultats ne confirment d'aucune façon, le solide corpus théorique (MacArthur & Wilson 1963, 1967; Mouquet & Loreau 2003) largement supporté par les études empiriques expérimentales (e.g. Damschen *et al.* 2019); pour d'autres références cf. ARTICLE 1), affirmant l'importance de la connectivité pour favoriser la diversité spécifique, et en particulier la richesse au sein des tâches d'habitat. Plusieurs hypothèses, non exclusives, peuvent être mobilisées pour expliquer cette absence d'effet sur la diversité spécifique et l'abondance totale des espèces, tout comme sur la similarité de composition spécifique dans le cas particulier des tâches de culture céréalière.

Premièrement, deux théories, ancrées dans la vision paysagère « tâche-matrice », suggèrent que l'importance de la connectivité pour la structure taxonomique des communautés au sein des tâches d'habitat est moindre, voire nulle (i) lorsque quantité totale d'habitat dans le paysage est supérieure à 30 % [cas des cultures céréalières, hypothèse du seuil de fragmentation (*fragmentation threshold hypothesis*; Andrén 1994; Hanski 2005; Pardini *et al.* 2010) ou (ii) pour une quantité totale d'habitat donnée dans son paysage environnant (selon une distance de dispersion donnée; *habitat amount hypothesis*; Fahrig 2013). Ces théories sont toutefois avancées avec une certaine précaution puisqu'elles sont jusqu'ici réservées au concept de fragmentation (i.e. surface de la tâche et isolement entre tâches), et doivent encore être transposées à la connectivité fonctionnelle. De surcroît, isoler les effets respectifs de la connectivité et de la quantité d'habitat environnant nécessitent une absence de corrélation entre ces deux phénomènes. Or, cette condition est généralement non satisfaite dans les études observationnelles, puisque tous deux agissent simultanément (Fahrig 2003; Collinge 2009; Hanski 2015).

Deuxièmement, l'importance de la connectivité pour la structure taxonomique des communautés peut être masquée par les processus locaux, qu'ils soient abiotiques ou biotiques (cf. introduction, section 3 et ARTICLE 2). Au sein du site agricole de Pleine-Fougères, les processus locaux, qu'ils soient ou non en prise directe avec les pratiques de gestion, pourraient tendre à contrôler le recrutement des plantules (cf. partie I, section 2). L'effet des

processus locaux pourrait ainsi occulter tout effet de la connectivité sur la structure taxonomique des communautés du couvert végétal au sein des tâches d'habitat. Afin de s'affranchir des processus locaux, et de se concentrer sur le seul processus de dispersion des graines, un échantillonnage de la banque de graines du sol a été réalisé au sein de 25 tâches de bois, de prairie temporaire et de culture céréalière (cf. partie I, section 3.2). Ces travaux, en cours d'exploitation, visent plus particulièrement à tester l'hypothèse selon laquelle une forte connectivité accroît davantage la diversité spécifique des communautés de la banque de graines que celles du couvert végétal. Des résultats préliminaires menés au sein des bois tendent à confirmer nos premières attentes, puisqu'ils révèlent qu'une forte connectivité fournie par les habitats boisés favorise la diversité spécifique des communautés de la banque de graines, tandis qu'elle n'affecte pas celle des communautés du couvert végétal (Planes 2019).

Enfin, la connectivité pourrait affecter la composition spécifique des communautés, c'est-à-dire l'identité des espèces, même lorsqu'aucune relation entre la connectivité et la diversité n'est établie. Comme observée dans les schémas temporels de biodiversité (Dornelas *et al.* 2014; Blowes *et al.* 2019), la composition spécifique des communautés peut être indépendante de la richesse spécifique lorsque les immigrations et les extinctions se compensent, entraînant un remplacement (*turnover*) d'espèces (Hillebrand *et al.* 2018). A mesure que la connectivité varie, certaines espèces coloniseraient des tâches d'habitat précédemment occupées par d'autres espèces venant de s'éteindre, de sorte que la richesse spécifique au sein des tâches resterait identique. La présence d'un tel phénomène, déjà observé le long d'un gradient de perte d'habitat (Banks-Leite *et al.* 2012), suggère la présence de seuils d'extinction spécifiques aux espèces repartis le long du gradient de connectivité (Lande 1987; Fahrig 2002; Banks-Leite *et al.* 2012). En somme, la connectivité pourrait ne pas modifier la richesse spécifique, mais agir essentiellement sur l'identité des espèces, en favorisant certaines espèces au détriment d'autres espèces, selon les traits fonctionnels qui les caractérisent. Cette dernière hypothèse s'accorde particulièrement avec les résultats issus des approches fonctionnelles réalisées dans le cadre de cette thèse.

1.2. La connectivité spatiale et sa dynamique temporelle, des filtres sélectionnant l'identité des espèces selon la valeur de leurs traits fonctionnels

Conformément à nos attentes (ARTICLE 1), la connectivité spatiale et sa dynamique temporelle agissent comme un filtre, sélectionnant l'identité des espèces selon les valeurs de traits qui vont permettre à leurs graines d'arriver sur le sol depuis la plante mère, et – probablement de

manière plus surprenante – de s'établir au sein de la communauté (traits de réponse; *sensu* (Lavorel *et al.* 1997; Lavorel & Garnier 2002; Suding *et al.* 2008).

Nos travaux démontrent en effet que la connectivité spatiale (ARTICLES 3 et 4) et sa dynamique temporelle (ARTICLE 5) agissent principalement sur les traits impliqués dans la dispersion, depuis la production de graines (nombre de graines, ARTICLE 4; mais cf. ARTICLE 5) jusqu'à leur arrivée via son effet sur le transfert des graines. Par exemple, une forte connectivité spatiale favorise et/ou entrave la colonisation des espèces boisées et prairiales zoochores, selon le comportement et le mouvement des animaux transférant les graines au sein des différents habitats reliant les tâches d'habitat (ARTICLE 3). Au-delà du mode de dispersion, la connectivité spatiale (ARTICLE 4) ou sa dynamique (ARTICLE 5) agit sur les traits déterminant finement la distance à laquelle les graines des espèces adventices ou des espèces boisées, respectivement, sont dispersées, tels que (i) l'allocation à la reproduction clonale (ARTICLES 4 et 5) et (ii) la masse des graines (ARTICLE 5). Les résultats à l'égard de l'interaction entre la connectivité spatiale et le mode de dispersion (ARTICLE 3) d'une part, et les traits fonctionnels déterminant la production et la distance de dispersion (ARTICLE 4) d'autre part, coïncident, dans l'ensemble, avec nos hypothèses. En revanche, contrairement à nos attentes, l'intensité et la variabilité des changements temporels de connectivité spatiale n'ont pas nécessairement entraîné la sélection de valeurs de traits restreignant la dispersion à de courtes distances (i.e. grosses graines, allocation à la reproduction végétative, cf. introduction, section 1.3). Ces résultats suggèrent que les effets cumulés des changements temporels de connectivité façonnent les communautés végétales de manière complexe, en agissant probablement de concert avec de multiples processus impliqués dans l'assemblage des communautés (régionaux, locaux, historiques, existence de compromis, cf. ARTICLE 5, section discussion).

Outre les traits impliqués dans la dispersion *stricto sensu*, nos travaux soulignent l'importance des traits définissant la capacité d'établissement des espèces au sein des tâches d'habitat dans la réponse des espèces à la connectivité spatiale (ARTICLE 4) ou à sa dynamique temporelle (ARTICLE 5). Des relations entre ces patrons de connectivité et la composition des valeurs de taux de germination (ARTICLE 4) ou la diversité de masse des graines (ARTICLE 5), respectivement, au sein des communautés, ont été établies. La connectivité, dans l'espace et/ou dans le temps, agirait ainsi non seulement sur la production de graines, le transport des graines, mais également sur le recrutement des plantules (i.e. germination, établissement et survie). Elle constituerait un facteur important dans la régulation de la dispersion efficace, et

ainsi de l'établissement d'une population viable, autrement dit, de la colonisation des tâches d'habitat par les espèces végétales. Toutefois, les mécanismes à l'origine de ces effets sur les traits d'établissement sont vraisemblablement indirects. Ils pourraient se produire selon les traits de dispersion des espèces en raison de l'existence de compromis (e.g. compromis entre capacités de colonisation et de compétition). Les effets de la connectivité sur les traits d'établissement observés au sein des communautés du couvert végétal pourraient également résulter de l'effet des processus locaux (facteurs abiotiques et biotiques), à l'issue de la sélection des espèces. Les données issues de la banque de graines seront ainsi mobilisées, afin d'étudier si la connectivité agit (i) seulement sur les traits de dispersion ou (ii) simultanément sur les traits de dispersion et d'établissement des espèces au sein des communautés de la banque de graines, à l'image de nos observations au sein des communautés du couvert végétal. Ainsi, si la connectivité agit seulement sur les traits de dispersion des communautés de la banque de graines, alors les patrons observés au sein des communautés du couvert végétal seraient dus à la prépondérance des processus locaux. En revanche, l'existence de patrons similaires au sein des communautés de la banque de graines et du couvert végétal suggérerait que la connectivité, en sélectionnant les espèces selon les traits définissant leur capacité de dispersion, agirait indirectement sur les traits définissant leur capacité d'établissement au sein des tâches.

En définitive, la prise en compte des traits fonctionnels impliqués dans l'ensemble des étapes définissant le processus de dispersion efficace des espèces permet de mieux comprendre les mécanismes impliqués dans la réponse des espèces végétales, aussi bien à la connectivité fournie par les différents habitats qu'à la dynamique temporelle de connectivité (ARTICLES 3 à 5).

1.3. La connectivité modifie la structure fonctionnelle des communautés végétales dans l'espace et dans le temps

La connectivité varie selon de multiples d'échelles spatiales et temporelles hiérarchiquement imbriquées (O'Neill *et al.* 1986; Allen & Starr 1988). Elle agit ainsi sur les traits fonctionnels des espèces végétales dans l'espace (ARTICLES 4 et 5) et dans le temps (ARTICLE 5).

En transposant le principe d'isolement par la résistance issue de la génétique des populations (McRae 2006; McRae & Beier 2007; McRae *et al.* 2008) à l'étude des communautés (cf. aussi Thiele *et al.* 2017, 2018b), des relations entre la connectivité fournie par les habitats boisées et/ou cultivées et la similarité de composition des communautés zoochores ont été

établies (ARTICLE 3). Toutefois, cette approche ne permettait pas de définir l'échelle spatiale à laquelle la connectivité du paysage prédisait le mieux la réponse des communautés végétales [l'échelle d'effet (*scale of effect*); Jackson & Fahrig 2012, 2015)]. Dans ce but, nous nous sommes intéressés à l'effet de la connectivité spatiale « environnante », et de sa dynamique temporelle, les tâches d'habitat dans lesquelles les espèces coexistent (ARTICLES 4 et 5). Grâce à cette approche, nous avons montré que la connectivité spatiale et sa dynamique temporelle agissaient à une échelle infra-kilométrique (< 750 m) sur la structure fonctionnelle des communautés végétales boisées et adventices. Ce résultat confirme nos prédictions, compte-tenu de mode de vie sessile des plantes, et de leur distance de dispersion limitée (e.g. van Ruremonde & Kalkhoven 1991 pour les espèces boisées, Benvenuti 2007 pour les espèces adventices). De façon intéressante, la connectivité fournie par les habitats prairiaux à une échelle de 750 m prédisait mieux les réponses fonctionnelles des communautés adventices que la connectivité à une échelle locale (250 m) et intermédiaire (500 m), la valeur agrégée du taux de germination étant seulement affectée par la connectivité à plus large échelle (ARTICLE 4). En démontrant que les patrons de connectivité agissent sur les traits des espèces à de multiples échelles spatiales (de 250 m à 750 m), ces travaux alimentent les recherches menées quant à l'échelle d'effet du paysage pour les espèces végétales (e.g. Gaba *et al.* 2010; Avon *et al.* 2015; Mony *et al.* 2018).

Non sans lien, la dynamique temporelle de connectivité à une échelle spatiale intermédiaire (500m) s'est avérée déterminante pour expliquer les communautés végétales boisées actuelles (ARTICLE 5). Comme souvent démontrés pour les communautés végétales prairiales (e.g. Lindborg & Eriksson 2004; Helm *et al.* 2006), ces résultats soulignent l'importance des changements de connectivité à long terme pour les communautés végétales boisées (ARTICLE 5) probablement en raison de leur longue durée de vie et de leurs faibles capacités de dispersion (cf. aussi (Naaf & Kolk 2015). Toutefois, l'exploration du rôle de la dynamique temporelle de connectivité peut apparaître encore limitée, puisqu'à l'instar de nombreux auteurs, nous nous sommes exclusivement concentrés sur un habitat permanent, ne représentant qu'une petite fraction de notre paysage agricole [e.g. tâches de bois (e.g. Kolk & Naaf 2015; Naaf & Kolk 2015; ARTICLE 5) ou de prairie (e.g. Lindborg & Eriksson 2004) relativement anciennes]. Le rôle de la dynamique temporelle de connectivité pour les habitats non-permanents (e.g. prairies temporaires, cultures céréalières) qui dominent notre paysage, demeure inconnu. Or, les changements transitoires de connectivité, qui se produisent au cours de la durée d'existence de ces habitats, devraient également affecter les communautés végétales actuelles, qu'elles soient prairiales ou adventices. Cette dernière hypothèse s'insère

dans la lignée d'observations personnelles récentes, soulignant le rôle essentiel de la dynamique temporelle à court terme du contexte paysager pour les communautés végétales prairiales (ARTICLE A1). A la lumière de la théorie de la hiérarchie (O'Neill *et al.* 1986; Allen & Starr 1988), ces constatations pourraient suggérer que les modifications à court terme (e.g. interannuelles; ARTICLE A1), imbriquées dans ces modifications à long terme (e.g. inter-décennies; ARTICLE 5) agissent simultanément dans les mécanismes d'assemblages des communautés végétales. Seulement, nos observations (ARTICLES 5 et A1) ne permettent pas d'appuyer cette hypothèse, puisqu'elles pourraient simplement être le reflet d'échelles temporelles de réponses différentes entre les espèces boisées et les espèces prairiales, en raison de longévités et de capacités de dispersion distinctes. L'utilisation de modèles théoriques, par type d'habitat, permettrait d'élucider le rôle de la structure hiérarchiquement imbriquée de la dynamique temporelle de connectivité sur les mécanismes de coexistence des espèces végétales au sein des métacommunautés.

1.4. Les modifications de la structure fonctionnelle des communautés exercée par la connectivité entraînent des conséquences potentielles sur le fonctionnement des écosystèmes

Les transformations fonctionnelles que subissent les communautés végétales face aux modifications de connectivité dans l'espace et dans le temps entraînent des conséquences potentielles sur le fonctionnement des écosystèmes (traits d'effet; *sensu* Lavorel *et al.* 1997; Lavorel & Garnier 2002; Suding *et al.* 2008).

Nos travaux fournissent une des premières preuves que la connectivité agit, via son effet sur les traits des plantes, sur le fonctionnement des écosystèmes, et plus particulièrement sur la fonction de la résistance de la culture céréalière à la colonisation des adventices (ARTICLE 4). Une forte connectivité réduit l'abondance totale des adventices au sein des cultures de céréales, en favorisant le taux de germination des espèces adventices au sein des communautés (cf. discussion, section 1.3). Les espèces à fort succès de germination – en raison d'une faible dormance des graines (Colbach *et al.* 2006; Baskin & Baskin 2014) – ne peuvent synchroniser leur germination lorsque l'espèce céréalière est semée afin d'échapper aux herbicides, et ainsi maximiser leur établissement (Gunton *et al.* 2011; Fried *et al.* 2012).

En distinguant les traits qui sont uniquement des traits de réponse à la connectivité de ceux qui sont également des traits d'effets concernant l'abondance totale des adventices, nos travaux franchissent une première étape vers la compréhension des effets de la connectivité

sur les fonctions écosystémiques, en intégrant les interactions plantes – plantes (ARTICLE 4). Cette compréhension pourrait aller bien au-delà, en identifiant, parmi les traits de réponse des espèces (ARTICLES 2 à 5), les traits qui affectent également les interactions entre niveaux trophiques, qu’elles soient positives (e.g. plantes – microorganismes, plantes - pollinisateurs) ou négatives (e.g. plantes – prédateurs), ces dernières étant à l’origine de multiples fonctions écosystémiques. Parmi les traits de réponses identifiés, la hauteur des plantes (ARTICLE 2), liée à l’attraction des pollinisateurs (Lortie & Aarssen 1999), mais également la masse des graines (ARTICLES 2 et 5), liée à la préférence des prédateurs de graines (voir Hulme 1998; Celis-Diez *et al.* 2004) mais aussi Moles & Westoby 2004; Gaba *et al.* 2019) pourraient, par exemple, agir sur les fonctions de pollinisation et de prédation. De multiples traits de réponse à la connectivité sont également susceptibles d’agir sur les interactions plantes – microorganismes, bien qu’ils n’ont, à notre connaissance, jamais été explorés à cette fin. Si elles sont souvent invisibles à l’œil nu, les communautés microbiennes favorisent la croissance, l’absorption des nutriments, la tolérance au stress et la résistance aux agents pathogènes de leurs plantes hôtes (cf. Trivedi *et al.* 2020 et références incluses) et sont ainsi essentielles pour la santé des plantes, la productivité et la fertilité des sols. A l’instar des macroorganismes, la connectivité semble être un facteur clé, bien qu’encore négligé, pour la dispersion des microorganismes, en particulier pour les espèces associées à un hôte, dont le mouvement, qu’il soit végétal ou animal, dépend de la connectivité (cf. ARTICLE A2 pour une revue). Présents au niveau des différents organes des plantes, les microorganismes peuvent notamment coloniser (Clay & Schardl 2002; Selosse *et al.* 2004) ou s’attacher via leur spores (Ramadhani *et al.* 2018; Séné *et al.* 2018) aux graines et disperser ainsi via ces vecteurs. Ainsi, les effets de la connectivité et sa dynamique temporelle sur la dispersion des microorganismes et le maintien des fonctions écosystémiques supportées par le microbiote des plantes pourraient être médiés par les traits des plantes, tels que la masse des graines, le nombre de graines produites ou encore le mode de dispersion des plantes. Une forte masse de graines ou une forte production de graines pourrait, en effet, favoriser la dispersion des microorganismes, en augmentant la surface ou la probabilité de colonisation ou d’attachement, mais également la probabilité de survie à l’issue d’un établissement réussi de la plante hôte. Quant à la dispersion zoochore, elle pourrait favoriser le transport des graines colonisées par les microorganismes ou des graines auxquelles des spores sont accrochées (Correia *et al.* 2019). Grâce à la dispersion orientée des animaux, la dispersion zoochore pourrait, de plus, permettre l’arrivée simultanée des graines et des (spores de)

microorganismes jusqu'à une tâche d'habitat favorable, correspondant à la niche écologique du microbiote de la plante.

En vue de ces nouvelles considérations, la transposition du cadre « trait de réponse – trait d'effet » aux fonctions écosystémiques supportées par les interactions entre les plantes et les autres organismes apparaît désormais essentielle pour déterminer le rôle de la connectivité sur les communautés végétales et les fonctions écosystémiques associées. Les mécanismes à l'origine des multiples fonctions écosystémiques supportées par les plantes grâce à la connectivité pourraient être identifiés, tout comme d'éventuels synergies ou conflits potentiels entre fonctions.

2. La considération conjointe des différents types d'habitat et de la dynamique temporelle, une voie vers une méthodologie pertinente de l'évaluation de la connectivité pour les communautés végétales

En second lieu, nos travaux permettent d'améliorer la méthodologie d'évaluation de la connectivité pour les communautés végétales, en affirmant la nécessité de considérer les différents types d'habitat contribuant à la connectivité (ARTICLES 3 et 4), mais également la dynamique temporelle de connectivité (ARTICLES 1 et 5). Ces avancées méthodologiques divulguent des informations nouvelles quant à l'interaction entre la structure physique du paysage et la dispersion des plantes. (ARTICLES 3 à 5). La particularité du phénomène de connectivité pour les plantes suggère des perspectives, visant à promouvoir l'inclusion explicite de la dynamique temporelle de connectivité (ARTICLE 1).

2.1. Le choix de mesures de connectivité spatiale potentielle multiples et complémentaires

La connectivité spatiale pour les communautés végétales est souvent mesurée selon sa nature structurelle (basée sur une modélisation Euclidienne de la dispersion potentielle). Néanmoins, l'utilisation des mesures de connectivité fonctionnelle potentielle, reconnaissant, par opposition, le rôle de la perméabilité de la matrice sur les mouvements de dispersion des plantes, s'est récemment démocratisée pour les espèces végétales, mais reste peu répandue à l'échelle des communautés (mais cf. Thiele *et al.* 2017, 2018a, b; Mony *et al.* 2018).

Avant tout, l'ensemble de nos travaux a été réalisé à partir de mesures de connectivité (fonctionnelle) potentielle, qui requièrent l'utilisation de cartes de résistance et d'un algorithme de connectivité (méthode des chemins de moindre coût ou la théorie des circuits, cf. introduction, section 2.2.1). Des preuves empiriques récentes montrent que les distances

Euclidiennes et effectives (ou fonctionnelles, i.e. issues des algorithmes de connectivité), fortement corrélées, affectent semblablement la similarité de composition spécifique entre communautés végétales. Toutefois, elles diffèrent dans leur capacité prédictive (Uroy *et al.* résultats non présentés; Thiele *et al.* 2017), à l'image d'observations antérieures sur la similarité génétique entre populations végétales (e.g. McRae & Beier 2007). La distance Euclidienne, la distance du chemin de moindre coût, et la distance de résistance semblent se répartir le long d'un gradient croissant de capacité à prédire la similarité de composition spécifique entre communautés végétales (i.e. distance Euclidienne < distance du chemin de moindre coût < distance de résistance).

Pour évaluer la connectivité potentielle, nous avons utilisé plusieurs algorithmes de connectivité, à savoir, la méthode des chemins de moindre coût (ARTICLE 4) et la théorie des circuits (ARTICLES 3 et 5). En dépit de sa performance pour prédire la dispersion des espèces végétales entre tâches, dépendant vraisemblablement de la redondance des chemins et se réalisant selon un mouvement non optimal, l'utilisation de la théorie des circuits soulève plusieurs réserves. La théorie des circuits exige des moyens de calculs très importants (temps et puissance), notamment lorsque la connectivité est calculée à partir de cartes disposant de fines résolutions et recouvrant de larges superficies. Ces contraintes restreignent son application, et ce, même en dépit d'avancées très récentes visant à contourner ce problème [e.g. GFlow (Leonard *et al.* 2017), Circuitscape dans Julia (Anantharaman *et al.* 2019), cf. Marrec *et al.* 2020]. Malgré ces obstacles, la théorie des circuits a été privilégiée pour sa performance accrue dans l'estimation du processus de dispersion des plantes, lorsque nos travaux visaient à examiner si l'intégration d'éléments nouveaux dans l'évaluation de la connectivité prédisait mieux les communautés végétales (ARTICLES 3 et 5). L'appréciation des apports de considérer simultanément différents types d'habitat contribuant à la connectivité (ARTICLE 3) ou différentes composantes de la dynamique temporelle de connectivité (ARTICLE 5) exige une approche, qui, bien que complexe, semble se rapprocher plus fidèlement du processus de dispersion des plantes. En revanche, la méthode des chemins de moindre coût a été valorisée lorsqu'il s'agissait de comprendre non seulement le rôle des différents habitats contribuant à la quantité d'habitat, mais aussi à la connectivité, sur la diversité et l'abondance des adventices au sein des agrosystèmes (ARTICLE 4). La méthode des chemins de moindre coût semble ainsi rester pertinente pour mesurer la connectivité potentielle, sa performance restant proche de celle de la théorie des circuits, malgré son fondement moins réaliste (Uroy *et al.* résultats non présentés; Thiele *et al.* 2017; Simpkins *et al.* 2018). Cette approche confère également de nombreux avantages, puisqu'elle permet de s'affranchir des moyens et de la

complexité des calculs imposés par la théorie des circuits, mais également des difficultés essentiellement techniques, jusqu'ici non reportées dans la littérature, pouvant aboutir à des mesures de connectivité potentielles erronées (e.g. conversion en distance métrique).

Quel que soit l'algorithme utilisé, des cartes de résistance individuelles ont été créées, selon le(s) type(s) d'habitat considéré(s) contribuant à la connectivité, afin de s'affranchir de la hiérarchisation des types d'habitat de la matrice. Néanmoins, deux paramétrages des valeurs de résistances ont été menés, l'un se basant sur une vision « multimodale » (ARTICLES 3 et 4), l'autre sur une vision « bimodale » de la matrice paysagère (ARTICLE 5). La vision « multimodale » de la matrice a été obtenue grâce à l'utilisation d'une analyse par fenêtre glissante (McGarigal & Cushman 2005). Cette approche reflète la façon dont les multiples valeurs de la perméabilité de matrice (ici, la proportion de l'habitat considéré) sont « perçues » localement par les espèces végétales lors des événements de dispersion à courte distance qui se produisent sur quelques dizaines de mètres (Howe & Smallwood 1982; Nathan 2006). Cette approche, offrant une représentation particulièrement fonctionnelle (i.e. centrée sur l'organisme) de la matrice paysagère, a soulevé toutefois quelques mises en garde lorsqu'il s'agissait de créer des cartes de résistances pour étudier la dynamique temporelle de connectivité (ARTICLE 5). En utilisant les cartes de résistances produites via l'analyse par fenêtre glissante, seules des modifications minimales de connectivité potentielle fournies par les habitats boisés ont été captées entre 1952 et aujourd'hui (Uroy *et al.* résultats non présentés). L'analyse par fenêtre glissante semble masquer les profondes modifications auxquelles les habitats boisés ont été soumis au cours de cette période, probablement en raison de l'échelle particulièrement fine à laquelle elles se sont produites (e.g. haies). Ces constatations ont motivé un paramétrage « bimodal » des valeurs de résistances pour l'étude de la dynamique temporelle de connectivité (ARTICLE 5). En particulier, l'attribution de la valeur de résistance de chaque pixel était fonction de la présence (ou de l'absence) d'habitat perméable à la dispersion des espèces végétales boisées, à savoir les habitats boisés (bois et haies). Ce paramétrage « bimodal » rend compte du déclin observé des éléments boisés sur la période étudiée dans les cartes de résistance, tout en se fondant sur des valeurs de résistances fonctionnelles et fiables, compte-tenu des preuves empiriques obtenues en amont (ARTICLE 3).

Face à l'absence de lignes directrices dans la littérature, la comparaison et la validation fonctionnelle des multiples approches pour mesurer la connectivité potentielle fait particulièrement défaut. Dans un tel contexte, des analyses préliminaires, dénotant l'incertitude ou la sensibilité de ces diverses méthodes, sont cruciales afin d'adopter le

meilleur compromis en fonction de l'optimal recherché. La décision de l'approche à utiliser doit, en effet, être basée sur les exigences individuelles de l'étude. En fin de compte, l'étude des relations entre la connectivité et les communautés végétales ne se réalise pas au travers d'une seule mais de multiples approches, celles-ci se complétant pour capter le plus fidèlement possible la façon complexe dont la dispersion des plantes interagit avec la structure du paysage.

2.2. La spécificité de la connectivité pour les plantes

Par la considération (i) des différents habitats contribuant à la connectivité (ARTICLES 3 et 4), mais aussi (ii) des différentes composantes de la dynamique temporelle de connectivité (ARTICLE 5), nous avons été en mesure d'offrir une vision nouvelle de la façon spécifique, particulière, dont la connectivité agit sur la dispersion des espèces végétales.

La première particularité de cette thèse a été de s'affranchir de la priorisation du rôle exercé par les différents types d'habitat sur la connectivité (potentielle) spatiale. En considérant les effets additifs de la connectivité fournie par les habitats boisés, prairiaux et cultivés, nous apportons un éclairage nouveau sur la dispersion des plantes en paysage fragmenté. A l'image des résultats contrastés des études empiriques (ARTICLE 2), la dispersion des espèces inféodées à un type d'habitat peut être favorisée (communautés boisées, ARTICLE 3) ou non affectée par une forte connectivité fournie par ce même habitat (communautés prairiales, ARTICLE 3 et adventices ARTICLE 4). De façon plus originale, nous avons mis en évidence qu'une forte connectivité fournie par des habitats auxquels ne sont pas inféodés les espèces peut avoir un effet négatif sur la dispersion des espèces [communautés boisées (ARTICLE 3)], mais également un effet positif [communautés prairiales (ARTICLE 3) et adventices (ARTICLE 3)]. Ces effets positifs exercés par d'autres types d'habitat ont été démontrés pour des espèces animales, aboutissant au concept de supplémentation paysagère (Dunning *et al.* 1992). Les organismes inféodés à un type d'habitat suppléent leur apport en ressources en utilisant des ressources dans des tâches proches du même habitat, ou en utilisant une ressource substituable dans des tâches proches d'un autre type d'habitat. Suivant Dunning *et al.* (1992), les espèces végétales suppléeraient leur chemin de dispersion « naturel » (c'est-à-dire les habitats auxquels elles sont inféodées) en utilisant d'autres types d'habitat. La supplémentation des chemins de dispersion observée chez les espèces zoochores prairiales est probablement liée à la supplémentation des ressources des animaux impliqués dans leur dispersion (ARTICLE 3). L'hypothèse du vecteur de dispersion ne pouvant être avancée pour les espèces adventices (cf. ARTICLE 3), l'observation d'un tel phénomène suggère

que les habitats prairiaux correspondent aux préférences écologiques des adventices (habitats riches en nutriments, ensoleillés et secs; Bourgeois *et al.* 2019). Ce phénomène de supplémentation pour les espèces adventices est toutefois discutable; puisque les habitats prairiaux pourraient, en réalité, constituer leur chemin de dispersion « naturel ». Dans nos paysages, la plupart des espèces adventices sont en effet originaires d'habitats naturels ouverts, tels que les prairies sèches (Jauzein 2011) et comprennent à la fois des espèces présentes dans les cultures et dans les habitats ouverts non cultivés (e.g. prairies).

Jusqu'ici, les tentatives de prise en compte de la dynamique temporelle de connectivité n'ont porté que sur le degré de connectivité à certains moments dans le temps. Dans ce contexte, la seconde originalité de cette thèse a été d'explorer, pour l'une des toutes premières fois, les effets cumulés de sept décennies de changements de connectivité spatiale sur les communautés végétales. Or, nous avons mis en évidence que seules l'intensité et la variabilité temporelle de ces changements temporels se produisant au cours de ces décennies affectent la structure fonctionnelle des communautés végétales boisées actuelles (ARTICLE 5). *A contrario*, le degré de connectivité n'exerce aucun effet sur la structure fonctionnelle actuelle des communautés végétales boisées. Ces résultats corroborent plusieurs études théoriques (Keymer *et al.* 2000) et empiriques (Metzger *et al.* 2009) démontrant le rôle prépondérant des changements temporels du contexte paysager pour les espèces évoluant au sein des paysages dynamiques. Ces observations semblent s'étendre aux changements temporels de connectivité pour les espèces végétales boisées. La colonisation des espèces végétales boisées, majoritairement pérennes et longévives (Ehrlén & Lehtilä 2002), est en effet l'aboutissement d'une dispersion particulièrement lente, se produisant au moyen de plusieurs étapes de dispersion à courte distance (Matlack 2005), dont la distance moyenne ne dépasse pas quelques mètres par an (Hermy & Verheyen 2007). Compte-tenu de ces caractéristiques, les communautés végétales boisées actuelles résultent essentiellement des effets cumulatifs de décennies de changements de connectivité, qui façonnent l'intensité et la variabilité des flux successifs de dispersion locale depuis une tâche d'habitat à une autre.

En somme, la connectivité est un phénomène bien particulier pour les espèces végétales, qui dépend de l'éventail des interactions possibles entre la structure du paysage et la dispersion des plantes qui se produisent au fil du temps. Au vu de nos résultats, faire fi des aspects susmentionnés dans l'évaluation de la (dynamique temporelle de) connectivité peuvent conduire à des conclusions erronées quant au rôle exercé par la connectivité dans la structuration des communautés végétales.

2.3. Laissez le concept de connectivité être dynamique !

Au milieu des années 2000, la connectivité a été reconnue comme un concept « dynamique », devant être quantifiée au regard des processus physiques (e.g. changements d'occupation du sol) et biologiques (e.g. capacités de dispersion) opérant à des échelles temporelles variables (Crooks & Sanjayan 2006; Taylor *et al.* 2006; cf. introduction, section 2.1.4). Depuis cette même période, le concept connectivité a bénéficié d'un intérêt grandissant (Correa Ayram *et al.* 2016; Fletcher *et al.* 2016), à l'instar de sa quantification par la théorie des graphs, qui s'est démocratisée au début des années 2000 (Foltête *et al.* 2020).

Malgré la relative ancienneté du caractère dynamique de la connectivité, couplée à l'ensemble de ces prérequis et des appels lancés pour quantifier cette dynamique temporelle (e.g. Kool *et al.* 2013; Zeigler & Fagan 2014; Lira *et al.* 2019), rares sont les études qui abordent la dynamique temporelle de connectivité de manière explicite (*stricto sensu*, i.e. changement temporels de connectivité spatiale ou connectivité spatio-temporelle ARTICLE 1). Seules 32 études caractérisant la dynamique temporelle de connectivité ont, en effet, été identifiées pour notre revue littéraire.

Cette paucité d'étude apparaît particulièrement préoccupante, compte-tenu des effets avérés de l'intensité (ARTICLES 1 et 5) et/ou de la variabilité (ARTICLE 5) des changements temporels de connectivité spatiale pour les plantes (ARTICLE 5; Metzger *et al.* 2009; Raatikainen *et al.* 2018), bien qu'ils ne sont parfois testés que de manière indirecte (i.e. influence de l'intensité des changements temporels sur la présence d'un délai de réponse au degré de connectivité; e.g. Raatikainen *et al.* 2018; cf. introduction, section 1.2.6). Les effets des changements temporels de connectivité spatiale semblent être tout aussi importants – sinon plus (ARTICLE 5) – que le degré de connectivité pour déterminer les communautés végétales actuelles. Si l'intensité et la variabilité des changements temporels de la connectivité spatiale, couplée à sa tendance (dénommée sens dans l'ARTICLE 1), doivent encore être alimentées par des prévisions théoriques et des études empiriques, l'effet de la rapidité (brusque *versus* progressif) de ces changements pourrait également être exploré. Seuls les géotypes les plus plastiques dans leurs traits de dispersion pourraient, par exemple, survivre à un changement temporel brusque de connectivité. Pris dans son ensemble, il semble crucial de poursuivre nos efforts dans la prise en compte des changements temporels de connectivité spatiale, en particulier potentielle, pour avancer notre compréhension de l'interaction entre la structure physique du paysage et de la dispersion spatiale des espèces végétales au cours du temps.

Développée en 2017 par Martensen *et al.* (2017), la connectivité spatio-temporelle fournit une métrique synthétique, intégrant l'importance de modifications de la structure physique des tâches d'habitat favorable au fil du temps [i.e. renouvellement des tâches (*habitat turnover*) : gain, perte, ou stabilité] pour la dispersion spatiale, mais également temporelle entre tâches d'habitat favorable (ARTICLE 1). Le renouvellement des tâches fournit, en effet, des « pas japonais » reliant des tâches selon une perspective spatio-temporelle : les organismes peuvent se disperser au fil du temps d'une tâche à une autre grâce à la présence de tâches éphémères, même si ces deux tâches sont isolées spatialement à un moment donné (Keymer *et al.* 2000; Matlack & Monde 2004; Wimberly 2006). L'inclusion de la dispersion spatiale et temporelle dans la caractérisation de connectivité semble ainsi fournir une évaluation plus réaliste de la connectivité des tâches d'habitat. Partant de ce constat, l'évaluation de la connectivité spatio-temporelle semble être une voie prometteuse pour mieux comprendre le rôle de la connectivité sur la structuration des communautés végétales. Toutefois, la connectivité spatio-temporelle ne peut, pour l'instant, qu'être appréhendée (i) selon sa nature structurelle et (ii) à partir de deux moments (ARTICLE 1).

Pour pallier à ses limites, nous cherchons désormais, dans le cadre d'un projet en collaboration avec Pr M.-J Fortin (Université de Toronto), Dr A.C. Martensen (Université Fédérale de São Carlos) et Dr J.-L Huang (Université de Wuhan), à caractériser la connectivité spatio-temporelle à partir de multiples moments, tout en intégrant des informations sur les capacités de dispersion spatio-temporelle des espèces végétales. Les capacités de dispersion spatiale des espèces végétales, susceptibles de varier au fil du temps selon la perméabilité de la matrice entre tâches aux multiples moments considérés, peuvent aisément être incorporées (e.g. ARTICLE 5). En revanche, il est nécessaire d'intégrer le fait que les capacités de dispersion temporelle des espèces végétales diffèrent selon la durée d'existence simultanée des tâches d'habitat favorable, c'est-à-dire du temps dont elles disposent pour se disperser d'une tâche favorable à une autre (cf. ARTICLE 1). La transposition du concept de connectivité spatio-temporelle à de multiples moments nécessite, dès lors, une pondération des liens spatiaux entre tâches basée sur une probabilité de dispersion dépendante de la distance effective du lien à chaque moment (cf. introduction, section 2.2.1.1). Une pondération des liens temporels dépendant non seulement de la (possible) existence simultanée des tâches d'habitat favorable (Martensen *et al.* 2017), mais aussi de la durée de celle-ci (ARTICLE 1; Rayfield 2009) doit également être faite. Au-delà de ces aspects, l'objectif final de ce projet serait d'inclure directement la présence de réponses décalées dans le temps des espèces, observées ou potentielles, dans l'évaluation de la connectivité spatio-temporelle (ARTICLE 1). Une telle

estimation holistique et unique de la connectivité spatio-temporelle permettra également de fournir un lien entre les études traitant de manière implicite la façon dont les communautés végétales sont affectées par la dynamique temporelle de connectivité, tout en s'affranchissant de tout problème de corrélation entre métriques. Toutefois, les calculs mathématiques complexes sur lesquels repose cette approche novatrice constitueront probablement un frein important au panel d'améliorations possibles, tout comme à ses possibilités d'applications futures.

Si nos travaux rendent compte des progrès réalisés dans les méthodes d'évaluation de la dynamique temporelle de connectivité, ils suggèrent également que les deux approches principales, à savoir, la caractérisation des changements temporels de connectivité spatiale (ARTICLES 1 et 5) et la connectivité spatio-temporelle (ARTICLE 1), reflètent des processus physiques et biologiques différents. Pour discerner les mécanismes captés au travers de ces deux approches, il est indispensable d'étudier et de confronter ces deux types d'estimation de la dynamique temporelle de connectivité à des indices de structuration des communautés végétales. Compte tenu des éléments susmentionnés dans cette seconde partie (cf. aussi discussion, section 1.2 et 1.3), ce discernement doit être évalué en tenant compte de la capacité des espèces végétales à suivre les changements de la structure physique du paysage à des échelles spatiales et temporelles variées.

3. Implications pour la conservation de la biodiversité floristique au sein des paysages agricoles

En troisième lieu, nos travaux peuvent avoir des implications de portée non négligeable pour la conservation de la biodiversité floristique au sein des paysages bocagers, en mettant l'accent sur les rôles variés qu'exercent les différents habitats sur la dispersion des espèces végétales. Ils fournissent également des méthodes et outils d'aide à la décision transférables aux gestionnaires et aménageurs des territoires ruraux pour prioriser les actions visant à évaluer et restaurer (ou maintenir) efficacement la connectivité, telles qu'encouragées par la Trame Verte et Bleue (TVB), non pas pour une espèce particulière mais pour de multiples espèces simultanément.

3.1. De multiples rôles exercés par les différents types d'habitat contribuant à la connectivité sur la dispersion des plantes

Si nos travaux réaffirment le rôle fondamental des habitats boisés, qui, en augmentant la connectivité dans l'espace et/ou dans le temps, favorise la dispersion des espèces végétales

boisées (ARTICLES 3 et 5), ils révèlent également des rôles moins connus des habitats prairiaux et cultivés pour la dispersion des espèces végétales boisées, prairiales et adventices (ARTICLES 3 et 4).

En dépit du faible nombre d'études caractérisant la connectivité selon sa nature fonctionnelle pour les espèces boisées (mais cf. Mony *et al.* 2018), de nombreuses études ont montré que les haies reliant des tâches de bois anciennes autrement isolées, facilitait la dispersion des espèces boisées (e.g. Lenoir *et al.* sous presse; Corbit *et al.* 1999; Wehling & Diekmann 2009; Paal *et al.* 2017; cf. aussi CHAPITRE A1). En considérant les habitats boisés dans leur ensemble, nos résultats suggèrent, qu'à l'instar des haies anciennes, les bois, y compris ceux établis plus récemment, augmentent la perméabilité de la matrice, facilitant ainsi la dispersion des espèces boisées d'une tâche de bois ancienne à une autre (ARTICLES 3 et 5). Les habitats boisés semblent offrir des conditions requises à la dispersion lente des espèces végétales, se réalisant via des événements de dispersion à courte distance sur plusieurs générations (Matlack 2005; Hermy & Verheyen 2007), probablement parce qu'ils comptent parmi les habitats les plus stables de la matrice agricole (Petit & Usher 1998). Maintenir des haies et des bois de bonne qualité au sein des paysages bocagers s'avère être un objectif majeur de conservation, d'autant plus qu'ils n'agissent pas seulement en tant que continuités écologiques pour les espèces boisées, mais contribuent aussi à un éventuel bouquet de fonctions écologiques (CHAPITRE A1; Valdés *et al.* 2020). Les stratégies de verdissement de la politique agricole commune (e.g. bonnes conditions agricoles et environnementales, mesures agro-environnementales et climatiques) et les dispositifs régionaux existants (e.g. programmes Breizh bocage) vont dans ce sens, en reconnaissant davantage la nécessité d'agir pour maintenir, restaurer, et replanter ces habitats bocagers, désormais considérés comme des systèmes agroforestiers (Observatoire de l'environnement en Bretagne 2018). Toutefois, les communautés boisées actuelles résultent de l'ensemble des changements de connectivité fournie par ces mêmes habitats qui se sont produits depuis le milieu des années 1950 (ARTICLE 5). Les conséquences de ces actions futures ne seront ainsi probablement visibles qu'à (très) long terme sur les communautés végétales, et elles devront être évaluées en tenant compte que ces communautés continueront, à l'avenir et pour une durée indéterminée, d'être hantées par nos actions passées.

Quant aux habitats prairiaux et cultivés, insérés et gérés de manière plus ou moins intensives au sein de la matrice agricole, ils n'apparaissent pas *a priori* comme des habitats offrant des conditions optimales à la dispersion des espèces végétales. Pourtant, ces habitats

agissent bel et bien sur la dispersion des espèces, et en particulier, des espèces qui ne leur sont pas inféodées (ARTICLES 3 et 4).

A l'inverse des habitats boisés, le rôle des habitats prairiaux pour les espèces cultivées semble plus complexe. Ils n'agissent pas sur la dispersion des espèces selon leur mode de dispersion (ARTICLE 3), mais facilitent en revanche la dispersion de certaines espèces aux valeurs de traits particulières, réduisant ainsi l'abondance totale des espèces adventices (ARTICLE 4; cf. discussion, section 1.4). Si la supplémentation du chemin de dispersion des espèces adventices semble ainsi attribuable à leurs préférences écologiques plutôt qu'à leur mode de dispersion (cf. discussion, section 2.2), ces résultats suggèrent aussi que l'augmentation de connectivité fournie par les habitats prairiaux pourrait présenter un intérêt pour la production céréalière. En l'absence de tout effet de la quantité d'habitat sur la diversité et l'abondance totale des adventices, médié (ou non) par les traits des espèces (ARTICLE 4), les agriculteurs pourraient en effet profiter d'une réduction de l'abondance des adventices sans même compromettre l'affectation de leurs champs à la production végétale ou animale (i.e. pâturage ou foin). De tels résultats sont importants, puisqu'ils contribuent à favoriser l'acceptation progressive par les agriculteurs des efforts encouragés par les politiques publiques pour rétablir la connectivité au sein des territoires ruraux.

Jusqu'ici occultés de toute stratégie de conservation et de restauration de la connectivité, les habitats cultivés ont pourtant un rôle double, ambivalent. Lorsqu'ils relient des tâches d'habitat autrement isolés, les habitats cultivés peuvent entraver (cas des communautés boisées), mais aussi faciliter (cas des communautés prairiales) la dispersion des espèces zoochores (ARTICLE 3). L'ambivalence des habitats cultivés, oscillant entre continuités écologiques et barrières à la dispersion, est probablement indirectement liée à des phénomènes de supplémentation et d'évitement des habitats cultivés par les espèces animales impliquées dans la dispersion des espèces boisées et prairiales, respectivement (ARTICLE 3).

Bien que les rôles des habitats prairiaux et cultivés mériteraient d'être approfondis, nos travaux soulignent le besoin de considérer de manière simultanée les divers habitats qui contribuent à la connectivité dans les stratégies et opérations visant à promouvoir la conservation des communautés végétales à l'échelle des territoires, même si leurs effets respectifs diffèrent.

3.2. Des méthodes et des outils mobilisables pour évaluer et restaurer la connectivité efficacement pour de multiples espèces végétales

Pour envisager des stratégies et prioriser des zones où il est nécessaire d'agir, les gestionnaires et les aménageurs du territoire doivent disposer de méthodes et d'outils d'aide à la décision. En ce sens, l'ensemble des réflexions méthodologiques menées dans le cadre de cette thèse (ARTICLES 1 à 5) peut être transféré vers l'élaboration de directives claires sur la manière d'évaluer et restaurer la connectivité pour les plantes, telles que voulues par la réglementation TVB. Cette section décrit les points clés qui peuvent être mobilisés pour atteindre cet objectif.

Premièrement, nos travaux fournissent une évaluation pertinente de la connectivité, fonctionnelle à l'échelle des communautés végétales, à travers l'amélioration des mesures de connectivité pluri-habitat existantes (ARTICLES 3 et 4), mais également la synthèse (ARTICLE 1) et le développement (ARTICLE 2) de mesures innovantes de la dynamique temporelle de connectivité. En l'absence de méthodologie standardisée, l'identification des différentes continuités écologiques constituant la TVB repose sur une interprétation visuelle ou sur la modélisation des chemins de dispersion potentiels entre tâches pour quelque(s) espèce(s) cible(s), le plus souvent patrimoniale(s). Si des analyses de conflits sont réalisées par des experts, le suivi et la validation de l'effet des continuités identifiées sur le(s) espèce(s) cible(s) restent le plus souvent absents (Amsallem *et al.* 2010, 2018). En ce sens, l'ensemble des outils et méthodes mobilisés et développés pour mesurer la connectivité potentielle fournie par les différents types d'habitat peut être mobilisé – voire étendu – pour identifier séparément les continuités par type d'habitat souhaité, tout en répondant à un objectif simultané de conservation multi-espèces. Si la plupart des habitats, contribuant à la connectivité favorise bel et bien la dispersion des espèces végétales, nous soulignons qu'ils n'agissent pas toujours comme des continuités écologiques *per se*, mais aussi comme des barrières à la dispersion (e.g. cultures). Bien qu'il soit nécessaire d'évaluer l'effet des continuités écologiques identifiées, et ce à une échelle cohérente avec la distance de dispersion des plantes, nos résultats soulignent qu'il est également indispensable de suivre leur dynamique. L'intégration de la dynamique temporelle de connectivité dans la TVB est cruciale, des décalages pouvant se produire entre l'élaboration des politiques, la mise en œuvre des stratégies et les résultats escomptés pour certaines espèces, qui portent toujours l'empreinte des modifications de connectivités passées. Pour se faire, les gestionnaires et les aménageurs peuvent bénéficier des métriques existantes, développées, ou en cours de développement pour s'adapter au processus de dispersion des plantes, pour caractériser la dynamique temporelle de connectivité. Ces métriques aideraient

les professionnels à mieux comprendre les patrons de biodiversité actuels et futurs, mais aussi à prioriser des zones spécifiques où il est nécessaire d'intervenir, en testant *a priori* l'impact des actions envisagées à plus ou moins long terme pour façonner la dynamique future souhaitée.

Deuxièmement, nos travaux permettent d'alimenter les réflexions quant aux listes d'espèces végétales régionales pour la cohérence nationale TVB, telles que voulues par le comité opérationnel TVB (Sordello *et al.* 2011). A l'issue de réflexions antérieures, la Fédération des Conservatoires botaniques Nationaux (FCBN) jugeait qu'il n'était pas envisageable de définir des espèces végétales dites de « cohérence », au-delà du premier filtre caractérisant les espèces pour lesquelles la région porte une responsabilité nationale (Chaurand 2011). La FCBN souligne que le deuxième filtre, définissant le caractère pertinent de la mise en œuvre de la TVB pour les espèces végétales n'a pu être établi, faute de généralisation possible quant au rôle des traits fonctionnels pour définir la sensibilité des espèces à la perte de connectivité (Chaurand 2011). Ici encore, nos travaux ouvrent des perspectives appliquées prometteuses, la sensibilité des espèces à la perte de connectivité spatiale semblant être associée à la possession d'un ensemble de traits fonctionnels dont les valeurs induisent de faibles capacités de dispersion, celles-ci étant déterminées par la production et la distance de transport des graines (ARTICLE 2 à 4). Certains traits impliqués dans le recrutement des plantules peuvent également avoir un rôle non négligeable pour la sensibilité des espèces à la perte de connectivité spatiale (cf. discussion, section 1.3). Enfin, et non des moindres, la considération des différentes composantes de la dynamique temporelle semble importante pour les espèces qui ont une capacité de dispersion faible, mais en revanche une capacité de persistance forte (e.g. cas des espèces boisées, ARTICLE 3, cf. aussi ARTICLE 2). En revanche, il est encore impossible de déterminer, à ce stade, l'arrangement des valeurs de traits déterminant la sensibilité des espèces aux différentes composantes de la dynamique temporelle de connectivité et selon les tendances qui y sont associées. Lorsque ces derniers aspects seront résolus, les gestionnaires pourront sélectionner, sur la base de leur valeur de traits, les espèces végétales pour lesquelles la TVB est pertinente, non seulement dans l'espace, mais également dans le temps; et ce, grâce à la disponibilité accrue des bases de données mondiales sur les traits des plantes (e.g. TRY, Kattge *et al.* 2011, 2020).

Troisièmement, à l'issue de nos travaux, des perspectives pourraient être envisagées afin d'évaluer la nécessité et le potentiel des actions de restauration de la connectivité pour la recolonisation des espèces végétales au sein des tâches d'habitat. Certaines espèces végétales

sont actuellement absentes de certaines tâches d'habitat favorable, alors qu'elles appartiennent au pool d'espèces de cet habitat (Pärtel *et al.* 2011). Ces espèces végétales, caractéristiques de la diversité dite sombre (*dark diversity*), sont caractérisées par de faibles capacités de dispersion et d'établissement, et dépendent aussi fortement ou obligatoirement des mycorhizes (Riibak *et al.* 2015; Moeslund *et al.* 2017). Certaines espèces, actuellement absentes de la communauté au sein d'une tâche d'habitat, pourraient alors y être recrutées dans le futur, grâce à une augmentation de la connectivité. Les tâches d'habitat à forte complétude (i.e. forte diversité observée et faible diversité sombre; *completeness*; Pärtel *et al.* 2013) représentent un enjeu de conservation majeur (Lewis *et al.* 2016). Il est alors crucial d'évaluer si, et dans quelle mesure, la restauration de la connectivité des tâches d'habitat augmente la complétude des communautés végétales, en favorisant les espèces à faibles capacités de dispersion (Török & Helm 2017). Si cette hypothèse est vérifiée (mais cf. Belinchón *et al.* sous presse), les professionnels impliqués dans la TVB pourraient alors identifier les tâches d'habitat prioritaires, sur lesquelles des actions de restauration ont le potentiel de favoriser une forte recolonisation. Avec des continuités écologiques appropriées à leur dispersion, et suffisamment de temps, les plantes piètres colonisatrices finiront par atteindre les tâches d'habitat favorable éloignées de la plante mère (Moeslund *et al.* 2017).

Enfin, l'ensemble des opérations implémentées dans le cadre de la TVB doit reposer sur des suivis à long terme, qui seront essentiels compte tenu de la sensibilité des espèces aux modifications de connectivité s'opérant au fil du temps.

4. Conclusion

En dépit de l'importance présumée de maintenir et de restaurer la connectivité pour enrayer la perte de biodiversité floristique, aucun consensus n'a pu être dégagé quant à l'efficacité de cette stratégie pour les communautés végétales. Concept aux multiples facettes, la connectivité est en réalité une interaction particulière, mais aussi plurielle, entre la structure physique du paysage et la dispersion des plantes, qu'il convient d'appréhender. Ces travaux apportent des éléments nouveaux quant au rôle de la connectivité sur la structuration des communautés végétales, en tentant de saisir, parmi l'éventail des interactions possibles, la contribution des différents types d'habitat à la connectivité, mais aussi sa dynamique temporelle. La connectivité apparaît ainsi comme un phénomène complexe, façonnant bel et bien l'assemblage des communautés végétales. Plutôt que d'agir sur leur diversité spécifique, elle semble davantage affecter leur composition spécifique, c'est-à-dire leur identité, en agissant sur les traits fonctionnels des espèces, et ainsi modifier potentiellement le

fonctionnement des écosystèmes. Nos travaux présentent des implications non négligeables pour la conservation de la biodiversité floristique au sein des paysages agricoles bocagers, en particulier pour les espèces piètres colonisatrices, dont la survie sur le territoire national face au changement climatique dépend de la pertinence et de l'efficacité des actions menées dans le cadre de Trame Verte et Bleue.

Annexes

Article A1. Small but not the least: transient changes in landscape patterns drive grassland plant aboveground and seed bank assemblages

Article A2. Ecological corridors for the invisibles

Chapitre A1. The role of hedgerows to support biodiversity and associated ecosystem services in intensive agricultural landscapes

List of publications

Article A1. Small but not the least: transient changes in landscape patterns drive grassland plant aboveground and seed bank assemblages

Léa Uroy, Jérémie Guy, Olivier Jambon, Romain Georges, Cendrine Mony

In preparation to be submitted to *Biodiversity and Conservation*

Abstract

Plant biodiversity conservation in fragmented semi-natural grasslands is a key challenge. In intensive agricultural landscapes, transient semi-natural habitats, such as temporary grasslands, can be interesting refuges for plant biodiversity. Because of their effect on plant dispersal, landscape spatial patterns are considered as key factors determining plant assemblages in grassland patches. Yet, these spatial patterns within the agricultural mosaic are strongly changing over grassland lifetime as a consequence of crop rotations, likely affecting seed dispersal and subsequent plant establishment. We examined how seed bank and plant aboveground assemblages of 30 temporary grassland patches were affected by changes of their surrounding landscape encountered over the grassland patch lifespan (from its setting up to its destruction). We especially evaluated the spatial (mean) and temporal (variation coefficient) changes in landscape heterogeneity and habitat amount surrounding patches across a range of spatial scales (250 to 750m) covering the range of dispersal distances of grassland plants. Despite changes of small intensity, the temporal variability of landscape characteristics was a better driver than its mean in shaping plant assemblages. Aboveground species richness increased with temporal variability in landscape composition (Shannon habitat diversity) and configuration (mean patch size), whereas habitat amount (percentage of grassland area) did not have any effect. In seed-bank, the richness and seed abundance of species with a short-dispersal distance increased with the temporal variability in landscape composition, while the richness decreased with the temporal variability in habitat amount. For species with long-dispersal distance, species richness decreased with mean landscape composition but seed abundance respectively increased and decreased with the temporal variability of landscape configuration and habitat amount. The spatial scale of effect differed between plants, depending on the distance they are dispersed (long vs. short) and the compartment they occupy (aboveground or seed bank). This study stressed the need for taking into account temporal landscape patterns effect in species assembly and revealed the strong discrepancy between seed bank and plant aboveground responses to landscape structure, which calls for the integration of seed bank potential into management actions.

Article A2. Ecological corridors for the invisibles

Cendrine Mony, Léa Uroy, Fadwa Khalfallah, Nick Haddad, Philippe Vandenkoornhuysse

To be submitted to *Ecology*

Abstract

A massive decrease in biodiversity is underway all over the world, mostly driven by habitat degradation and fragmentation. As a complement to local restoration actions, the use of ecological corridors has been proposed as a key landscape-level management strategy to counterbalance these negative effects by promoting movement between local patches, thereby maintaining species diversity throughout the landscape matrix. A lively debate has emerged on the efficiency of such corridors for macroorganisms, resulting in a large theoretical and conceptual framework. However, the “invisible” microbial compartment has been largely neglected despite their biodiversity which is greater than that of all other living forms on earth, and the important role microorganisms play in many ecosystem services that are fundamental to our society. Whether this conceptual framework can be applied to microorganisms remains an open question because of their particular characteristics such as small size, high propagule production, their short lifespan and generation time that likely shape their response to the landscape. We analyzed if and how the corridor hypothesis applies to the microbial world and reviewed existing evidence and the methods used to test this hypothesis on microorganisms. To obtain general patterns, we accounted for all types of microorganisms, from symbiotic to pathogenic and free-living, across all ecosystems. We demonstrate that the response of microorganisms to their landscape does not only result from environmental patchiness. However, in micro- and macroorganisms, we identified major differences in the mechanisms and processes underlying the corridor effect, due to the effects of temporal and spatial scales, interaction with hosts, and evolutionary processes. In the context of global change, a high priority for ecology in the future will be to tackle this loss of microbial diversity. Incorporating the corridor theory in the rules governing microbial community assembly offers new research avenues on this pressing issue.

Introduction

The massive worldwide decline in biodiversity is referred to by many scientists as the sixth biodiversity extinction crisis (Barnosky *et al.* 2011; Ceballos *et al.* 2015). Habitat degradation and fragmentation are considered to be the main drivers of the decline, by reducing the availability of favorable habitat patches (**Box 1**), increasing edge effects and habitat isolation (Haddad *et al.* 2015). Ecological corridors have been proposed as a key landscape-level strategy to mitigate the negative effects of habitat fragmentation (Hilty *et al.* 2006), by promoting dispersal movement, thereby preserving genetic fluxes (Wilson & Willis 1975) and protecting local populations from extinction (rescue effect; Brown & Kodric-Brown 1977). The corridor hypothesis posits that corridors facilitate the movement of organisms among habitat patches, generally contributing to dispersal movements (Rosenberg *et al.* 1997; Beier & Noss 1998). This hypothesis has been modulated by the drift fence hypothesis, which suggests that the movement of organisms, even located in the landscape matrix, is guided by the corridors once encountered (Anderson & Danielson 1997; Haddad & Baum 1999). Corridors can be of several types and forms depending on the concept used to assess how organisms respond to dispersal in the landscape, including via habitat strips (called corridors) to landscape patches that represent landscape connectivity (**Box 1** and **Fig. 1**). Recent meta-analyses comparing results demonstrated the generally positive effect of corridors on population dynamics, population genetic diversity and species richness in macroorganisms (Beier & Noss 1998; Gilbert-Norton *et al.* 2010; Fletcher *et al.* 2016 but see also Haddad *et al.* 2014).

Microorganisms display more than $\sim 10^6$ fold biodiversity than the total species richness of classified Eukaryotes (i.e. 1,233,000 species in Eukaryotes; Mora *et al.* 2011) vs. more than a trillion (10^{12}) microbial species richness estimated on earth (Locey & Lennon 2016). Microorganisms are predominant in all compartments of all ecosystems and life forms. These microorganisms are crucial to human society, as they support many ecosystem services, including soil fertility (Adhikari & Hartemink 2016; Guo *et al.* 2019) food production, health (McKenney *et al.* 2018) and water purification (Adhikari & Hartemink 2016), among others.

Evidence for diversity loss in microbial communities is starting to emerge, in soils for instance (e.g. Wang *et al.* 2018). The global biodiversity crisis is thus likely to downscale to this invisible compartment, leading to important changes in the related provision of services (Delgado-Baquerizo *et al.* 2016).

Biodiversity results from random variations and from a set of drivers that shape species assembly, among which dispersal is of huge importance (MacArthur & Wilson 1967; Mouquet & Loreau 2003). Dispersal limitation has indeed been demonstrated for microbial communities (Martiny *et al.* 2006; Hanson *et al.* 2012). In microorganisms, dispersal is either passive (i.e. achieved through particular vectors), or active (i.e. achieved through cilia or flagella). It has been shown to follow a distance-decay relationship, as predicted by the biogeography theory (MacArthur & Wilson 1967), over distances ranging from centimeters to hundreds of meters for bacteria (Horner-Devine *et al.* 2004) and fungi (Peay *et al.* 2010). Like for macroorganisms, dispersal might also depend on how the landscape promotes or hinders species movement, especially in the case of microorganisms associated with hosts whose movement depends on a landscape mosaic. This may depend on the type of landscape elements composing the matrix (landscape composition), but also on their configuration (landscape configuration), which may provide corridors for these microorganisms.

Whether the hypotheses explaining the dispersal promoting effect of corridors can be applied to microorganisms remains questionable. The fact the hypotheses apply to microorganisms suggests that dispersal-limitation in microorganisms is independent of environmental patchiness. Microorganisms have characteristics that differ markedly from those of macroorganisms, such as their small size. The size-dispersal hypothesis indeed predicts that smaller organisms are more likely affected by species sorting than by dispersal limitation because smaller organisms can disperse over longer distances than macroorganisms (Cottenie 2005; Beisner *et al.* 2006; Shurin *et al.* 2009). Microorganisms usually also produce numbers of propagules, many more than macroorganisms. In ectomycorrhizal fungi, for instance, production is estimated at billions to trillions of spores per km² (Peay *et al.* 2012). Despite limited knowledge about the dispersal of microorganisms, it appears that the production of so many propagules is offset by the fact the vast majority of spores falls close to the source of emission and by the very low probability of achieving viable germination (Peay *et al.* 2012). Microorganisms usually have a short generation time ranging from minutes to at the most a few days. In this particular case, dispersal can thus extend over several generations, meaning the corridor effect can affect not only movement of an individual but the movement achieved over several generations of individuals.

In this review, we investigate whether the corridor hypothesis applies to microorganisms and determine to what extent the underlying mechanisms and processes

resemble those observed in macroorganisms. To achieve a general overview, we considered all types of symbiotic, pathogens, or free-living microorganisms, over all ecosystems.

Box 1 Main definitions

Habitat patches: discrete areas of ‘homogeneous’ environmental conditions where the patch boundaries are distinguished by discontinuities in environmental character states from their surroundings of magnitudes that are perceived by or relevant to the organism or ecological phenomenon under consideration (Wiens 1976; Kotliar & Wiens 1990).

Ecological corridor: strip (habitat-strip corridor) or nonlinear, discontinuous permeable landscape element that connects otherwise isolated habitat patches (Beier & Noss 1998; Burel & Baudry 1999; Chetkiewicz *et al.* 2006).

Rescue effect: the effect due to ease population size (demographic rescue) or fitness (genetic rescue), thereby preventing local (Brown & Kodric-Brown 1977).

Landscape connectivity: the degree to which a landscape facilitates or prevents movement, and especially dispersal movements, among habitat patches (Taylor *et al.* 1993).

Extinction debt: the number of species yet to go extinct in the patch following a loss of connectivity (Cristofoli *et al.* 2010). This time-lag represents the delay in species response to environmental change (Tilman *et al.* 1994).

Colonization credit: the number of species yet to colonize a patch following a gain in connectivity (Cristofoli *et al.* 2010). Time delay reflects a lag in immigration lag, which leads to immigration credit (Kuussaari *et al.* 2009).

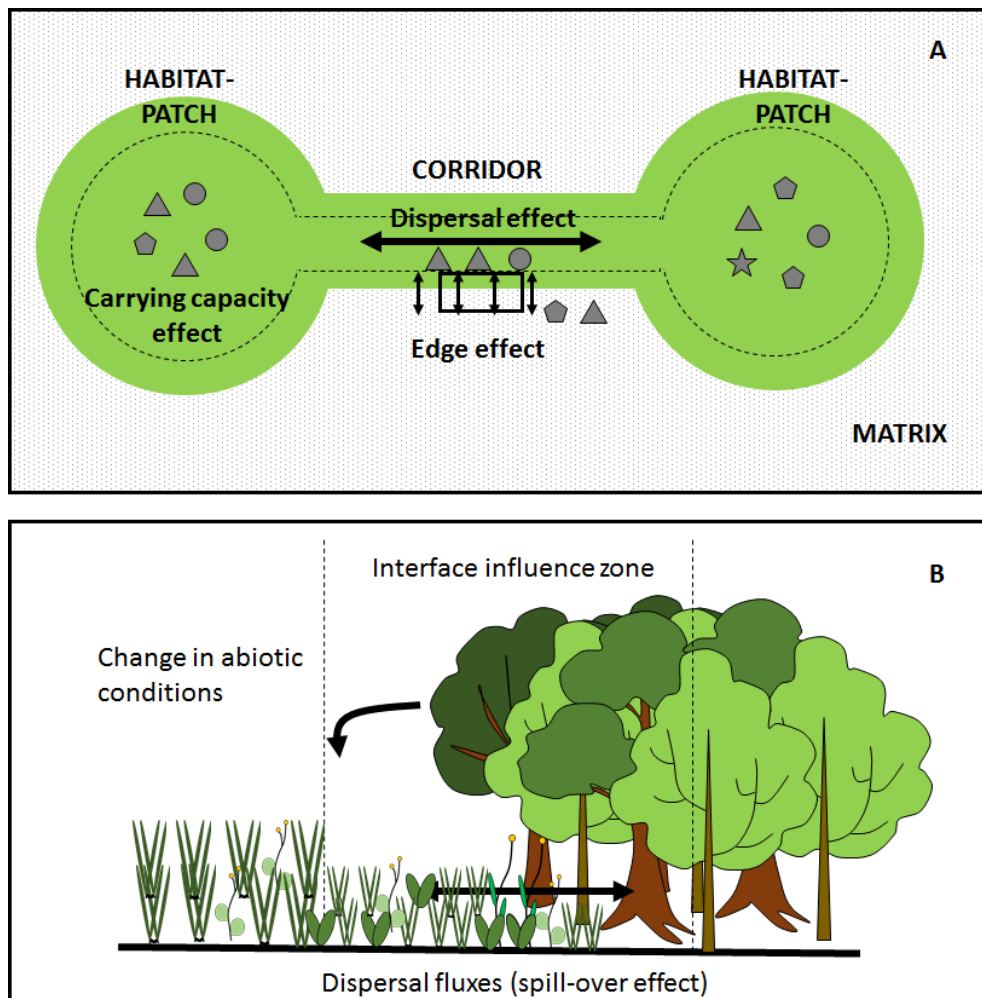
Cross habitat spillover: the movement of organisms from one habitat type to another for the purpose of dispersal and/or foraging (Tschardtke *et al.* 2012).

Microbial rescue effect: It reflects the ability of modified microbiomes to increase host-fitness and population densities, thereby preventing host extinction (Mueller *et al.* in press).

The different mechanisms underlying the corridor hypothesis

The corridor hypothesis states that, whatever their form and type, ecological corridors counteract the negative effects of habitat fragmentation by facilitating the dispersal of organisms among local habitat patches (Haddad *et al.* 2003; Gilbert-Norton *et al.* 2010). The dispersal effect concept is challenged by other views arguing that corridors also increase the edge effect due to interfaces with other habitat types and the amount of habitat available for organisms to coexist. All these processes (dispersal, edge or habitat amount effects) are assumed to have an overall positive impact on biodiversity (**Fig. 1**).

Fig. 1 Mechanisms underlying the corridor effects. This is an illustration of the simplest spatial pattern of ecological corridors, habitat-strip corridor. **(A)** Different mechanisms related to the presence of a corridor. Dispersal effect is linked to the movement of species from one habitat patch to another. Edge effect is linked to the influence of the interface on dispersal fluxes and abiotic conditions (see B). High edge amounts due to an extensive perimeter of habitat patches and thin corridors increase the influence of the interface. The effect of carrying capacity is linked to the amount of habitat related to the corridor and habitat patches. Large amounts of habitat due to large habitat patches and corridors increase the carrying capacity effect. **(B)** Focus on influences linked with the interface zone between the corridor and the matrix habitats (example here of a forest corridor close to a grassland matrix). These influences include dispersal fluxes between the corridor and the matrix habitat (spill-over effect) and changes in the abiotic conditions.



The dispersal effect is associated with the movement of organisms within a landscape, which is hypothesised to be easier in corridors than in less permeable landscape elements. Microorganisms display a wide range of dispersal strategies including frequent long-distance dispersal events, partly due to their ability to be dispersed by vectors such as flowing water, wind or animals. There is also increasing evidence for very short-dispersal distances via small vectors (e.g. worms or collembola in the case of soil microorganisms), active dispersal thanks to flagella in bacteria or cilia in protists; and vegetative mycelium multiplication in fungi. In these species, “dispersal capacity” refers to a few micrometers to decimeters (Martiny *et al.*

2006). In fungi, motion (i.e. active and passive movements) and navigation capacity vary considerably among taxonomic groups and species (Bielčik *et al.* 2019). This has led to highly divergent scales of dispersal depending on the microorganism's life-history traits such as the type of vector, body size and dispersal strategies; which may render them more or less sensitive to large-scale corridors. The notable diversity of dispersal-related traits determines differences in colonization ability (Peay *et al.* 2010). But to our knowledge, up to now, no studies have included detailed analyses of either active or passive dispersal movement of microorganisms along corridors.

Disentangling the dispersal effect from the edge effect or the habitat effect is difficult. Corridor edges can indeed act as barriers or as filters to movement, or facilitate the arrival of organisms from the matrix and their dispersal along corridors (Fagan *et al.* 1999). Corridor edges can also modify the environmental conditions, which, in turn, may affect the germination and survival of microorganisms. To our knowledge, only a few studies have quantified these different mechanisms and those that did were based on experimental designs that test the presence of a corridor but also its shape, which modifies the amount of edge (Tewksbury *et al.* 2002). Other designs have been based on nested-experimental treatments in which connected and unconnected treatments are used with different distances to the edge. For instance, edge effects were detected in the Savannah Corridor Experimental site for four wind-dispersed and splash-dispersed fungi (foliar fungi on *Solidago odora* and three *Lespedeza* spp.), by comparing the proportion of infected plants close to the edge compared to the proportion in the center of the patch. Depending on the fungal species, edges either favored or hampered pathogen abundance, which was assessed by counting leaf lesions. In another experiment using the same experimental design but based on plant transplants, a higher proportion of diseased plants and therefore a higher abundance of the leaf fungal pathogen *Cochliobolus heterostrophus*, was found in patches with fewer edges, independently of the presence or absence of a corridor (Johnson & Haddad 2011). These negative or positive edge effects were related to two major effects: (i) a change in microclimatic conditions that affected the development of fungal species and (ii) a change in wind turbulence and hence in the spore deposition patterns within the patch (Sullivan *et al.* 2011). Lastly, no analysis of whether the corridor's carrying capacity overrides the dispersal or the edge effect has been performed so far in microorganisms. Independently of the corridor context, there is a range of evidence that the size of the habitat patch size determines species richness (see for instance Peay *et al.* 2007), suggesting that corridors act positively on microorganism coexistence by increasing the total habitat amount.

Many research questions concerning the mechanisms behind the corridor effect of microorganisms thus remain open. Investigating the role of dispersal in corridor response is a new avenue worth exploring, as recent hedge studies have started to quantify the role of host movement in microbiota dispersal (see for instance Correia *et al.* 2019 for microorganism transmission via birds; Shade *et al.* 2017 for transmission through seeds).

Modelling ecological connectivity for microorganisms: should matrix effects be taken into account?

Studies on corridors are based on different conceptual models of landscapes (Sirami 2016); **Fig. 1**) and different types of metrics to analyze connectivity among landscape patches (**Fig. 2**), and the choice of model and its development have produced a wide range of studies (see (Moilanen & Nieminen 2002; Kindlmann & Burel 2008; Rayfield *et al.* 2011 for reviews).

Considering the microbial compartment, there is a large set of studies framed by the island-biogeography theory that considers connectivity to be the Euclidean distance between patches (“island” model, MacArthur & Wilson 1967). Euclidean distance is directly associated with the well-known distance-decay pattern predicted by the biogeography theory (MacArthur & Wilson 1967). This metric does not include the landscape elements that comprise the matrix. As assumed by biogeography theory, the closest patches display more similar assemblages than isolated ones (Nekola & White 1999). However, in landscape ecology, connectivity generally includes the type and quality of matrix composition, because the habitat patches within the matrix show varying degrees of permeability to the movement of organisms (Murphy & Lovett-Doust 2004). A first approximation of the matrix effect was based on a binary view of the landscape, composed of habitat patches embedded in an inhospitable matrix of non-habitats (“patch-matrix” model, **Fig. 2**). The simplest spatial pattern is a habitat strip that acts as a corridor between patches. This pattern is not easy to find in nature but consider the case of river networks connecting aquatic elements or networks of hedgerow connecting forest fragments. More common situations include discontinuous habitat patches distributed within the matrix, formalized as stepping-stone corridors. Most studies dealing with microorganisms in which the matrix was taken into account were conducted in the framework of the “patch-matrix” landscape model. For instance, connectivity among patches was assessed through the distance to the mainland patch or as the distance to the nearest habitat patch of the same type. The type of measurement used influenced the results. For instance, in Peay *et al.* (2007), fungal species richness associated with *Pinus muricata* roots decreased when connectivity was measured as

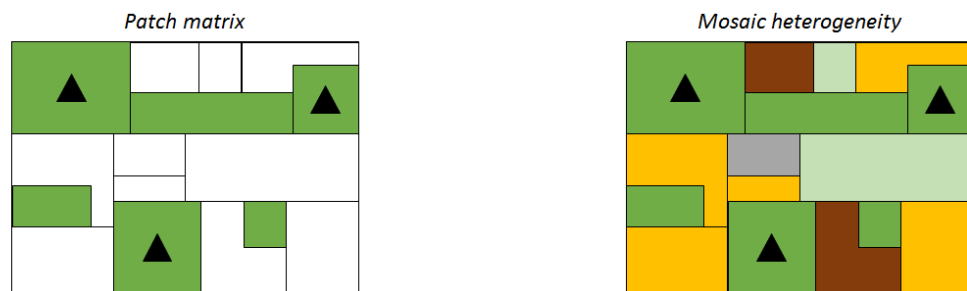
the distance to the mainland, but was independent of the distance to the nearest individual, suggesting that species dispersal does not follow a stepping stone connectivity model. More realistic distances (i.e. functional distances) that account for preferential dispersal routes across the landscape matrix require creating cost (or resistance) maps, in which cost (or resistance) values reflect the ecological cost of species to move through habitat and non-habitat patches. Using an approach of this type, Becker *et al.* (2017) analyzed the composition of the bacterial microbiota on amphibian skin in individual treefrogs located forests connected with each other to varying extents. Forest connectivity was estimated in two ways: the first was based on the Euclidean distance and the second on a functional distance, calculated from cost maps that classified forest habitats with a minimum cost (i.e. highly permeable) and other habitat types with a maximum cost (i.e. slightly permeable). The authors demonstrated that bacterial assemblages bore more resemblance to one another in better connected patches. However, the effect was only detected when the connectivity index was based on functional distance and not on Euclidean distance. These findings suggest that more functional-based connectivity indexes are better predictors of amphibian movement and of the associated microbiota dispersal than geographical isolation alone.

The second landscape model considers the heterogeneity of the entire landscape matrix, that is, its composition made up of different types of landscape elements (“mosaic landscape” model, **Fig. 2**). This model accounts for all the different habitat types in the landscape matrix that enable dispersal with different degrees of permeability. To date, such models have been only been used in a descriptive way in microorganisms. For instance, Ferrari *et al.* (2016) based their sampling design on the use of sites considered to be well-connected areas compared with others considered to be disconnected. The disconnected areas were made up of patchy landforms with vegetated patches separated by small circular mounds of fresh soil material formed by the action of frost, and the patches were assumed to be barriers that isolated the sampling areas. These authors demonstrated that the soils in the patchy landforms contained more similar communities but fewer biological associations than connected areas. In the same way as for macroorganisms, the assumption of an inhospitable matrix needs to be relaxed for microorganisms, by considering the permeability of the different habitat types that make up the landscape matrix. Distinguishing between such costs is the next step in microorganisms studies but requires a better description of the microorganisms’ ecological preferendum (both in terms of abiotic conditions and in the case of biotrophic organisms, of hosts) and dispersal movement. Such mechanisms can be approximated by taking the life-history traits of the microorganisms into account. Overall,

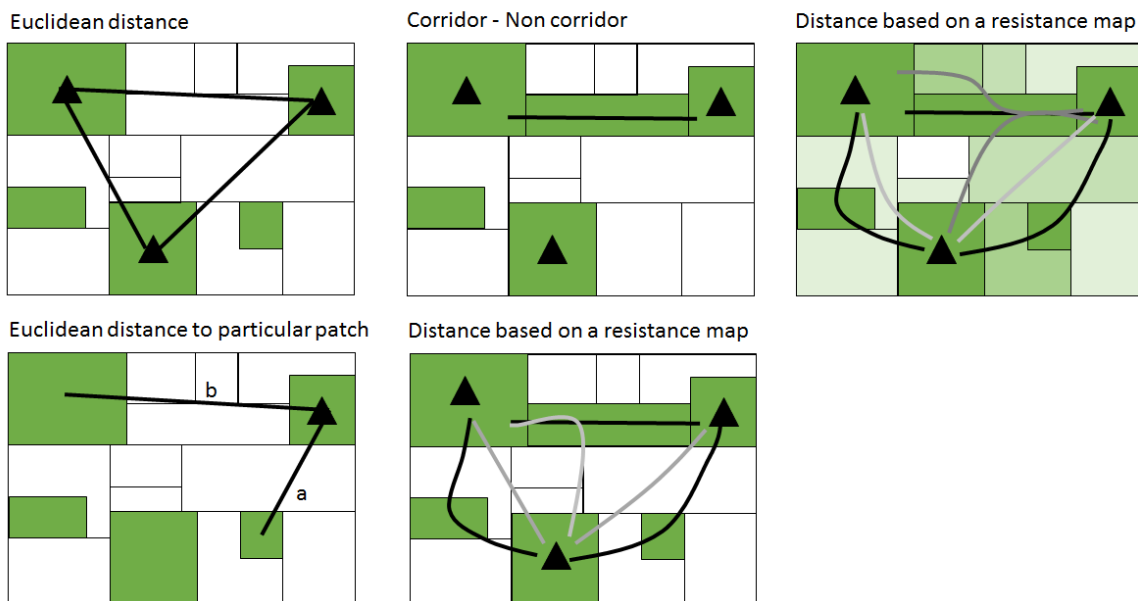
transposing these more realistic representations of the landscape developed for macroorganisms to microorganisms is a promising way to reach a more functional understanding of the corridor effect.

Fig. 2 The different types of corridors and their assumed dispersal pathways and metrics. **(A)** Landscape conceptual model (conceptual models are based on Sirami (2016). Models are of two types: the “patch-matrix” model which considers landscape as a binary representation of habitat-non-habitat and the “mosaic landscape” model which is a multi-patch extension of the patch-matrix model (Wiens 1995). Landscapes are described as discrete patches of different land-cover classes (Forman & Godron 1986; Forman 1995). **(B)** Connectivity metrics. Black lines represent the assumed dispersal pathways. Colors represent different patch types. Black triangles identify the sampling patches where the microbial assemblages were studied.

A-Landscape conceptual model



B-Connectivity metrics and assumed dispersal pathways



Are the impacts of corridors on microbial biodiversity positive or negative?

Landscape connectivity is expected to have positive effects on genetic diversity, population abundance, species richness, and in general, by promoting species coexistence at the landscape scale (Haddad *et al.* 2003; Gilbert-Norton *et al.* 2010; Uroy *et al.* 2019a). Our current knowledge of the effect of corridors on microbial communities is limited to a couple of explanatory variables including species richness, composition, and in the case of species-

focused studies, abundance, possibly measured using symptoms (for instance to describe a pathogen infection).

The analysis of empirical evidence for the corridor effect on microorganisms produced contrasted responses. A number of studies reported a positive effect of hydrological corridors on the transport of microorganisms downstream (Lindström & Bergström 2005; Griffin 2007). A positive impact of connectivity on species richness was found in terrestrial systems, for instance in ectomycorrhizal fungi (Peay *et al.* 2012). In a lava-fragmented landscape, Vannette *et al.* (2016) demonstrated an increase in similarity in fungal species composition in fungi associated with the roots of a tree *Metrosideros polymorpha*, growing in highly connected fragments compared to species composition in the roots of the same species of tree growing in poorly connected fragments. This study is one of the very few to analyze a shift in species composition linked with their dispersal strategies: species characterized by airborne spore dispersal were more abundant in isolated fragments while fungi with poorly characterized dispersal or biotrophic lifestyle were more abundant in well-connected fragments. More in-depth inclusion of traits in studies of how microbial communities respond to connectivity loss should be encouraged in future. In contrast to these studies, others demonstrated the absence of relationships between arbuscular mycorrhizal fungal communities and landscape connectivity in sandy coastal plains in response to the distance to mainland environments (e.g. da Silva *et al.* 2017), or in assemblages associated with the roots of the herbaceous *Stachys sylvatica* that grows in forest fragments in response to the distance to the nearest forest stand (Boeraeve *et al.* 2019). The absence of impacts was explained by the authors as the consequence of a dominant effect of abiotic local factors on this taxonomic group. But an alternative explanation might be that the corridor effect needs to be considered at a much smaller scale because of the short dispersal distance of these organisms.

In macroorganisms, corridors have been also reported to have a negative impact by spreading antagonists, such as pathogens, parasites, predators, or strong competitors (see Haddad *et al.* 2014 for a review). The great majority of studies of landscape effects on microorganisms concern pathogen dispersal (see Plantegenest *et al.* 2007; Suzán *et al.* 2012 for reviews). Particular landscape elements, not necessarily of the same habitat type, have been repeatedly identified as corridors for these pathogens. For instance, rivers were shown to disperse *Phytophthora alni* among alder trees through waterborne zoospores (Ioos *et al.* 2005). Human dispersal caused by vehicles moving along roads has also been demonstrated as a major corridor for pathogens: for example, Laine & Hanski (2006) demonstrated a strong

correlation between pathogen occurrence (*Podosphaera plantagenis*, an obligate pathogen of *Plantago lanceolata*) and the proximity of a road. Another example can be found in a study by Jules *et al.* (2002) who demonstrated a major role for roads through both foot traffic and vehicles, in the propagation of the root pathogen, *Phytophthora lateralis* of *Chamaecyparis lawsoniana*. In the existing literature, the negative effects of corridors are still limited to the spread of pathogens, but other negative interactions also need to be taken into consideration.

Time-lag responses to corridors

In macroorganisms, especially sessile ones, there is increasing evidence that assemblages do not respond instantaneously to changes in connectivity (see Lira *et al.* 2019 for a review on landscape patterns). These time-lagged responses result from an extinction debt or a colonization credit (**Box 1**, see Kuussaari *et al.* 2009 and Jackson & Sax 2010 for reviews on these concepts), following either a loss or gain in connectivity, respectively. Yet, few studies have demonstrated time-lagged responses to connectivity in microorganisms. One exception is a study by Berglund & Jonsson (2005), who demonstrated a delay in the decline in species richness of wood-inhabiting fungi in recently fragmented landscapes compared to old isolates. In such fragments, these authors recorded a progressive decline in population densities before complete disappearance of the species, suggesting the existence of an extinction debt. Evidence for an extinction debt in bacteria has not yet been provided but this phenomenon is likely due to the ability of bacteria to remain dormant for long periods of time (Gray *et al.* 2019) and to be present in a patch even if it is isolated from other patches. By extension, evidence for colonization credit of ectomycorrhizal fungi was reported in a study by Peay *et al.* (2012), who compared the composition of a fungal community associated with the roots of oaks developing in old forest stands with those on the roots of oaks developing in recent stands, the recent stands being either isolated from or connected to, old forests. Oaks in the recent stands had lower fungal species richness, suggesting a colonization credit, but the credit was even bigger in isolated stands than in connected ones. These time-lagged responses by microbial assemblages are likely related to their dispersal strategies, such as short dispersal distances (for colonization credit), high vegetative multiplication and strong dormancy (for extinction debt). In addition, while colonizing new patches, early-arriving species have a competitive advantage over later-arriving species (“priority effect” *sensu* Kennedy & Bruns 2005) and community composition may then depend on historical variations in arrival order (Dickie *et al.* 2012). Analyzing the mechanisms of the delayed-responses to connectivity also requires accounting for one of the particularities that make microorganisms unique, which is

their very short generation time. For this reason, the effect of connectivity is likely to affect several generations of microorganisms with short dispersal distances, compared to the effect on macroorganisms, whose dispersal movement occurs within the life-span of the individual or within a few generations. In contrast to macroorganisms, microorganisms may experience evolutionary processes during their passage along the dispersal route, with adaptations, mutations, and possibly even speciation. Genetic differentiation among microbial populations between donor and recipient patches could indeed occur as a result of the time it takes to pass through the corridor. Thus, one would expect detection of time-lagged responses to be challenging in some groups in which species delimitation is technically difficult (e.g. unknown species).

The particular case of biotic corridors

Many microorganisms are associated with either animal or plant hosts, sometimes with a high degree of host-specificity (e.g. *Rhizobium leguminosarum*, which forms nodules with legumes). These different hosts may represent a set of ecological niches whose favorability depends on the degree of host-association: microorganisms can indeed be classified along a specialist-generalist gradient depending on the degree of host specialization. Microbial distribution is thus the result of a direct effect of this biotic landscape and hence depends on the metapopulation dynamics of the hosts. Metapopulation dynamics is itself driven by the ecological landscape. In biotic landscapes, corridors may be ephemeral, depending on the probability of contacts among hosts; or mobile, depending on hosts ability to move across the landscape. These characteristics – time spent in the corridor and mobility - likely depend on their host's strategy for colonizing space, and their host's behavioral traits.

Another key particularity of biotic corridors is the existence of an interaction loop between hosts and the associated microorganisms that affects their metacommunity dynamics (Miller *et al.* 2018). Microbiota has indeed a major effect on its hosts' performance through several ecological functions including nutrition, resistance to environmental and pathogenic stresses (for a review, see Vannier *et al.* 2015). Pathogens may even cause the death of their host in the case of severe infection. Beyond their effect on performance, some microorganisms also influence some of the above mentioned traits that influence the probability of contacts among hosts: for instance, depending on the inocula of fungi, a plant's clonal growth may be modified either through elongation and/or increased branching of stolons (for a review, see Bittebiere *et al.* 2020). For instance, in *Prunella vulgaris*, stolons were shown to vary two- to three-fold in length and up to two-fold in branching intensity

depending on the arbuscular mycorrhizal fungal isolate inoculated (Streitwolf-Engel *et al.* 1997). Some pathogens can also control the behavior of their animal hosts by influencing their social interactions and the transmission of the microorganisms among a set of hosts (see examples in the review of Klein (2003). In this situation, connectivity results from the relationships between a host and its microbiota.

Micro-corridors for microorganisms

Spatial heterogeneity of microorganisms has been reported in many studies at the scale of a few centimeters (see for instance review by Franklin & Mills 2007 and Bahram *et al.* 2015). Ecological corridors may thus be considerably downscaled, i.e. to less than 1m². In this section, we review these micro-corridor studies.

The first set of studies developed experimental micro-corridors. For instance, Rantalainen *et al.* (2004) set up microcosms less than one m² in size to analyze the microbial colonization of sterile patches connected to a source patch, the patches of which were not connected. Corridors increased species richness of soil fungi consistently at all sampling dates throughout the experiment. An increase in species richness was only found only in bacteria on some sampling dates. The sometimes-negative effect of corridors on bacteria was explained by increased competition for resources in the connected patches due to the higher fungal species richness. This work suggests the importance of accounting for possible interactions among groups of microorganisms in response to corridors. To advance our understanding of the effect of these micro-corridors, Rantalainen *et al.* (2005) used a similar experimental design to test the inclusion of enchytraeid worms in connected and unconnected systems, and showed that saprophytic fungi dispersal in the corridors was promoted by the movement of these worms, and to a lesser extent, in the absence of worms, by vegetative growth. However, bacteria were not affected by these treatments, suggesting passive dispersal through water rainfall or microarthropods. The nature of the matrix surrounding the connected or isolated patches also matters. Using experimental micro-landscapes, Spiesman *et al.* (2018) analyzed the response of bacterial communities to the degree of connectivity in two matrix habitats with connected and isolated patches of oak leaf litter (*Quercus germinata*) embedded in a matrix of bare soil or pine litter (*Pinus clausa*). These authors reported higher bacterial richness in isolated oak litter patches than in connected ones, and in patches surrounded by pine litter compared to bare soil, indicating a cross habitat spillover effect from the neighboring matrix (**Box 1**), probably of generalist species.

In real field situations, there is some evidence that these ecological micro-corridors exist: the existence of ecological connectivity and/or the existence of biotic corridors (i.e. based on host connectivity). For instance, microbial communities were shown to be structured by soil pore connectivity that represent discrete habitat patches. Bacteria dispersal depended on the mode of motility, pore size and matrix potential (Wolf *et al.* 2013). However, in a study to test this effect, Carson *et al.* (2010) reported that, contrary to what the corridor hypothesis would lead one to expect, lower pore connectivity in soils increased microbial diversity. The authors explained this by a sheltering effect of isolated particles from highly competitive organisms. In biotic landscapes, recent works by our team demonstrated that the spatial configuration of hosts affected endophytic fungal assemblages (Mony *et al.* 2020a, b). For instance, fungal species richness was more closely related to the resistance distance among hosts calculated based on the probability of the presence of hosts of the same identity, rather than to the Euclidean distances among hosts (Mony *et al.* 2020b). Following the corridor hypothesis, Basidiomycota richness was shown to increase with host connectivity, in contrast to Glomeromycotina, which were richer in less connected plants, probably due to an increased edge effect (Mony *et al.* 2020b).

An individual host can also constitute a biotic micro landscape for microorganisms: for instance, Vannier *et al.* (2018) demonstrated transmission of bacteria and arbuscular mycorrhizal fungi along the stolons of *Glechoma hederacea*, the connections thus acted as structural corridors for the microorganisms. This confirmed the results of other experiments performed by Watson *et al.* (2002) on the clonal plant *Podophyllum peltatum*. For these assemblages, plant clonal growth may help spread microorganisms at short scales. Even within the microbial compartment, fungal hyphae can be a vector for the dispersion of bacteria (Yang *et al.* 2017), because a continuous film of water develops along the hyphae thereby letting motile microorganisms swim (Kohlmeier *et al.* 2005). Because hyphae allow the translocation of nutrients, as well as foraging for nutrient-rich patches or crossing nutrient-poor habitats (e.g. Boer *et al.* 2005), hyphal networks can thus be regarded as a guide for a variety of soil microorganisms to move toward attractive nutrient-rich patches (Bravo *et al.* 2013). Communication among the microbial compartments that allows such active movement is an emerging research question (Leach *et al.* 2017), and in the second step should be linked to the theoretical framework of corridor ecology.

Corridors for the invisibles

The extent to which ecological corridors are useful for a wide range of taxonomic groups has been the subject of debate in many reviews (Beier & Noss 1998; Murphy & Lovett-Doust 2004; Haddad & Tewksbury 2006; Gilbert-Norton *et al.* 2010; Haddad *et al.* 2011, 2015; Fletcher *et al.* 2016), although not including the microbial compartment. Here we propose that the corridor hypothesis is valid for microorganisms and that microorganisms respond to their landscape independently of only environmental patchiness. However, we also highlight major differences among macroorganisms in the mechanisms and processes involved, due to spatial and temporal scale-effects, interactions with hosts, and evolutionary processes. This review provides new insights into the rules governing microbial community assembly depending on ecological corridors, and suggests new avenues for further research in the field. Future studies will need to provide guidelines for the concrete implementation of corridors that take microorganisms into account. If corridors are introduced as a key component of landscape-scale management plans worldwide, this would benefit part of the microbial compartment, other microorganisms challenge our common perception of the landscape. Therefore, land-use planners should rethink the landscape, including transposing it to finer scales so that corridors benefit the entire microbial compartment. In the context of global change, the huge role played by microorganisms in climate regulation, soil fertility, i.e. nutrient cycling and in making nutrients available for plants, and, more broadly, effects on their host, food and fiber production (e.g. Delgado-Baquerizo *et al.* 2016), microbial ecology will have to make loss of microbial diversity a priority in future research. Given the urgency of this issue, transposition of the corridor hypothesis and landscape ecology to the “*invisibles*” appears timely. A microbial rescue effect (Mueller *et al.* in press) that could be promoted by these microorganism-dedicated corridors, both at small and large scales, exemplifies the need to expand such corridors for the “*invisibles*”.

Chapitre A1. The role of hedgerows to support biodiversity and associated ecosystem services in intensive agricultural landscapes

Audrey Alignier, Léa Uroy, Stéphanie Aviron

Reconciling agricultural production with biodiversity conservation (2020). Eds. Bàrberi, P. & Moonen, A.-C. Burleigh Dodds Science Publishing, London.

Abstract

Over the past half century, agricultural intensification has severely modified agricultural landscapes and farming systems. These changes have been beneficial to provisioning services, i.e. agricultural yields, but detrimental for biodiversity and associated ecosystem services. As a contribution to halting and reversing the decline, it has been suggested that conserving and/or restoring hedgerows would be a positive action. Hedgerows are key features of agricultural landscapes. They have a wide range of roles, including agronomical, ecological and cultural functions. In particular, hedgerows provide habitats, refuges and resources for many plant and animal species. Generally viewed as stable landscape elements, their management and history are often not considered in ecological studies. At the landscape scale, hedgerows can contribute to species movements by acting as corridors and ensure landscape connectivity. Focusing on pest regulation and pollination services, we highlight how hedgerows contribute to the multifunctionality of agroecosystems even in intensively managed agricultural landscapes.

Introduction

Hedgerows are key features of agricultural landscapes, especially in northwestern Europe (e.g. hedgerow networks, “bocage”) where they are the dominant type of semi-natural habitat (Burel & Baudry 1999) and assume a wide range of roles, including agronomical, ecological and cultural functions (Baudry *et al.* 2000). They benefit crop growth by acting as windbreak and shelter for husbandry (Forman & Baudry 1984) and contribute to the reduction of soil erosion and pesticide drift from neighboring crops (Marshall & Moonen 2002). They are critical features for biodiversity conservation, agroecosystem functioning and associated ecosystem services (Pywell *et al.* 2015). They supply habitat, shelter and resources (Marshall & Moonen 2002; Hannon & Sisk 2009; Vickery *et al.* 2009) for a wide range of plant and animal species. By providing high levels of floral diversity, they contribute to the maintenance of pollinator populations (Morandin & Kremen 2013) and to enhance the community of natural enemies (Bianchi *et al.* 2006; Chaplin-Kramer & Kremen 2012). However, hedgerows may also be reservoirs of weeds and pests, which can spread into the fields (Forman & Baudry 1984; Pollard & Holland 2006). At larger scales, hedgerows may contribute to species movement and spillover by acting as corridors and ensuring connectivity through the landscape (Baudry *et al.* 2000; Concepción *et al.* 2012). Communities of natural enemies and pollinators are often found to be more abundant in complex landscapes where hedgerows are better conserved (Chaplin-Kramer *et al.* 2011; Kennedy *et al.* 2013). Based upon the Millennium Ecosystem Assessment (2005), Cole *et al.* (2009) identified 20 positive ecosystem services (i.e. direct and indirect benefits people obtain from ecosystems) delivered by hedgerows including provisioning (e.g. food, fiber), regulating (e.g. air quality, pest regulation, pollination), cultural (e.g. recreation, aesthetics), supporting (e.g. soil fertility, primary production) and biodiversity conservation services (**Table 1**). Despite this abundant literature, more research is needed to elucidate the role of hedgerows in supporting multiple ecosystem services at different spatial scales.

Table 1 Ecosystem services delivered by hedgerows as identified by Cole *et al.* (2009). Examples are from Forman & Baudry (1984), Baudry *et al.* (2000), Dainese *et al.* (2017) and Dover 2019.

Service	Specific service	Examples
Supporting	Soil formation	Soil formation
	Photosynthesis	Production of oxygen
	Primary production	Production of chemical energy e.g. organic matter
Provisioning	Food	Fruits, vegetables, fodder
	Fibre	Timber
	Fuel	Wood (e.g. from pruning trees and cutting shrubs)
Regulating	Air quality	Removal of particulates
	Climate regulation	Radiation interception, windbreak effect
	Water regulation	Runoff and flood control
	Erosion regulation	Soil retention (by roots)
	Water quality / purification	Removal of pollutants
	Pest control	Source of natural enemies
	Pollination	Nectar, pollen and nesting resources provision
	Hazard reduction	Prevention of landslides
Cultural	Recreation (field sports)	Field sports e.g. walking along footpaths
	Cultural heritage	Cultural and historical values
	Education	Outdoor classroom: natural history education
	Aesthetics / inspiration	Source of inspiration
	Sense of place	Regional identity
Biodiversity	Habitat	Living space for plants and animals
	Refuge	Shelter, overwintering site
	Corridor	Facilitation of the movement through the landscape
	Complementary resources	Provision of additional resources

This chapter will tackle these different issues focusing predominantly on the role of hedgerows in supporting biodiversity and associated ecosystem services by:

- examining the evidence that hedgerows offer habitat for a wide range of species,
- considering hedgerows as management unit and part of farming systems,
- considering hedgerows as part of the hedgerow network landscape,
- highlighting the role of hedgerows for ecosystem services of agricultural importance, with the examples of pollination and pest regulation,
- exploring hedgerow planting and bocage restoration and its contribution to agroecosystem multifunctionality.

Each part of this chapter will be illustrated with case studies resulting from different projects carried out on the “Zone Atelier Armorique”, a Long-Term Socio-Ecological Research (LTSER) site in northern Brittany, France (48°36'0" N, 1°32'0" W). This study site is characterized by an extensive hedgerow network, with relatively small fields (on average 1.3 ha) being separated by woody habitats (mainly hedgerows and few woodlands; **Fig. 1**). In this study site, the hedgerows are made of rows of oak (*Quercus robur*) or chestnut (*Castanea sativa*) generally planted on an earthen bank 0.5–0.8 m high surrounded by ditches and managed as trees by farmers (pruning for firewood every 9–12 years). The shrub layer, dominated by hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), broom (*Cytisus scoparius*), spindle (*Euonymus europaeus*), or gorse (*Ulex europaeus*), is rarely continuous and can be even absent.



Fig. 1 Hedgerow network (“bocage”) of the LTSER Zone Atelier Armorique site. Source: © Air Papillon.

What is a hedgerow?

Hedgerows can be found throughout the World including Europe, North and South America, Africa and China, and have been a large component of managed landscapes for over 2000 years (Deckers *et al.* 2004; Hannon & Sisk 2009). Such countries/regions show marked differences in hedgerow structure, species composition, and the type of management. The diversity of hedgerows stems from their multiple origins and includes their role in the landscape, as well their contribution to biodiversity and ecosystem functioning (Baudry *et al.* 2000).

Characterized by lines of trees and/or shrubs, hedgerows also encompass the herbaceous layer, the bank and ditch separating agricultural fields (Forman & Baudry 1984) (**Fig. 2**). So, hedgerows may vary according to the predominance of shrubs, trees, or both, single or multiple species dominance, species composition, height and width, and structures such as ditch, bank, stonewall, wood or wire fence. They represent relatively permanent habitats within a constantly disturbed environment, i.e. the agricultural matrix, acting as suitable habitats for many plant and animal species.

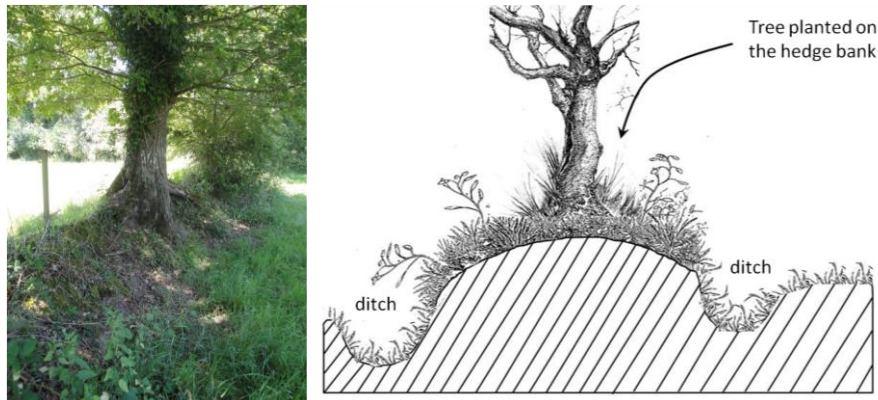


Fig. 2 On the left, hedgerow with trees planted on a bank in the Zone Atelier Armorique, France. On the right, schematic representation of a typical hedgerow from Brittany (France) with tree planted on a bank and surrounded by ditches. Source: © A. Alignier.

Historically, hedgerows constitute limits, physical as well as symbolic. They delineate physical property limits, i.e. crop fields, and prevent cattle mixing with neighbors' like in Britain (Baudry *et al.* 2000). Hedgerows provide wood (e.g. firewood, timber) as well as fodder used as winter forage in several regions in Europe and, fruits and medicinal plants. They also cover a broad range of agri-environmental issues including microclimate modification, radiation interception, water infiltration, windbreak effect, soil erosion and runoff prevention (Burel & Baudry 1995; Kiepe 1995; Oyarzun *et al.* 2007; Sánchez *et al.* 2009) although perhaps the greatest volume of scientific literature concerns ecological benefits issues.

The role of hedgerows as habitat for biodiversity

The value of hedgerows as habitat for native plants, butterflies, birds and mammals within intensively managed agricultural landscapes has been widely recognized (Burel 1996; Baudry *et al.* 2000; Dover & Sparks 2000; Hinsley & Bellamy 2000; Gelling *et al.* 2007; Dondina *et al.* 2016). The Royal Society for the Protection of birds reports that hedgerows support up to 80 per cent of British woodland birds, 50 per cent of mammals and 30 per cent of butterflies (Anon. 2019).

Hundreds of vascular plant species are known to grow in hedgerows but they are generally not restricted to hedgerows and are found in other nearby habitats. For example, Wehling & Diekmann (2009) showed that hedgerows contained 77 % of all forest species observed in the matrix of neighboring woodlands in Germany. This proportion is comparable to findings from the USA, where about 70 % of all forest species were able to colonize hedgerows of the same region Corbit *et al.* (1999). By comparing vegetation in forest patches and hedgerows in intensively managed agricultural landscapes in Belgium, Van Den Berge *et al.* (2019) showed that hedgerow species are typical forest edge species. Hedgerows include shaded parts but they are also more exposed to solar radiation and wind. Thus, light-tolerant plant species as well as species with various degrees of shade tolerance can be found in hedgerows, like ivy (*Hedera helix*), herb Robert (*Geranium robertianum*), and foxglove (*Digitalis purpurea*).

Hedgerows may also shelter a suite of annual species under disturbed conditions. The perception that weeds spread from hedgerows into crops is prevalent among farmers, leading to accentuated and sometimes damaging hedgerow management. Resulting disturbances and the removal of perennial species encourage the installation of annual weed species capable of colonizing the field (Marshall & Moonen 2002). However, studies in Britain have indicated that weed spread from hedgerows/field margins into croplands is limited to a few annual species such as barren brome (*Bromus sterilis*) and cleavers (*Galium aparine*) (e.g. Smith *et al.* 1999).

In natural conditions, the composition of vegetation is a result of soil type, climate, dispersal and regeneration of plant species. In agricultural landscapes, management affects habitats that in turn, shapes the colonization success of species. By surveying 511 hedgerows in Belgium, Deckers *et al.* (2004) found that adjacent land use, management, soil conditions and hedgerow structure all affected hedgerow plant communities. Hedgerow structure, partly determined by management, influences light levels and microclimate with a large influence on the composition of plant communities (McCollin *et al.* 2000; Van Den Berge *et al.* 2019).

Hedgerows as managed elements

Hedgerows are traditionally managed to prevent encroachment on adjacent agricultural land (Baudry *et al.* 2000). Tree layer management includes infrequent management techniques such as coppicing, applied every 20 to 40 years, pruning (**Fig. 3**) and trimming which rejuvenate hedgerows by encouraging them to produce new shoots from the base of woody

species. Over 50 % of the woody hedge biomass is removed during hedge-laying or coppicing, and between this infrequent rejuvenation management, hedgerows are generally trimmed every few years to maintain their shape (Staley *et al.* 2013). Over the last 70 years frequent cutting with a mechanized flail has become the dominant form of management across Europe (Croxtton *et al.* 2004).



Fig. 3 Hedgerow with pruned trees in the Zone Atelier Armorique, France. Source: © C. Codet.

Herbaceous layer management is much more frequent. Indeed, direct herbicide spraying by farmers at the base of the hedge or on the ditch bank is common to prevent weed invasion into crop fields, e.g. spot-wise spraying against species such as creeping thistle (*Cirsium arvense*), bramble (*Rubus fruticosus* agg.) and common nettle (*Urtica dioica*) (Kleijn & Verbeek 2000; Alignier & Baudry 2015). Adjacent agricultural activities (especially ploughing or tillage, stock (e.g. cattle, sheep) grazing and herbicide drift; **Fig. 4**), together with management techniques directly applied to the herbaceous layer of hedgerows result in a high level of disturbances and potential soil nutrient enrichment (Marshall & Moonen 2002) affecting local environmental heterogeneity and thus plant and animal communities within.



Fig. 4 Hedgerow along ploughed field in the Zone Atelier Armorique, France. Source: © A. Alignier.

Hedgerows as part of farming systems

The way hedgerows are managed and their structure depends on the farming system (Le Cœur *et al.* 2002). Cash crop farms mainly have hedgerows with few trees and shrubs. In contrast, diversified productive dairy farms have dense hedgerows. Diversified dairy farms with low production exhibit an intermediate pattern (Le Cœur *et al.* 2002). In turn, hedgerow structure, by modulating light and moisture, influences plant species composition: dense hedgerows include plant species requiring conditions of forest environments (e.g. false-brome (*Brachypodium sylvaticum*), Solomon's seal (*Polygonatum multiflorum*) and ivy (*Hedera helix*). Hygrophilous or meso-hygrophilous species (e.g. common fleabane (*Pulicaria dysenterica*), greater bird's-foot trefoil (*Lotus pedunculatus*) and wild angelica (*Angelica sylvestris*) were significantly more frequent in hedgerows with wide and deep banks (Le Cœur *et al.* 2002).

At the micro-regional scale, Thenail (2002) showed that hedgerow density in bocage landscapes of Brittany (France) can also be related to farming systems. By comparing farms located along a gradient of density of the hedgerow networks in the landscape, the author found that the production, economic levels, productivity and technical means of farms increase from the dense to the open bocage area. Especially, from the dense to the open bocage area, dairy farms contain an increasing proportion of maize used for silage and grain, short duration grassland and cash crops, which can be seen as a gradient of land use intensification. The fodder system is based on relatively more maize silage in the open bocage area, and relatively more on a multi-functionality of grassland in the dense bocage area. Complementary studies in the same study site showed that the system of activities implemented for the management of the hedgerows in the farms of the dense bocage

landscape, does not only take more time, but is also more complex than in the more open bocage landscapes (Burel *et al.* 1998).

Generally considered as semi-natural elements, i.e. stable and undisturbed, few ecological studies investigated the effect of hedgerow management on biodiversity patterns. The management of hedgerows is dependent on farming systems which can be thus envisaged as a driving factor of the evolution of the biodiversity. However, comparative studies of hedgerows in different farming systems (in a region but also between countries) are rarely carried out.

Case study: The importance of taking into account of the management of hedgerows as well as their history for biodiversity conservation

We assessed the relative influence of current and past management practices and landscape context on the local biodiversity of 101 hedgerows in the northern part of the Zone Atelier Armorique. The study focused on the species richness and composition of carabid assemblages. Carabids were trapped partly in 2001 and the other part in 2002. To homogenize, the sampling year of carabids was referred as the year 1. Presence-absence of management practices applied to the herbaceous component of hedgerows was monitored every year between 1995 and 2002, i.e. grazing with or without cattle trampling, mechanical management (i.e. mowing, shrub cutting, crushing with or without exportation of plant residues), herbicide spraying and tillage or ploughing (**Fig. 5**). Landscape context of each hedgerow was yearly described over the study period in 50 m and 500 m buffer radii with: percent cover (%) of woodland, grassland, spring crops and winter crops as landscape composition metrics; and hedge density (total hedge length, in meters) and mean patch size (m²) as landscape configuration metrics.

We found that carabid species richness and diversity were best explained by past management practices and landscape heterogeneity (4 to 5 years before carabid surveys) than current ones (higher values of explained variance; **Fig. 6**). Overall, the influence of past management practices dedicated to hedgerows was higher than the influence of past landscape heterogeneity except for year 5. This can be explained by the fact that few management operations occurred this particular year. Carabid diversity was higher in grazed or herbicide sprayed hedgerows probably due to increased heterogeneity in habitat conditions. Hedgerows surrounded by grasslands and crops harbored carabid species associated with open habitats whilst forest carabid species dominated those surrounded by

woodland. A landscape effect was scale-dependent and mostly detected at the finest spatial scale, within 50 m around hedgerows. Such distribution of farmland and forest carabid species is consistent with results from previous studies (Millán de la Peña *et al.* 2003; Aviron *et al.* 2005). Our results support the idea that the contribution of hedgerows to the maintenance of biodiversity relies on the way they are managed. Although they are usually considered as semi-natural elements and so, suffering low disturbances, hedgerows should be considered as management units being part of farming activities, as for arable fields. In addition, our results highlight the importance of taking account of time to understand current patterns of carabid assemblages. According to Dover (1996), we therefore suggest that researchers and land managers consider both hedgerow management and history when studying biodiversity patterns in agricultural landscapes.

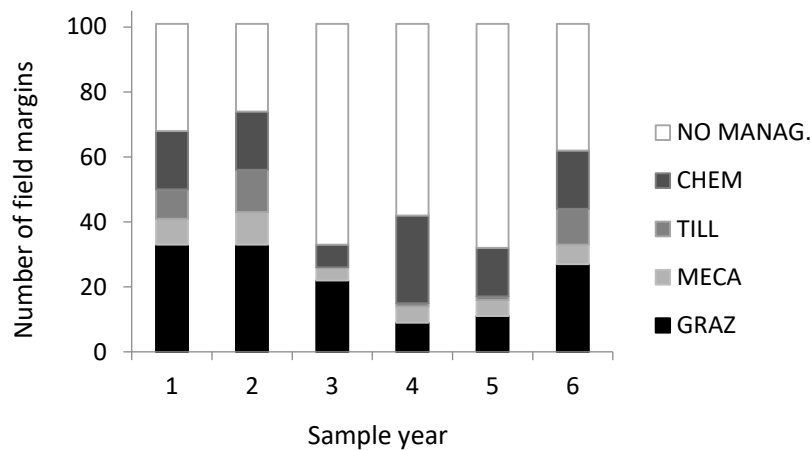


Fig. 5 Occurrence frequency of the four management practices over the 101 studied hedgerows, in the sampling year of carabids (year 1) and years before, year 6 being the oldest. NO MANAG. = no management, CHEM = herbicide spraying, TILL = tillage, MECA= mechanical management, GRAZ = cattle grazing. Source: Alignier & Aviron (2017).

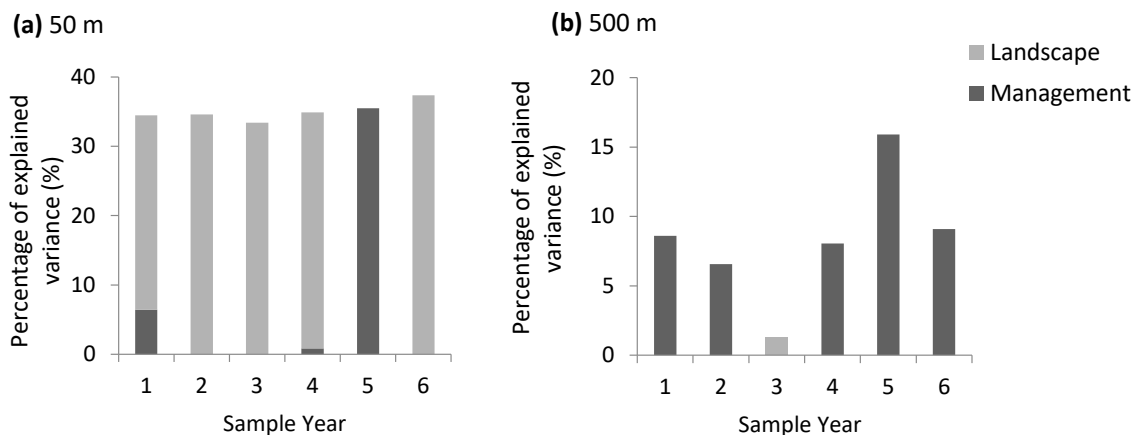


Fig. 6 Hierarchical partitioning of explained variance (%) in carabid species richness explained each year (year 1 being the sampling year for carabids and year 6, the eldest) by management practices and landscape metrics at (a) 50 m and (b) 500 m. Source: Alignier & Aviron (2017).

Hedgerows and hedgerow network

Brief overview of hedgerow evolution

Since the mid-20th century and as a consequence of agricultural intensification, land consolidation programs and urban expansion, hedgerows have suffered from a marked decline in their density in agricultural landscapes. Pointereau (2002) reported that the hedgerow network lost almost 12,000 ha (8 %) every year between 1991 and 2000 in France. Barr & Gillespie (2000) indicated a net loss of almost 121,000 km of hedgerows between 1984 and 1990 in UK. In 2007, the Countryside Commission Survey showed a 1.7 % decrease in the length of woody linear features between 1998 and 2007 (Carey *et al.* 2008). This trend has led to severe biodiversity loss and the deterioration of key ecosystem services to agriculture (Tilman *et al.* 2001). For example, species richness in vegetation associated with all types of landscape boundaries in Great Britain decreased by 4.0 % between 1998 and 2007 and by 14.6 % between 1978 and 2007. To mitigate the negative effects of agricultural intensification, it has been proposed to focus on the conservation and restoration of hedgerows and hedgerow networks (Batáry *et al.* 2011; Ponisio *et al.* 2016; Dainese *et al.* 2017).

Hedgerows and landscape connectivity

As linear features of the landscape, hedgerows may serve as a potential corridor for biodiversity and ensure landscape connectivity. Corridors have been proposed as an important conservation tool (Diamond 1975b; Verkaar 1990), assuming that the connectivity of forest fragments is crucial for the survival of many forest species (Jacquemyn *et al.* 2003). The efficiency of hedgerows as conservation corridors has mostly been studied in animals (Simberloff & Cox 1987). For plants, especially animal-dispersed species, corridors may help to maintain viable populations (Corbit *et al.* 1999; Wehling & Diekmann 2009).

However, negative effects of hedgerows can also be observed. Corridors can indeed facilitate flows of organisms and matter (e.g. pollen flow) along hedgerows but impede dispersal across (Dover & Settele 2009). For example, Quin *et al.* (2008) showed that hedgerows guided individual butterfly movements in bocage landscapes of Brittany (France). Hedgerows which were oriented towards the receiver forest patch (*i.e.* parallel hedgerows) clearly promoted butterfly movements whereas perpendicular hedgerows impeded butterfly movements and acted as barriers. Other negative effects of the hedgerow network are encountered, such as increased spread of contagious diseases, parasites and invasive species (Simberloff *et al.* 1992; Deckers *et al.* 2005).

Case study: Increasing landscape connectivity provided by hedgerows increases similarity in plant assemblages for animal-dispersed species in woodlands

We investigated whether and how wooded elements (i.e. hedgerows and woodlots) participated in connectivity and drove composition of plant assemblages according to three dispersal modes: animal-, wind- and unassisted dispersal. We performed exhaustive surveys of plant assemblages in 25 woodlands, 25 temporary grasslands and 25 winter wheat crops, the three main habitat types of agricultural landscapes in the northern part of the Zone Atelier Armorique. We characterized dispersal mode of each plant species (i.e. animal-dispersal, wind-dispersal or unassisted dispersal). We assessed landscape connectivity provided by wooded elements (i.e. hedgerows, woodlots and forests) using resistance distance, a measure derived from the circuit theory (McRae 2006; McRae *et al.* 2008). This method evaluates all possible paths between two habitat patches assuming that dispersal follows random walks (McRae *et al.* 2008). The resulting connectivity measure is a measure of isolation called resistance distance: the higher the resistance distance, the lower the connectivity. We then evaluated the similarity in composition between pairs of plant assemblages. We found that the similarity in plant assemblages' composition in woodlands was significantly related to the connectivity provided by wooded elements by contrast with temporary grasslands and winter wheat crops. More specifically, only animal-dispersed plant assemblages were more similar in composition than expected by hazard when the connectivity provided by wooded elements increased (**Fig. 7**). Our results suggest that a high connectivity between patches of woodlands provided by wooded elements (i.e. hedgerows) facilitates the dispersal of animal-dispersal plants species inhabiting these woodlands, hence increasing the similarity in plant composition between patches of woodlands. Overall, this study highlights the fundamental role of wooded habitats as corridor for wood-dwelling animal-dispersed plant species.

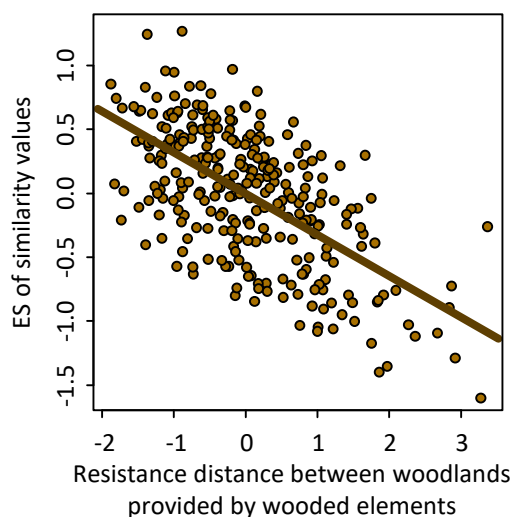


Fig. 7 Partial residual plot denoting the significant effect of the resistance distance (higher the resistance distance, the lower the connectivity) between woodlands provided by wooded elements on the effect size (ES) of similarity values for animal-dispersed plant assemblages in woodlands. The ES of similarity indicates the extent to which the observed value of the similarity between pairs of habitat patches is different from its random expectation based on the regional species pool. Positive ES values indicates a higher similarity than expected, due to a dispersal enhancing effect of the connectivity, whereas negative ES values indicate a lower similarity than expected, due to a dispersal barrier effect of the connectivity. Source: Uroy *et al.* (2019).

Case study: Effective dispersal of plants from woodlands along hedgerows is enhanced by connected hedgerow network of a good quality

Assessing how connectivity provided by hedgerows affects plant dispersal by studying the established (i.e. above ground) plant assemblages may be difficult, as local factors (e.g. habitat quality) can counterbalance the corridor role of hedgerows. To assess the direct effect of the connectivity provided by hedgerows on seed dispersal, Mony *et al.* (submitted) analyzed seed dispersal from 16 woodlands along connected and unconnected hedgerow networks in the northern part of the Zone Atelier Armorique. The connected and unconnected hedgerow networks were identified using a least-cost path analysis and their quality (i.e. three-dimensional structure) was also quantified. Using seed traps located along the paths during the peak of seed dispersal, they quantified the species composition, species abundance and richness of trapped seeds after germination in greenhouse conditions. They also analyzed the seed-removal by animals of two species, millet (*Panicum miliaceum*) and buckwheat (*Fagopyrum esculentum*), as a proxy of seed dispersal by animals. They reported that connected hedgerow networks displayed both higher abundance and richness compared to unconnected ones. Mony *et al.* (submitted) also reported that a greater proportion of seeds of *Panicum miliaceum* was removed in connected hedgerow networks compared to unconnected ones (Fig. 8). The connectivity effect was, however, probably partly correlated to the hedgerow quality that was lower in unconnected networks compared to connected ones. This study provides the first empirical evidence that a connected hedgerow network harboring a complex structure enhances plant dispersal from woodlands. Overall, maintaining hedgerow of a good quality should be a major issue of conservation in agricultural landscapes.

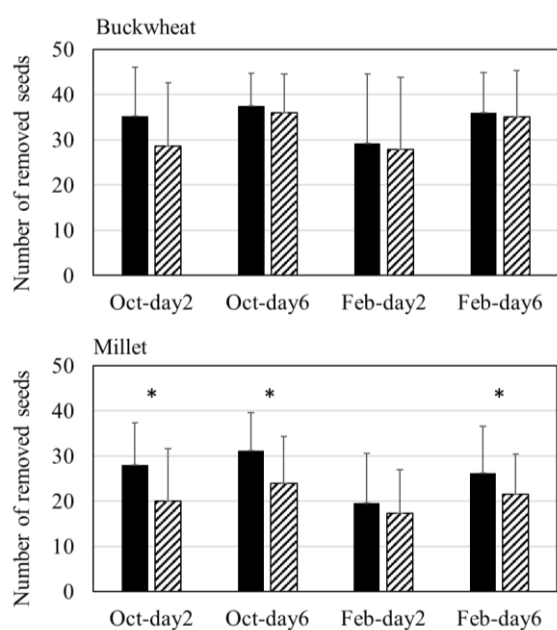


Fig. 8 Number of removed seeds of the two studied species, of two species, millet (*Panicum miliaceum*) and buckwheat (*Fagopyrum esculentum*) in connected (solid black bar) and unconnected (hatched bar) hedgerow networks for each sampling period (October and February) and date of survey (Day 2 and Day 6). Asterisks indicate significant difference in seed removal ($P < 0.05$). Source: Mony *et al.* (submitted).

Case study: Increasing hedgerow network connectivity contributes to the maintenance of forest carabid species

Hedgerows and other remnant woody habitats are crucial for the dispersal and persistence of forest species with low dispersal abilities in agricultural landscapes. Among them, forest carabid beetles are low mobile species whose populations are spatially fragmented and located in small woodlots, forests and structurally dense hedgerows (Petit & Burel 1998; Neumann *et al.* 2016). By contrast, generalist carabid species, which are also commonly found in hedgerows, are more mobile and less sensitive to the connectivity of the hedgerow network. For this reason, a decrease in hedgerow density and connectivity is expected to cause the replacement of forest species by generalist carabid species. We investigated the contribution of hedgerow density and connectivity for the maintenance of forest carabid species in bocage landscapes. We sampled carabid beetles in 40 hedgerows located in 20 landscapes characterized by varying amount (4.5-28 %) and configuration of woody habitats (5-25 km of edges between woody and farmland habitats) in the northern part of the Zone Atelier Armorique. We characterized the amount and spatial connectivity of woody habitats in three radius circles: 50 m in order to account for the immediate context of habitats, as well as 250 m and 500 m to account for the wider landscape context. Spatial connectivity of woody habitats was measured by two metrics: the spatial connectivity index developed by Hanski & Thomas (1994), accounting for woodland area and distance to nearest woody habitat; and the length (in km) of edges between woody habitats and farmland, reflecting the length of the hedgerow network. The results showed that forest carabid species were dominated by two species, *Abax parallelepipedus* and *Pterostichus madidus* (79 % of trapped species), which are brachypterous species, i.e. species without or with short, unusable wings. Abundances of forest carabid species were significantly, and positively related to the length of edges between woody elements and farmland at the finest spatial scale (50 m) (Fig. 9). By contrast, their abundance was reduced in landscapes where annuals crops were directly adjacent, i.e. with high edge length between annual crops at the largest spatial scale (500 m). This landscape pattern is typical from intensive agricultural landscapes where hedgerows have been removed and the hedgerow network has been fragmented. In such landscapes, forest carabid species were found to disappear whilst generalist and highly mobile species, which are adapted to disturbed and open habitats, dominate carabid assemblages (Millán de la Peña *et al.* 2003). This case study underlines the importance of hedgerow network connectivity for the dispersal and maintenance of forest carabid species in agricultural landscapes.

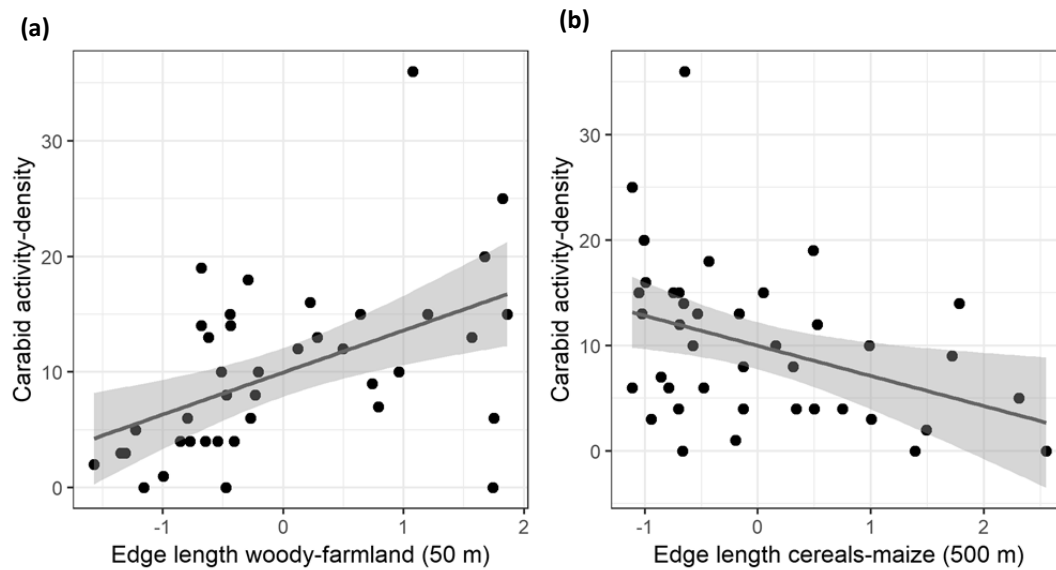


Fig. 9 Relationships between activity-density (as proxy of abundance) of forest carabid species in hedgerows and **(a)** length of edges between woody elements and farmland at 50 m or **(b)** edge length between annual crops at 500 m). Source: Aviron, unpublished data.

Hedgerows and ecosystem services

The ways that ecosystems benefit people are known as ecosystem services. These services can broadly be divided into four categories: (i) Regulating services – those that regulate processes such as water purification, crop pollination and pest control; (ii) Provisioning services – those generating products such as food and energy; (iii) Cultural services – those that assist our recreation and well-being, or provide aesthetic experiences and spiritual enrichment or learning opportunities and (iv) Supporting services – those that are necessary for the production of all other ecosystem services including soil formation, photosynthesis, primary production and nutrient cycling (Wolton *et al.* 2014; **Table 1**). Among regulating services underpinned by biodiversity, pest and weed control and pollination have been demonstrated to have a substantial impact on crop production worldwide. These ecosystem services are also those most at risk from agricultural intensification (Tschardt *et al.* 2005). By promoting pest natural enemies (e.g. presence and diversity of predator arthropods) and pollinators, hedgerows sustain these ecosystem services.

Case study: Hedgerow density and configuration promote pest natural enemies in agricultural landscapes

Many generalist insect species in agricultural landscapes use alternately hedgerows and cultivated habitats during their life cycle (Morandin & Kremen 2013; Garratt *et al.* 2017; Dover 2019; Holland 2019). Among them, natural enemies of crop pests use hedgerows as

overwintering sites or refuges when crops do not offer suitable habitat conditions (after harvest for instance), or to find alternative resources (animal preys or nectar resources for adult parasitoids or hoverflies) (Rand *et al.* 2006; Blitzer *et al.* 2012; Garratt *et al.* 2017; Holland 2019). For this reason, landscape heterogeneity related to the amount of semi-natural habitats including hedgerows is often found to enhance the diversity of natural enemies (Tschardt *et al.* 2005; Bianchi *et al.* 2006) and levels of pest regulation (Thies *et al.* 2003; Gardiner *et al.* 2009; Rusch *et al.* 2011) in agricultural landscapes. This predominant effect of landscape heterogeneity can even be more important than local farming practices to explain the variations in the diversity of natural enemies in crop fields (Rundlöf & Smith 2006).

We investigated how landscape heterogeneity related to hedgerow networks, in-field habitat quality related to local farming practices (organic *versus* conventional farming) and habitat conditions (crop density, crop height, weed cover), and farming heterogeneity (surface area of organic *versus* conventional crops) influence the diversity of natural enemies in crop fields. Communities of ladybirds, predatory carabid beetles, and parasitoids (aphid mummies) were sampled in 2012 and 2013 in 20 pairs of winter wheat fields (one under organic farming, one under conventional farming) in the southern part of the Zone Atelier Armorique. The pairs of studied fields were distributed along two orthogonal landscape gradients in terms of amount of semi-natural habitats (0.5-20 %) and farming heterogeneity (6-35 % of organic crops).

During the study, 657 ladybirds, 54,742 carabid beetles and 1,120 mummies were collected. We showed that the diversity of natural enemies was mainly related to the abundance of ladybirds. Abundances of natural enemies were influenced by land-cover heterogeneity and in-field habitat quality (**Fig. 10**). Specifically, the abundance of natural enemies was increased by increasing hedgerow density and increasing complexity in hedgerow configuration (positive correlation value: $R = 0.24$). Local farming type has a stronger and positive effect on the abundances of natural enemies in fields as expressed by the higher, positive correlation value ($R = 0.56$). These results confirm that the abundances of natural enemies in fields are promoted in complex agricultural landscapes by high density and complex configuration of semi-natural habitats such as hedgerows (Chaplin-Kramer *et al.* 2011). However, the effects of local crop management are also crucial, and even more important than those of landscape complexity, contrary to results from existing literature (Bengtsson *et al.* 2005). This result suggests that the relative effects of local farming type and landscape complexity on natural enemies are highly context-dependent. Our study shows,

however, that the adoption of low-input farming practices and the restoration of hedgerow networks are both valuable management options to promote natural enemies in agricultural landscapes.

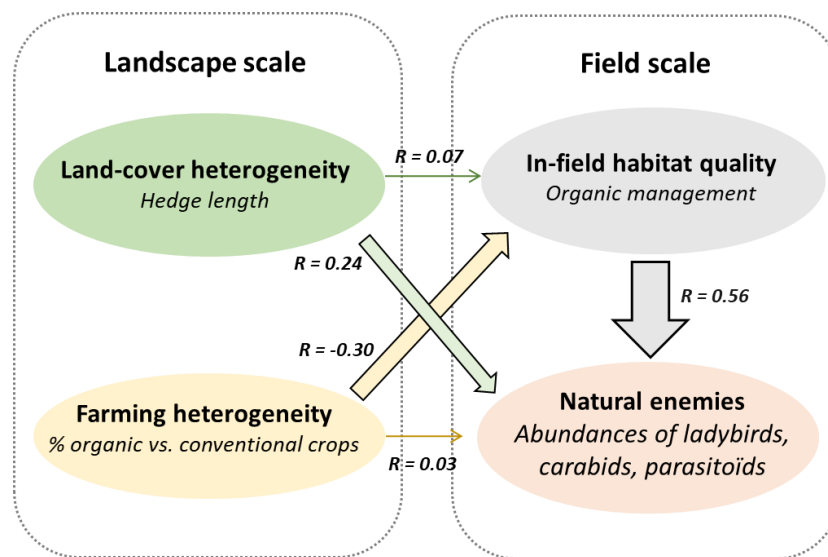


Fig. 10. Summary of the relationships between (i) natural enemy abundance in crop fields (related to abundances of ladybirds, carabid beetles, and parasitoids) and (ii) variables describing in-field habitat quality at the field scale (in pairs organic and conventional fields), (iii) metrics describing land-cover heterogeneity and (iv) metrics describing farming heterogeneity. Relationships between these four (latent) variables were assessed using PLS-Path modelling. R is the correlation value (path effect) between two latent variables. Depicted exogenous variables (in italics) are variables that significantly contributed to explain latent variables. Source: modified from Puech *et al.* (2015).

Case study: Hedgerows enhance pollinators in intensive agricultural landscapes

Pollinators play an important functional role in most terrestrial ecosystems and contribute to a key ecosystem service, i.e. pollination, that is vital to the maintenance of both wild plant communities and agricultural productivity. Pollinators contribute to 35 % of global crop production (Klein *et al.* 2007). Insects, particularly both domesticated and wild bees, are the primary pollinators of most agricultural crops and wild plants and so our case study will focus on these insects.

We investigated the contribution of hedgerows to the provision of diversified resources for a wide range of pollinators as well as to the support of plant-pollinator network. Twenty winter cereal fields bordered by at least one hedgerow were selected in the southern part of the Zone Atelier Armorique. We quantified plant-pollinator interactions by recording the number of visits between pollinators and flowering plant species (i.e. the number of contacts between a pollinator and flower's reproductive part). Pollinators were observed along two transects, one along the hedgerow, and another, parallel to the first one, 50 m from

the field edge in the field interior. Pollinators were classified into eight groups: domestic bees, solitary bees, bumblebees, syrphids, butterflies, diptera, coleoptera and other hymenoptera. Due to the very few number of observations, domestic bees were excluded from analyses. On the same transects, we estimated the cover (in percentage) of each flowering plant species.

In total, we observed the seven groups of pollinators interacting with 62 flowering plant species. We showed that the cover of flowering plant species in hedgerows was positively related to the abundance of wild bees and bumblebees in hedgerows and, to the abundance of syrphids in both hedgerows and field interiors. Specifically, bumblebees were sensitive to the cover of ligneous flowering plant species whereas syrphids were sensitive to the cover of herbaceous flowering plant species. Plant-pollinator networks shown in **Fig. 10** revealed a more complex structure in hedgerows (1,008 interaction events involving 55 flowering plant species) than in inner fields (883 interaction events involving 29 flowering plant species).

In fields, mayweed (*Matricaria inodora*) was the most frequently visited plant species (855 visits) and represented a key resource for most pollinator groups. In hedgerows, bramble (*Rubus fruticosus agg.*) was the most frequently visited plant species and was particularly important for wild bees, butterflies and bumblebees. Besides herbaceous species, shrub/tree species like common holly (*Ilex aquifolium*), spindle (*Euonymus europaeus*), chestnut (*Castanea sativa*) contributed to the interaction network. We showed that hedgerows offer a wide range of resources (through higher diversity of flowering plants than inner fields) as suggested by Venjakob *et al.* (2016). Our results emphasize the positive role and the need to maintain hedgerows to provide diversified resources for pollinators and support their maintenance in intensive agricultural landscapes.

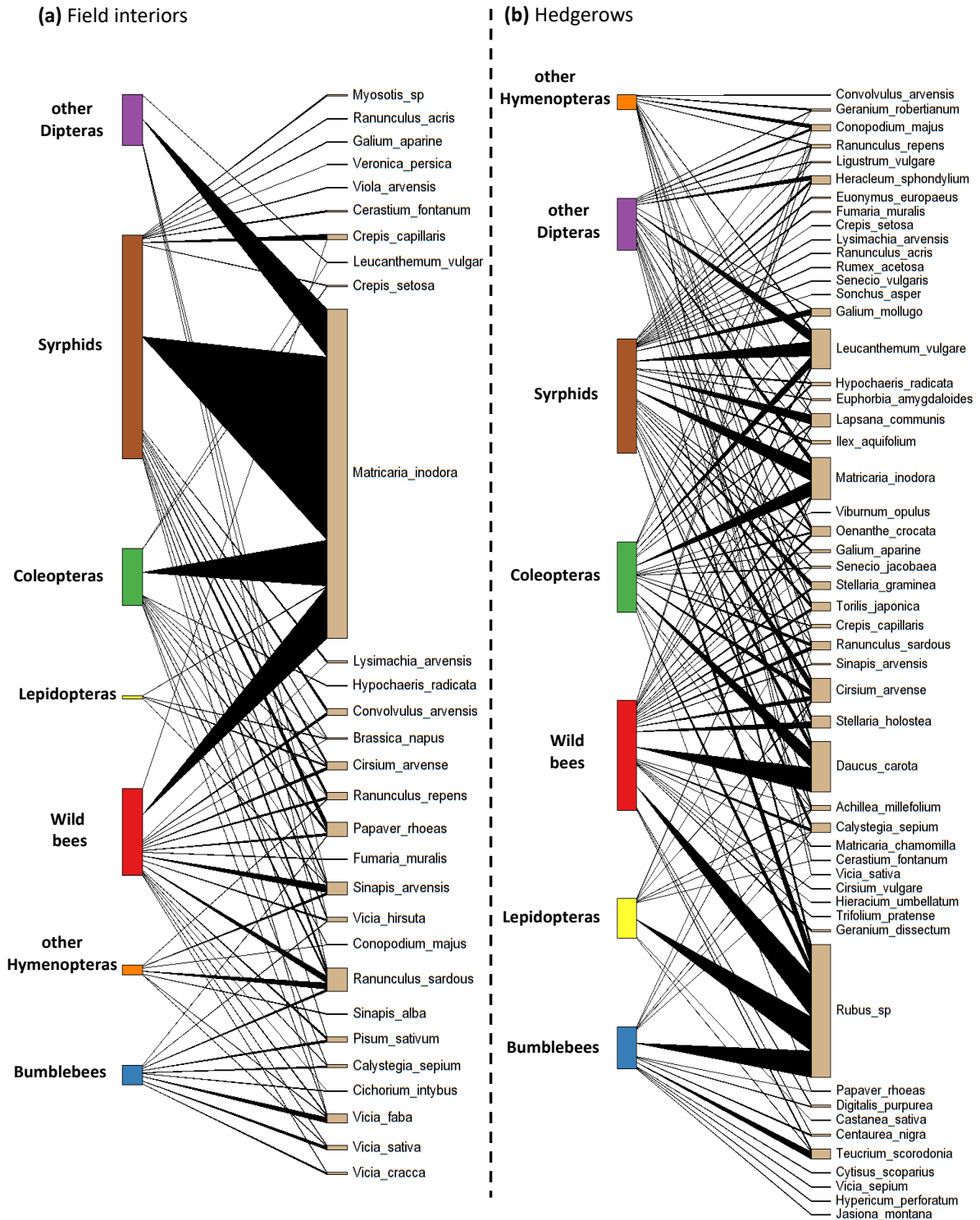


Fig. 10 Interaction networks between pollinator groups (N = 7) and flowering plant species in **(a)** inner fields and **(b)** hedgerows. The width of links (in black) represents the frequency of interactions. The length of bars (in color) corresponds to the relative abundance of pollinator groups and to the cover of flowering plants (as a proxy of their abundance). Source: Berry, unpublished data.

Case study: hedgerow plantation and bocage restoration enhance biodiversity involved in multifunctionality on farms

Studies addressing the effect of conservation and restoration of hedgerows have mostly focused on one particular ecosystem service or ecological function like pollination (e.g. Morandin & Kremen 2013), while there are only a few studies that study the impacts of hedgerows on multiple ecosystem services, simultaneously (e.g. Van Vooren *et al.* 2018). Here, we assessed the multifunctionality of recently planted hedgerows (i.e. 15 years ago; N = 16) compared to old traditional field margins (old hedgerows: N = 8; grassy margins: N = 8) on several farms pertaining to hedgerow network landscapes in Brittany, northwestern France. Multifunctionality was assessed by considering the ability of field margins to support (i) biodiversity of conservation interest, (ii) functional biodiversity involved in regulation functions (pest control and pollination), and (iii) biodiversity associated with negative disservices for agriculture, related to pest infestations in crops.

We showed that recent hedgerows harbor, 15 years after planting, similar levels of species diversity than old, traditional field margins (**Fig. 11**). Some recent hedgerows harbor species that are not found in old traditional hedgerows (and *vice versa*), suggesting that the diversity of field margins contributes to biodiversity conservation at farm / landscape level. Recent hedgerows also had carabid species that are typically associated with forest habitats, showing that these hedgerows fulfilled the suitable microclimatic conditions and vegetation density required by these forest species.

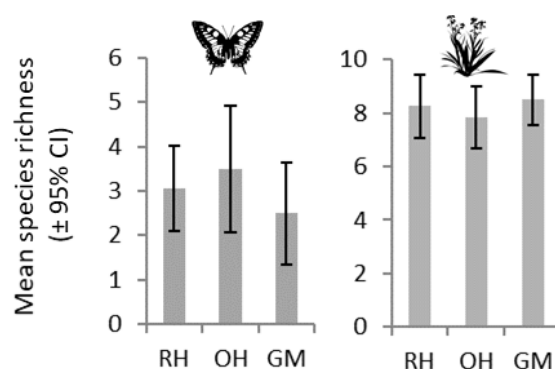


Fig. 11 Species richness of biodiversity of conservation interest (butterflies and vascular plants) in recent hedgerows (RH), old hedgerows (OH) and grassy field margins (GM). Differences in species richness between the different types of field margins are not significant (tested in mixed Generalized Linear Models, combined with Multi-Model Inference and model averaging procedures). Source: Aviron, unpublished data.

Recent hedgerows also harbored comparable levels of functional biodiversity, 15 years after planting. Recent hedgerows had similar abundance levels of predatory carabid beetles (**Fig. 12**) as well as pollinating insects. Annual crops adjacent to recent hedgerows also tended

to have higher activity-density of predatory arthropods than field adjacent to traditional margins (Fig. 12). It suggests that recent hedgerows might play a similar role of refuge and reservoir of predatory arthropods to other field margins. They do not increase weed infestation in crops as suggested by comparable levels of weed cover between field margin types.

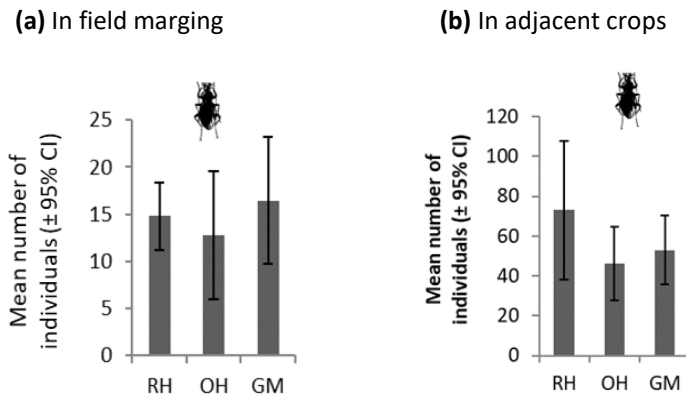


Fig. 12 Abundances (activity-density) of predatory carabid beetles observed (a) in field margins and (b) in adjacent fields. RH: recent hedgerows; OH: old hedgerows; GM: grassy field margins. Differences in species richness between the different types of field margins are not significant (tested in mixed Generalized Linear Models, combined with Multi-Model Inference and model averaging procedures). Source: Aviron, unpublished data.

At the landscape scale, the configuration of hedgerow networks had a strong impact on the different type of biodiversity. But we observed antagonistic responses for the different species groups. Hedgerow density had a positive effect on vascular plants and pollinators but a negative effect on carabid abundance (Fig. 13). These results suggest that enhancing multifunctionality on farms through bocage restoration might not simultaneously enhance contrasted ecological functions and that management measures should be targeted according to required functions.

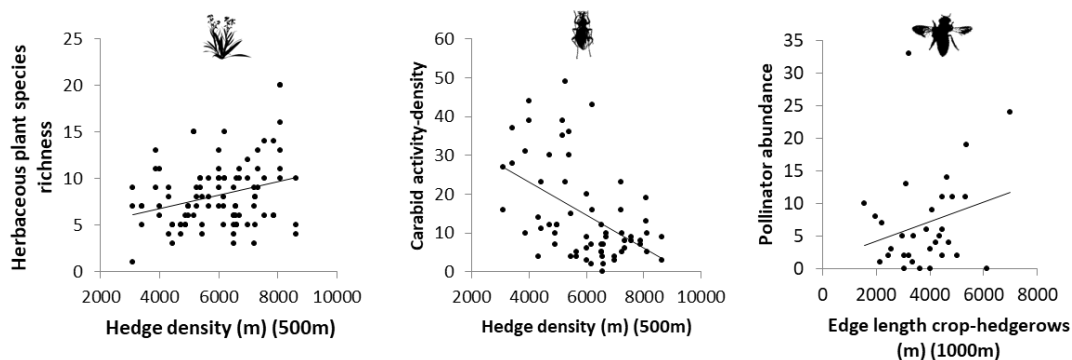


Fig. 13 Impact of the configuration of hedgerow networks (hedgerow density or edge length between crops and hedgerows) on local biodiversity Relationships are all significant at $P < 0.05$ (tested in mixed Generalized Linear Models, combined with Multi-Model Inference and model averaging procedures). Source: Aviron, unpublished data.

Summary and future trends

The way in which hedgerows are managed as well as their management history can affect their structure and composition. Often considered as semi-natural elements, studies considering the effect of hedgerow management on biodiversity and associated ecosystem services are exceptions. There is a dearth of information on the effect of frequency, type and timing of hedgerow management particularly on ecosystem services. As an example, it can be expected that hedgerow management will influence the availability and quantity of floral resources for pollinators.

The connectivity of the landscape, and thereby the ability of plants and animals to disperse across the landscape is also important for biodiversity conservation. But, tracking the movement of organisms through landscapes is difficult. Thus evidence, of the value of hedgerow networks in providing effective landscape connectivity, remains scarce. If hedgerows promote the abundance and dispersal of pest natural enemies, they may also favor the abundance and dispersal of pests. Whether hedgerows have any impacts on levels of pest regulation will be the outcome of highly complex interactions that are not well understood (Dover 2019).

To conclude, conservation and/or restoration of hedgerows appears to be a promising intervention that can promote both biodiversity conservation and associated ecosystem services. However, cost-benefit studies are needed to provide convincing evidence to farmers of the interest of such interventions and over what time-frame benefits might be realized (Garbach & Long 2017).

List of publications

ARTICLES

- Published in peer-reviewed journals

Barbe, L., Mony, C., Jung, V., **Uroy, L.** & Prinzing, A. (2020). Associational decomposition: After-life traits and interactions among decomposing litters control during-life aggregation of plant species. *Functional Ecology*, 34, 1956–1966

Uroy, L., Mony, C. & Ernoult, A. (2019). Additive effects of connectivity provided by different habitat types drive plant assembly. *Scientific Reports*, 9, 13952.

Uroy, L., Ernoult, A. & Mony, C. (2019). Effect of landscape connectivity on plant communities: a review of response patterns. *Landscape Ecology*, 34, 203–225.

- (To be) submitted to peer-reviewed journals

Uroy, L., Alignier, A., Mony, C., Foltête, J.-C. & Ernoult A. (in major revision). How to assess the temporal dynamics of landscape connectivity in ever-changing landscapes: a literature review. *Landscape Ecology*.

Uroy, L., Mony, C., Ernoult, A. & Alignier, A. (to be resubmitted). Using the response-effect trait framework reveals that high habitat connectivity reduces weed abundance in winter cereals.

Uroy, L., Ernoult, A., Alignier, A. & Mony, C. (to be resubmitted). Unveiling the ghosts of landscapes past: changes in landscape connectivity over the last decades are still shaping current woodland plant assemblages.

Mony, C., **Uroy, L.**, Khalfallah, F., Haddad, N. & Vandenkoornhuys, P. (to be submitted). Ecological corridors for the invisible.

- In preparation

Uroy, L., Guy, J., Georges, R., Jambon, O. & Mony, C. (in preparation). Small but not the least: transient changes in landscape patterns drive grassland plant aboveground and seed bank assemblages.

BOOK CHAPTERS

Alignier, A., **Uroy, L.** & Aviron, S. (2020). The role of hedgerows to support biodiversity and associated ecosystem services in intensive agricultural landscapes. In: *Reconciling agricultural production with biodiversity conservation* (eds. Bàrberi, P. & Moonen, A.-C.). Burleigh Dodds Science Publishing, London.

COMMUNICATIONS IN NATIONAL AND INTERNATIONAL CONFERENCES

- Talks (*: speaker)

Uroy, L.*, Ernoult, A., Alignier, A. & Mony, C. (accepted). Current forest plant assemblages result from landscape connectivity dynamics over the past decades. *Historical Ecology for the Future*, Metz, France, May 25-29 2020 [Postponed due to COVID-19].

Uroy, L.*, Mony, C., Ernoult, A. & Alignier, A. A trait-based approach to unravel the effects of habitat connectivity and habitat amount on weeds. *10th IALE World Congress*, Milano, Italy, July 1-5 2019.

Uroy, L.*, Mony, C., Alignier, A. & Ernoult, A. Trame verte et bleue et biodiversité: une vue d'ensemble des outils et méthodes pour caractériser la connectivité paysagère et son effet sur les communautés végétales. *La cartographie de la flore, un outil au service des politiques publiques de la biodiversité*, Nantes, France, June 7-8 2019.

Uroy, L.*, Mony, C. & Ernoult, A. Additive effects of ecological continuities drive plant assembly rules. *SFEcologie 2018*, Rennes, France, October 22-25 2018.

Mony, C.* , Berges, L., Alignier, A., Baudry, J., Burel, F., Ernoult, A., Lecoq, L., **Uroy, L.**, Avon, C., Archaux, F., Chauchard, S. & Dupouey, J.-L. Time as a driver of biodiversity response to landscape connectivity. *SFEcologie 2018*, Rennes, France, October 22-25 2018.

Uroy, L.* Biodiversité et Services Ecosystémiques associés aux complémentarités entre continuités écologiques boisées et cultivées dans les paysages agroforestiers. *4^{ème} Rencontres des agroforesteries tempérées sur le thème Agroforesterie et élevage*, Venours, France. September 12-13 2018.

Uroy, L.*, Mony, C. & Ernoult, A. Influence de la connectivité paysagère sur la structuration des communautés végétales: prise en compte des différentes continuités écologiques. *Rencontres d'Ecologie des Paysages 2017*, Toulouse, France, October 23-26 2017.

○ Posters (*: presenter)

Uroy, L.*, Mony, C., Ernoult, A. & Alignier, A. Effect of landscape connectivity provided by wooded and cultivated elements on weeds: a response-effect trait framework. *4th World Congress on Agroforestry*, Montpellier, France, May 20-22 2019.

POPULAR SCIENCE

○ Talks

Uroy, L. Paysage et flore des prairies temporaires. *Repas annuel des agriculteurs de la Zone-Atelier Armorique de Pleine-Fougères*, Pleine-Fougères, France, May 28 2018.

○ Medias

Uroy, L. 2020. Interview : "Restaurer les corridors est bénéfique". *Sciences Ouest*, 383, 7.

Participation to the documentary film "La Grace du Sillon" by Cyril Le Tourneur d'Ison.

Références

A

- Aavik, T. & Helm, A. (2018). Restoration of plant species and genetic diversity depends on landscape-scale dispersal. *Restor. Ecol.*, 26, S92–S102.
- Aavik, T., Holderegger, R. & Bolliger, J. (2014). The structural and functional connectivity of the grassland plant *Lychnis flos-cuculi*. *Heredity*, 112, 471–478.
- Adhikari, K. & Hartemink, A.E. (2016). Linking soils to ecosystem services — A global review. *Geoderma*, 262, 101–111.
- Adriaens, D., Honnay, O. & Hermy, M. (2006). No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. *Biol. Conserv.*, 133, 212–224.
- Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., *et al.* (2003). The application of ‘least-cost’ modelling as a functional landscape model. *Landsc. Urban Plan.*, 64, 233–247.
- Alignier, A. & Aviron, S. (2017). Time-lagged response of carabid species richness and composition to past management practices and landscape context of semi-natural field margins. *J. Environ. Manage.*, 204, 282–290.
- Alignier, A. & Baudry, J. (2015). Changes in management practices over time explain most variation in vegetation of field margins in Brittany, France. *Agric. Ecosyst. Environ.*, 211, 164–172.
- Alignier, A., Bretagnolle, V. & Petit, S. (2012). Spatial patterns of weeds along a gradient of landscape complexity. *Basic Appl. Ecol.*, 13, 328–337.
- Allen, T.F.H. & Starr, T.B. (1988). *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.
- Amsallem, J., Deshayes, M. & Bonneville, M. (2010). Analyse comparative de méthodes d’élaboration de trames vertes et bleues nationales et régionales. *Sci. Eaux Territ.*, Numéro 3, 40–45.
- Amsallem, J., Sordello, R., Billon, L. & Vanpeene, S. (2018). Bilan des Schémas régionaux de cohérence écologique en France : quels apports méthodologiques pour l’identification et la cartographie de la Trame verte et bleue ? *Sci. Eaux Territ.*, Numéro 25, 4–11.
- Anantharaman, R., Hall, K., Shah, V. & Edelman, A. (2019). Circuitscape in Julia: High Performance Connectivity Modelling to Support Conservation Decisions. *ArXiv190603542 Q-Bio*.
- Anderson, G.S. & Danielson, B.J. (1997). The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landsc. Ecol.*, 12, 261–271.

- Andersson, E. & Nilsson, C. (2002). Temporal variation in the drift of plant litter and propagules in a small boreal river. *Freshw. Biol.*, 47, 1674–1684.
- Andreasen, C., Stryhn, H. & Streibig, J.C. (1996). Decline of the Flora in Danish Arable Fields. *J. Appl. Ecol.*, 33, 619–626.
- Andrén, H. (1994). Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos*, 71, 355.
- Anon. (2019). *The value of hedgerows for wildlife*. The RSPB. Available at: <https://www.rspb.org.uk/our-work/conservation/conservation-and-sustainability/advice/conservation-land-management-advice/farm-hedges/the-value-of-hedgerows-for-wildlife/>. Last accessed 18 November 2019.
- Arellano-Rivas, A., De-Nova, J.A. & Munguía-Rosas, M.A. (2016). Patch isolation and shape predict plant functional diversity in a naturally fragmented forest. *J. Plant Ecol.*, 1–11.
- Auffret, A.G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., *et al.* (2017a). HistMapR: Rapid digitization of historical land-use maps in R. *Methods Ecol. Evol.*, 8, 1453–1457.
- Auffret, A.G., Rico, Y., Bullock, J.M., Hooftman, D.A.P., Pakeman, R.J., Soons, M.B., *et al.* (2017b). Plant functional connectivity – integrating landscape structure and effective dispersal. *J. Ecol.*
- Aviron, S., Burel, F., Baudry, J. & Schermann, N. (2005). Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agric. Ecosyst. Environ.*, Agri-Environmental Schemes as Landscape Experiments, 108, 205–217.
- Avon, C., Bergès, L. & Dupouey, J.-L. (2015). Landscape effects on plants in forests: Large-scale context determines local plant response. *Landsc. Urban Plan.*, 144, 65–73.

B

- Baessler, C. & Klotz, S. (2006). Effects of changes in agricultural land-use on landscape structure and arable weed vegetation over the last 50 years. *Agric. Ecosyst. Environ.*, 115, 43–50.
- Baeten, L., Davies, T.J., Verheyen, K., Calster, H.V. & Vellend, M. (2015). Disentangling dispersal from phylogeny in the colonization capacity of forest understorey plants. *J. Ecol.*, 103, 175–183.
- Bagaria, G., Rodà, F. & Pino, J. (2019). Extinction and colonisation of habitat specialists drive plant species replacement along a Mediterranean grassland-forest succession. *J. Veg. Sci.*, 30, 331–340.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks: Dispersal, connectivity and networks. *Biol. Rev.*, 88, 310–326.
- Bahram, M., Peay, K.G. & Tedersoo, L. (2015). Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. *New Phytol.*, 205, 1454–1463.
- Bakker, J.P., Bakker, E.S., Rosén, E., Verweij, G.L. & Bekker, R.M. (1996a). Soil Seed Bank Composition along a Gradient from Dry Alvar Grassland to Juniperus Shrubland. *J. Veg. Sci.*, 7, 165–176.

- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. (1996b). Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerlandica*, 45, 461–490.
- Banks-Leite, C., Ewers, R.M. & Metzger, J.P. (2012). Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology*, 93, 2560–2569.
- Bàrberi, P., Bocci, G., Carlesi, S., Armengot, L., Blanco-Moreno, J.M. & Sans, F.X. (2018). Linking species traits to agroecosystem services: a functional analysis of weed communities. *Weed Res.*
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.
- Barr, C.J. & Gillespie, M.K. (2000). Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *J. Environ. Manage.*, 60, 23–32.
- Barton, K. (2018). *MuMIn: Multi-Model Inference*.
- Baskin, C.C. & Baskin, J.M. (2014). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. 2nd edn. Academic Press, San Diego, CA.
- Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. Biol. Sci.*, 278, 1894–1902.
- Baudry, J., Bunce, R.G.H. & Burel, F. (2000). Hedgerows: An international perspective on their origin, function and management. *J. Environ. Manage.*, 60, 7–22.
- Baudry, J., Burel, F., Aviron, S., Martin, M., Ouin, A., Pain, G., *et al.* (2003). Temporal variability of connectivity in agricultural landscapes: do farming activities help? *Landsc. Ecol.*, 18, 303–314.
- Baudry, J. & Papy, F. (2001). The role of landscape heterogeneity in the sustainability of cropping systems. In: *Crop science: progress and prospects. Papers presented at the Third International Crop Science Congress, Hamburg, Germany, 17-22 August 2000* (eds. Nösberger, J., Geiger, H.H. & Struik, P.C.). CABI, Wallingford, pp. 243–259.
- Becker, C.G., Longo, A.V., Haddad, C.F.B. & Zamudio, K.R. (2017). Land cover and forest connectivity alter the interactions among host, pathogen and skin microbiome. *Proc. R. Soc. B Biol. Sci.*, 284, 20170582.
- Beier, P. & Noss, R.F. (1998). Do Habitat Corridors Provide Connectivity? *Conserv. Biol.*, 12, 1241–1252.
- Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A. & Longhi, M.L. (2006). The Role of Environmental and Spatial Processes in Structuring Lake Communities from Bacteria to Fish. *Ecology*, 87, 2985–2991.
- Belinchón, R., Hemrová, L. & Münzbergová, Z. (sous presse). Functional traits determine why species belong to the dark diversity in a dry grassland fragmented landscape. *Oikos*.
- de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., *et al.* (2009). Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *J. Veg. Sci.*, 20, 475–486.
- Belyea, L.R. & Lancaster, J. (1999). Assembly Rules within a Contingent Ecology. *Oikos*, 86, 402–416.
- Bender, D.J. & Fahrig, L. (2005). Matrix Structure Obscures the Relationship Between Interpatch Movement and Patch Size and Isolation. *Ecology*, 86, 1023–1033.

- Bengtsson, J., Ahnström, J. & Weibull, A.-C. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.*, 42, 261–269.
- Bennett, A.F. (2003). *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation*. IUCN-The World Conservation Union, Gland, Cambridge.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18, 182–188.
- Benvenuti, S. (2007). Weed seed movement and dispersal strategies in the agricultural environment. *Weed Biol. Manag.*, 7, 141–157.
- Berg, R.Y. (1983). Plant distribution as seen from plant dispersal: general principles and basic modes of plant dispersal. In: *Dispersal and Distribution* (ed. Kubitzki, K.). Paul Parey, Hamburg, pp. 13–36.
- Berglund, H. & Jonsson, B.G. (2005). Verifying an Extinction Debt among Lichens and Fungi in Northern Swedish Boreal Forests. *Conserv. Biol.*, 19, 338–348.
- Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A. & Garnier, E. (2012). Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *J. Ecol.*, 100, 1422–1433.
- Betbeder, J., Hubert-Moy, L., Burel, F., Corgne, S. & Baudry, J. (2015). Assessing ecological habitat structure from local to landscape scales using synthetic aperture radar. *Ecol. Indic.*, 52, 545–557.
- Betbeder, J., Nabucet, J., Pottier, E., Baudry, J., Corgne, S. & Hubert-Moy, L. (2014). Detection and Characterization of Hedgerows Using TerraSAR-X Imagery. *Remote Sens.*, 6, 3752–3769.
- Bianchi, F. j. j. a, Booij, C. j. h & Tscharrntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B Biol. Sci.*, 273, 1715–1727.
- Biedermann, R. (2004). Modelling the spatial dynamics and persistence of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Oikos*, 107, 645–653.
- Bielčik, M., Aguilar-Trigueros, C.A., Lakovic, M., Jeltsch, F. & Rillig, M.C. (2019). The role of active movement in fungal ecology and community assembly. *Mov. Ecol.*, 7, 36.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., *et al.* (2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, 313, 351–354.
- Bishop-Taylor, R., Tulbure, M.G. & Broich, M. (2015). Surface water network structure, landscape resistance to movement and flooding vital for maintaining ecological connectivity across Australia's largest river basin. *Landsc. Ecol.*, 30, 2045–2065.
- Bishop-Taylor, R., Tulbure, M.G. & Broich, M. (2018). Impact of hydroclimatic variability on regional-scale landscape connectivity across a dynamic dryland region. *Ecol. Indic.*, 94, 142–150.
- Bittebiere, A.-K., Benot, M.-L. & Mony, C. (2020). Clonality as a key but overlooked driver of biotic interactions in plants. *Perspect. Plant Ecol. Evol. Syst.*, 43, 125510.
- Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A. & Tscharrntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.*, 146, 34–43.
- Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., *et al.* (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339–345.

- Bodin, Ö. & Saura, S. (2010). Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. *Ecol. Model.*, 221, 2393–2405.
- Boedeltje, G., Bakker, J.P., Bekker, R.M., Van Groenendael, J.M. & Soesbergen, M. (2003). Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *J. Ecol.*, 91, 855–866.
- Boedeltje, G., Bakker, J.P., Ten Brinke, A., Van Groenendael, J.M. & Soesbergen, M. (2004). Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *J. Ecol.*, 92, 786–796.
- Boer, W. de, Folman, L.B., Summerbell, R.C. & Boddy, L. (2005). Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiol. Rev.*, 29, 795–811.
- Boeraeve, M., Honnay, O. & Jacquemyn, H. (2019). Local abiotic conditions are more important than landscape context for structuring arbuscular mycorrhizal fungal communities in the roots of a forest herb. *Oecologia*, 190, 149–157.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., *et al.* (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127–135.
- Bommarco, R., Lindborg, R., Marini, L. & Öckinger, E. (2014). Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Divers. Distrib.*, 20, 591–599.
- Bond, W.J. & Midgley, J.J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.*, 16, 45–51.
- Bonte, D., Dyck, H.V., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., *et al.* (2012). Costs of dispersal. *Biol. Rev.*, 87, 290–312.
- Boorman, S.A. & Levitt, P.R. (1973). Group selection on the boundary of a stable population. *Theor. Popul. Biol.*, 4, 85–128.
- Borgy, B., Perronne, R., Kohler, C., Grison, A.-L., Amiaud, B. & Gaba, S. (2016). Changes in functional diversity and intraspecific trait variability of weeds in response to crop sequences and climate. *Weed Res.*, 56, 102–113.
- Bornette, G., Amoros, C. & Lamouroux, N. (1998). Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshw. Biol.*, 39, 267–283.
- Botta-Dukát, Z. & Czúcz, B. (2016). Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods Ecol. Evol.*, 7, 114–126.
- Bourgeois, B., Munoz, F., Fried, G., Mahaut, L., Armengot, L., Denelle, P., *et al.* (2019). What makes a weed a weed? A large-scale evaluation of arable weeds through a functional lens. *Am. J. Bot.*, 106, 90–100.
- Boussard, H. & Baudry, J. (2014). *Chloe2012: a software for landscape pattern analysis*.
- Boutin, C., Baril, A. & Martin, P. (2008). Plant diversity in crop fields and woody hedgerows of organic and conventional farms in contrasting landscapes. *Agric. Ecosyst. Environ.*, 123, 185–193.
- Bowne, D.R. & Bowers, M.A. (2004). Interpatch movements in spatially structured populations: a literature review. *Landsc. Ecol.*, 19, 1–20.
- Bravo, D., Cailleau, G., Bindschedler, S., Simon, A., Job, D., Verrecchia, E., *et al.* (2013). Isolation of oxalotrophic bacteria able to disperse on fungal mycelium. *FEMS Microbiol. Lett.*, 348, 157–166.

- Bretagnolle, V. & Gaba, S. (2015). Weeds for bees? A review. *Agron. Sustain. Dev.*, 35, 891–909.
- Brown, J.H. & Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, 58, 445–449.
- Brückmann, S.V., Krauss, J. & Steffan-Dewenter, I. (2010). Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *J. Appl. Ecol.*, 47, 799–809.
- Brudvig, L.A. (2016). Interpreting the effects of landscape connectivity on community diversity. *J. Veg. Sci.*, 27, 4–5.
- Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M. & Levey, D.J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proc. Natl. Acad. Sci.*, 106, 9328–9332.
- Brudvig, L.A., Leroux, S.J., Albert, C.H., Bruna, E.M., Davies, K.F., Ewers, R.M., *et al.* (2017). Evaluating conceptual models of landscape change. *Ecography*, 40, 74–84.
- Brunet, J., De Frenne, P., Holmström, E. & Mayr, M.L. (2012). Life-history traits explain rapid colonization of young post-agricultural forests by understory herbs. *For. Ecol. Manag.*, 278, 55–62.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.*, 18, 119–125.
- Bull, J.W., Suttle, K.B., Singh, N.J. & Milner-Gulland, E. (2013). Conservation when nothing stands still: moving targets and biodiversity offsets. *Front. Ecol. Environ.*, 11, 203–210.
- Bunn, A.G., Urban, D.L. & Keitt, T.H. (2000). Landscape connectivity: A conservation application of graph theory. *J. Environ. Manage.*, 59, 265–278.
- Burel, F. (1996). Hedgerows and Their Role in Agricultural Landscapes. *Crit. Rev. Plant Sci.*, 15, 169–190.
- Burel, F. & Baudry, J. (1995). Social, aesthetic and ecological aspects of hedgerows in rural landscapes as a framework for greenways. *Landsc. Urban Plan.*, Greenways, 33, 327–340.
- Burel, F. & Baudry, J. (1999). *Ecologie du paysage. Concepts, méthodes et applications*. Editions TEC et DOC, Paris.
- Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Coeur, D., *et al.* (1998). Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecologica*, 19, 47–60.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- van Buuren, S. & Groothuis-Oudshoorn, K. (2011). mice: Multivariate Imputation by Chained Equations in R. *J. Stat. Softw.*, 45, 1–67.

C

- Cadotte, M.W. & Tucker, C.M. (2017). Should Environmental Filtering be Abandoned? *Trends Ecol. Evol.*, 32, 429–437.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000). Long-distance seed dispersal in plant populations. *Am. J. Bot.*, 87, 1217–1227.
- Calabrese, J.M. & Fagan, W.F. (2004). A comparison-shopper's guide to connectivity metrics. *Front. Ecol. Environ.*, 2, 529–536.

- Campbell, L.A. & Meinke, L.J. (2006). Seasonality and Adult Habitat Use by Four Diabrotica Species at Prairie-Corn Interfaces. *Environ. Entomol.*, 35, 922–936.
- Cardina, J., Johnson, G.A. & Sparrow, D.H. (1997). The nature and consequence of weed spatial distribution. *Weed Sci.*, 45, 364–373.
- Carey, P.D., Wallis, S., Chamberlain, P., Cooper, A., Emmett, B.A., Maskell, L.C., *et al.* (2008). *Countryside survey: UK results from 2007* (CEH Project Number: C03259). NERC/Centre for Ecology and Hydrology.
- Carson, J.K., Gonzalez-Quiñones, V., Murphy, D.V., Hinz, C., Shaw, J.A. & Gleeson, D.B. (2010). Low Pore Connectivity Increases Bacterial Diversity in Soil. *Appl. Environ. Microbiol.*, 76, 3936–3942.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.*, 1, e1400253.
- Celis-Diez, J.L., Bustamante, R.O. & Vásquez, R.A. (2004). Assessing frequency-dependent seed size selection: a field experiment. *Biol. J. Linn. Soc.*, 81, 307–312.
- Chaplin-Kramer, R. & Kremen, C. (2012). Pest control experiments show benefits of complexity at landscape and local scales. *Ecol. Appl.*, 22, 1936–1948.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.*, 14, 922–932.
- Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M. & Inouye, B.D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere*, 2, 1–11.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.
- Chaurand, J. (2011). *Trame verte et bleue – Réflexion et essai méthodologique de définition de listes d'espèces végétales pour la cohérence nationale de la Trame Verte et Bleue*. Fédération des Conservatoires botaniques nationaux.
- Chesson, P. (1991). A need for niches? *Trends Ecol. Evol.*, 6, 26–28.
- Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Chetkiewicz, C.-L.B., Clair, C.C.S. & Boyce, M.S. (2006). Corridors for Conservation: Integrating Pattern and Process. *Annu. Rev. Ecol. Syst.*, 37, 317–342.
- Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C., *et al.* (2011). Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecol. Lett.*, 14, 1273–1287.
- Clarke, R.T., Rothery, P. & Raybould, A.F. (2002). Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. *J. Agric. Biol. Environ. Stat.*, 7, 361–372.
- Clauzel, C., Bannwarth, C. & Foltête, J.-C. (2015). Integrating regional-scale connectivity in habitat restoration: An application for amphibian conservation in eastern France. *J. Nat. Conserv.*, 23, 98–107.
- Clay, K. & Schardl, C. (2002). Evolutionary origins and ecological consequences of endophyte symbiosis with grasses. *Am. Nat.*, 160 Suppl 4, S99–S127.
- Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

- Colbach, N., Dürr, C., Roger-Estrade, J., Chauvel, B. & Caneill, J. (2006). AlomySys: Modelling black-grass (*Alopecurus myosuroides* Huds.) germination and emergence, in interaction with seed characteristics, tillage and soil climate: I. Construction. *Eur. J. Agron.*, 24, 95–112.
- Cole, L., Deane, R. & Rayment, M. (2009). *Provision of ecosystem services through the environmental stewardship scheme* (Research contract NR0121). DEFRA, London, UK.
- Collinge, S.K. (2009). *Ecology of Fragmented Landscapes*. JHU Press.
- Commission Européenne. (2017). *Modernising and Simplifying the Common Agricultural Policy (CAP)* (Background Document: Climate and Environmental challenges facing EU agriculture and rural areas). European Commission, Brussels.
- Concepción, E.D., Fernández-González, F. & Díaz, M. (2012). Plant diversity partitioning in Mediterranean croplands: effects of farming intensity, field edge, and landscape context. *Ecol. Appl. Publ. Ecol. Soc. Am.*, 22, 972–981.
- Connor, E.F. & McCoy, E.D. (1979). The Statistics and Biology of the Species-Area Relationship. *Am. Nat.*, 113, 791–833.
- Corbit, M., Marks, P.L. & Gardescu, S. (1999). Hedgerows as habitat corridors for forest herbs in central New York, USA. *J. Ecol.*, 87, 220–232.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.
- Correa Ayram, C.A., Mendoza, M.E., Etter, A. & Salicrup, D.R.P. (2016). Habitat connectivity in biodiversity conservation: A review of recent studies and applications. *Prog. Phys. Geogr. Earth Environ.*, 40, 7–37.
- Correia, M., Heleno, R., Silva, L.P. da, Costa, J.M. & Rodríguez-Echeverría, S. (2019). First evidence for the joint dispersal of mycorrhizal fungi and plant diaspores by birds. *New Phytol.*, 222, 1054–1060.
- Cosyns, E., Claerbout, S., Lamoot, I. & Hoffmann, M. (2005). Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. *Plant Ecol.*
- Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.*, 8, 1175–1182.
- Cousins, S.A.O. (2009). Extinction debt in fragmented grasslands: paid or not? *J. Veg. Sci.*, 20, 3–7.
- Cousins, S.A.O., Ohlson, H. & Eriksson, O. (2007). Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. *Landsc. Ecol.*, 22, 723–730.
- Cousins, S.A.O. & Vanhoenacker, D. (2011). Detection of extinction debt depends on scale and specialisation. *Biol. Conserv.*, 144, 782–787.
- Couvreur, M., Couvreur, M., Vandenberghe, B., Verheyen, K. & Hermy, M. (2004). An experimental assessment of seed adhesivity on animal furs. *Seed Sci. Res.*, 14, 147–159.
- Crawley, M.J. (2000). Seed predators and plant population dynamics. In: *Seeds: the ecology of regeneration in plant communities* (ed. Fenner, M.). CABI, Wallingford, pp. 167–182.
- Cristofoli, S., Monty, A. & Mahy, G. (2010). Historical landscape structure affects plant species richness in wet heathlands with complex landscape dynamics. *Landsc. Urban Plan.*, 98, 92–98.
- Crooks, K.R. & Sanjayan, M. (2006). *Connectivity Conservation*. Cambridge University Press.

- Croxton, P.J., Franssen, W., Myhill, D.G. & Sparks, T.H. (2004). The restoration of neglected hedges: a comparison of management treatments. *Biol. Conserv.*, 117, 19–23.
- Cushman, S.A., Gutzweiler, K., Evans, J.S. & McGarigal, K. (2010). The Gradient Paradigm: A Conceptual and Analytical Framework for Landscape Ecology. In: *Spatial Complexity, Informatics, and Wildlife Conservation* (eds. Cushman, S.A. & Huettmann, F.). Springer Japan, Tokyo, pp. 83–108.

D

- Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M. & Marini, L. (2017). High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *J. Appl. Ecol.*, 54, 380–388.
- Dale, M.R.T. (2017). Spatio-temporal Graphs. In: *Applying graph theory in ecological research*. Cambridge University Press, Cambridge, pp. 222–251.
- Damschen, E.I., Baker, D.V., Bohrer, G., Nathan, R., Orrock, J.L., Turner, J.R., *et al.* (2014). How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proc. Natl. Acad. Sci.*, 111, 3484–3489.
- Damschen, E.I., Brudvig, L.A., Burt, M.A., Fletcher, R.J., Haddad, N.M., Levey, D.J., *et al.* (2019). Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science*, 365, 1478–1480.
- Damschen, E.I., Brudvig, L.A., Haddad, N.M., Levey, D.J., Orrock, J.L. & Tewksbury, J.J. (2008). The movement ecology and dynamics of plant communities in fragmented landscapes. *Proc. Natl. Acad. Sci.*, 105, 19078–19083.
- Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. & Levey, D.J. (2006). Corridors increase plant species richness at large scales. *Science*, 313, 1284–1286.
- De Ryck, D.J.R., Robert, E.M.R., Schmitz, N., Van der Stocken, T., Di Nitto, D., Dahdouh-Guebas, F., *et al.* (2012). Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules. *Aquat. Bot.*, 103, 66–73.
- Deckers, B., Hermy, M. & Muys, B. (2004). Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica*, 26, 23–37.
- Deckers, B., Verheyen, K., Hermy, M. & Muys, B. (2005). Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. *Ecography*, 28, 99–109.
- Decocq, G., Valentin, B., Toussaint, B., Hendoux, F., Saguez, R. & Bardat, J. (2004). Soil seed bank composition and diversity in a managed temperate deciduous forest. *Biodivers. Conserv.*, 13, 2485–2509.
- Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R. & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Front. Ecol. Environ.*, 12, 212–217.
- Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., *et al.* (2016). Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.*, 7, 10541.
- Diamond, J.M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proc. Natl. Acad. Sci.*, 69, 3199–3203.

- Diamond, J.M. (1975a). Assembly of species communities. In: *Ecology and Evolution of Communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge, MA, pp. 342–444.
- Diamond, J.M. (1975b). The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.*, 7, 129–146.
- Dickie, I.A., Fukami, T., Wilkie, J.P., Allen, R.B. & Buchanan, P.K. (2012). Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecol. Lett.*, 15, 133–141.
- Didham, R.K. (2010). *Ecological Consequences of Habitat Fragmentation*. eLS, Major Reference Works.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B Biol. Sci.*, 268, 25–29.
- Dondina, O., Kataoka, L., Orioli, V. & Bani, L. (2016). How to manage hedgerows as effective ecological corridors for mammals: A two-species approach. *Agric. Ecosyst. Environ.*, 231, 283–290.
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., *et al.* (2014). Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*, 344, 296–299.
- van Dorp, D., Schippers, P. & van Groenendael, J.M. (1997). Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. *Landsc. Ecol.*, 12, 39–50.
- Dover, J. & Settele, J. (2009). The influences of landscape structure on butterfly distribution and movement: a review. *J. Insect Conserv.*, 13, 3–27.
- Dover, J. & Sparks, T. (2000). A review of the ecology of butterflies in British hedgerows. *J. Environ. Manage.*, 60, 51–63.
- Dover, J.W. (1996). Factors Affecting the Distribution of Satyrid Butterflies on Arable Farmland. *J. Appl. Ecol.*, 33, 723–734.
- Dover, J.W. (2019). *The Ecology of Hedgerows and Field Margins*. Routledge, London, New York.
- Drake, J.A. (1991). Community-Assembly Mechanics and the Structure of an Experimental Species Ensemble. *Am. Nat.*, 137, 1–26.
- Dray, S. & Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Softw.*, 22, 1–20.
- Driscoll, D.A. (2007). How to find a metapopulation This review is one of a series dealing with some aspects of the impact of habitat fragmentation on animals and plants. This series is one of several virtual symposia focussing on ecological topics that will be published in the Journal from time to time. *Can. J. Zool.*, 85, 1031–1048.
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992). Ecological Processes That Affect Populations in Complex Landscapes. *Oikos*, 65, 169–175.
- Dzwonko, Z. & Loster, S. (1988). Species richness of small woodlands on the western Carpathian foothills. *Vegetatio*, 76, 15–27.

E

- Ehrlén, J. & Lehtilä, K. (2002). How perennial are perennial plants? *Oikos*, 98, 308–322.
- Elton, C.S. (1927). *Animal ecology*. Sidgwick and Jackson, London.

- Eriksson, O. (1996). Regional Dynamics of Plants: A Review of Evidence for Remnant, Source-Sink and Metapopulations. *Oikos*, 77, 248–258.
- Eriksson, O. (1997). Clonal life histories and the evolution of seed recruitment. In: *The ecology and evolution of clonal plants*. (eds. de Kroon, H. & van Groenendael, J.M.). Backhuys Publishers, Leiden, pp. 221–226.
- Eriksson, O. (2000). Seed Dispersal and Colonization Ability of Plants: Assessment and Implications for Conservation. *Folia Geobot.*, 35, 115–123.
- Eriksson, O. & Ehrlén, J. (1992). Seed and microsite limitation of recruitment in plant populations. *Oecologia*, 91, 360–364.
- Eriksson, O. & Ehrlén, J. (2001). Landscape fragmentation and the viability of plant populations. In: *Integrating Ecology and Evolution in a Spatial Context: 14th Special Symposium of the British Ecological Society*. Silvertown J. and Antonovics, J., Oxford, pp. 157–175.
- Eriksson, O. & Eriksson, Å. (1998). Effects of arrival order and seed size on germination of grassland plants: Are there assembly rules during recruitment? *Ecol. Res.*, 13, 229–239.
- van Etten, J. (2017). R Package gdistance: Distances and Routes on Geographical Grids. *J. Stat. Softw.*, 76, 1–21.
- Evju, M., Blumentrath, S., Skarpaas, O., Stabbetorp, O.E. & Sverdrup-Thygeson, A. (2015). Plant species occurrence in a fragmented grassland landscape: the importance of species traits. *Biodivers. Conserv.*, 24, 547–561.

F

- Fagan, W.F., Cantrell, R.S. & Cosner, C. (1999). How Habitat Edges Change Species Interactions. *Am. Nat.*, 153, 165–182.
- Fahrig, L. (2002). Effect of Habitat Fragmentation on the Extinction Threshold: A Synthesis*. *Ecol. Appl.*, 12, 346–353.
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.
- Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.*, 40, 1649–1663.
- Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annu. Rev. Ecol. Evol. Syst.*, 48, 1–23.
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., et al. (2019). Is habitat fragmentation bad for biodiversity? *Biol. Conserv.*, 230, 179–186.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., et al. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.*, 14, 101–112.
- Fahrig, L. & Merriam, G. (1985). Habitat Patch Connectivity and Population Survival. *Ecology*, 66, 1762–1768.
- Faraway, J.J. (2016). *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models, Second Edition*. 2nd edn. Chapman and Hall/CRC, Boca Raton.

- Favre-Bac, L., Ernoult, A., Mony, C., Rantier, Y., Nabucet, J. & Burel, F. (2014). Connectivity and propagule sources composition drive ditch plant metacommunity structure. *Acta Oecologica*, 61, 57–64.
- Favre-Bac, L., Lamberti-Raverot, B., Puijalon, S., Ernoult, A., Burel, F., Guillard, L., *et al.* (2017a). Plant dispersal traits determine hydrochorous species tolerance to connectivity loss at the landscape scale. *J. Veg. Sci.*, 28, 605–615.
- Favre-Bac, L., Mony, C., Burel, F., Seimandi-Corda, G. & Ernoult, A. (2017b). Connectivity drives the functional diversity of plant dispersal traits in agricultural landscapes: the example of ditch metacommunities. *Landsc. Ecol.*, 32, 2029–2040.
- Fenner, M.K. & Thompson, K. (2005). *The Ecology of Seeds*. Cambridge University Press.
- Ferrari, B.C., Bissett, A., Snape, I., Dorst, J. van, Palmer, A.S., Ji, M., *et al.* (2016). Geological connectivity drives microbial community structure and connectivity in polar, terrestrial ecosystems. *Environ. Microbiol.*, 18, 1834–1849.
- Fischer, J. & Lindenmayer, D.B. (2006). Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, 112, 473–480.
- Fischer, J. & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.*, 16, 265–280.
- Fischer, M. & Stöcklin, J. (1997). Local Extinctions of Plants in Remnants of Extensively Used Calcareous Grasslands 1950 –1985. *Conserv. Biol.*, 11, 727–737.
- Flatrès, P. (1979). L'évolution des bocages: la région Bretagne. *Noréis*, 103, 303–320.
- Fletcher, R. & Fortin, M.-J. (2018). *Spatial Ecology and Conservation Modeling: Applications with R*. Springer International Publishing.
- Fletcher, R.J., Acevedo, M.A. & Robertson, E.P. (2014). The matrix alters the role of path redundancy on patch colonization rates. *Ecology*, 95, 1444–1450.
- Fletcher, R.J., Burrell, N.S., Reichert, B.E., Vasudev, D. & Austin, J.D. (2016). Divergent Perspectives on Landscape Connectivity Reveal Consistent Effects from Genes to Communities. *Curr. Landsc. Ecol. Rep.*, 1, 67–79.
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., *et al.* (2018). Is habitat fragmentation good for biodiversity? *Biol. Conserv.*, 226, 9–15.
- Foltête, J.-C. (2018). A parcel-based graph to match connectivity analysis with field action in agricultural landscapes: Is node removal a reliable method? *Landsc. Urban Plan.*, 178, 32–42.
- Foltête, J.-C., Clauzel, C. & Vuidel, G. (2012). A software tool dedicated to the modelling of landscape networks. *Environ. Model. Softw.*, 38, 316–327.
- Foltête, J.-C., Girardet, X. & Clauzel, C. (2014). A methodological framework for the use of landscape graphs in land-use planning. *Landsc. Urban Plan.*, 124, 140–150.
- Foltête, J.-C., Savary, P., Clauzel, C., Bourgeois, M., Girardet, X., Saharoui, Y., *et al.* (2020). Coupling landscape graph modeling and biological data: a review. *Landsc. Ecol.*
- Forman, R.T.T. (1995). *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press.
- Forman, R.T.T. & Baudry, J. (1984). Hedgerows and hedgerow networks in landscape ecology. *Environ. Manage.*, 8, 495–510.
- Forman, R.T.T. & Godron, M. (1986). *Landscape Ecology*. Wiley.
- Franklin, R. & Mills, A. (Eds.). (2007). *The Spatial Distribution of Microbes in the Environment*. Springer Netherlands.

- French, B.W., Elliott, N.C., Berberet, R.C. & Burd, J.D. (2001). Effects of Riparian and Grassland Habitats on Ground Beetle (Coleoptera: Carabidae) Assemblages in Adjacent Wheat Fields. *Environ. Entomol.*, 30, 225–234.
- Fried, G., Kazakou, E. & Gaba, S. (2012). Trajectories of weed communities explained by traits associated with species' response to management practices. *Agric. Ecosyst. Environ.*, 158, 147–155.
- Fried, G., Villers, A. & Porcher, E. (2018). Assessing non-intended effects of farming practices on field margin vegetation with a functional approach. *Agric. Ecosyst. Environ.*, 261, 33–44.
- Fukami, T. (2015). Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Annu. Rev. Ecol. Evol. Syst.*, 46, 1–23.
- Fukami, T. & Nakajima, M. (2013). Complex plant–soil interactions enhance plant species diversity by delaying community convergence. *J. Ecol.*, 101, 316–324.

G

- Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V. & Petit, S. (2010). Weed species richness in winter wheat increases with landscape heterogeneity. *Agric. Ecosyst. Environ.*, 138, 318–323.
- Gaba, S., Deroulers, P., Bretagnolle, F. & Bretagnolle, V. (2019). Lipid content drives weed seed consumption by ground beetles (Coleoptera, Carabidae) within the smallest seeds. *Weed Res.*, 59, 170–179.
- Gaba, S., Perronne, R., Gardarin, A., Bretagnolle, F., Biju-Duval, L., Colbach, N., *et al.* (2017). Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge. *Weed Res.*, 57, 123–147.
- Galpern, P., Manseau, M. & Fall, A. (2011). Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. *Biol. Conserv.*, 144, 44–55.
- Garbach, K. & Long, R.F. (2017). Determinants of field edge habitat restoration on farms in California's Sacramento Valley. *J. Environ. Manage.*, 189, 134–141.
- García-Feced, C., Saura, S. & Elena-Rosselló, R. (2011). Improving landscape connectivity in forest districts: A two-stage process for prioritizing agricultural patches for reforestation. *For. Ecol. Manag.*, 261, 154–161.
- Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O'Neal, M., Chacon, J.M., *et al.* (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl. Publ. Ecol. Soc. Am.*, 19, 143–154.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., *et al.* (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.*, 14, 1062–1072.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., *et al.* (2004). Plant Functional Markers Capture Ecosystem Properties During Secondary Succession. *Ecology*, 85, 2630–2637.
- Garratt, M.P.D., Senapathi, D., Coston, D.J., Mortimer, S.R. & Potts, S.G. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agric. Ecosyst. Environ.*, 247, 363–370.

- Gause, G.F. (1934). *The Struggle for Existence*. Williams and Wilkins Company, Baltimore.
- Gelling, M., Macdonald, D.W. & Mathews, F. (2007). Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landsc. Ecol.*, 22, 1019–1032.
- Gignac, L.D. & Dale, M.R.T. (2007). Effects of size, shape, and edge on vegetation in remnants of the upland boreal mixed-wood forest in agro-environments of Alberta, Canada. *Can. J. Bot.*, 85, 273–284.
- Gilbert-Norton, L., Wilson, R., Stevens, J.R. & Beard, K.H. (2010). A meta-analytic review of corridor effectiveness. *Conserv. Biol.*, 24, 660–668.
- Gilpin, M. & Hanski, I. (1991). *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London, UK.
- Gilpin, M.E. & Diamond, J.M. (1976). Calculation of immigration and extinction curves from the species-area-distance relation. *Proc. Natl. Acad. Sci.*, 73, 4130–4134.
- Gil-Tena, A., Lecerf, R. & Ernoult, A. (2013). Disentangling community assemblages to depict an indicator of biological connectivity: A regional study of fragmented semi-natural grasslands. *Ecol. Indic.*, 24, 48–55.
- Godefroid, S. & Koedam, N. (2003). How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Glob. Ecol. Biogeogr.*, 12, 287–298.
- Götzenberger, L., Bello, F. de, Bräthen, K.A., Davison, J., Dubuis, A., Guisan, A., *et al.* (2012). Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol. Rev.*, 87, 111–127.
- Grandin, U. & Rydin, H. (1998). Attributes of the seed bank after a century of primary succession on islands in Lake Hjälmaren, Sweden. *J. Ecol.*, 86, 293–303.
- Gray, D.A., Dugar, G., Gamba, P., Strahl, H., Jonker, M.J. & Hamoen, L.W. (2019). Extreme slow growth as alternative strategy to survive deep starvation in bacteria. *Nat. Commun.*, 10, 890.
- Greene, D.F. & Johnson, E.A. (1996). Wind Dispersal of Seeds from a Forest Into a Clearing. *Ecology*, 77, 595–609.
- Griffin, D.W. (2007). Atmospheric Movement of Microorganisms in Clouds of Desert Dust and Implications for Human Health. *Clin. Microbiol. Rev.*, 20, 459–477.
- Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *J. Veg. Sci.*, 17, 255–260.
- Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. *The Auk*, 34, 427–433.
- van Groenendael, J.M. & de Kroon, H. (1990). *Clonal growth in plants: regulation and function*. SPB Academic Publishing, The Hague.
- Gross, N., Suding, K.N. & Lavorel, S. (2007). Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *J. Veg. Sci.*, 18, 289–300.
- Groupe Mammalogique Breton. (2015). *Atlas des mammifères de Bretagne*. Locus Solus.
- Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., *et al.* (2002). Planning for Biodiversity Conservation: Putting Conservation Science into Practice A seven-step framework for developing regional plans to conserve biological diversity, based upon principles of conservation biology and ecology, is being used extensively

- by the nature conservancy to identify priority areas for conservation. *BioScience*, 52, 499–512.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, 8, 993–1009.
- Gunton, R.M., Petit, S. & Gaba, S. (2011). Functional traits relating arable weed communities to crop characteristics: Traits relating weed communities to crops. *J. Veg. Sci.*, 22, 541–550.
- Guo, Z., Liu, H., Wan, S., Hua, K., Wang, D., Guo, X., *et al.* (2019). Fertilisation practice changes rhizosphere microbial community structure in the agroecosystem. *Ann. Appl. Biol.*, 174, 123–132.
- Gurrutxaga, M., Rubio, L. & Saura, S. (2011). Key connectors in protected forest area networks and the impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW Europe). *Landsc. Urban Plan.*, 101, 310–320.

H

- Haddad, N.M. & Baum, K.A. (1999). An Experimental Test of Corridor Effects on Butterfly Densities. *Ecol. Appl.*, 9, 623–633.
- Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., *et al.* (2003). Corridor use by diverse taxa. *Ecology*, 84, 609–615.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., *et al.* (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.*, 1, e1500052.
- Haddad, N.M., Brudvig, L.A., Damschen, E.I., Evans, D.M., Johnson, B.L., Levey, D.J., *et al.* (2014). Potential negative ecological effects of corridors. *Conserv. Biol. J. Soc. Conserv. Biol.*, 28, 1178–1187.
- Haddad, N.M., Gonzalez, A., Brudvig, L.A., Burt, M.A., Levey, D.J. & Damschen, E.I. (2017). Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography*, 40, 48–55.
- Haddad, N.M., Hudgens, B., Damschen, E.I., Levey, D.J., Orrock, J.L., Tewksbury, J.J., *et al.* (2011). Assessing positive and negative ecological effects of corridors. In: *Sources, Sinks and Sustainability* (eds. Liu, J., Hull, V., Morzillo, A.T. & Wiens, J.A.). Cambridge University Press, Cambridge, pp. 475–503.
- Haddad, N.M. & Tewksbury, J.J. (2006). Impacts of corridors on populations and communities. In: *Connectivity Conservation: maintaining connections for nature* (eds. Crooks, K.R. & Sanjayan, M.). Cambridge University Press, Cambridge, pp. 390–415.
- Haila, Y. (2002). A Conceptual Genealogy of Fragmentation Research: From Island Biogeography to Landscape Ecology*. *Ecol. Appl.*, 12, 321–334.
- Hair, J.F., Black, W.C., Babin, B.J., Anderson, R.E. & Tatham, R.L. (2014). *Multivariate Data Analysis*. Pearson custom library. 7th edn. Pearson, Harlow.
- Hannon, L.E. & Sisk, T.D. (2009). Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biol. Conserv.*, 142, 2140–2154.
- Hanski, I. (1985). Single-Species Spatial Dynamics May Contribute to Long-Term Rarity and Commonness. *Ecology*, 66, 335–343.
- Hanski, I. (1994a). A Practical Model of Metapopulation Dynamics. *J. Anim. Ecol.*, 63, 151–162.

- Hanski, I. (1994b). Patch-occupancy dynamics in fragmented landscapes. *Trends Ecol. Evol.*, 9, 131–135.
- Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I. (2005). *The Shrinking World: Ecological Consequences of Habitat Loss*. International Ecology Institute, Oldendorf/Luhe.
- Hanski, I. (2015). Habitat fragmentation and species richness. *J. Biogeogr.*, 42, 989–993.
- Hanski, I. & Gilpin, M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.*, 42, 3–16.
- Hanski, I. & Simberloff, D. (1997). The Metapopulation Approach, Its History, Conceptual Domain, and Application to Conservation. In: *Metapopulation Biology* (eds. Hanski, I. & Gilpin, M.E.). Academic Press, San Diego, pp. 5–26.
- Hanski, I. & Thomas, C.D. (1994). Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. *Biol. Conserv.*, 68, 167–180.
- Hanski, I.A. & Gilpin, M.E. (1997). *Metapopulation Biology: Ecology, Genetics, and Evolution*. Elsevier Science.
- Hanson, C.A., Fuhrman, J.A., Horner-Devine, M.C. & Martiny, J.B.H. (2012). Beyond biogeographic patterns: processes shaping the microbial landscape. *Nat. Rev. Microbiol.*, 10, 497–506.
- Hanzlik, K. & Gerowitt, B. (2016). Methods to conduct and analyse weed surveys in arable farming: a review. *Agron. Sustain. Dev.*, 36, 11.
- Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London.
- Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biol. J. Linn. Soc.*, 42, 73–88.
- Harrison, S. & Taylor, A.D. (1997). Empirical Evidence for Metapopulation Dynamics. In: *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds. Hanski, I. & Gilpin, M.E.). Academic Press, San Diego, pp. 27–42.
- Hastings, A. (1991). Structured models of metapopulation dynamics. *Biol. J. Linn. Soc.*, 42, 57–71.
- Helm, A., Hanski, I. & Pärtel, M. (2006). Slow response of plant species richness to habitat loss and fragmentation. *Ecol. Lett.*, 9, 72–77.
- Herben, T. & Goldberg, D.E. (2014). Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits. *J. Ecol.*, 102, 156–166.
- Herben, T., Nováková, Z. & Klimešová, J. (2014). Clonal growth and plant species abundance. *Ann. Bot.*, 114, 377–388.
- Hermy, M. & Verheyen, K. (2007). Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecol. Res.*, 22, 361–371.
- Hernández, A., Miranda, M., Arellano, E.C., Saura, S. & Ovalle, C. (2015). Landscape dynamics and their effect on the functional connectivity of a Mediterranean landscape in Chile. *Ecol. Indic.*, 48, 198–206.
- Higgins, S.I., Nathan, R. & Cain, M.L. (2003). Are Long-Distance Dispersal Events in Plants Usually Caused by Nonstandard Means of Dispersal? *Ecology*, 84, 1945–1956.

- Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., *et al.* (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *J. Appl. Ecol.*, 55, 169–184.
- HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012). Rethinking Community Assembly through the Lens of Coexistence Theory. *Annu. Rev. Ecol. Evol. Syst.*, 43, 227–248.
- Hilty, J.A., Jr, W.Z.L. & Merenlender, A.M. (2006). *Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation*. Island Press.
- Hinsley, S.A. & Bellamy, P.E. (2000). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *J. Environ. Manage.*, 60, 33–49.
- Hodgson, J.A., Moilanen, A. & Thomas, C.D. (2009). Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. *Ecology*, 90, 1608–1619.
- Holland, J. (2019). Contribution of hedgerows to biological control. In: *The Ecology of Hedgerows and Field Margins* (ed. Dover, J.W.). Routledge, London, New York, pp. 123–146.
- Honnay, O. & Bossuyt, B. (2005). Prolonged clonal growth: escape route or route to extinction? *Oikos*, 108, 427–432.
- Honnay, O., Hermy, M. & Coppin, P. (1999). Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. *Biol. Conserv.*, 87, 73–84.
- Hooftman, D.A.P., Edwards, B. & Bullock, J.M. (2016). Reductions in connectivity and habitat quality drive local extinctions in a plant diversity hotspot. *Ecography*, 39, 583–592.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecol. Monogr.*, 75, 3–35.
- Horner-Devine, M.C., Carney, K.M. & Bohannan, B.J.M. (2004). An ecological perspective on bacterial biodiversity. *Proc. R. Soc. Lond. B Biol. Sci.*, 271, 113–122.
- Horváth, Z., Ptacnik, R., Vad, C.F. & Chase, J.M. (2019). Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecol. Lett.*, 22, 1019–1027.
- Howe, H.F. & Smallwood, J. (1982). Ecology of Seed Dispersal. *Annu. Rev. Ecol. Syst.*, 13, 201–228.
- Huang, J.-L., Andrello, M., Martensen, A.C., Saura, S., Liu, D.-F., He, J.-H., *et al.* (2020). Importance of spatio-temporal connectivity to maintain species experiencing range shifts. *Ecography*, 43, 591–603.
- Hubbell, S.P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16, S9–S21.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- Huber, S., Huber, B., Stahl, S., Schmid, C. & Reisch, C. (2017). Species diversity of remnant calcareous grasslands in south eastern Germany depends on litter cover and landscape structure. *Acta Oecologica*, 83, 48–55.
- Hulme, P.E. (1998). Post-dispersal seed predation and seed bank persistence. *Seed Sci. Res.*, 8, 513–519.

- Hutchings, M.J. (1986). Plant population biology. In: *Methods in plant ecology* (eds. Moore, P.D. & Chapman, S.B.). Blackwell Scientific, Oxford.
- Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*, 22, 415–427.
- Huyghe, C. (2009). Evolution des prairies et cultures fourragères et de leurs modalités culturales et d'utilisation en France au cours des cinquante dernières années. *Fourrages*, 200, 404–428.
- Hylander, K. & Ehrlén, J. (2013). The mechanisms causing extinction debts. *Trends Ecol. Evol.*, 28, 341–346.

I

- Ibáñez, I., Katz, D.S.W., Peltier, D., Wolf, S.M. & Barrie, B.T.C. (2014). Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess–multiresponse dynamics. *J. Ecol.*, 4, 882–895.
- Ioos, R., Husson, C., Andrieux, A. & Frey, P. (2005). SCAR-based PCR primers to detect the hybrid pathogen *Phytophthora alni* and its subspecies causing alder disease in Europe. *Eur. J. Plant Pathol.*, 112, 323–335.

J

- Jackson, H.B. & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landsc. Ecol.*, 27, 929–941.
- Jackson, H.B. & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale? *Glob. Ecol. Biogeogr.*, 24, 52–63.
- Jackson, S.T. & Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.*, 25, 153–160.
- Jacquemyn, H., Butaye, J. & Hermy, M. (2003). Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography*, 26, 768–776.
- Jakobsson, A. & Eriksson, O. (2000). A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, 88, 494–502.
- Jauzein, P. (2011). *Flore des champs cultivés*. Editions Quae.
- Johnson, B.L. & Haddad, N.M. (2011). Edge effects, not connectivity, determine the incidence and development of a foliar fungal plant disease. *Ecology*, 92, 1551–1558.
- Johst, K., Brandl, R. & Eber, S. (2002). Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, 98, 263–270.
- Joly, D., Brossard, T., Cardot, H., Cavailles, J., Hilal, M. & Wavresky, P. (2010). Les types de climats en France, une construction spatiale. *Cybergeo Eur. J. Geogr.*
- Jules, E.S., Kauffman, M.J., Ritts, W.D. & Carroll, A.L. (2002). Spread of an Invasive Pathogen Over a Variable Landscape: A Nonnative Root Rot on Port Orford Cedar. *Ecology*, 83, 3167–3181.
- Julve, P. (1998). Baseflor. Index botanique, écologique et chorologique de la flore de France.

K

- Katoh, K., Sakai, S. & Takahashi, T. (2009). Factors maintaining species diversity in satoyama, a traditional agricultural landscape of Japan. *Biol. Conserv.*, The Conservation and Management of Biodiversity in Japan, 142, 1930–1936.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., *et al.* (2020). TRY plant trait database – enhanced coverage and open access. *Glob. Change Biol.*, 26, 119–188.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., *et al.* (2011). TRY – a global database of plant traits. *Glob. Change Biol.*, 17, 2905–2935.
- Keitt, T., Urban, D.L. & Milne, B.T. (1997). Detecting Critical Scales in Fragmented Landscapes. *Conserv. Ecol.*, 1, art4.
- Kelt, D.A., Taper, M.L. & Meserve, P.L. (1995). Assessing the Impact of Competition on Community Assembly: A Case Study using Small Mammals. *Ecology*, 76, 1283–1296.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., *et al.* (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.*, 16, 584–599.
- Kennedy, P.G. & Bruns, T.D. (2005). Priority Effects Determine the Outcome of Ectomycorrhizal Competition between Two *Rhizopogon* Species Colonizing *Pinus muricata* Seedlings. *New Phytol.*, 166, 631–638.
- Keymer, J.E., Marquet, P.A., Velasco-Hernández, J.X. & Levin, S.A. (2000). Extinction Thresholds and Metapopulation Persistence in Dynamic Landscapes. *Am. Nat.*, 156, 478–494.
- Kiepe, P. (1995). No runoff, no soil loss: soil and water conservation in hedgerow barrier systems. Doctoral thesis. Agricultural University, Wageningen, Netherlands.
- Kindlmann, P. & Burel, F. (2008). Connectivity measures: a review. *Landsc. Ecol.*, 23, 879–890.
- Kivimäki, I., Shimbo, M. & Saerens, M. (2014). Developments in the theory of randomized shortest paths with a comparison of graph node distances. *Phys. Stat. Mech. Its Appl.*, 393, 600–616.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., *et al.* (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. Biol. Sci.*, 276, 903–909.
- Kleijn, D. & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary vegetation. *J. Appl. Ecol.*, 37, 256–266.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.*, 274, 303–313.
- Klein, S.L. (2003). Parasite manipulation of the proximate mechanisms that mediate social behavior in vertebrates. *Physiol. Behav.*, 79, 441–449.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., *et al.* (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J. Ecol.*, 96, 1266–1274.
- Klimeš, L., Klimešová, J., Hendricks, R. & van Groenendael, J.M. (1997). Clonal plant architecture: a comparative analysis of form and function. In: *The ecology and evolution*

- of clonal plants*. (eds. de Kroon, H. & van Groenendael, J.M.). Backhuys Publishers, Leiden, pp. 1–9.
- Klimešová, J. & Klimeš, L. (2003). Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow’s model? *Oikos*, 103, 225–229.
- Koen, E.L., Bowman, J. & Walpole, A.A. (2012). The effect of cost surface parameterization on landscape resistance estimates. *Mol. Ecol. Resour.*, 12, 686–696.
- Kohlmeier, S., Smits, T.H.M., Ford, R.M., Keel, C., Harms, H. & Wick, L.Y. (2005). Taking the Fungal Highway: Mobilization of Pollutant-Degrading Bacteria by Fungi. *Environ. Sci. Technol.*, 39, 4640–4646.
- Kolb, A. & Diekmann, M. (2005). Effects of Life-History Traits on Responses of Plant Species to Forest Fragmentation. *Conserv. Biol.*, 19, 929–938.
- Kolk, J. & Naaf, T. (2015). Herb layer extinction debt in highly fragmented temperate forests – Completely paid after 160 years? *Biol. Conserv.*, 182, 164–172.
- Kool, J.T., Moilanen, A. & Treml, E.A. (2013). Population connectivity: recent advances and new perspectives. *Landsc. Ecol.*, 28, 165–185.
- Kotliar, N.B. & Wiens, J.A. (1990). Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity. *Oikos*, 59, 253–260.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.*, 29, 592–599.
- Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008). Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science*, 322, 580–582.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R., Helm, A., Kuussaari, M., *et al.* (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.*, 13, 597–605.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999). The second Silent Spring? *Nature*, 400, 611–612.
- Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F. & Thurgate, N. (2010). The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology*, 91, 944–950.
- Kühn, I., Durka, W. & Klotz, S. (2004). BioFlor: a new plant-trait database as a tool for plant invasion ecology. *Divers. Distrib.*, 10, 363–365.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., *et al.* (2009). Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.*, 24, 564–571.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *J. Stat. Softw.*, 82, 1–26.

L

- Laine, A.-L. & Hanski, I. (2006). Large-scale spatial dynamics of a specialist plant pathogen in a fragmented landscape. *J. Ecol.*, 94, 217–226.
- Laita, A., Kotiaho, J.S. & Mönkkönen, M. (2011). Graph-theoretic connectivity measures: what do they tell us about connectivity? *Landsc. Ecol.*, 26, 951–967.
- Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.

- Laliberté, E., Legendre, P. & Shipley, B. (2014). *Package “FD.”*
- Lande, R. (1987). Extinction Thresholds in Demographic Models of Territorial Populations. *Am. Nat.*, 130, 624–635.
- Laughlin, D.C., Joshi, C., Richardson, S.J., Peltzer, D.A., Mason, N.W.H. & Wardle, D.A. (2015). Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. *J. Veg. Sci.*, 26, 46–57.
- Lausch, A., Blaschke, T., Haase, D., Herzog, F., Syrbe, R.-U., Tischendorf, L., *et al.* (2015). Understanding and quantifying landscape structure – A review on relevant process characteristics, data models and landscape metrics. *Ecol. Model.*, 295, 31–41.
- Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.*, 16, 545–556.
- Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.*, 12, 474–478.
- Le Cœur, D., Baudry, J., Burel, F. & Thenail, C. (2002). Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agric. Ecosyst. Environ.*, The Ecology of Field Margins in European Farming Systems, 89, 23–40.
- Leach, J.E., Triplett, L.R., Argueso, C.T. & Trivedi, P. (2017). Communication in the Phytobiome. *Cell*, 169, 587–596.
- Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000). The evolutionary ecology of seed size. In: *Seeds: the ecology of regeneration in plant communities* (ed. Fenner, M.). CABI, Wallingford, pp. 31–57.
- Lenoir, J., Decocq, G., Spicher, F., Gallet-Moron, E., Buridant, J. & Closset-Kopp, D. (sous presse). Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: Evidence from the species–time–area relationship. *J. Veg. Sci.*
- Leonard, P.B., Duffy, E.B., Baldwin, R.F., McRae, B.H., Shah, V.B. & Mohapatra, T.K. (2017). gflow: software for modelling circuit theory-based connectivity at any scale. *Methods Ecol. Evol.*, 8, 519–526.
- Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005). Effects of landscape corridors on seed dispersal by birds. *Science*, 309, 146–148.
- Levin, D.A. (1981). Dispersal Versus Gene Flow in Plants. *Ann. Mo. Bot. Gard.*, 68, 233–253.
- Levins, R. (1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.*, 15, 237–240.
- Levins, R. (1970). Extinction. In: *Some Mathematical Problems in Biology*. The American Mathematical Society, Providence, Rhode Island, pp. 77–107.
- Levins, R. & Culver, D. (1971). Regional Coexistence of Species and Competition between Rare Species. *Proc. Natl. Acad. Sci.*, 68, 1246–1248.
- Lewis, R.J., Szava-Kovats, R. & Pärtel, M. (2016). Estimating dark diversity and species pools: an empirical assessment of two methods. *Methods Ecol. Evol.*, 7, 104–113.

- Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., *et al.* (2008). Plant functional group composition and large-scale species richness in European agricultural landscapes. *J. Veg. Sci.*, 19, 3–14.
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, 68, 619–640.
- Lindborg, R. (2007). Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. *J. Ecol.*, 95, 555–564.
- Lindborg, R. & Eriksson, O. (2004). Historical Landscape Connectivity Affects Present Plant Species Diversity. *Ecology*, 85, 1840–1845.
- Lindborg, R., Helm, A., Bommarco, R., Heikkinen, R.K., Kühn, I., Pykälä, J., *et al.* (2012). Effect of habitat area and isolation on plant trait distribution in European forests and grasslands. *Ecography*, 35, 356–363.
- Lindgren, J.P. & Cousins, S.A.O. (2017). Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants. *Landscape Ecol.*, 32, 1895–1906.
- Lindström, E.S. & Bergström, A.-K. (2005). Community composition of bacterioplankton and cell transport in lakes in two different drainage areas. *Aquat. Sci.*, 67, 210–219.
- Lira, P.K., de Souza Leite, M. & Metzger, J.P. (2019). Temporal Lag in Ecological Responses to Landscape Change: Where Are We Now? *Curr. Landscape Ecol. Rep.*, 4, 70–82.
- Liu, S., Dong, Y., Deng, L., Liu, Q., Zhao, H. & Dong, S. (2014). Forest fragmentation and landscape connectivity change associated with road network extension and city expansion: A case study in the Lancang River Valley. *Ecol. Indic.*, 36, 160–168.
- Liu, S., Yin, Y., Liu, X., Cheng, F., Yang, J., Li, J., *et al.* (2017). Ecosystem Services and landscape change associated with plantation expansion in a tropical rainforest region of Southwest China. *Ecol. Model.*, Special Issue of China-Korea Joint Seminars on multi-disciplinary and multi-method approaches toward sustainable human and nature interactions, 353, 129–138.
- Locey, K.J. & Lennon, J.T. (2016). Scaling laws predict global microbial diversity. *Proc. Natl. Acad. Sci.*, 113, 5970–5975.
- Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.*, 26, 482–491.
- Lõhmus, K., Paal, T. & Liira, J. (2014). Long-term colonization ecology of forest-dwelling species in a fragmented rural landscape - dispersal versus establishment. *Ecol. Evol.*, 4, 3113–3126.
- Lomolino, M.V. (1990). The Target Area Hypothesis: The Influence of Island Area on Immigration Rates of Non-Volant Mammals. *Oikos*, 57, 297–300.
- Loreau, M. & Mouquet, N. (1999). Immigration and the Maintenance of Local Species Diversity. *Am. Nat.*, 154, 427–440.
- Lortie, C.J. & Aarssen, L.W. (1999). The advantage of being tall: Higher flowers receive more pollen in *Verbascum thapsus* L. (Scrophulariaceae). *Écoscience*, 6, 68–71.
- Luoto, M., Rekolainen, S., Aakkula, J. & Pykälä, J. (2003). Loss of Plant Species Richness and Habitat Connectivity in Grasslands Associated with Agricultural Change in Finland. *AMBIO J. Hum. Environ.*, 32, 447–452.

M

- MacArthur, R. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am. Nat.*, 101, 377–385.
- MacArthur, R.H. & Wilson, E. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MacArthur, R.H. & Wilson, E.O. (1963). An Equilibrium Theory of Insular Zoogeography. *Evolution*, 17, 373–387.
- Madeira, F., Tschardtke, T., Elek, Z., Kormann, U.G., Pons, X., Rösch, V., *et al.* (2016). Spillover of arthropods from cropland to protected calcareous grassland – the neighbouring habitat matters. *Agric. Ecosyst. Environ.*, 235, 127–133.
- Marrec, R., Abdel Moniem, H.E., Irvani, M., Hricko, B., Kariyeva, J. & Wagner, H.H. (2020). Conceptual framework and uncertainty analysis for large-scale, species-agnostic modelling of landscape connectivity across Alberta, Canada. *Sci. Rep.*, 10, 6798.
- Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. & Ward, L.K. (2003). The role of weeds in supporting biological diversity within crop fields*. *Weed Res.*, 43, 77–89.
- Marshall, E.J.P. & Moonen, A.C. (2002). Field margins in northern Europe: their functions and interactions with agriculture. *Agric. Ecosyst. Environ.*, The Ecology of Field Margins in European Farming Systems, 89, 5–21.
- Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I. & Metzger, J.P. (2012). Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. *Conserv. Biol.*, 26, 1100–1111.
- Martensen, A.C., Saura, S. & Fortin, M.-J. (2017). Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes. *Methods Ecol. Evol.*, 8, 1253–1264.
- Martin, C.A. (2018). An early synthesis of the habitat amount hypothesis. *Landsc. Ecol.*, 33, 1831–1835.
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., *et al.* (2006). Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.*, 4, 102–112.
- Mason, N.W.H., Lanoiselée, C., Mouillot, D., Wilson, J.B. & Argillier, C. (2008). Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *J. Anim. Ecol.*, 77, 661–669.
- Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111, 112–118.
- Matějková, I., Diggelen, R. van & Prach, K. (2003). An attempt to restore a central European species-rich mountain grassland through grazing. *Appl. Veg. Sci.*, 6, 161–168.
- Matias, M.G., Mouquet, N. & Chase, J.M. (2013). Dispersal stochasticity mediates species richness in source–sink metacommunities. *Oikos*, 122, 395–402.
- Matisziw, T.C. & Murray, A.T. (2009). Connectivity change in habitat networks. *Landsc. Ecol.*, 24, 89–100.
- Matlack, G.R. (2005). Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *J. Ecol.*, 93, 50–59.

Références

- Matlack, G.R. & Monde, J. (2004). Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *J. Ecol.*, 92, 1025–1035.
- Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997). Agricultural Intensification and Ecosystem Properties. *Science*, 277, 504–509.
- Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.*, 13, 1085–1093.
- Mazaris, A.D., Papanikolaou, A.D., Barbet-Massin, M., Kallimanis, A.S., Jiguet, F., Schmeller, D.S., *et al.* (2013). Evaluating the Connectivity of a Protected Areas' Network under the Prism of Global Change: The Efficiency of the European Natura 2000 Network for Four Birds of Prey. *PLOS ONE*, 8, e59640.
- McCollin, D., Jackson, J.I., Bunce, R.G.H., Barr, C.J. & Stuart, R. (2000). Hedgerows as habitat for woodland plants. *J. Environ. Manage.*, 60, 77–90.
- McGarigal, K. & Cushman, S.A. (2005). The Gradient Concept of Landscape Structure. In: *Issues and Perspectives in Landscape Ecology*. pp. 112–119.
- McGarigal, K., Cushman, S.A. & Ene, E. (2012). *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps*. Computer software program produced by the authors at the University of Massachusetts, Amherst.
- McIntyre, N.E., Collins, S.D., Heintzman, L.J., Starr, S.M. & van Gestel, N. (2018). The challenge of assaying landscape connectivity in a changing world: A 27-year case study in the southern Great Plains (USA) playa network. *Ecol. Indic.*, 91, 607–616.
- McKenney, E.A., Koelle, K., Dunn, R.R. & Yoder, A.D. (2018). The ecosystem services of animal microbiomes. *Mol. Ecol.*, 27, 2164–2172.
- McRae, B.H. (2006). Isolation by Resistance. *Evolution*, 60, 1551–1561.
- McRae, B.H. & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proc. Natl. Acad. Sci.*, 104, 19885–19890.
- McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008). Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation. *Ecology*, 89, 2712–2724.
- Meeus, J.H.A. (1993). The transformation of agricultural landscapes in Western Europe. *Sci. Total Environ.*, 129, 171–190.
- Merriam, G. (1991). Corridors and connectivity: Animal populations in heterogenous environments. In: *Nature conservation 2: the role of corridors* (eds. Saunders, D.A. & Hobbs, R.J.). Surrey Beatty and Sons, NSW, Australia.
- Metzger, J.P., Martensen, A.C., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Teixeira, A.M.G., *et al.* (2009). Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. *Biol. Conserv.*, 142, 1166–1177.
- Meynier, A. & Deniel, J. (1965). Les talus et l'aménagement de l'espace rural. *Penn Ar Bed*, 41, 41–54.
- Millán de la Peña, N., Butet, A., Delettre, Y., Morant, P. & Burel, F. (2003). Landscape context and carabid beetles (Coleoptera: Carabidae) communities of hedgerows in western France. *Agric. Ecosyst. Environ.*, 94, 59–72.
- Millennium Ecosystem Assessment (Ed.). (2005). *Ecosystems and human well-being: synthesis*. Island Press, Washington, DC.
- Miller, E.T., Svanbäck, R. & Bohannan, B.J.M. (2018). Microbiomes as Metacommunities: Understanding Host-Associated Microbes through Metacommunity Ecology. *Trends Ecol. Evol.*, 33, 926–935.

- Miller-Rushing, A.J., Primack, R.B., Devictor, V., Corlett, R.T., Cumming, G.S., Loyola, R., *et al.* (2019). How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biol. Conserv.*, 232, 271–273.
- Minor, E.S. & Gardner, R.H. (2011). Landscape connectivity and seed dispersal characteristics inform the best management strategy for exotic plants. *Ecol. Appl. Publ. Ecol. Soc. Am.*, 21, 739–749.
- Minor, E.S., Tessel, S.M., Engelhardt, K.A.M. & Lookingbill, T.R. (2009). The role of landscape connectivity in assembling exotic plant communities: a network analysis. *Ecology*, 90, 1802–1809.
- Minor, E.S. & Urban, D.L. (2008). A Graph-Theory Framework for Evaluating Landscape Connectivity and Conservation Planning. *Conserv. Biol.*, 22, 297–307.
- Mittelbach, G.G. & Schemske, D.W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends Ecol. Evol.*, 30, 241–247.
- Moeslund, J.E., Brunbjerg, A.K., Clausen, K.K., Dalby, L., Fløjgaard, C., Juel, A., *et al.* (2017). Using dark diversity and plant characteristics to guide conservation and restoration. *J. Appl. Ecol.*, 54, 1730–1741.
- Moggridge, H.L., Gurnell, A.M. & Mountford, J.O. (2009). Propagule input, transport and deposition in riparian environments: the importance of connectivity for diversity. *J. Veg. Sci.*, 20, 465–474.
- Moilanen, A. & Hanski, I. (2001). On the use of connectivity measures in spatial ecology. *Oikos*, 95, 147–151.
- Moilanen, A. & Nieminen, M. (2002). Simple Connectivity Measures in Spatial Ecology. *Ecology*, 83, 1131–1145.
- Moles, A.T. & Westoby, M. (2004). Seedling survival and seed size: a synthesis of the literature. *J. Ecol.*, 92, 372–383.
- Mony, C., Abadie, J., Gil-Tena, A., Burel, F. & Ernoult, A. (2018). Effects of connectivity on animal-dispersed forest plant communities in agriculture-dominated landscapes. *J. Veg. Sci.*, 29, 167–178.
- Mony, C., Brunellière, P., Vannier, N., Bittebiere, A.-K. & Vandenkoornhuysse, P. (2020a). Effect of floristic composition and configuration on plant root mycobiota: a landscape transposition at a small scale. *New Phytol.*, 225, 1777–1787.
- Mony, C., Landais, Q., Georges, R., Butet, A., Burel, F., Jambon, O., *et al.* (submitted). Effects of connectivity on forest actual plant dispersal in agriculture-dominated landscapes: a community-scale analysis.
- Mony, C., Vannier, N., Brunellière, P., Biget, M., Coudouel, S. & Vandenkoornhuysse, P. (2020b). The influence of host-plant connectivity on fungal assemblages in the root microbiota of *Brachypodium pinnatum*. *Ecology*, 101, e02976.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How Many Species Are There on Earth and in the Ocean? *PLOS Biol.*, 9, e1001127.
- Morandin, L.A. & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl. Publ. Ecol. Soc. Am.*, 23, 829–839.
- Morato, R.G., Ferraz, K.M.P.M. de B., de Paula, R.C. & de Campos, C.B. (2014). Identification of Priority Conservation Areas and Potential Corridors for Jaguars in the Caatinga Biome, Brazil. *PLoS ONE*, 9.

- Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.*, 24, 867–876.
- Mouquet, N., E. Miller, T., Daufresne, T. & M. Kneitel, J. (2006). Consequences of varying regional heterogeneity in source–sink metacommunities. *Oikos*, 113, 481–488.
- Mouquet, N., Leadley, P., Mériguet, J. & Loreau, M. (2004). Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos*, 104, 77–90.
- Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.*, 162, 544–557.
- Mueller, E.A., Wisnoski, N.I., Peralta, A.L. & Lennon, J.T. (in press). Microbial rescue effects: How microbiomes can save hosts from extinction. *Funct. Ecol.*
- Mueller-Dombois, D. & Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. John Wiley & Sons.
- Mui, A.B., Caverhill, B., Johnson, B., Fortin, M.-J. & He, Y. (2017). Using multiple metrics to estimate seasonal landscape connectivity for Blanding’s turtles (*Emydoidea blandingii*) in a fragmented landscape. *Landscape Ecol.*, 32, 531–546.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R. & Hubbell, S.P. (2008). Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.*, 96, 653–667.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Hubbell, S.P. & Foster, R.B. (2002). Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation* (eds. Levey, D.J., Silva, W.R. & Galetti, M.). CABI, Oxfordshire, pp. 35–54.
- Murphy, H.T. & Lovett-Doust, J. (2004). Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos*, 105, 3–14.
- Myers, J.A. & Harms, K.E. (2009). Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecol. Lett.*, 12, 1250–1260.
- Myers, J.A. & LaManna, J.A. (2016). The promise and pitfalls of β -diversity in ecology and conservation. *J. Veg. Sci.*, 27, 1081–1083.

N

- Naaf, T. & Kolk, J. (2015). Colonization credit of post-agricultural forest patches in NE Germany remains 130–230years after reforestation. *Biol. Conserv.*, 182, 155–163.
- Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.
- Nathan, R. (2006). Long-distance dispersal of plants. *Science*, 313, 786–788.
- Nathan, R., Katul, G.G., Bohrer, G., Kuparinen, A., Soons, M.B., Thompson, S.E., *et al.* (2011). Mechanistic models of seed dispersal by wind. *Theor. Ecol.*, 4, 113–132.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., *et al.* (2002). Mechanisms of long-distance dispersal of seeds by wind. *Nature*, 418, 409–413.
- Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.*, 15, 278–285.
- Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. *J. Biogeogr.*, 26, 867–878.

Neumann, J.L., Griffiths, G.H., Hoodless, A. & Holloway, G.J. (2016). The compositional and configurational heterogeneity of matrix habitats shape woodland carabid communities in wooded-agricultural landscapes. *Landscape Ecol.*, 31, 301–315.

Nilsson, C., Brown, R.L., Jansson, R. & Merritt, D.M. (2010). The role of hydrochory in structuring riparian and wetland vegetation. *Biol. Rev. Camb. Philos. Soc.*, 85, 837–858.

O

O'Brien, R.M. (2007). A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Qual. Quant.*, 41, 673–690.

Observatoire de l'environnement en Bretagne. (2018). *Le bocage en Bretagne* (No. 13). Les dossiers de l'environnement en Bretagne. Observatoire de l'environnement en Bretagne.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* (2019). *Package "vegan."* Community Ecology Package.

O'Neill, R.V., Deangelis, D.L., Waide, J.B. & Allen, T.F.H. (1986). *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton.

Opdam, P. (1991). Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecol.*, 5, 93–106.

Orelien, J.G. & Edwards, L.J. (2008). Fixed-effect variable selection in linear mixed models using R² statistics. *Comput. Stat. Data Anal.*, 52, 1896–1907.

Orrock, J.L. & Damschen, E.I. (2005). Corridors Cause Differential Seed Predation. *Ecol. Appl.*, 15, 793–798.

Orrock, J.L., Danielson, B.J., Burns, M.J. & Levey, D.J. (2003). Spatial Ecology of Predator–Prey Interactions: Corridors and Patch Shape Influence Seed Predation. *Ecology*, 84, 2589–2599.

Ouborg, N.J., Vergeer, P. & Mix, C. (2006). The rough edges of the conservation genetics paradigm for plants. *J. Ecol.*, 94, 1233–1248.

Ouin, A., Martin, M. & Burel, F. (2008). Agricultural landscape connectivity for the meadow brown butterfly (*Maniola jurtina*). *Agric. Ecosyst. Environ.*, 124, 193–199.

Ovaskainen, O. & Hanski, I. (2002). Transient Dynamics in Metapopulation Response to Perturbation. *Theor. Popul. Biol.*, 61, 285–295.

Oyarzun, R.A., Stöckle, C.O. & Whiting, M.D. (2007). A simple approach to modeling radiation interception by fruit-tree orchards. *Agric. For. Meteorol.*, 142, 12–24.

Ozinga, W.A., Bekker, R.M., Schaminée, J.H.J. & Van Groenendael, J.M. (2004). Dispersal potential in plant communities depends on environmental conditions. *J. Ecol.*, 92, 767–777.

P

Paal, T., Kütt, L., Lõhmus, K. & Liira, J. (2017). Both spatiotemporal connectivity and habitat quality limit the immigration of forest plants into wooded corridors. *Plant Ecol.*, 218, 417–431.

Pacala, S.W. & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.*, 143, 222–257.

- Panzacchi, M., Moorter, B.V., Strand, O., Saerens, M., Kivimäki, I., Clair, C.C.S., *et al.* (2016). Predicting the continuum between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths. *J. Anim. Ecol.*, 85, 32–42.
- Pardini, R., Bueno, A. de A., Gardner, T.A., Prado, P.I. & Metzger, J.P. (2010). Beyond the Fragmentation Threshold Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. *PLOS ONE*, 5, e13666.
- Pardini, R., de Souza, S.M., Braga-Neto, R. & Metzger, J.P. (2005). The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol. Conserv.*, 124, 253–266.
- Pärtel, M., Szava-Kovats, R. & Zobel, M. (2011). Dark diversity: shedding light on absent species. *Trends Ecol. Evol.*, 26, 124–128.
- Pärtel, M., Szava-Kovats, R. & Zobel, M. (2013). Community Completeness: Linking Local and Dark Diversity within the Species Pool Concept. *Folia Geobot.*, 48, 307–317.
- Pascual-Hortal, L. & Saura, S. (2006). Comparison and development of new graph-based landscape connectivity indices: towards the prioritization of habitat patches and corridors for conservation. *Landsc. Ecol.*, 21, 959–967.
- Patterson, B.D. & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.*, 96, 65–82.
- Peay, K.G., Bruns, T.D., Kennedy, P.G., Bergemann, S.E. & Garbelotto, M. (2007). A strong species-area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecol. Lett.*, 10, 470–480.
- Peay, K.G., Garbelotto, M. & Bruns, T.D. (2010). Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology*, 91, 3631–3640.
- Peay, K.G., Schubert, M.G., Nguyen, N.H. & Bruns, T.D. (2012). Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. *Mol. Ecol.*, 21, 4122–4136.
- Penone, C., Davidson, A.D., Shoemaker, K.T., Marco, M.D., Rondinini, C., Brooks, T.M., *et al.* (2014). Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.*, 5, 961–970.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., *et al.* (2010). Scenarios for Global Biodiversity in the 21st Century. *Science*, 330, 1496–1501.
- Perronne, R., Gaba, S., Cadet, E. & Le Corre, V. (2014). The interspecific and intraspecific variation of functional traits in weeds: diversified ecological strategies within arable fields. *Acta Bot. Gallica*, 161, 243–252.
- Perry, G.L.W. & Lee, F. (2019). How does temporal variation in habitat connectivity influence metapopulation dynamics? *Oikos*, 128, 1277–1286.
- Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.
- Petit, S., Alignier, A., Colbach, N., Joannon, A., Le Cœur, D. & Thenail, C. (2013). Weed dispersal by farming at various spatial scales. A review. *Agron. Sustain. Dev.*, 33, 205–217.
- Petit, S. & Burel, F. (1998). Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agric. Ecosyst. Environ.*, 69, 243–252.

- Petit, S., Griffiths, L., Smart, S.S., Smith, G.M., Stuart, R.C. & Wright, S.M. (2004). Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecol.*, 19, 463–471.
- Petit, S. & Usher, M.B. (1998). Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. *Biodivers. Conserv.*, 7, 1549–1561.
- Piessens, K., Honnay, O. & Hermy, M. (2005). The role of fragment area and isolation in the conservation of heathland species. *Biol. Conserv.*, 122, 61–69.
- Piessens, K., Honnay, O., Nackaerts, K. & Hermy, M. (2004). Plant Species Richness and Composition of Heathland Relics in North-Western Belgium: Evidence for a Rescue-Effect? *J. Biogeogr.*, 31, 1683–1692.
- van der Pijl, L. (1972). *Principles of Dispersal in Higher Plants*. 2nd edn. Springer-Verlag, Berlin Heidelberg.
- Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., *et al.* (1995). Environmental and economic costs of soil erosion and conservation benefits. *Science*, 267, 1117–1123.
- Pinheiro, J. & Bates, D. (2000). *Mixed-Effects Models in S and S-PLUS*. Statistics and Computing. Springer-Verlag, New York.
- Piquot, Y., Petit, D., Valero, M., Cuguen, J., de Laguerie, P. & Vernet, P. (1998). Variation in Sexual and Asexual Reproduction among Young and Old Populations of the Perennial Macrophyte *Sparganium erectum*. *Oikos*, 82, 139–148.
- Planes, M. (2019). *Influence de la connectivité et de sa dynamique sur les patrons de diversité actuels des communautés végétales boisées exprimées et potentielles* (Rapport de stage). Université de Rennes 1, Rennes.
- Plantegenest, M., Le May, C. & Fabre, F. (2007). Landscape epidemiology of plant diseases. *J. R. Soc. Interface*, 4, 963–972.
- Pocheville, A. (2015). The Ecological Niche: History and Recent Controversies. In: *Handbook of Evolutionary Thinking in the Sciences* (eds. Heams, T., Huneman, P., Lecointre, G. & Silberstein, M.). Springer Netherlands, Dordrecht, pp. 547–586.
- Pointereau, P. (2002). Les haies : évolution du linéaire en France depuis quarante ans. *Courr. Environ. INRA*, 46, 69–73.
- Pollard, K.A. & Holland, J.M. (2006). Arthropods within the woody element of hedgerows and their distribution pattern. *Agric. For. Entomol.*, 8, 203–211.
- Pollux, B.J.A., Luteijn, A., Van Groenendael, J.M. & Ouborg, N.J. (2009). Gene flow and genetic structure of the aquatic macrophyte *Sparganium emersum* in a linear unidirectional river. *Freshw. Biol.*, 54, 64–76.
- Ponisio, L.C., M’Gonigle, L.K. & Kremen, C. (2016). On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Glob. Change Biol.*, 22, 704–715.
- Price, B., McAlpine, C.A., Kutt, A.S., Phinn, S.R., Pullar, D.V. & Ludwig, J.A. (2009). Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach. *Ecography*, 32, 745–756.
- Puech, C., Poggi, S., Baudry, J. & Aviron, S. (2015). Do farming practices affect natural enemies at the landscape scale? *Landscape Ecol.*, 30, 125–140.
- Pulliam, H.R. (1988). Sources, Sinks, and Population Regulation. *Am. Nat.*, 132, 652–661.

- Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecol. Lett.*, 3, 349–361.
- Pyke, D.A. & Archer, S. (1991). Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. *J. Range Manag.*, 44, 550–557.
- Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M., *et al.* (2015). Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proc. R. Soc. B Biol. Sci.*, 282, 20151740.

Q

- Quéré, E. & Geslin, J. (2016). Liste des plantes vasculaires invasives de Bretagne.

R

- Raatikainen, K.J., Oldén, A., Käyhkö, N., Mönkkönen, M. & Halme, P. (2018). Contemporary spatial and environmental factors determine vascular plant species richness on highly fragmented meadows in Central Finland. *Landsc. Ecol.*, 33, 2169–2187.
- Ramadhani, I., Sukarno, N. & Listiyowati, S. (2018). Basidiospores attach to the seed of *Shorea leprosula* in lowland tropical dipterocarp forest and form functional ectomycorrhiza on seed germination. *Mycorrhiza*, 28, 85–92.
- Rand, T.A., Tylianakis, J.M. & Tschardtke, T. (2006). Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.*, 9, 603–614.
- Rantalainen, M.-L., Fritze, H., Haimi, J., Kiikkilä, O., Pennanen, T. & Setälä, H. (2004). Do enchytraeid worms and habitat corridors facilitate the colonisation of habitat patches by soil microbes? *Biol. Fertil. Soils*, 39, 200–208.
- Rantalainen, M.-L., Fritze, H., Haimi, J., Pennanen, T. & Setälä, H. (2005). Species richness and food web structure of soil decomposer community as affected by the size of habitat fragment and habitat corridors. *Glob. Change Biol.*, 11, 1614–1627.
- Rao, C.R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theor. Popul. Biol.*, 21, 24–43.
- Rapinel, S., Mony, C., Lecoq, L., Clément, B., Thomas, A. & Hubert-Moy, L. (2019). Evaluation of Sentinel-2 time-series for mapping floodplain grassland plant communities. *Remote Sens. Environ.*, 223, 115–129.
- Rappaport, D.I., Tambosi, L.R. & Metzger, J.P. (2015). A landscape triage approach: combining spatial and temporal dynamics to prioritize restoration and conservation. *J. Appl. Ecol.*, 52, 590–601.
- Rayfield, B. (2009). *Maintaining Habitat Connectivity for Conservation*. University of Toronto, Toronto.
- Rayfield, B., Fortin, M.-J. & Fall, A. (2010). The sensitivity of least-cost habitat graphs to relative cost surface values. *Landsc. Ecol.*, 25, 519–532.
- Rayfield, B., Fortin, M.-J. & Fall, A. (2011). Connectivity for conservation: a framework to classify network measures. *Ecology*, 92, 847–858.
- Rayfield, B., James, P.M.A., Fall, A. & Fortin, M.-J. (2008). Comparing static versus dynamic protected areas in the Québec boreal forest. *Biol. Conserv.*, 141, 438–449.

- Reigada, C., Schreiber, S.J., Altermatt, F. & Holyoak, M. (2015). Metapopulation dynamics on ephemeral patches. *Am. Nat.*, 185, 183–195.
- Ricketts, T.H. (2001). The Matrix Matters: Effective Isolation in Fragmented Landscapes. *Am. Nat.*, 158, 87–99.
- Riibak, K., Reitalu, T., Tamme, R., Helm, A., Gerhold, P., Znamenskiy, S., *et al.* (2015). Dark diversity in dry calcareous grasslands is determined by dispersal ability and stress-tolerance. *Ecography*, 38, 713–721.
- Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.*, 39, 157–176.
- Robleño, I., Storkey, J., Solé-Senan, X.O. & Recasens, J. (2018). Using the response–effect trait framework to quantify the value of fallow patches in agricultural landscapes to pollinators. *Appl. Veg. Sci.*, 21, 267–277.
- Rodríguez, A., Andrén, H. & Jansson, G. (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos*, 95, 383–396.
- Ronce, O. (2007). How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution. *Annu. Rev. Ecol. Evol. Syst.*, 38, 231–253.
- Rosalino, L.M., Ferreira, D., Leitão, I. & Santos-Reis, M. (2011). Usage patterns of Mediterranean agro-forest habitat components by wood mice *Apodemus sylvaticus*. *Mamm. Biol. - Z. Für Säugetierkd.*, 76, 268–273.
- Rosenberg, D.K., Noon, B.R. & Meslow, E.C. (1997). Biological Corridors: Form, Function, and Efficacy. *BioScience*, 47, 677–687.
- Ross, M.A. & Harper, J.L. (1972). Occupation of Biological Space During Seedling Establishment. *J. Ecol.*, 60, 77–88.
- Rossetti, M.R., Tschardtke, T., Aguilar, R. & Batáry, P. (2017). Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. *Ecol. Lett.*, 20, 264–272.
- Rothley, K.D. & Rae, C. (2005). Working backwards to move forwards: Graph-based connectivity metrics for reserve network selection. *Environ. Model. Assess.*, 10, 107–113.
- Row, J.R., Knick, S.T., Oyler-McCance, S.J., Loughheed, S.C. & Fedy, B.C. (2017). Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. *Ecol. Evol.*, 7, 3751–3761.
- Rubio, L., Bodin, Ö., Brotons, L. & Saura, S. (2015). Connectivity conservation priorities for individual patches evaluated in the present landscape: how durable and effective are they in the long term? *Ecography*, 38, 782–791.
- Rundlöf, M. & Smith, H.G. (2006). The effect of organic farming on butterfly diversity depends on landscape context. *J. Appl. Ecol.*, 43, 1121–1127.
- van Ruremonde, R.H.A.C. van & Kalkhoven, J.T.R. (1991). Effects of Woodlot Isolation on the Dispersion of Plants with Fleshy Fruits. *J. Veg. Sci.*, 2, 377–384.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., *et al.* (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agric. Ecosyst. Environ.*, 221, 198–204.
- Rusch, A., Valantin-Morison, M., Sarthou, J.-P. & Roger-Estrade, J. (2011). Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landsc. Ecol.*, 26, 473–486.

Rybicki, J., Abrego, N. & Ovaskainen, O. (2020). Habitat fragmentation and species diversity in competitive communities. *Ecol. Lett.*, 23, 506–517.

S

Saerens, M., Achbany, Y., Fouss, F. & Yen, L. (2009). Randomized shortest-path problems: two related models. *Neural Comput.*, 21, 2363–2404.

Sahraoui, Y., Foltête, J.-C. & Clauzel, C. (2017). A multi-species approach for assessing the impact of land-cover changes on landscape connectivity. *Landsc. Ecol.*, 32, 1819–1835.

Sánchez, I.A., Lassaletta, L., McCollin, D. & Bunce, R.G.H. (2009). The effect of hedgerow loss on microclimate in the Mediterranean region: an investigation in Central Spain. *Agrofor. Syst.*, 78, 13.

Sandström, U.G. (2002). Green Infrastructure Planning in Urban Sweden. *Plan. Pract. Res.*, 17, 373–385.

Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A. & Dubois, G. (2019). Global trends in protected area connectivity from 2010 to 2018. *Biol. Conserv.*, 238, 108183.

Saura, S., Estreguil, C., Mouton, C. & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecol. Indic.*, 11, 407–416.

Saura, S. & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landsc. Urban Plan.*, 83, 91–103.

Saura, S. & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33, 523–537.

Saura, S. & Torné, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environ. Model. Softw.*, 24, 135–139.

Scanlan, M. (1981). Biogeography of forest plants in the Prairie-Forest Ecotone in Western Minnesota. In: *Forest Island Dynamics in Man-dominated Landscapes* (eds. Burges, R.L. & Sharpe, D.M.). Springer, Berlin, pp. 97–124.

Schleicher, A., Biedermann, R. & Kleyer, M. (2011). Dispersal traits determine plant response to habitat connectivity in an urban landscape. *Landsc. Ecol.*, 26, 529–540.

Schoener, T.W. (1989). The ecological niche. In: *Ecological concepts: The contribution of ecology to an understanding of the natural world* (ed. Cherrett, J.M.). Blackwell, Oxford and Boston, pp. 79–113.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.*, 188, 333–353.

Schurr, F.M., Steinitz, O. & Nathan, R. (2008). Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *J. Ecol.*, 96, 628–641.

Selosse, M.-A., Baudoin, E. & Vandenkoornhuyse, P. (2004). Symbiotic microorganisms, a key for ecological success and protection of plants. *C. R. Biol.*, 327, 639–648.

- Séne, S., Selosse, M.-A., Forget, M., Lambourdière, J., Cissé, K., Diédhiou, A.G., *et al.* (2018). A pantropically introduced tree is followed by specific ectomycorrhizal symbionts due to pseudo-vertical transmission. *ISME J.*, 12, 1806–1816.
- Shade, A., Jacques, M.-A. & Barret, M. (2017). Ecological patterns of seed microbiome diversity, transmission, and assembly. *Curr. Opin. Microbiol.*, 37, 15–22.
- Shmida, A. & Wilson, M.V. (1985). Biological Determinants of Species Diversity. *J. Biogeogr.*, 12, 1–20.
- Shurin, J.B., Cottenie, K. & Hillebrand, H. (2009). Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia*, 159, 151–159.
- da Silva, I.R., de Souza, F.A., da Silva, D.K.A., Oehl, F. & Maia, L.C. (2017). Patterns of Arbuscular Mycorrhizal Fungal Distribution on Mainland and Island Sandy Coastal Plain Ecosystems in Brazil. *Microb. Ecol.*, 74, 654–669.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605–611.
- Simberloff, D. & Cox, J. (1987). Consequences and Costs of Conservation Corridors. *Conserv. Biol.*, 1, 63–71.
- Simberloff, D., Farr, J.A., Cox, J. & Mehlman, D.W. (1992). Movement Corridors: Conservation Bargains or Poor Investments? *Conserv. Biol.*, 6, 493–504.
- Simpkins, C.E., Dennis, T.E., Etherington, T.R. & Perry, G.L.W. (2018). Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. *Ecol. Model.*, 367, 13–23.
- Sirami, C. (2016). Biodiversity in heterogeneous and dynamic landscapes. In: *Oxford Research Encyclopedia of Environmental Science*.
- Smith, H., Firbank, L.G. & Macdonald, D.W. (1999). Uncropped edges of arable fields managed for biodiversity do not increase weed occurrence in adjacent crops. *Biol. Conserv.*, 89, 107–111.
- Solé-Senan, X.O., Juárez-Escario, A., Robleño, I., Conesa, J.A. & Recasens, J. (2017). Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services by Mediterranean arable plants. *Agric. Ecosyst. Environ.*, 247, 255–264.
- Soomers, H., Winkel, D.N., Du, Y. & Wassen, M.J. (2010). The dispersal and deposition of hydrochorous plant seeds in drainage ditches. *Freshw. Biol.*, 55, 2032–2046.
- Sordello, R., Comolet-Tirman, J., De Massary, J.-C., Dupont, P., Haffner, P., Rogeon, G., *et al.* (2011). *Trame verte et bleue – Critères nationaux de cohérence – Contribution à la définition du critère sur les espèces.* (Rapport MNHN-SPN). Muséum National d’Histoire Naturelle, Service du Patrimoine Naturel.
- Sorensen, A.E. (1986). Seed Dispersal by Adhesion. *Annu. Rev. Ecol. Syst.*, 17, 443–463.
- Spasojevic, M.J., Copeland, S. & Suding, K.N. (2014). Using functional diversity patterns to explore metacommunity dynamics: a framework for understanding local and regional influences on community structure. *Ecography*, 37, 939–949.
- Spear, S.F., Balkenhol, N., Fortin, M.-J., Mcrae, B.H. & Scribner, K. (2010). Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol. Ecol.*, 19, 3576–3591.
- Spiesman, B.J., Stapper, A.P. & Inouye, B.D. (2018). Patch size, isolation, and matrix effects on biodiversity and ecosystem functioning in a landscape microcosm. *Ecosphere*, 9, e02173.

- Sprugel, D.G. (1991). Disturbance, equilibrium, and environmental variability: What is 'Natural' vegetation in a changing environment? *Biol. Conserv.*, 58, 1–18.
- Staley, J.T., Bullock, J.M., Baldock, K.C.R., Redhead, J.W., Hooftman, D.A.P., Button, N., *et al.* (2013). Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management. *Biol. Conserv.*, 167, 97–105.
- Starfinger, U. & Stöcklin, J. (1996). Seed, Pollen, and Clonal Dispersal and Their Role in Structuring Plant Populations. In: *Progress in Botany / Fortschritte der Botanik: Structural Botany Physiology Genetics Taxonomy Geobotany / Struktur Physiologie Genetik Systematik Geobotanik*, Progress in Botany/Fortschritte der Botanik (eds. Behnke, H.-D., Lüttge, U., Esser, K., Kadereit, J.W. & Runge, M.). Springer, Berlin, Heidelberg, pp. 336–355.
- Stier, A., Lee, S. & O'Connor, M. (2019). Temporal variation in dispersal modifies dispersal-diversity relationships in an experimental seagrass metacommunity. *Mar. Ecol. Prog. Ser.*, 613, 67–76.
- Stoate, C., Boatman, N., Borralho, R., Rio Carvalho, C., de Snoo, G. & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *J. Environ. Manage.*, 63, 337–365.
- Stöcklin, J. & Winkler, E. (2004). Optimum reproduction and dispersal strategies of a clonal plant in a metapopulation: a simulation study with *Hieracium pilosella*. *Evol. Ecol.*, 18, 563–584.
- Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. (1997). Clonal Growth Traits of Two *Prunella* Species are Determined by Co-Occurring Arbuscular Mycorrhizal Fungi from a Calcareous Grassland. *J. Ecol.*, 85, 181–191.
- Strykstra, R.J., Verweij, G. I. & Bakker, J. p. (1997). Seed dispersal by mowing machinery in a Dutch brook valley system. *Acta Bot. Neerlandica*, 46, 387–401.
- Suárez-Esteban, A., Delibes, M. & Fedriani, J.M. (2013). Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal. *J. Appl. Ecol.*, 50, 767–774.
- Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., *et al.* (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.*, 14, 1125–1140.
- Sullivan, L.L., Johnson, B.L., Brudvig, L.A. & Haddad, N.M. (2011). Can dispersal mode predict corridor effects on plant parasites? *Ecology*, 92, 1559–1564.
- Suzán, G., Esponda, F., Carrasco-Hernández, R. & Aguirre, A. (2012). Habitat fragmentation and infectious disease ecology. In: *New Directions in Conservation Medicine: Applied Cases of Ecological Health* (eds. Aguirre, A., Ostfeld, R. & Daszak, P.). Oxford University Press, New York, pp. 135–150.
- Swenson, N.G. & Enquist, B.J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90, 2161–2170.

T

- Tackenberg, O. (2003). Modeling Long-Distance Dispersal of Plant Diaspores by Wind. *Ecol. Monogr.*, 73, 173–189.
- Tackenberg, O., Poschlod, P. & Kahmen, S. (2003). Dandelion Seed Dispersal: The Horizontal Wind Speed Does Not Matter for Long-Distance Dispersal - it is Updraft! *Plant Biol.*, 5, 451–454.

- Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O. & Amiaud, B. (2014). Filling the gap in functional trait databases: use of ecological hypotheses to replace missing data. *Ecol. Evol.*, 4, 944–958.
- Taylor, P.D., Fahrig, L., Heinen, K., Merriam, G., Crooks, K.R. & Sanjayan, M. (2006). Landscape connectivity: a return to the basics. In: *Connectivity Conservation: maintaining connections for nature*. Cambridge University Press, Cambridge, pp. 29–43.
- Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, 68, 571–573.
- Ter Heerd, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996). An Improved Method for Seed-Bank Analysis: Seedling Emergence After Removing the Soil by Sieving. *Funct. Ecol.*, 10, 144–151.
- Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., *et al.* (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci.*, 99, 12923–12926.
- Thenail, C. (2002). Relationships between farm characteristics and the variation of the density of hedgerows at the level of a micro-region of bocage landscape. Study case in Brittany, France. *Agric. Syst.*, 71, 207–230.
- Thiele, J., Buchholz, S. & Schirmel, J. (2017). Using resistance distance from circuit theory to model dispersal through habitat corridors. *J. Plant Ecol.*, rtx004.
- Thiele, J., Kellner, S., Buchholz, S. & Schirmel, J. (2018a). Connectivity or area: what drives plant species richness in habitat corridors? *Landsc. Ecol.*, 1–9.
- Thiele, J., Schirmel, J. & Buchholz, S. (2018b). Effectiveness of corridors varies among phytosociological plant groups and dispersal syndromes. *PLOS ONE*, 13, e0199980.
- Thies, C., Steffan-Dewenter, I. & Tschardt, T. (2003). Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, 101, 18–25.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Thompson, K., Bakker, J.P. & Bekker, R.M. (1997). *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press.
- Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.*, 99, 1299–1307.
- Tikka, P.M., Högmander, H. & Koski, P.S. (2001). Road and railway verges serve as dispersal corridors for grassland plants. *Landsc. Ecol.*, 16, 659–666.
- Tilman, D., Fargione, J., Wolff, B., D’Antonio, C., Dobson, A., Howarth, R., *et al.* (2001). Forecasting Agriculturally Driven Global Environmental Change. *Science*, 292, 281–284.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature*, 371, 65–66.
- Tischendorf, L. & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos*, 90, 7–19.
- Tischendorf, L. & Fahrig, L. (2001). On the Use of Connectivity Measures in Spatial Ecology. A Reply. *Oikos*, 95, 152–155.
- Török, P. & Helm, A. (2017). Ecological theory provides strong support for habitat restoration. *Biol. Conserv.*, 206, 85–91.

- Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T. & Singh, B.K. (2020). Plant–microbiome interactions: from community assembly to plant health. *Nat. Rev. Microbiol.*, 1–15.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.*, 8, 857–874.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.*, 87, 661–685.
- Tulbure, M.G., Kininmonth, S. & Broich, M. (2014). Spatiotemporal dynamics of surface water networks across a global biodiversity hotspot—implications for conservation. *Environ. Res. Lett.*, 9, 114012.
- Turcotte, Y. & Desrochers, A. (2003). Landscape-dependent response to predation risk by forest birds. *Oikos*, 100, 614–618.
- Turner, B. (1993). *The Earth as Transformed by Human Action: Global and Regional Changes in the Biosphere over the Past 300 Years*. Revised edition. Cambridge University Press.
- Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kaźmierczak, A., Niemela, J., *et al.* (2007). Promoting ecosystem and human health in urban areas using Green Infrastructure: A literature review. *Landsc. Urban Plan.*, 81, 167–178.

U

- Urban, D. & Keitt, T. (2001). Landscape Connectivity: A Graph-Theoretic Perspective. *Ecology*, 82, 1205–1218.
- Urban, D.L., Minor, E.S., Treml, E.A. & Schick, R.S. (2009). Graph models of habitat mosaics. *Ecol. Lett.*, 12, 260–273.
- Uroy, L., Ernoult, A. & Mony, C. (2019a). Effect of landscape connectivity on plant communities: a review of response patterns. *Landsc. Ecol.*, 34, 203–225.
- Uroy, L., Mony, C. & Ernoult, A. (2019b). Additive effects of connectivity provided by different habitat types drive plant assembly. *Sci. Rep.*, 9, 13952.
- Usher, M.B., Brown, A.C. & Bedford, S.E. (1992). Plant Species Richness in Farm Woodlands. *For. Int. J. For. Res.*, 65, 1–13.

V

- Valanko, S., Norkko, J. & Norkko, A. (2015). Does stability in local community composition depend on temporal variation in rates of dispersal and connectivity? *J. Sea Res.*, Protecting Marine Biodiversity to Preserve Ecosystem Functioning: a Tribute to Carlo Heip, 98, 24–32.
- Valdés, A., Lenoir, J., Frenne, P.D., Andrieu, E., Brunet, J., Chabrierie, O., *et al.* (2020). High ecosystem service delivery potential of small woodlands in agricultural landscapes. *J. Appl. Ecol.*, 57, 4–16.
- van der Valk, A.G. (1981). Succession in Wetlands: A Gleasonian Approach. *Ecology*, 62, 688–696.

- Van Den Berge, S., Tessens, S., Baeten, L., Vanderschaeve, C. & Verheyen, K. (2019). Contrasting vegetation change (1974–2015) in hedgerows and forests in an intensively used agricultural landscape. *Appl. Veg. Sci.*, 22, 269–281.
- Van Strien, M.J., Keller, D. & Holderegger, R. (2012). A new analytical approach to landscape genetic modelling: least-cost transect analysis and linear mixed models. *Mol. Ecol.*, 21, 4010–4023.
- Van Vooren, L., Reubens, B., Ampoorter, E., Broekx, S., Pardon, P., Van Waes, C., *et al.* (2018). Monitoring the Impact of Hedgerows and Grass Strips on the Performance of Multiple Ecosystem Service Indicators. *Environ. Manage.*, 62, 241–259.
- Vander Wall, S.B., Forget, P.M., Lambert, J.E. & Hulme, P.E. (2005). Seed fate pathways: filling the gap between parent and offspring. In: *Seed fate: predation, dispersal and seedling establishment* (eds. Forget, P.M., Lambert, J.E., Hulme, P.E. & Vander Wall, S.B.). CABI, Wallingford, pp. 1–8.
- Vandermeer, J.H. (1972). Niche Theory. *Annu. Rev. Ecol. Syst.*, 3, 107–132.
- Vanesse, R. (1997). Un exemple d'analyse du stock grainier dans un sol forestier. In: *Actes du Vème colloque international sur la biologie et l'écologie des mauvaises herbes*. Dijon, France, pp. 141–147.
- Vanneste, T., Valdés, A., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Andrieu, E., *et al.* (2019). Functional trait variation of forest understorey plant communities across Europe. *Basic Appl. Ecol.*, 34, 1–14.
- Vannette, R.L., Leopold, D.R. & Fukami, T. (2016). Forest area and connectivity influence root-associated fungal communities in a fragmented landscape. *Ecology*, 97, 2374–2383.
- Vannier, N., Mony, C., Bittebiere, A.-K., Michon-Coudouel, S., Biget, M. & Vandenkoornhuysse, P. (2018). A microorganisms' journey between plant generations. *Microbiome*, 6, 79.
- Vannier, N., Mony, C., Bittebière, A.-K. & Vandenkoornhuysse, P. (2015). Epigenetic Mechanisms and Microbiota as a Toolbox for Plant Phenotypic Adjustment to Environment. *Front. Plant Sci.*, 6.
- Vellend, M. (2010). Conceptual Synthesis in Community Ecology. *Q. Rev. Biol.*, 85, 183–206.
- Vellend, M., Myers, J.A., Gardescu, S. & Marks, P.L. (2003). Dispersal of Trillium seeds by deer: implications for long-distance migration of forest herbs. *Ecology*, 84, 1067–1072.
- Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., *et al.* (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, 87, 542–548.
- Venjakob, C., Klein, A.-M., Ebeling, A., Tschardt, T. & Scherber, C. (2016). Plant diversity increases spatio-temporal niche complementarity in plant-pollinator interactions. *Ecol. Evol.*, 6, 2249–2261.
- Verbeke, G. & Molenberghs, G. (2000). *Linear Mixed Models for Longitudinal Data*. Springer-Verlag New York.
- Verheyen, K., Vellend, M., Calster, H.V., Peterken, G. & Hermy, M. (2004). Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology*, 85, 3302–3312.
- Verkaar, H. (1990). Corridors as a tool for plant species conservation? In *Species dispersal in agricultural habitats*. In: *Species dispersal in agricultural habitats* (eds. Bunce, R.G.H. & Howarth, R.). Belhaven Press, London, pp. 82–97.

- Vickery, J.A., Feber, R.E. & Fuller, R.J. (2009). Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. *Agric. Ecosyst. Environ.*, 133, 1–13.
- Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology*, 89, 2290–2301.
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Pothier, C., Blanchard, A., *et al.* (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, 160, 747–755.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Vittoz, P. & Engler, R. (2007). Seed dispersal distances: a typology based on dispersal modes and plant traits. *Bot. Helvetica*, 117, 109–124.

W

- Wang, C., Liu, D. & Bai, E. (2018). Decreasing soil microbial diversity is associated with decreasing microbial biomass under nitrogen addition. *Soil Biol. Biochem.*, 120, 126–133.
- Watling, J.I., Nowakowski, A.J., Donnelly, M.A. & Orrock, J.L. (2011). Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Glob. Ecol. Biogeogr.*, 20, 209–217.
- Watson, M.A., Scott, K., Griffith, J., Dieter, S., Jones, C.S. & Nanda, S. (2002). The developmental ecology of mycorrhizal associations in mayapple, *Podophyllum peltatum*, Berberidaceae. In: *Ecology and Evolutionary Biology of Clonal Plants: Proceedings of Clone-2000. An International Workshop held in Obergurgl, Austria, 20–25 August 2000* (eds. Stuefer, J.F., Erschbamer, B., Huber, H. & Suzuki, J.-I.). Springer Netherlands, Dordrecht, pp. 203–220.
- Watts, A.G., Schlichting, P.E., Billerman, S.M., Jesmer, B.R., Micheletti, S., Fortin, M.-J., *et al.* (2015). How spatio-temporal habitat connectivity affects amphibian genetic structure. *Front. Genet.*, 6.
- Wehling, S. & Diekmann, M. (2009). Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biol. Conserv.*, 142, 2522–2530.
- Weihner, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos. Trans. R. Soc. B Biol. Sci.*, 366, 2403–2413.
- Weihner, E. & Keddy, P.A. (1995). The Assembly of Experimental Wetland Plant Communities. *Oikos*, 73, 323–335.
- Wereszczuk, A. & Zalewski, A. (2015). Spatial Niche Segregation of Sympatric Stone Marten and Pine Marten – Avoidance of Competition or Selection of Optimal Habitat? *PLoS ONE*, 10.
- Westoby, M., Jurado, E. & Leishman, M. (1992). Comparative evolutionary ecology of seed size. *Trends Ecol. Evol.*, 7, 368–372.
- Whitcomb, B.L., Whitcomb, R.F. & Bystrak, D. (1977). Island biogeography and “Habitat Islands” of eastern forest. III. Long-term turnover and effects of selective logging on the avifauna of forest fragments. *Am. Birds*, 31, 7.

- Wiens, J.A. (1976). Population Responses to Patchy Environments. *Annu. Rev. Ecol. Syst.*, 7, 81–120.
- Wiens, J.A. (1995). Landscape mosaics and ecological theory. In: *Mosaic Landscapes and Ecological Processes* (eds. Hansson, L., Fahrig, L. & Merriam, G.). Springer Netherlands, Dordrecht, pp. 1–26.
- Wiens, J.A. (1997). Metapopulation Dynamics and Landscape Ecology. In: *Metapopulation Biology* (eds. Hanski, I. & Gilpin, M.E.). Academic Press, San Diego, pp. 43–62.
- Wilcove, D.S., McLellan, C.H. & Dobson, A.P. (1986). Habitat fragmentation in the temperate zone. In: *Conservation biology: the science of scarcity and diversity* (ed. Soulé, M.E.). Sinauer Associates, Sunderland, MA, pp. 237–256.
- Williams, P.D., Hastings, A., Křivan, A.E.V. & McPeck, E.M.A. (2013). Stochastic Dispersal and Population Persistence in Marine Organisms. *Am. Nat.*, 182, 271–282.
- Willson, M.F. (1993). Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, 107, 261–280.
- Willson, M.F., Rice, B.L. & Westoby, M. (1990). Seed dispersal spectra: a comparison of temperate plant communities. *J. Veg. Sci.*, 1, 547–562.
- Wilson, D.S. (1992). Complex Interactions in Metacommunities, with Implications for Biodiversity and Higher Levels of Selection. *Ecology*, 73, 1984–2000.
- Wilson, E.O. & Willis, E.O. (1975). Applied Biogeography. In: *Ecology and Evolution of Communities* (eds. Cody, M.L. & Diamond, J.M.). Harvard University Press, Cambridge, pp. 522–534.
- Wimberly, M.C. (2006). Species Dynamics in Disturbed Landscapes: When does a Shifting Habitat Mosaic Enhance Connectivity? *Landsc. Ecol.*, 21, 35–46.
- Winkler, E. & Stöcklin, J. (2002). Sexual and Vegetative Reproduction of *Hieracium pilosella* L. under Competition and Disturbance: a Grid-based Simulation Model. *Ann. Bot.*, 89, 525–536.
- With, K.A. (2019). *Essentials of Landscape Ecology*. Oxford University Press.
- Wolf, A.B., Vos, M., Boer, W. de & Kowalchuk, G.A. (2013). Impact of Matric Potential and Pore Size Distribution on Growth Dynamics of Filamentous and Non-Filamentous Soil Bacteria. *PLOS ONE*, 8, e83661.
- Wolton, R.J., Pollard, K.A., Goodwin, A. & Norton, L. (2014). *Regulatory services delivered by hedges: the evidence base* (Report of Defra project LM0106).
- Wright, S. (1934). The method of path coefficients. *Ann. Math. Stat.*, 5, 161–215.

Y

- Yang, P., Zhang, M. & van Elsas, J.D. (2017). Role of flagella and type four pili in the co-migration of *Burkholderia terrae* BS001 with fungal hyphae through soil. *Sci. Rep.*, 7, 2997.

Z

- Zacharias, D. & Brandes, D. (1990). Species Area-Relationships and Frequency: Floristical Data Analysis of 44 Isolated Woods in Northwestern Germany. *Vegetatio*, 88, 21–29.

- Zambrano, J., Garzon-Lopez, C.X., Yeager, L., Fortunel, C., Cordeiro, N.J. & Beckman, N.G. (2019). The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? *Oecologia*.
- Zeigler, S.L. & Fagan, W.F. (2014). Transient windows for connectivity in a changing world. *Mov. Ecol.*, 2, 1–10.
- Zeller, K.A., Jennings, M.K., Vickers, T.W., Ernest, H.B., Cushman, S.A. & Boyce, W.M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Divers. Distrib.*, 24, 868–879.
- Zeller, K.A., McGarigal, K. & Whiteley, A.R. (2012). Estimating landscape resistance to movement: a review. *Landsc. Ecol.*, 27, 777–797.
- Ziółkowska, E., Ostapowicz, K., Radeloff, V.C. & Kuemmerle, T. (2014). Effects of different matrix representations and connectivity measures on habitat network assessments. *Landsc. Ecol.*, 29, 1551–1570.
- Zobel, M. (1997). The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.*, 12, 266–269.
- Zobel, M., Moora, M. & Herben, T. (2010). Clonal mobility and its implications for spatio-temporal patterns of plant communities: what do we need to know next? *Oikos*, 119, 802–806.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Statistics for Biology and Health. Springer-Verlag, New York.

Titre : Effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales

Mots-clés : fragmentation, paysages agricoles, corridors, dynamique temporelle, dispersion des graines, traits fonctionnels

Résumé : Le maintien et la restauration de la connectivité sont proposés comme une stratégie majeure pour enrayer la perte de biodiversité en paysage fragmenté. Pour autant, aucun consensus n'a pu être dégagé quant à l'efficacité de cette stratégie pour les communautés végétales. Pour accroître et généraliser notre compréhension du rôle de la connectivité, cette thèse vise à déterminer l'effet de la connectivité et de sa dynamique temporelle sur la structuration taxonomique et fonctionnelle des communautés végétales. Menée au sein de la Zone Atelier Armorique, cette étude se concentre sur trois habitats dominants les paysages agricoles (bois, prairies temporaires et cultures céréalières). Cette thèse montre que la connectivité fournie par les différents types d'habitat et sa dynamique temporelle (intensité et variabilité des changements temporels de connectivité) n'affectent ni la diversité spécifique ni l'abondance totale des espèces au sein des communautés végétales. Elles agissent plutôt sur la composition spécifique des communautés, en sélectionnant les espèces selon la valeur de leurs traits fonctionnels liés à la production, au transport des graines, mais aussi au recrutement des plantules. En deçà du kilomètre, et au cours des décennies, la connectivité façonne alors la structure fonctionnelle des communautés végétales, affectant ainsi le fonctionnement des agroécosystèmes. Ces résultats offrent une nouvelle vision de l'interaction entre le paysage et la dispersion des plantes. De façon originale, une forte connectivité fournie par des habitats auxquels ne sont pas inféodées les espèces peut avoir un effet positif ou négatif sur la dispersion des espèces. De surcroît, l'intensité et la variabilité des changements de connectivité opérés au cours des sept dernières décennies continuent de façonner les communautés actuelles. Nos travaux suggèrent ainsi de fortes implications pour la conservation de la biodiversité floristique au sein des paysages agricoles, dont le maintien dépend, en partie, de la pertinence et de l'efficacité des actions menées dans le cadre de la Trame Verte et Bleue.

Title: Effect of connectivity and its temporal dynamics on the taxonomic and the functional structure of plant communities

Key-words: habitat fragmentation, agricultural landscapes, corridors, temporal dynamics, seed dispersal, functional traits

Abstract: Maintaining and restoring connectivity are proposed as a key landscape-level strategy to mitigate biodiversity loss in fragmented landscapes. However, there is a limited consensus about its efficiency for plant communities. To deepen and broaden our understanding about the role of connectivity, this PhD thesis aims to determine the effect of connectivity and its temporal dynamics on the taxonomic and the functional structure of plant communities. Carried out in the Zone Atelier Armorique, this study focuses on three dominant habitat types in agricultural landscapes (woodlands, grasslands and winter cereal crops). The connectivity provided by the different habitat types and its temporal dynamics (the magnitude and the variability of the temporal changes in connectivity) do not affect species diversity nor the total abundance of species. Rather, they shape species composition of plant communities, selecting species identity depending on their functional trait values related to seed production and transport, as well as seedling recruitment. Below one kilometre, and over decades, connectivity thus shapes the functional structure of plant communities, thereby affecting agroecosystem functioning. We reveal then new insights into the specific interaction between landscape and plant dispersal. Of note, the connectivity provided by other habitat types can impede or facilitate the dispersal of species of a given habitat type. We also showed that the magnitude and the variability of changes in connectivity over the last seven decades are still shaping current communities. Overall, our results may have far-reaching implications for plant biodiversity in agricultural landscapes, its conservation depending, in part, on the relevance and the effectiveness of the actions deployed under the Green and Blue Belt Network policy.