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Effet de l'hétérogénéité du paysage sur la diversité fonctionnelle des communautés végétales et les fonctions écologiques associées

Lucie Lecoq

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Lucie Lecoq. Effet de l'hétérogénéité du paysage sur la diversité fonctionnelle des communautés végétales et les fonctions écologiques associées. Ecologie, Environnement. Université de Rennes, 2021. Français. NNT : 2021REN1B029 . tel-03585644

HAL Id: tel-03585644

<https://theses.hal.science/tel-03585644v1>

Submitted on 23 Feb 2022

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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

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Effet de l'hétérogénéité du paysage sur la diversité fonctionnelle des communautés végétales et les fonctions écologiques associées

Thèse présentée et soutenue à Rennes, le 18 Octobre 2021

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Les recherches présentées dans ce manuscrit ont été réalisées au sein de l'unité mixte de recherche Ecosystèmes, Biodiversité, Evolution - UMR CNRS 6553 ECOBIO Université de Rennes 1



Cette thèse a été financée par le projet européen Interreg ALICE, la Région Bretagne et la Zone Atelier Armorique.



Remerciements

Me voilà à la fin de cette tumultueuse aventure ! Il y a eu des hauts, il y a aussi eu des bas, mais j'avoue être fière de tout le travail accompli. Et même si j'ai frôlé la folie à plusieurs reprises, j'ai toujours été épaulée, de près ou de loin, par un grand nombre de personnes sans qui tout ça n'aurait pas été possible. J'espère seulement que ces quelques lignes suffiront à vous faire parvenir l'immense gratitude que j'ai envers vous tous.

Je remercie tout d'abord mes deux encadrantes, Cendrine et Aude. Merci de m'avoir offert la possibilité de travailler avec vous depuis mes stages de master et de m'avoir toujours soutenue dans la réalisation de cette thèse. Merci de m'avoir accordé une grande confiance tout au long de ces 3 ans, que ce soit pour les questions de recherches mais aussi pour les missions d'enseignement que j'ai tant appréciées.

Je souhaite remercier les membres du jury qui ont accepté d'évaluer mes travaux: Cécile Albert, Didier Alard, Sandra Luque et François Munoz. Je remercie également les membres de mon comité de thèse : Marie-Lise Benot, Françoise Burel, Simon Chollet, Sébastien Rapinel et Hervé Quénot pour leur aide et leurs réflexions pertinentes tout au long de cette thèse.

Je remercie chaleureusement toutes les agricultrices et les agriculteurs du bassin versant du Couesnon qui ont accepté de me laisser crapahuter dans leurs champs et échapper (parfois de justesse) à leurs vaches. Je les remercie pour leur patience et leur gentillesse, en espérant qu'un jour nous devenions collègues.

Ce fameux terrain dans les champs n'aurait pas été le même sans l'aide précieuse de Myriam qui, même sous des averses de grêle, continuait à me demander si 'la ligule de cette graminée était tronquée ou non'. Je remercie également mes deux autres stagiaires, Enora et Benjamin, pour m'avoir accompagnée pendant la fin de ce terrain et pour m'avoir soutenue quand la motivation m'échappait.

Un grand merci à Elodie, pour avoir pris le temps de me former aux joies de la télédétection. Merci également à Gaëtan et Thomas pour notre collaboration et pour les moments de détente qui allaient avec, que ça soit en France ou en Irlande.

Un grand merci à toutes les personnes du laboratoire ECOBIO, pour leur aide et leurs petits mots de soutien tout le long de cette thèse.

Merci notamment à Philippe, pour les nombreux points Bon Mayennais donnés gracieusement, qui me permettent aujourd'hui de porter haut et fière mes couleurs. Merci également de m'avoir intégrée dans le master EFCE qui m'a menée à cette thèse.

Merci beaucoup à JP Caudal pour son aide sur la création des perches à Tinytags mais aussi pour toutes les discussions sur la vie en général. Que de sagesse en un seul homme...

Je remercie également Olivier pour sa très grande aide sur la récolte des données climatiques. Je lui envoie toute ma force pour continuer cette douce aventure remplie de vaches et de papillons métalliques.

Un immense merci au gang des terribles, j'ai nommé Isabelle, Bertrand et Patricia. Merci d'avoir fait de ce labo un lieu convivial, rempli de scotch, de musique douteuse et de post-its. En espérant recroiser votre route très vite.

Un grand merci à la triplète Vincent, Simon, Lou, pour les soirées scientifiques houblonnées et pour leurs coups de main sur l'identification des fameuses 'plantes sp'. Et merci à toutes celles et ceux qui m'ont accompagnée pendant les différentes missions d'enseignement, notamment Céline pour nos discussions et ses encouragements pendant cette dernière ligne droite.

Sans aucun doute, un immense merci à toutes les doctorantes du Bureau 112 girl power, sans qui je n'aurais sûrement pas survécu. Marine, Léa, Eve, Claire, Solène, Lorine, Alice et Victor. Merci pour l'infatigable écoute, entraide et surtout renwouennage qui ont rempli ce bureau pendant 3 ans. Même si la dernière année aura forcément été beaucoup plus silencieuse, sachez que je n'aurais pas tenu sans vous alors merci infiniment.

Un merci spécial à Djadja, pour toutes nos discussions sur le paysage, sur la recherche, et pour le voyage à Milan qui aura été, en bien comme en mal, un tournant dans ma vision du monde de la recherche.

Je tiens aussi à remercier tous les copains des masters EFCE, MODE ou PNB pour m'avoir soutenue (et supportée) durant ces années d'études supérieures : Pierre-Gilles, Benoit, Coco, Alexis, Théo M., Malo, Valentin, Claire, Dudul, Pauline et Théo. Un grand merci notamment à Pauline pour son soutien durant ces derniers mois de rédaction !

Enfin, merci énormément à Colin Favret pour m'avoir fait découvrir la recherche au sein du Centre sur la biodiversité de l'Université de Montréal. Merci (ou pas d'ailleurs) de m'avoir montré à quel point se poser une question et essayer d'y répondre pouvait devenir addictif.

Je ne sais pas s'il lira ces lignes un jour, mais je tenais aussi à remercier Mr Prodhomme, mon professeur de primaire, pour m'avoir appris très tôt à m'émerveiller devant la Nature et pour m'avoir donné envie de chercher à la comprendre.

La science c'est bien, mais soyons honnêtes, je n'aurais pas pu écrire cette thèse sans toutes les personnes qui m'ont toujours apporté leur soutien en dehors du travail.

Merci infiniment à toutes les coéquipières et coéquipiers des clubs de basket-ball de Rennes et de Saint-Malo. Merci de m'avoir permis de relâcher toute la pression dans le sport, et de m'avoir permis de passer des moments forts en émotion, sur et en dehors du terrain. Je suis désolée pour tous les coups de coudes qui ne vous étaient pas (toujours) destinés, et je m'engage à ralentir les massages intensifs de vos côtes dans les années à venir.

Merci à toute la troupe de Branféré, qui finalement est aussi là depuis le début ! Merci d'avoir fait de mes étés des bulles de bonheur hors du temps, inexplicables tant qu'on ne les a pas vécues. Une pensée particulière aux Clems pour leur accueil sans limite et pour leur inspiration à vivre la vie autrement. Une petite dédicace à Guytou, qui est le tout premier à avoir planté dans ma tête la graine de la recherche.

Merci à toutes les autres copines et tous les autres copains rencontrés tout le long de ce parcours, que ce soit en France, au Canada ou en Australie. Je pense particulièrement à Gabriel et Nora qui ont grandement aidé mon adaptation à Montréal, et à Maud qui m'a accompagnée durant l'une des plus belles aventures de ma vie.

Merci à Flo, pour son soutien infailible qu'elle m'accorde depuis le début de nos frasques lycéennes, et merci à Nasti pour sa bienveillance et son optimisme à toute épreuve. Merci notamment pour votre écoute et vos encouragements pendant ces derniers mois de rédaction.

Merci à mes Guérines pour leur soutien sans faille durant ces trois ans, pour leur amour du Trivial et les weekends où on n'y allait pas vraiment 'dolo dolo'.

Merci à Marido pour m'avoir prêté un bout de son jardin qui m'a servi d'exutoire pendant ces derniers mois. Merci à Clem et Mathieu pour toutes leurs questions sur mon doctorat en brins d'herbe, ce qui ne veut absolument rien dire mais je trouvais ça assez dans le ton.

Et finalement un immense merci à tous les membres de ma famille pour leurs oreilles attentives et leurs conseils.

Merci notamment à mes grands-mères, pour m'avoir toujours encouragée et m'avoir transmis leur entêtement.

Je remercie tout particulièrement mon papa et ma maman. Merci de m'avoir toujours élevée dans la bienveillance et de m'avoir offert une enfance remplie d'amour, de voyages et de fêtes. Merci de m'avoir toujours soutenue, quelles que soient mes décisions, et d'avoir toujours compris mes besoins de liberté et d'aventure. Cette thèse n'aurait jamais pu être écrite sans vous.

Merci infiniment à ma grande sœur, Marion. Je ne te remercierai jamais assez pour tout ce que tu as fait et ce que tu continues de faire pour moi. C'est compliqué de ne pas être une drama queen en écrivant ces lignes, alors juste merci de m'avoir toujours montré le chemin. It's like one mind.

Merci à mon beau-frère Maxime qui, en me citant dans les remerciements de son mémoire, m'oblige à le citer en retour ici par politesse... Même si nous ne parlons pas la même langue car tu as un faible pour Python et moi pour R, merci d'avoir veillé à ce que votre frigo se remplisse de bières dès que j'arrivais chez vous.

Merci à Alix, mon Tipois, pour remplir mon cœur un peu plus tous les jours.

Merci à Marine, chérie. Je pense que je n'arriverai pas à trouver les bons mots pour exprimer à quel point je suis heureuse que tu te sois trouvée sur mon chemin. Disons juste que je suis ravie que la science (la bière ?) nous ait permis de nous croiser. Merci infiniment, pour tout. Que les aventures de Tic & Tac continuent très longtemps, dans une joyeuse ambiance de houblon et de blagues de tonton.


Et finalement, merci à Val. Si nous avions su, lorsque j'étais en première année de licence, que tu finirais par m'accompagner tout au long de ce tumultueux périple qu'auront été mes études supérieures. Je ne regretterai jamais d'avoir poussé les portes de cette salle de basket de la Harpe. Merci de m'avoir toujours soutenue et de m'avoir donné la force d'aller jusqu'au bout. J'ai tellement hâte que nous commencions de nouvelles aventures.

A ma mamie Jacqueline, qui m'a appris à apprendre. Sans ton dévouement au moment des devoirs, mon parcours n'aurait certainement pas été le même.

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Introduction générale

Le paysage est défini comme étant une « partie de territoire telle que perçue par les populations, dont le caractère résulte de l'action de facteurs naturels et/ou humains et de leurs interrelations » (Convention européenne du paysage, 2000). Le paysage est donc en constante évolution car il est l'expression de l'interaction dynamique entre la nature et les activités humaines (Antrop, 2005). Il évolue souvent de manière lente et imperceptible mais parfois suivant des mutations rapides et radicales (ESO, 2013). Les changements paysagers se produisent par l'action de différentes forces motrices qui s'exercent sur des pas de temps allant de la décennie au siècle (Burel & Baudry, 1999). Elles peuvent être socio-économiques, politiques, naturelles ou culturelles (Bürge et al., 2005). Aujourd'hui, ces forces motrices sont principalement liées au développement territorial, intimement corrélé aux enjeux de l'urbanisation (Antrop, 2005 ; Mazzocchi et al., 2013), et au développement agricole (Mazzocchi et al., 2013). Le paysage est au cœur d'enjeux sociaux et politiques qui dépassent la sphère étroite des acteurs de l'aménagement du territoire ou du milieu scientifique (Luginbühl, 2007).

En Europe, et notamment en France, les changements dans la structure du paysage depuis la fin de la deuxième guerre mondiale ont majoritairement été induits par l'intensification agricole (Burel & Baudry, 1999). La nécessité de nourrir la population a conduit à une politique agricole axée sur l'intensification, couplée à l'avènement de nouvelles techniques agricoles. Cette intensification agricole s'est effectuée - et s'effectue encore - via différents processus opérant de l'échelle locale à l'échelle paysagère (Tscharntke et al., 2005). A l'échelle locale, l'intensification agricole se traduit entre autre par une utilisation soutenue d'intrants chimiques et de produits phytosanitaires et à une forte mécanisation (Matson et al., 1997; Tscharntke et al., 2005). A l'échelle paysagère, l'intensification agricole se traduit par une simplification de la mosaïque, avec une augmentation de la taille des parcelles et une diminution en diversité des types d'occupation du sol (Burel & Baudry, 1999 ; Tscharntke et al., 2005). Elle se traduit également par une perte et un isolement des éléments semi-naturels comme les prairies permanentes, les haies, et les boisements (Tscharntke et al., 2005).

Les modifications dans la structure du paysage induites par l'intensification agricole sont aujourd'hui considérées comme une cause majeure de la perte de biodiversité (Fahrig et al., 2011). Cette perte n'épargne aucun taxon, que ce soit les plantes (Flohre et al., 2011), les insectes (Burel et al., 2004), les oiseaux (Sotherton, 1998), ou les mammifères (Gentili et al., 2014), et peut avoir des conséquences importantes sur le fonctionnement des écosystèmes (Newbold et al., 2019). En effet, au-delà de sa valeur morale intrinsèque, la biodiversité assure le bon fonctionnement des écosystèmes et fournit des services utiles à l'Homme (Hooper et al., 2005). Elle assure ainsi la production d'aliments, de combustibles et de matériel génétique, offre des possibilités éducatives et récréatives, et réduit les risques liés au dérèglement climatique (CBD, 2008). Les plantes plus particulièrement, en tant que producteurs primaires, sont les organismes à la base des flux de matière et d'énergie et sont donc des organismes fondamentaux à étudier pour comprendre et maintenir le fonctionnement des écosystèmes (Prevedello

& Vieira, 2010). Malgré les nombreuses alertes émises par les scientifiques, les mesures mises en place pour conserver la biodiversité se sont avérées jusqu'ici insuffisantes face aux impératifs sociaux et économiques croissants (Mace et al., 2010). Il est donc aujourd'hui essentiel de mettre la conservation de la biodiversité au premier plan, pour sa valeur intrinsèque mais aussi pour les services qu'elle rend et qui peuvent avoir des implications socioéconomiques importantes dans le présent et dans le futur.



Processus d'assemblage des communautés végétales

A. Cadre théorique de l'effet du paysage sur les communautés végétales

1. *La communauté végétale, la résultante d'une succession de filtres écologiques*

Comprendre les règles régissant la distribution et l'abondance des espèces au sein des écosystèmes a très tôt intéressé les scientifiques (Lotka, 1925). Force est de constater que les organismes vivants ne semblent pas être répartis au hasard dans l'environnement, les scientifiques tentent depuis des décennies de comprendre quels facteurs expliquent la présence d'une espèce à un endroit donné (Grinnell, 1917 ; Elton, 1927 ; Macarthur & Levins, 1967 ; Hubbell, 2001), comment les espèces coexistent et comment elles forment des communautés (i.e. ensemble d'individus d'espèces différentes coexistant à un endroit et un temps donné, Vellend, 2010). En 1975, Diamond fut le premier à faire émerger la notion de *règles d'assemblages* qui visait à décrire les lois qui régissent la coexistence des espèces et donc la structuration des communautés. Depuis, de nombreuses théories en étroite relation avec le concept de niche (Encadré 1) ont émergé afin d'expliquer quels processus influencent l'assemblage spatiotemporel des communautés végétales.

Les processus régissant l'assemblage des communautés peuvent être liés au hasard (i.e. processus non-déterministes) ou liés aux conditions abiotiques et biotiques de la communauté (i.e. processus déterministes). Une vision classique de l'assemblage des communautés est de considérer que ces processus agissent comme une hiérarchie de filtres successifs qui limitent quelles espèces peuvent persister sur un site à partir du pool d'espèces disponibles dans la région (Figure 1).

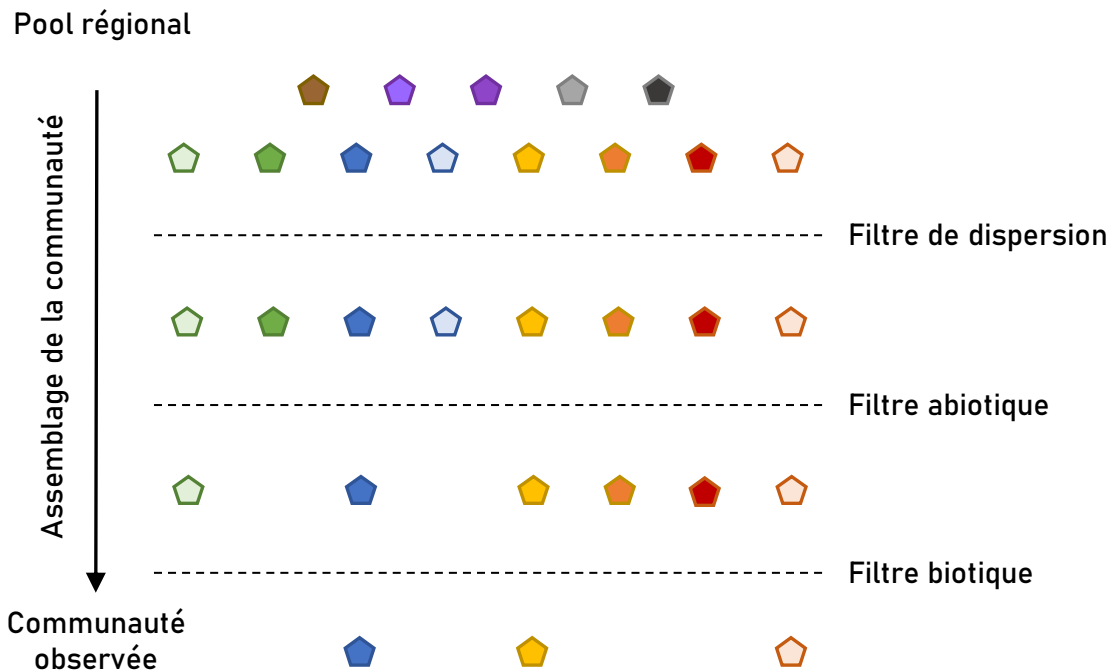


Figure 1 : Schéma de la théorie des filtres régissant l'assemblage des communautés végétales. Les hexagones de couleur représentent différentes espèces végétales. A partir d'un pool régional d'espèces, une succession de filtres agissent et déterminent la composition des communautés végétales observées. Adapté à partir de Lortie et al., (2004).

Cette théorie distingue trois filtres principaux. A partir d'un pool régional d'espèces, correspondant à l'ensemble des espèces disponibles à l'échelle d'une région, un premier filtre exclut les espèces selon des contraintes liées à la dispersion (Figure 1). Ce filtre sélectionne ainsi les espèces selon leur capacité à se disperser (Zobel, 1997). Il est considéré comme le plus soumis aux processus stochastiques (Lortie et al., 2004) et est principalement influencé par la structure du paysage car celle-ci facilite ou entrave la dispersion des espèces dans l'espace (Taylor et al., 1993). Les espèces capables de se disperser arrivent dans l'habitat considéré et sont soumises au filtre abiotique. Ce filtre représente l'ensemble des conditions physicochimiques de l'environnement (e.g. température, humidité édaphique, luminosité) et exclut les espèces incapables de tolérer ces conditions (Lortie et al., 2004). Théoriquement, ces conditions sont représentées comme la niche fondamentale de Hutchinson (Encadré 1). Finalement un dernier filtre, le filtre biotique, exclut certaines espèces en fonction des interactions biotiques au sein de la communauté (Mittelbach & Schemske, 2015). Ces interactions peuvent être considérées comme négatives (i.e. compétition) ou bénéfiques (i.e. facilitation) et sont définies théoriquement comme la niche réalisée de Hutchinson (Encadré 1). La succession de ces filtres permet ainsi la structuration de la communauté observée à partir du pool régional (Figure 1).

Encadré 1 : le concept de niche. Grinnell (1917) fut le premier à décrire la niche comme étant l'ensemble des conditions nécessaires dans l'environnement pour qu'un organisme puisse survivre et se développer. Par la suite, Elton (1927) a ajouté à cette définition la notion de la position de l'organisme dans les réseaux trophiques et sa fonction dans l'écosystème. Finalement, Hutchinson (1957) définit la niche comme un espace à n -dimensions (ou hypervolume), décrivant l'amplitude des conditions abiotiques et biotiques nécessaires pour la survie et le développement d'une espèce. Il distingue également deux types de niche : (i) la niche fondamentale qui correspond aux conditions abiotiques dans lesquelles une espèce peut survivre et (ii) la niche réalisée. Cette dernière correspond en fait à la niche fondamentale après interactions entre espèces, qu'elles soient négatives (i. e. compétition) ou positives (i.e. facilitation).

Cette théorie des filtres demeure aujourd'hui une base solide pour tenter de comprendre les processus structurant les communautés végétales mais elle a cependant récemment été soulignée comme incomplète (Mittelbach & Schemske, 2015). Premièrement, elle suppose que les filtres sont successifs et que l'assemblage des communautés est unidirectionnel. Or, il existe aussi des rétroactions des communautés vers le pool régional (Mittelbach & Schemske, 2015). Bien que la présence d'une espèce au sein d'une communauté locale soit effectivement conditionnée par son recrutement au sein du pool régional, sa présence dans celui-ci est tout autant tributaire de la capacité de cette espèce à se maintenir localement (Mittelbach & Schemske, 2015). Ainsi, le pool d'espèces régional n'est pas immuable mais bien en constant rééquilibrage au cours du temps et ce par différents processus: la spéciation ajoute par exemple de nouvelles espèces au pool régional alors que l'extinction en élimine d'autres, et la dispersion permet la persistance d'espèces qui pourraient autrement s'éteindre (Mittelbach & Schemske, 2015). Cette démonstration de Mittelbach & Schemske (2015) est partie du constat que le modèle classique de filtres ne prend pas explicitement en compte les interactions spatiales entre les différentes communautés (i.e. théorie des métacommunautés, Leibold et al., 2004). Pourtant, la dispersion entre les communautés locales peut être déterminante pour la coexistence régionale des espèces. De plus, l'effet de la dispersion, des conditions abiotiques et des interactions biotiques peuvent agir simultanément dans la structuration des communautés végétales (Loughnan & Gilbert, 2017).

2. *Les métacommunautés, ou comment les communautés interagissent spatialement*

L'une des premières théories reconnaissant l'importance de la dimension spatiale dans l'assemblage des communautés est la théorie de biogéographie insulaire de MacArthur & Wilson (1967). Dans leur théorie, la richesse en espèces sur une île est fonction de la taille de cette île et de sa distance au continent. Ainsi, l'assemblage des espèces est presque entièrement dépendant des taux d'immigration et d'extinction des espèces. Ces travaux, enrichis par divers auteurs au cours des dernières décennies (e.g. Hubbell, 2001) ont permis de grandes avancées dans l'écologie des communautés mais ont également

servi de base à bon nombre de travaux en écologie du paysage. En effet, cette théorie suggère implicitement l'existence de processus spatiaux dans la structuration de communautés plus ou moins isolées spatialement. Par la suite, la théorie de métapopulations (Levins, 1969), ensuite déclinée à l'échelle des communautés par Leibold et al. (i.e. métacommunautés ; 2004) a permis de mettre en lumière l'importance des processus spatiaux dans l'assemblage des communautés végétales.

La théorie des métacommunautés décrit explicitement les mécanismes de structuration des assemblages dans un cadre spatialisé (Leibold et al., 2004). Cette théorie reconnaît, en plus des processus déterministes de filtres abiotiques et biotiques, les processus stochastiques de dispersion ainsi que les processus neutralistes (Hubbel 2001). Une métacommunauté est définie comme étant un ensemble de communautés locales qui sont reliées entre elles par la dispersion d'espèces potentiellement en interaction (Leibold et al., 2004). Quatre paradigmes conceptuels ont été présentés pour décrire les métacommunautés, chacun décrivant différents mécanismes d'assemblage des communautés. Ils tentent d'expliquer la coexistence des espèces et de prédire les changements dans la composition en fonction du taux de dispersion et des caractéristiques de l'habitat et des espèces (Logue et al., 2011). Les quatre paradigmes sont (i) la dynamique des taches, (ii) le tri des espèces, (iii) l'effet de masse et (iv) le neutralisme (Figure 2).

Le paradigme de la dynamique des taches suppose qu'il existe de multiples taches identiques d'habitat dans un paysage et que chacune d'entre elles subissent des extinctions à la fois stochastiques et déterministes. Les extinctions déterministes sont affectées par des interactions entre espèces (i.e. compétition), et peuvent être compensées par une dispersion importante (Figure 2). Le paradigme de tri des espèces diffère du premier car il prend en compte les effets des caractéristiques abiotiques locales sur les taux de survie des populations et les interactions entre espèces. Ici, les taches d'habitat locales sont donc considérées comme hétérogènes pour certains facteurs (i.e. ronds ou carrés dans la Figure 2), et le résultat des interactions entre espèces locales dépend de cette hétérogénéité. Le paradigme de l'effet de masse suppose également que les différentes taches d'habitat présentent des conditions abiotiques différentes mais il suggère que la dispersion est suffisante entre ces taches pour entraîner des relations source-puits (Mouquet & Loreau, 2002). Le rôle de la dispersion ici est double puisque d'une part, l'immigration complète les taux de natalité locaux, et d'autre part l'émigration peut augmenter les taux de perte de ces populations locales. Finalement, le paradigme du neutralisme a sa propre dynamique de métacommunauté : il est principalement influencé par des modèles aléatoires lents de changement de composition dans l'espace et dans le temps, car cette théorie suppose que les espèces sont équivalentes en terme de *fitness* (Leibold et al., 2004).

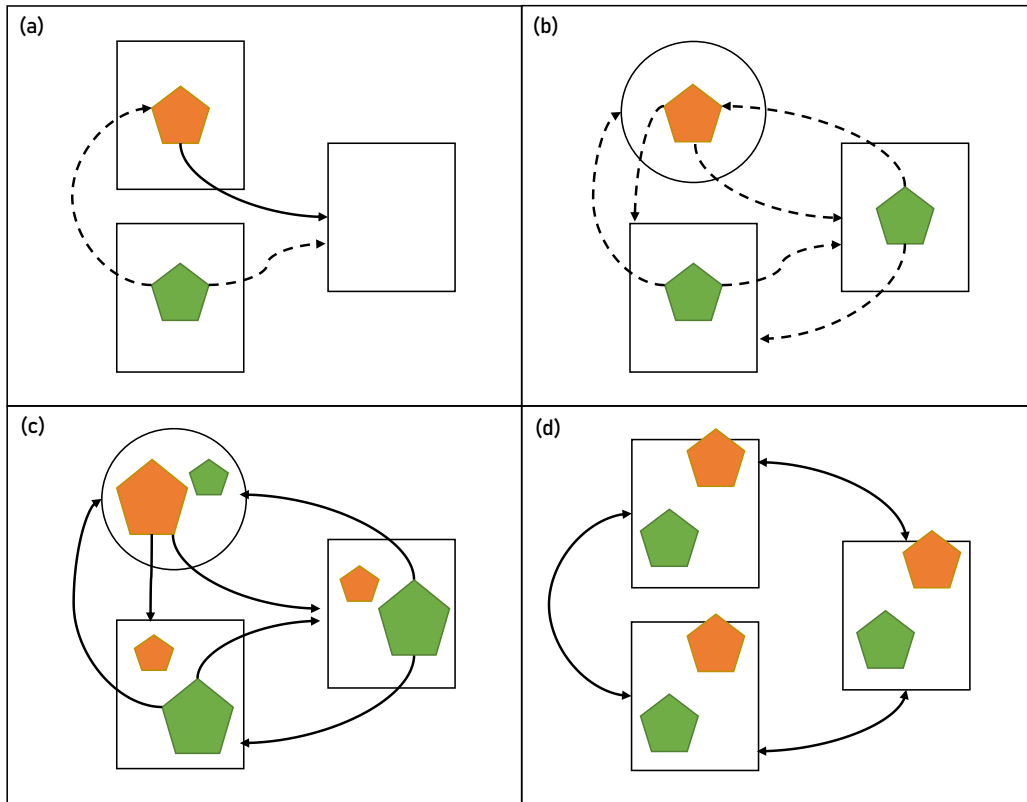


Figure 2 : Représentation schématique des quatre paradigmes de la théorie des métacommunautés pour deux espèces en compétition. La population de l'espèce A est représentée par un hexagone vert, et la population de l'espèce B est représentée par un hexagone orange. La dominance d'une espèce dans un site est représentée par la taille de l'hexagone qui le représente. Les ronds ou carrés représentent des taches d'habitats et leurs formes schématisent des caractéristiques abiotiques différentes. Les flèches pleines indiquent une dispersion plus importante que les flèches pointillées. Les quatre paradigmes illustrés sont (a) la dynamique des patchs, (b) le tri des espèces, (c) les effets de masse et (d) le neutralisme. D'après Leibold et al., (2004).

La théorie des métacommunautés a permis à l'écologie du paysage de se développer car elle souligne l'importance de la dispersion des espèces entre taches d'habitat, processus très largement influencé par la structure du paysage (Taylor et al., 1993). De plus, cette théorie souligne l'effet potentiel de caractéristiques spécifiques aux espèces (e.g. compétitivité, capacité de dispersion) leur permettant de se maintenir et de se développer dans des paysages plus ou moins hétérogènes. Ces caractéristiques spécifiques à chaque espèce sont à la base de l'approche fonctionnelle, approche qui est en plein développement pour comprendre les règles d'assemblages des communautés végétales à l'échelle du paysage.

B. L'approche fonctionnelle pour mieux comprendre les mécanismes d'assemblage des communautés végétales

1. De l'approche taxonomique à l'approche fonctionnelle

Les scientifiques se sont très longtemps appuyés sur la diversité taxonomique pour décrire les communautés végétales. La structure taxonomique peut être décrite comme la liste des espèces qui composent une communauté et leurs abondances relatives au sein de cette communauté. Bien qu'essentielle en écologie de la conservation, cette approche ne permet pas de comprendre sur quels caractères les filtres écologiques sélectionnent les espèces (voir 1.A.1.). Une approche complémentaire, basée sur la composante fonctionnelle des organismes, permet de prendre en compte l'ensemble des caractéristiques spécifiques à une espèce. La niche fonctionnelle (Rosenfeld, 2002) peut être considérée comme un hypervolume à n -dimensions analogue à la niche de Hutchinson (Encadré 1) à la différence que les différents axes ne représentent pas les différentes conditions abiotiques et biotiques dans lesquelles l'espèce peut survivre mais les différentes caractéristiques de l'espèce (e.g. compétitivité, performance photosynthétique). Ainsi, la niche d'Hutchinson définit où et dans quelles circonstances une espèce va exister, tandis que la niche fonctionnelle définit l'effet écologique qu'une espèce aura dans un habitat donné (Rosenfeld, 2002). S'intéresser à la facette fonctionnelle de la biodiversité est un concept relativement ancien et a été à la base de nombreuses classifications des organismes développées parallèlement à la taxonomie comme la classification de Raunkiær (1934), les stratégies r/K de MacArthur et Wilson (1967), les stratégies CRS de Grime (1974) ou encore les groupes fonctionnels de Lavorel et al. (1997).

Plus récemment, la volonté des scientifiques de s'approcher au plus près de la réalité biologique des communautés a mis l'approche basée sur les traits au centre du débat. Les traits fonctionnels sont définis comme tous les caractères morphologiques, physiologiques ou phénologiques mesurables à l'échelle de l'individu et qui impactent sa *fitness* (Violle et al. 2007). Ils permettent de comprendre la réponse des espèces aux caractéristiques environnementales et/ou leur effet sur le fonctionnement de l'écosystème (Díaz & Cabido, 2001). Cette approche basée sur les traits permet ainsi de décrire les espèces non pas via leur identité taxonomique ou leur appartenance à des groupes fonctionnels réducteurs, mais via des mesures quantitatives précises de valeurs de traits (Garnier et al., 2016).

Un large panel de traits fonctionnels est disponible pour les espèces végétales grâce notamment au développement de base de données mondiales (e.g. BiolFlor, Kühn et al., 2004 ; LEDA, Kleyer et al., 2008; TRY, Kattge et al., 2020). Les traits fonctionnels concernent de multiples organes de la plante (i.e. racines, fleurs, feuilles, graines) et peuvent être liés à différents processus et à différentes étapes de leur cycle de vie (Laughlin, 2014). Ces étapes incluent la production de graines, la dispersion et le transport de graines, la germination, l'établissement et la survie (Grubb, 1977). Tout comme il existe

des *trade-offs* et corrélations entre ces processus, il existe des *trade-offs* et corrélations entre les traits liés à ces processus (Wright et al., 2010). Dans les recherches en écologie du paysage, les traits étudiés sont souvent sur ceux liés au processus de dispersion car ce processus est supposé être le premier impacté par la structure du paysage. Mais plus récemment, certaines études ont mis en lumière l'intérêt de considérer les traits liés à d'autres étapes du cycle de vie des plantes comme ceux liés à l'établissement (Zambrano et al., 2019), ou à la phénologie (Duflot et al., 2014). Cependant, attribuer un trait à un processus précis reste un exercice difficile car un trait fonctionnel peut participer simultanément à plusieurs étapes dans le cycle de vie de la plante (Violle et al., 2007 ; Hevia et al., 2017). Par exemple, la masse des graines peut influencer la capacité de dispersion de la plante, mais peut également participer à son pouvoir compétitif (Turnbull et al., 1999). Ainsi, sélectionner des traits liés à différents processus et provenant de plusieurs organes est conseillé afin d'apprécier au mieux la niche fonctionnelle des communautés de plantes (Laughlin, 2014).

2. Décrire la structure fonctionnelle d'une communauté végétale

Le développement de l'approche basée sur les traits permet de mieux comprendre les règles d'assemblage des communautés à la lumière des caractéristiques de chaque espèce. Les filtres écologiques (voir 1.A.1.) peuvent ainsi sélectionner des espèces au sein d'un pool car elles possèdent un syndrome de traits appropriés pour un habitat donné (Keddy, 1992 ; Diaz et al., 1998). La distribution des valeurs de traits au sein des communautés est supposée être affectée par des mécanismes déterministes pouvant agir simultanément.

Classiquement il est attendu que le filtre abiotique, correspondant à un ensemble de conditions environnementales, sélectionne les espèces capables de survivre dans cet environnement (i.e. *habitat filtering*, Keddy, 1992). Ce « filtre de l'habitat » induit alors une convergence de valeurs de traits au sein de la communauté et tend donc à former des communautés d'espèces fonctionnellement similaires (Figure 3). A l'inverse, il est attendu que le filtre biotique, correspondant aux interactions entre espèces, induise une divergence des valeurs de traits au sein de la communauté (i.e. *limiting similarity*, MacArthur et Levins 1967). Cette théorie repose sur le principe d'exclusion compétitive (Gause, 1934) qui stipule que deux espèces fonctionnellement trop proches ne peuvent coexister sur le long terme et que leur interaction aboutira nécessairement à l'exclusion d'une des deux. La divergence de valeurs de traits permet de diminuer l'éventuelle compétition au sein de la communauté et d'ainsi garantir la coexistence des espèces. Cependant, les interactions biotiques peuvent également résulter en une convergence vers une stratégie optimale (Loughnan & Gilbert, 2017).

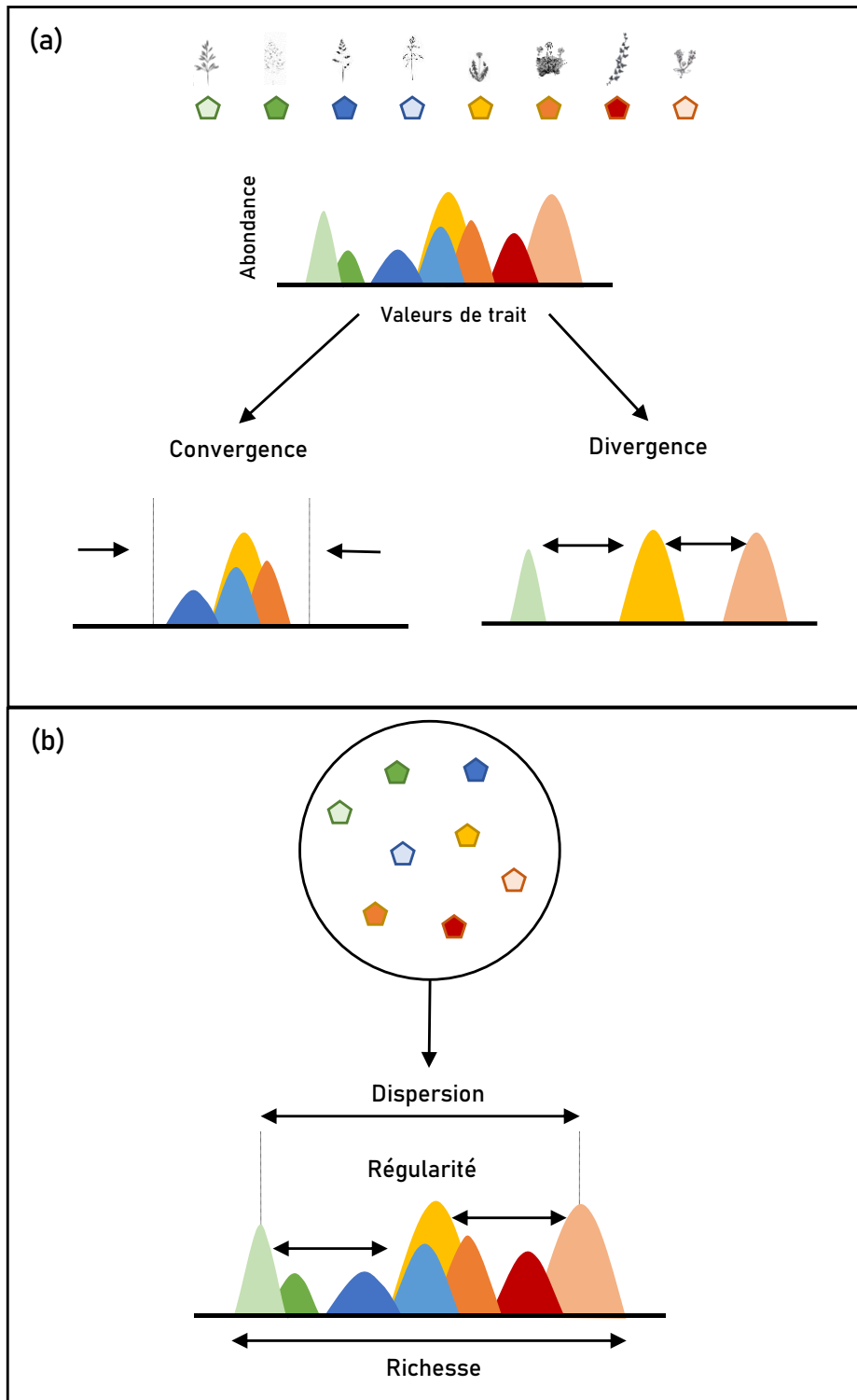


Figure 3 : L'approche basée sur les traits pour comprendre et décrire l'assemblage des espèces. Chaque hexagone de couleur représente une espèce végétale. Les courbes représentent l'abondance de l'espèce dans la communauté et sont réparties selon un gradient de valeurs de trait. (a) Les différents filtres environnementaux agissant dans la structuration des communautés peuvent amener à une convergence de valeurs de trait ou une divergence de valeurs de trait. (b) La diversité fonctionnelle peut être divisée en plusieurs composantes, comme sa composition (richesse) ou sa structure (régularité, dispersion). D'après Villéger et al. (2008) et Morel (2018).

Comme décrit par Rosenfeld (2002), le concept de niche fonctionnelle est multidimensionnel (i.e. hypervolume à n -dimensions). Il est possible de décrire les communautés végétales en prenant en compte plusieurs traits fonctionnels simultanément afin de capter les différentes dimensions de la niche fonctionnelle (Villéger et al., 2008). Cette approche permet de prendre en compte plus précisément les inévitables corrélations et *trade-offs* entre traits reflétant ainsi mieux la réalité biologique des communautés (Wright et al., 2010). Ainsi, de multiples avancées méthodologiques ont émergé depuis une dizaine d'années afin de quantifier la diversité fonctionnelle en prenant en compte simultanément plusieurs traits (e.g. Villéger et al., 2008 ; Maire et al., 2015). La diversité fonctionnelle comme définie dans ce manuscrit inclut la richesse fonctionnelle, mais également la régularité fonctionnelle et la dispersion fonctionnelle (Figure 3). Le développement de ces indices permet ainsi de mieux comprendre les processus régissant les assemblages des plantes.

3. *Les traits comme lien entre processus d'assemblage et services écosystémiques*

De par leurs effets sur la croissance, la reproduction et la survie des plantes, les traits fonctionnels peuvent également avoir un impact sur le fonctionnement global de l'écosystème. Ainsi, les recherches ont progressivement fait la distinction entre deux types de traits : les traits de réponse, supposés répondre aux variations de l'environnement, et les traits d'effet, supposés influencer le fonctionnement de l'écosystème (Lavorel & Garnier, 2002). Toutefois, les traits de réponse et les traits d'effets ne présentent pas de définition *stricto sensu* car une large gamme de traits peut à la fois répondre aux conditions environnementales et influencer le fonctionnement de l'écosystème (Figure 4). Malgré tout, le concept de traits de réponse-effet permet de mieux comprendre l'effet de l'environnement sur le fonctionnement de l'écosystème à travers la réponse de la biodiversité.

Comprendre le lien entre les traits fonctionnels et le fonctionnement de l'écosystème est depuis plusieurs années au centre des recherches en écologie. En effet, le bon fonctionnement de l'écosystème assure le maintien des services utiles à l'Homme (Hooper et al., 2005), définis sous le nom de services écosystémiques. Ce concept de services écosystémiques a été défini en premier lieu par Ehrlich & Mooney (1983) pour attirer l'attention au niveau mondial sur la perte de biodiversité et la dégradation des écosystèmes. Les services écosystémiques sont généralement classés en quatre grande catégories : (i) les services de support (e.g. formations des sols), (ii) services d'approvisionnement (e.g. alimentation), (iii) les services de régulation (e.g. climat), et (iv) les services récréatifs (e.g. développement cognitif). Le maintien de la biodiversité pour soutenir ces services s'est historiquement appuyé sur l'exemple liant la diversité en espèces végétales dans une communauté et la productivité de cette communauté (Encadré 2), mais s'est aujourd'hui élargi à d'autres fonctions des écosystèmes.

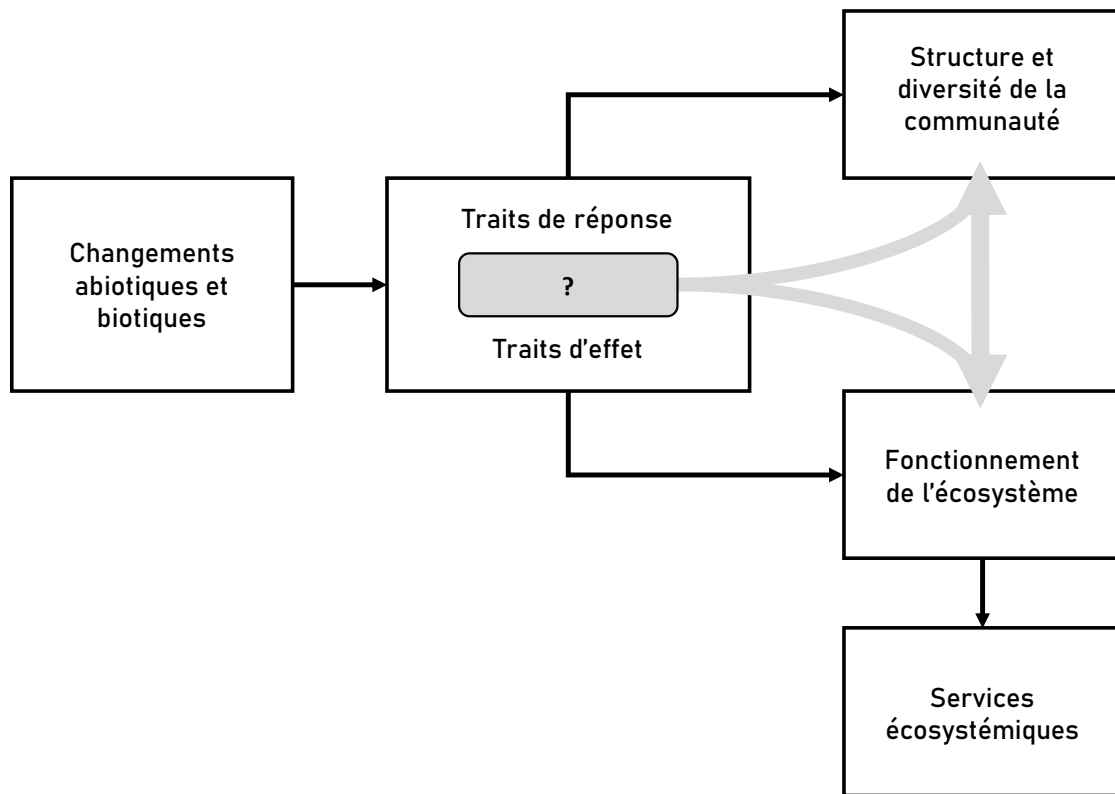
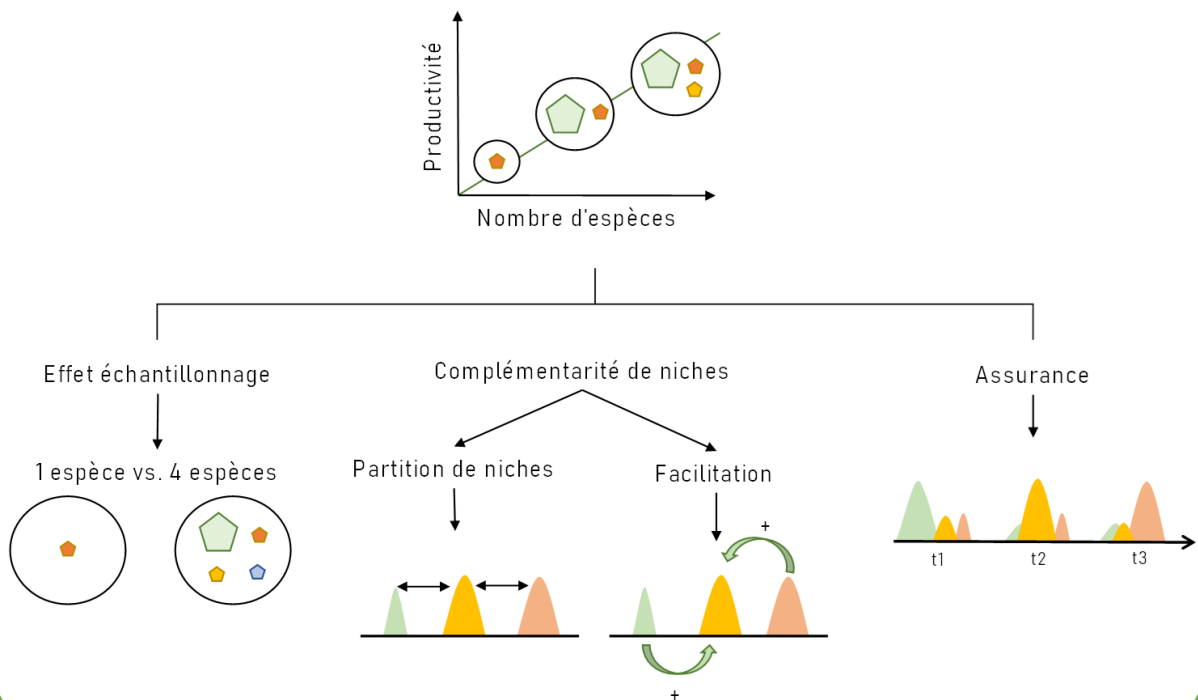


Figure 4 : Représentation du cadre conceptuel qui articule la réponse environnementale, les effets sur l'écosystème et les services écosystémiques à travers l'utilisation de l'approche basée sur des traits pertinents de réponse et d'effet. Adapté d'après Lavorel & Garnier (2002).

Il est primordial de comprendre au mieux les différentes forces agissant sur l'assemblage des espèces car le maintien de la diversité végétale est supposé assurer un meilleur fonctionnement de l'écosystème. De par leur mode de vie sessile, les plantes sont d'autant plus contraintes par la structure du paysage qui influence leur dispersion et la disponibilité de niches (Poggio et al., 2010). Cependant, tous les éléments dans le paysage ne vont pas influencer les mêmes processus, c'est pourquoi de plus en plus d'études s'efforcent à décomposer la structure du paysage en différents éléments pour en comprendre leurs effets sur la biodiversité.

Encadré 2 : le lien biodiversité-productivité. Les travaux de Tilman (1996) ont ouvert la voie des recherches sur le lien biodiversité-productivité. En s'appuyant sur un large dispositif expérimental, Tilman a démontré que les communautés végétales ayant un plus grand nombre d'espèces présentaient une plus grande productivité. L'hypothèse centrale pour expliquer ce résultat est la complémentarité des niches qui stipule que les communautés riches en espèces sont capables d'accéder et d'utiliser plus efficacement les ressources limitantes parce qu'elles contiennent des espèces ayant des niches écologiques variées. Cette théorie englobe à la fois le concept de partition de niches (i.e. utilisation différentielle des ressources pour la coexistence des espèces) et le concept de facilitation (i.e. interactions positives entre les organismes qui profitent à au moins un des participants et ne nuisent à aucun). Cependant, Huston (1997) suggère que ce résultat ne s'explique pas par la richesse en espèces elle-même mais par des « traitements cachés » définis comme des facteurs manipulés intentionnellement ou non au cours des expériences. Il décrit plus précisément l'effet d'échantillonnage: lorsque les espèces sont sélectionnées au hasard, plus le nombre d'espèces est grand, plus la probabilité qu'une espèce beaucoup plus productive que les autres soit sélectionnée est grande (représenté par le grand hexagone vert ci-dessous). Finalement, selon l'hypothèse de l'assurance (Yachi & Loreau, 1999), le maintien de la productivité dans les assemblages végétaux est plus probable lorsque le pool d'espèces est plus important car il offre de plus grandes garanties que certaines espèces maintiendront leur fonctionnement à travers le temps quand d'autres échoueront.



2

Le paysage, un facteur conditionnant les règles d'assemblage

Le paysage peut influencer la composition des communautés végétales en jouant le rôle de filtre écologique (Keddy, 1992). Cependant, au sein même de l'écologie du paysage, deux visions s'opposent ou se complètent selon les auteurs : la vision habitat centrée (i. e. tache-matrice, MacArthur & Wilson, 1967 ; Hanski & Gilpin, 1991) et la vision de la matrice globale (i.e. tache-mosaïque ; Wiens, 1995).

A. Les composantes du paysage et leurs effets sur les processus d'assemblage

1. *Habitat : quantité, isolement ou les deux ?*

La théorie de biogéographie insulaire de MacArthur et Wilson (1967) s'est très rapidement imposée comme centrale en écologie du paysage. En effet, les taches d'habitat d'intérêt dans le paysage sont considérées comme des îles plus ou moins isolées incluses dans une matrice homogène et hostile (i.e. analogue à la mer). Les études se concentrent alors sur l'effet de la taille et l'effet de l'isolement des taches d'habitat sur les communautés végétales, en analogie à la taille et à l'isolement des îles (Fahrig 2017). Les taches d'habitat de petite surface sont supposées avoir un taux d'extinction élevé (i.e. faible capacité d'accueil) et les taches fortement isolées de l'habitat source (i.e. habitat de qualité supérieure pouvant servir de réservoir) ont un taux de colonisation faible (MacArthur & Wilson, 1967). Cette vision du paysage a entraîné un développement conséquent des recherches sur le phénomène de la fragmentation des habitats. La fragmentation se définit comme une réduction et/ou une augmentation de l'isolement entre les taches d'habitat (Wilcove & McLellan, 1986). Pour comprendre les effets de cette fragmentation, il est aujourd'hui suggéré de faire la distinction entre les effets de la perte de la quantité d'habitat, et l'effet de l'isolement des taches d'habitat restantes sur la diversité des communautés végétales (Fletcher et al., 2018).

Comprendre les effets respectifs de la taille des taches d'habitat et de leur isolement nécessite une absence de corrélation entre ces deux phénomènes. Or tous deux agissent simultanément dans les paysages et il reste ardu de les étudier indépendamment dans des systèmes réels (Fahrig 2003; Hanski 2015). Ainsi, Fahrig (2013) a récemment proposé de résumer ces deux composantes via la théorie de quantité d'habitat (i.e. *habitat amount hypothesis*). L'hypothèse de la quantité d'habitat postule que, pour les taches d'habitat incluses dans une matrice paysagère inhospitalière, l'effet de la taille de la tache et l'effet de son isolement sont principalement déterminés par un seul processus sous-jacent, l'effet de la zone d'échantillonnage (i.e. *sampled area effect*). L'hypothèse stipule que la richesse en espèces dans des sites d'échantillonnage de taille égale devrait augmenter avec la quantité totale d'habitat dans le paysage environnant (Figure 5). Dans ce cas, le paysage environnant doit être situé à une distance jugée

appropriée du site d'échantillonnage selon la capacité de dispersion des organismes étudiés. L'hypothèse de la quantité d'habitat remplace donc les deux variables prédictives habituellement utilisées, la taille de la tache et son isolement, une seule variable prédictive : la quantité d'habitat. Cette hypothèse fait encore débat (Haddad et al., 2017 ; Martin, 2018) mais pourrait être d'importance pour la conservation des espaces naturels car elle implique que conserver plusieurs petites taches d'habitat ou une seule grande tache d'habitat serait équivalent (i.e. SLOSS - single large or several small; Fahrig, 2017).

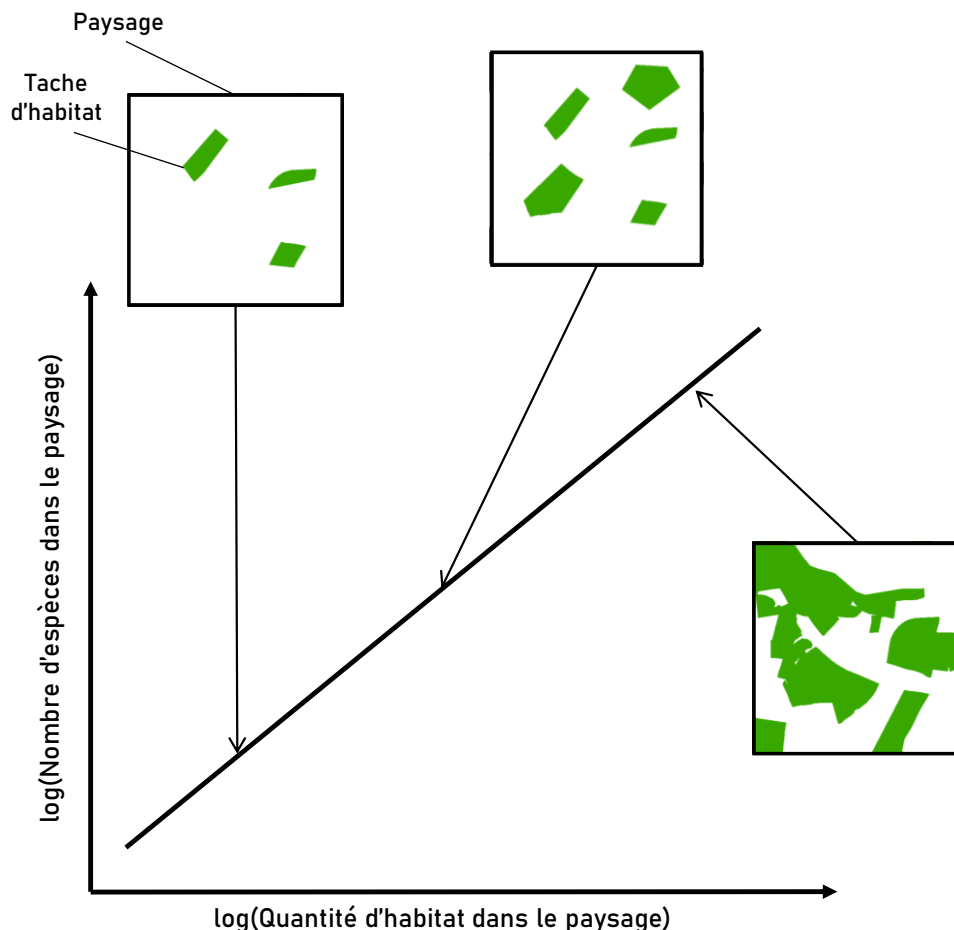


Figure 5 : Schéma représentant la théorie de la quantité d'habitat. Cette théorie stipule que le nombre total d'espèces dans un type d'habitat dans un paysage augmente avec la quantité totale de cet habitat dans le dit paysage. Ce phénomène se produit indépendamment de la taille des taches d'habitat et de leur isolement. D'après Fahrig (2013).

Toutefois, cette vision habitat-centrée est souvent considérée comme trop simpliste car elle fait abstraction de la nature de la matrice environnante (Kuefler et al., 2010). En effet, elle ne prend pas en compte les autres types d'occupations du sol adjacentes qui peuvent pourtant avoir des effets sur les processus de dispersion ou de disponibilité de niches (Poggio et al., 2010). Cette approche binaire du paysage peut sembler parfois inappropriée pour les plantes car elles répondent plutôt à des gradients de qualité des ressources, et sont tributaires de certains agents de dispersion eux-mêmes influencés par la structure de la matrice (Murphy & Lovett-Doust, 2004).

2. *Hétérogénéité de la matrice paysagère*

Proposée comme alternative à la vision tache d'habitat vs. matrice hostile, le modèle de mosaïque paysagère vise à prendre en compte la nature de la matrice environnante aux taches d'habitats étudiées (Deconchat & Sirami, 2017). Cette matrice n'est donc plus considérée comme neutre et homogène mais comme un ensemble d'habitats différents (i.e. mosaïque) pouvant influencer les processus d'assemblages des communautés végétales (Prevedello & Vieira, 2010). Certaines études considèrent l'hétérogénéité de la matrice paysagère uniquement via des mesures de proportions de terres arables au sein des paysages (e.g. Jonason et al., 2017). Pourtant, il est possible de distinguer la composition en éléments du paysage (richesse, abondance des types d'occupation du sol), et la configuration spatiale de ces éléments (taille des taches d'habitat, longueur de bordures entre habitats ; Fahrig et al., 2011). Ces deux composantes de l'hétérogénéité ont été définies par Fahrig et al. (2011) comme l'hétérogénéité de composition et l'hétérogénéité de configuration respectivement (Figure 6).

Classiquement, l'hétérogénéité de composition peut être quantifiée en identifiant le nombre de types d'occupations du sol différentes au sein d'un paysage (e.g. Lomba et al., 2011). Un paysage présentant quatre occupations du sol différentes est alors considéré comme plus hétérogène qu'un paysage n'en présentant que deux. Cependant, cette mesure rudimentaire ne prend pas en compte la dominance de certaines occupations du sol (Fahrig et al., 2011). Ainsi, deux paysages présentant le même nombre d'occupations du sol seront considérés comme équivalents en termes d'hétérogénéité, même si un des deux paysages est dominé par un seul type d'occupation du sol. Pour quantifier cette différence, l'indice de Shannon pour le paysage (McGarigal et al., 2012), analogue à l'indice de Shannon caractérisant les communautés d'organismes (Spellerberg & Fedor, 2003), prend en compte la richesse mais aussi l'équitabilité entre les types d'occupations du sol. Pour les mesures de l'hétérogénéité de configuration en revanche, on s'intéresse uniquement à la complexité spatiale des occupations du sol. Une des mesures les plus utilisées est la taille des parcelles : plus la taille des parcelles est petite, plus le paysage est considéré comme hétérogène (Fahrig et al., 2011). Mais l'hétérogénéité de configuration peut s'appréhender par de multiples autres indicateurs (Cushman et al., 2008) comme la densité des bordures entre les différents types d'occupation du sol ou encore la juxtaposition et l'agrégation des taches d'habitats (Ahlqvist & Shorridge, 2010; McGarigal et al., 2012).

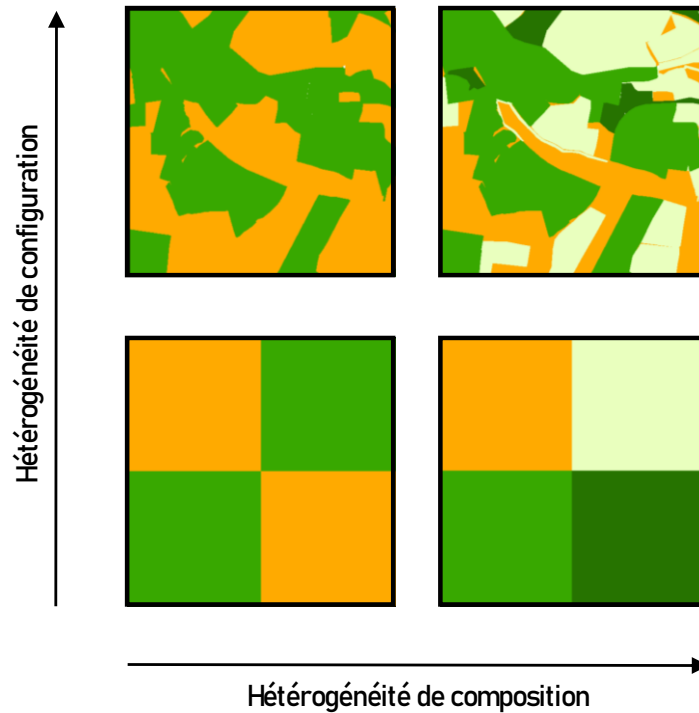


Figure 6 : Représentation schématique de la variation en hétérogénéité de composition et de configuration. Chaque carré représente un paysage et chaque couleur représente un type d'occupation du sol différent. Lorsque la diversité en occupations du sol augmente, l'hétérogénéité de composition augmente. Lorsque l'organisation spatiale des occupations du sol se complexifie, l'hétérogénéité de configuration augmente. D'après Fahrig et al. (2011).

Réussir à dissocier les deux descripteurs de l'hétérogénéité reste difficile dans les systèmes réels (Cushman et al., 2008 ; Fahrig et al. 2011 ; Pasher et al. 2013). Pourtant, ils n'influencent théoriquement pas les mêmes processus et peuvent donc régir différemment l'assemblage des communautés végétales. Une plus grande hétérogénéité de composition (i.e. une plus grande diversité/équitabilité des occupations du sol) va par exemple induire un plus grand réservoir d'espèces présentes dans le paysage environnant, qui sont potentiellement capables d'immigrer au sein des taches d'habitat (Öckinger et al., 2012). L'hétérogénéité de composition peut donc influencer les hiérarchies compétitives entre les taches d'habitat dans les modèles de métacommunautés (voir 1.A.2.). L'hétérogénéité de configuration quant à elle va influencer les flux et les taux de rencontres entre les espèces au sein des taches d'habitats et les occupations du sols adjacentes (Fahrig, 2017). L'hétérogénéité de composition va donc plutôt correspondre à quelles espèces peuvent immigrer et l'hétérogénéité de configuration à comment elles vont être en capacité d'immigrer au sein des taches d'habitat.

3. *La particularité du bocage sur les conditions climatiques locales*

Parmi les différents types de paysages, le bocage est particulier dans sa structure de par la présence d'un réseau de structures végétales ligneuses linéaires (i.e. réseaux de haies ; Baudry et Jouin 2003). Le réseau

de haies peut agir non seulement sur la dispersion des espèces (Montgomery et al., 2020) mais également sur la vitesse du vent, la température de l'air et l'évapotranspiration des plantes (Guyot et Seguin 1976). Au niveau régional, la densité de haies influence les régimes de flux d'air et peut ainsi influencer les conditions climatiques (Figure 7). Au niveau parcellaire, la présence d'une haie modifie le schéma normal d'atténuation du vent (Figure 7), et diminue la vitesse du vent près du sol en aval de cette haie. La courbe de température près du sol reflète la distribution de ce ralentissement avec une augmentation de la température dans les parties protégées du vent, excepté les zones d'ombres très proches de la haie.

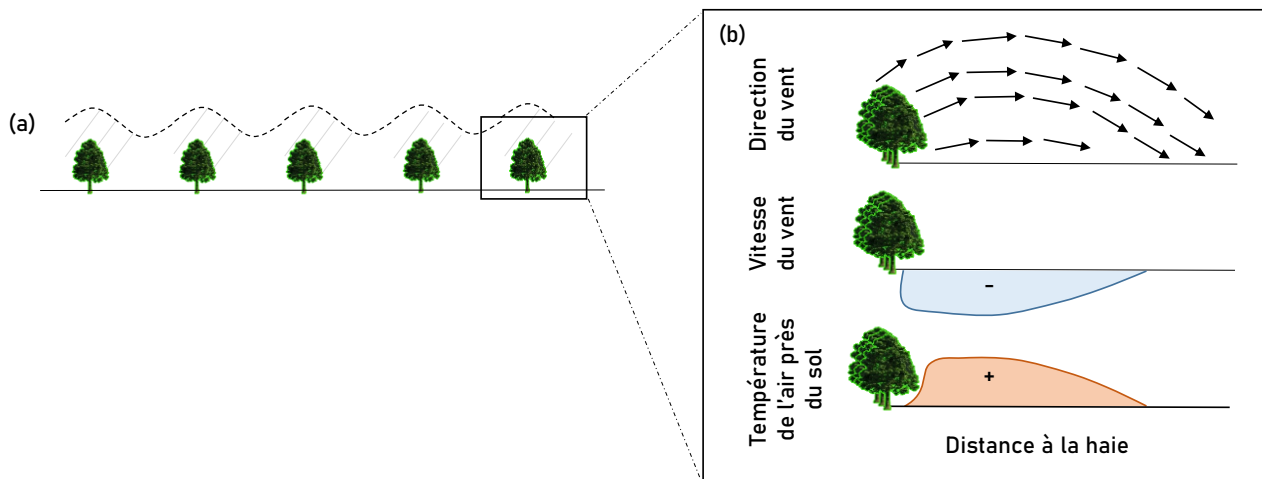


Figure 7 : Effets théoriques de la présence de haies sur la vitesse du vent et la température de l'air à l'échelle paysagère (a) et locale (b). D'après Guyot & Seguin (1976) et Forman & Baudry (1984).

Les différentes composantes du paysage influencent donc plusieurs processus prenant part à l'assemblage des communautés végétales, que ça soit sur le filtre de la dispersion, le filtre abiotique (e.g. climat local) et biotiques (i.e. disponibilité de niches). Cependant, ces composantes n'auront pas forcément les mêmes effets suivant l'échelle à laquelle la diversité des communautés végétales est appréhendée.

B. L'échelle du paysage: emboîtement hiérarchique de la biodiversité

La distinction entre les différentes échelles spatiales de la biodiversité est essentielle en écologie car elle permet de révéler des distributions d'espèces complémentaires. Il est possible d'appréhender ces échelles via un emboîtement hiérarchique de la diversité des communautés végétales. On peut ainsi séparer la diversité en trois niveaux principaux : (i) la diversité alpha (α) qui se réfère à la diversité locale moyenne (i.e. diversité de la communauté), (ii) la diversité beta (β) qui se réfère à la diversité intercommunautés moyenne, et la diversité gamma (γ) qui correspond à la diversité totale d'un paysage (Crist & Veech, 2006). Ces trois composantes ont d'abord été associées dans une vision multiplicative (Whittaker, 1960), puis dans une vision additive (Veech et al., 2002), ces deux visions coexistant encore

à l'heure actuelle (Veech & Crist, 2010). Dans la vision additive, la diversité gamma peut être considérée comme la somme de la diversité alpha et de la diversité beta (Figure 8), qui sont par ailleurs exprimées dans la même unité (Crist & Veech, 2006).

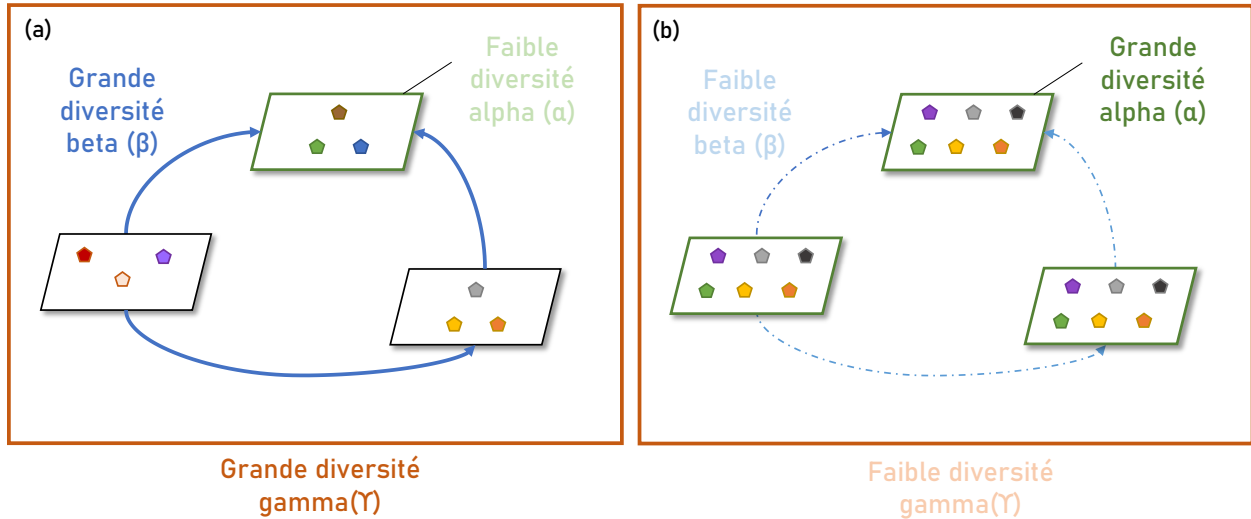


Figure 8 : Représentation de la diversité alpha, beta et gamma et leurs possibles variations. Les hexagones de couleur représentent des espèces végétales, les petits rectangles des taches d'habitat et le grand rectangle un paysage. La diversité alpha correspond à la diversité locale d'une tache d'habitat. La diversité beta correspond à la différence en espèces entre les taches d'habitat dans un paysage. La diversité gamma représente la diversité totale à l'échelle d'un paysage. (a) Dans ce paysage, les 3 taches d'habitats présentent des diversité alpha faibles. Cependant, ces taches sont très dissimilaires entre elles en termes de diversité, la diversité beta est donc importante. La diversité gamma, résultat additif de la diversité alpha et beta, est donc importante également. (b) A l'inverse du premier exemple, les taches d'habitat présentent une grande diversité alpha mais sont très similaires entre elles en termes de diversité. La diversité beta et la diversité gamma sont donc toutes les deux faibles.

Beaucoup d'études en écologie du paysage se concentrent sur la diversité alpha et l'intérêt pour les échelles beta et gamma reste relativement récent (Tscharntke et al., 2012). Pourtant, étudier la biodiversité à l'échelle beta et gamma est nécessaire pour pouvoir évaluer le statut des espèces végétales dans la mosaïque et peut permettre de déduire comment la structure du paysage influence la diversité à grande échelle (Bennett et al., 2006). Cette approche permet de mieux comprendre les règles d'assemblage des communautés végétales à l'échelle paysagère mais peut également permettre de protéger la diversité plus efficacement. En conservant des taches d'habitat dissimilaires en terme de diversité au sein d'un paysage, la diversité beta pourrait compenser les pertes locales d'espèces à l'échelle paysagère (Tscharntke et al., 2012 ; Figure 8).

C. Le paysage actuel et futur et les effets sur les communautés végétales

Le paysage peut influencer les communautés végétales suivant sa structure, qu'elle soit liée à l'habitat considéré ou à la matrice environnante. Cependant, le paysage est en constante évolution car il est l'expression de l'interaction dynamique entre la nature et les activités humaines (Antrop, 2005). Au cours

du siècle dernier, les modifications dans le paysage, et plus particulièrement dans l'utilisation des sols, ont été le principal moteur de la perte de biodiversité et il est probable que cela reste une menace majeure à l'avenir (Albert et al., 2020). C'est pourquoi depuis quelques années, la communauté scientifique se penche sur le développement de scénarios qui tentent d'évaluer l'impact de différents développements socio-économiques sur la biodiversité et les services écosystémiques (Pereira et al., 2010). Ces scénarios, basés sur des narrations de développement de la société, peuvent être projetés quantitativement et spatialement (Albert et al., 2020). Ces projections permettent ensuite de comparer les effets potentiels des différents scénarios de développements territoriaux sur la structure du paysage, la biodiversité et les services associés. Ils représentent ainsi de précieux outils d'aide à la décision qui sont transférables aux gestionnaires des territoires dans le but de maintenir et augmenter l'approvisionnement en services écosystémiques au sein des territoires.

Objectifs et organisation de la thèse

L'objectif général de cette thèse est de déterminer l'effet de la structure du paysage actuel et futur sur la diversité fonctionnelle des assemblages de plantes et les fonctions écologiques associées. Pour se faire nous nous sommes appuyés sur un dispositif à grande échelle composé de 30 fenêtres paysagères de 1km x 1km réparties au sein du bassin versant du Couesnon (France). Afin d'accroître la portée des résultats, deux types d'habitats semi-naturels typiques des paysages agricoles bretons ont été étudiés dans le chapitre 2 : les prairies permanentes et les haies. Les deux autres chapitres se concentrent uniquement sur les prairies permanentes et les fonctions écologiques associées.

Le Premier chapitre de ce manuscrit s'intéresse aux éléments méthodologiques mis en œuvre pour répondre aux questions de recherche. Il contient une description de la zone d'étude, une explication détaillée du processus de sélection des fenêtres paysagères et des méthodes d'échantillonnage des communautés végétales.

Dans le Deuxième Chapitre (ARTICLE 1), nous avons étudié les effets indépendants de la quantité d'habitat, de l'hétérogénéité de composition et de l'hétérogénéité de configuration sur la diversité fonctionnelle gamma des assemblages de plantes. Nous nous sommes appuyés sur le plan d'échantillonnage présenté dans le Premier chapitre et nous avons comparé la réponse de deux types d'habitats différents en terme de structure spatiale : les plantes herbacées des prairies permanentes (i.e. habitat surfacique) et les plantes herbacées des haies (i.e. habitat linéaire). Nous avons testé les effets des composantes du paysage sur trois indices décrivant les structures fonctionnelles globales des deux types de végétations (i.e. richesse fonctionnelle, régularité fonctionnelle et dispersion fonctionnelle) mais également les effets sur la contribution individuelle de chaque trait fonctionnel à la construction

de ces trois indices. Cette recherche a été réalisée en collaboration avec Hugo Saiz de l'Institut des sciences végétales de l'Université de Bern (Suisse).

Dans le Troisième chapitre (ARTICLE 2), nous nous sommes concentrés plus précisément sur les assemblages de prairies permanentes. L'objectif était de comprendre les relations entre la structure du paysage, la diversité fonctionnelle des assemblages de plantes prairiales et leur productivité. Nous avons exploré les théories biodiversité-productivité dans des systèmes *in situ*, pour essayer de comprendre les effets de la structure du paysage sur la productivité. Pour ce faire, nous nous sommes concentrés sur la diversité fonctionnelle multidimensionnelle des prairies (richesse, régularité, et dispersion) et leur productivité (moyenne annuelle, stabilité temporelle, variabilité spatiale) calculée à partir d'images acquises par la constellation de satellites Sentinel-2. Cette recherche a été réalisée en collaboration avec Elodie Fabre et Sébastien Rapinel de l'UMR LETG de l'Université de Rennes 2.

Dans le Quatrième chapitre (ARTICLE 3), l'objectif était d'estimer l'évolution des services écosystémiques de la zone d'étude sous différents scénarios de changements d'occupation du sol. Nous avons estimé la relation structure du paysage-services écosystémiques directement à partir de relevés floristiques et de la température de l'air mesurée sur le terrain. Nous avons d'abord estimé les valeurs actuelles des services écosystémiques (disponibilité de l'habitat, diversité taxonomique et fonctionnelle, productivité, régulation du climat). Ensuite, nous avons étudié les relations entre les services écosystémiques actuels et la structure du paysage. Enfin, nous nous sommes appuyés sur trois scénarios socio-économiques reflétant des trajectoires contrastées de développement agricole et territorial pour le bassin versant du Couesnon afin de projeter les conséquences possibles des changements d'occupation du sol sur les services écosystémiques. Cette recherche a été réalisée en collaboration avec Gaëtan Palka, Thomas Houet et Hervé Quénol de l'UMR LETG de l'Université de Rennes 2.

Ce manuscrit se conclut par une discussion générale où nous revenons sur l'ensemble des résultats au regard des cadres théoriques et méthodologiques mobilisés. Nous discutons les réponses apportées aux questions de recherche initiales par les analyses mises en œuvre. Des pistes de recherches futures pouvant être réalisées dans le prolongement de cette thèse sont également proposées (ARTICLE 4).

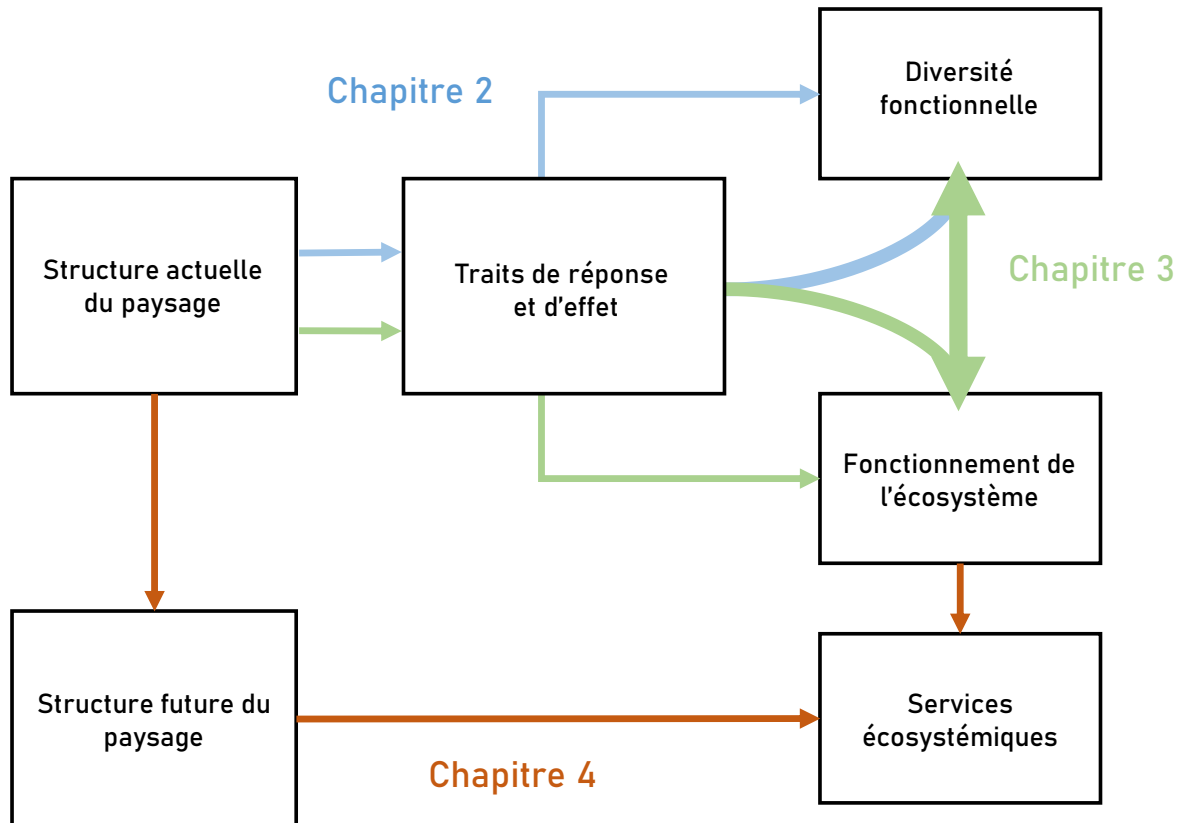


Figure 9 : Schéma adapté de Lavorel & Garnier (2002) représentant le cheminement scientifique et l'organisation des chapitres de la thèse. Les flèches bleues correspondent aux liens testés dans l'article du chapitre 2, les flèches vertes correspondent aux liens testés dans l'article du chapitre 3 et les flèches marrons correspondent aux liens testés dans l'article du chapitre 4.



Chapitre 1

Éléments méthodologiques

- A. Bassin versant du Couesnon et sélection des fenêtres paysagères
- B. Echantillonnage des communautés végétales
- C. Traits fonctionnels
- D. Mesure de la productivité des prairies

A. Bassin versant du Couesnon et sélection des fenêtres paysagères

L'ensemble des résultats présentés dans les Chapitres 2, 3 et 4 ont été obtenus à partir de données collectées dans le bassin versant du Couesnon situé à cheval entre la Bretagne et la Normandie (France). Ce petit bassin versant couvre une surface de 1130 km² et s'étale sur une soixantaine de communes d'Ille et Vilaine et 15 communes de la Manche, abritant ainsi plus 90 000 habitants. La rivière du Couesnon s'étend sur 115 km et se jette au pied du Mont-Saint-Michel. Elle est alimentée par des cours d'eau aux débits très largement tributaires de la pluviométrie. Le sous-sol est composé principalement de roches métamorphiques et plutoniques imperméables ; il contribue donc à la présence d'un réseau hydrographique très dense. Près de 1 700 km de linéaire de cours d'eau ont été recensés et les fonds de vallées sont marqués par la présence de nombreuses zones humides (SAGE Couesnon, 2021). Le bassin versant est dominé par les terres agricoles et englobe un large éventail de structures paysagères. Il présente tout de même deux zones principales qui se distinguent par des pratiques agricoles différentes, avec au Nord du territoire les polders du Mont-Saint-Michel caractérisés par de grandes cultures et cultures légumières, et au centre une zone caractérisée par un système de polyculture-élevage laitier dominant. Ce type de production se traduit dans le paysage par une grande proportion de prairies (temporaires et permanentes), avec également de grandes surfaces allouées au maïs et à d'autres céréales. Les zones forestières sont concentrées dans deux forêts principales (i.e. forêt de Fougères et forêt de Villecartier), le reste des zones boisées correspond à des petites parcelles de bois post-agricoles. Le bassin versant du Couesnon est également caractérisé par un réseau de haies plus ou moins dense selon la localisation.

Pourcentages des différentes occupations du sol dans le bassin versant du Couesnon

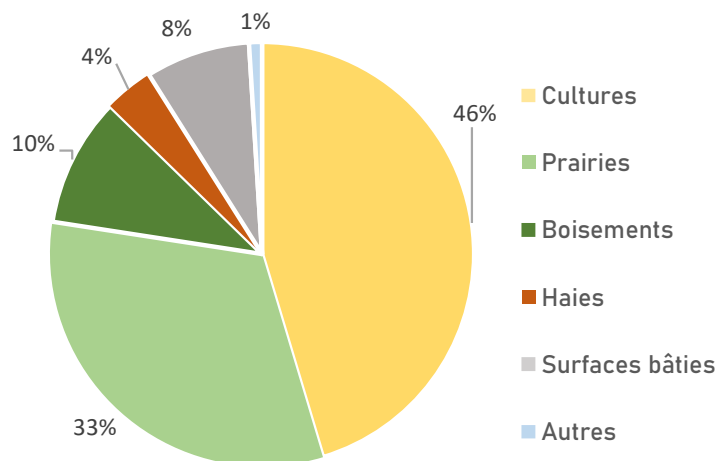


Figure 1 : Pourcentages des différentes occupations du sol au sein du bassin versant du Couesnon en 2017 (France). La carte d'occupation des sols a été fournie par le Centre français de données sur les sols Theia.

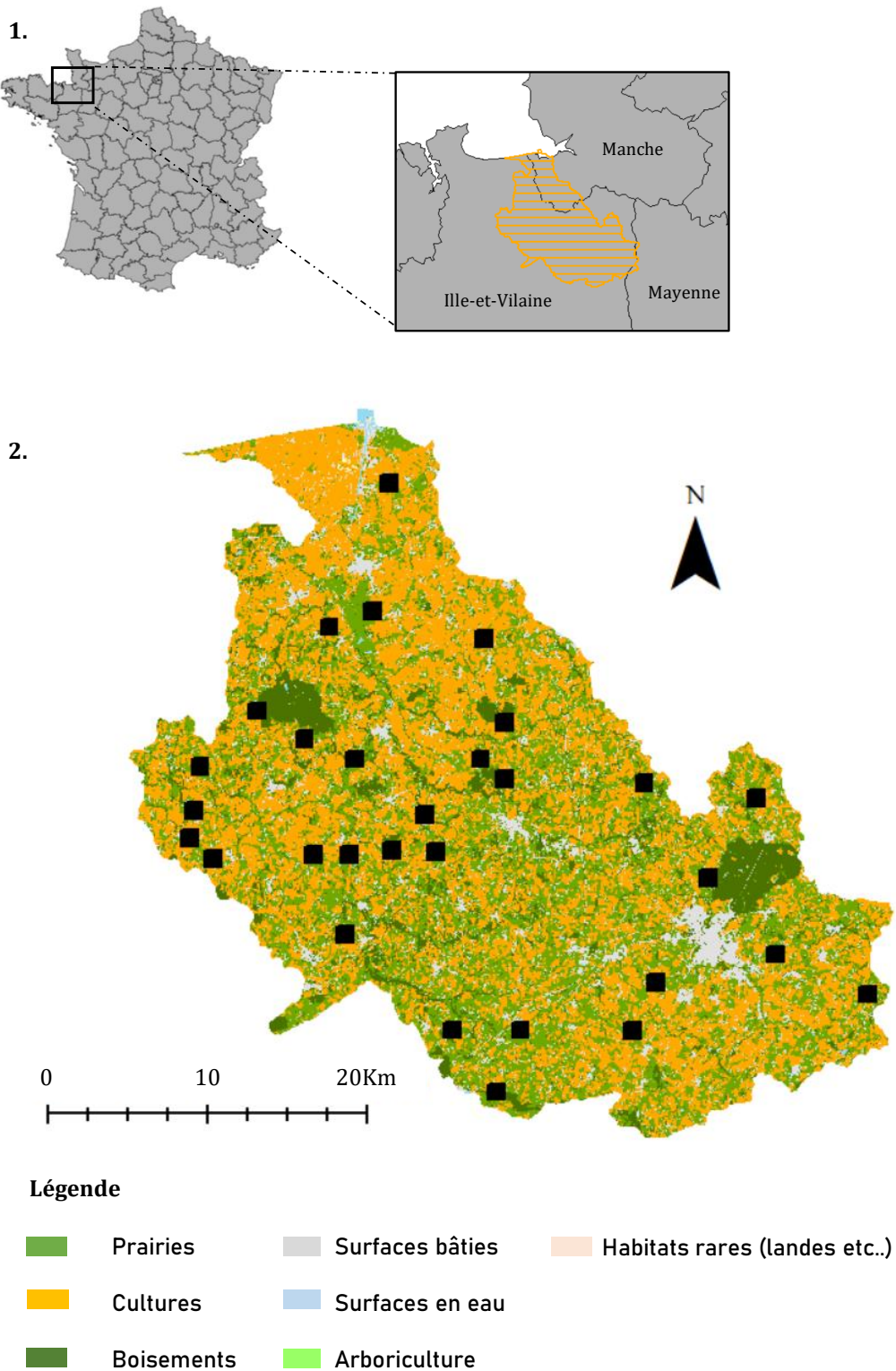


Figure 2 : Carte du bassin versant du Couesnon (France). 1. Le bassin versant couvre 1130km² et se situe à cheval entre la Bretagne et la Normandie. 2. Les carrés noirs indiquent la position des 30 fenêtres paysagères sélectionnées. La carte d'occupation des sols a été fournie par le Centre français de données sur les sols Theia.

Nous avons choisi de sélectionner nos sites d'études via un dispositif qui minimise *a priori* la corrélation des variables décrivant la structure du paysage. Nous nous sommes appuyés sur une carte détaillée de l'occupation des sols de 2017 d'une résolution de 10 m fournie par le Centre français de données sur les sols (Théia), et d'une carte du réseau de haies fournie par les gestionnaires locaux (SAGE Couesnon). La carte d'occupation du sol a été sous-échantillonnée à une résolution de 5m en utilisant l'approche du plus proche voisin et fusionnée avec la carte des réseaux de haies rasterisée à 5m. Nous avons obtenu une carte globale du bassin versant du Couesnon à une résolution de 5m où sept classes principales d'occupation du sol ont été identifiées : les prairies, les haies, les cultures, les vergers, les surfaces artificielles, les bois et les habitats rares (les landes, les surfaces en eau). A partir de cette carte, trente fenêtres paysagères (1km x 1km) ont été sélectionnées pour représenter la diversité du paysage à travers le bassin versant et quatre gradients indépendants décrivant la structure du paysage: deux gradients pour l'hétérogénéité du paysage, (i) hétérogénéité de composition, (ii) hétérogénéité de configuration, et deux gradients pour les quantités d'habitats semi-naturels, (iii) pourcentage de prairies, et (iv) pourcentage de haies (Figure 2). Les 30 fenêtres ont été sélectionnées sur la base d'autres critères qui limitent la probabilité de choisir des paysages atypiques : chaque fenêtre présentait ainsi moins de 2% de zone urbanisée ou d'habitats rares, au moins 5% de prairies, et au moins 1% de haies. Pour s'assurer que les sites sélectionnés étaient représentatifs du paysage environnant et pour éviter tout effet de bordure majeur, nous avons comparé la surface par type d'occupation du sol dans le paysage de 1km x 1km avec une zone plus grande (2km x 2km) centré sur chaque site et nous avons vérifié que les deux paysages (1km x 1km versus 2 km x 2km) présentaient moins de 10% de différence entre chaque occupation du sol (suivant la procédure de Dufлот et al., 2015). Ce processus de sélection a permis de représenter la diversité des paysages à travers le bassin versant sans sélectionner de fenêtre paysagère située aux extrêmes des 4 gradients (e.g. 0.5% de prairies vs. 100% de prairies).

Afin de rechercher un éventuel effet de la structure du paysage sur les conditions climatiques locales au sein des fenêtres paysagères, nous avons placé deux enregistreurs de température de l'air dans chaque fenêtre paysagère. Ces capteurs (Tinytag Plus 2 - TGP-4017) ont été placés dans des abris (ACS-5050) et fixés à 2 mètres du sol sur des poteaux de clôtures en bois adjacents à des parcelles de prairie (Figure 3). Avant et après la période d'enregistrement, des tests ont été effectués pour vérifier un éventuel 'effet enregistreur' : tous les enregistreurs ont été placés dans la même pièce pendant 24h et nous avons vérifié que les valeurs enregistrées étaient similaires. Les 60 capteurs répartis dans le bassin versant ont enregistré la température de l'air toutes les heures d'Octobre 2019 à Septembre 2020 compris.

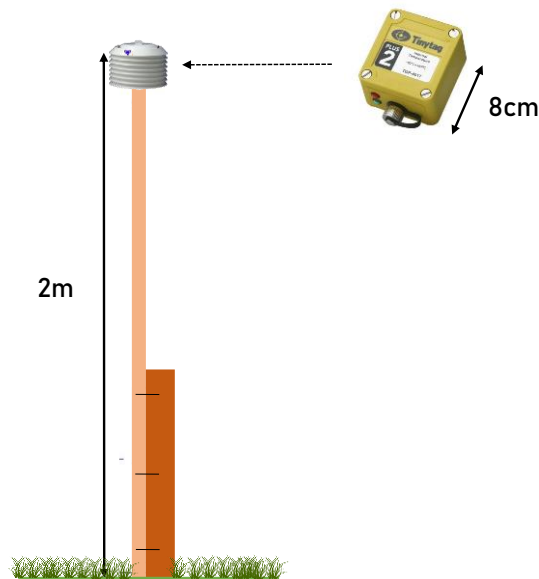


Figure 3 : Dispositif permettant l'acquisition des données de température de l'air. Le capteur de température est placé dans un abri météo et fixé sur une perche en bois à 2m du sol. Deux dispositifs ont été placés par fenêtre paysagère, représentant ainsi 60 dispositifs répartis sur le bassin versant du Couesnon.

B. Echantillonnage des communautés végétales

Dans chaque fenêtre paysagère, nous avons étudié les assemblages de plantes herbacées des prairies permanentes (i.e. prairies implantées depuis au moins 5 ans tel que défini par la PAC) et les assemblages de plantes herbacées des haies (i.e. élément linéaire présentant au moins les strates herbacée et arborée). Nous avons choisi ces modèles d'étude car ils font partie des principaux habitats semi-naturels des paysages agricoles et remplissent de nombreuses fonctions dont celle de refuge et de corridor pour les plantes. De plus, ces deux habitats sont intéressants à étudier car ils ont des structures très différentes : les haies sont des habitats boisés linéaires alors que les prairies sont des habitats couvrant de grandes surfaces. Dans chaque fenêtre paysagère, nous avons sélectionné 3 à 5 parcelles de prairie et 3 à 5 haies selon leur disponibilité. Dans chaque parcelle de prairie et chaque haie, nous avons effectué 5 relevés floristiques. Chaque relevé de prairie correspondait à un quadrat de 2m x 2m situé à au moins cinq mètres du bord de la parcelle (soit 20m² par parcelle de prairie). Chaque relevé de haie correspondait à un quadrat de 2m x la largeur de la haie. Nous avons décidé d'adapter la largeur du relevé plutôt que d'adopter un quadrat fixe afin de (i) capturer toutes les espèces dans les haies les plus larges et (ii) éviter d'intégrer la flore d'autres habitats adjacents dans les haies les plus étroites. Nous n'avons pas inclus les espèces ligneuses dans nos relevés car la plupart des espèces d'arbres et d'arbustes dans les haies de la zone d'étude ont été plantées et ne sont pas issues d'une croissance spontanée. De plus, nous avons exclu du plan d'échantillonnage les prairies inondables afin d'éviter d'échantillonner des communautés aux conditions abiotiques atypiques. Nous avons également contrôlé partiellement la composition des arbres dans les haies en évitant les haies dominées par des espèces de saules ou de conifères, ou les haies qui

avaient été récemment plantées, car ces haies atypiques pourraient influencer localement les assemblages des plantes herbacées.

C. Traits fonctionnels

Afin de caractériser la diversité fonctionnelle des communautés végétales, une série de traits a été sélectionnée à partir de bases de données. Nous avons sélectionné six traits fonctionnels provenant de plusieurs organes et correspondant à des aspects clés du cycle de vie des plantes : la masse des graines et la hauteur, le début et la durée de la floraison, la surface foliaire spécifique (i.e. SLA) et le taux de germination. Ces traits ont été sélectionnés car supposés pertinents pour comprendre la réponse des communautés végétales à la structure du paysage (i.e. traits de réponse) et pertinents pour regarder leurs effets sur les fonctions de l'écosystème (i.e. traits d'effet). Les valeurs de traits ont été extraites de différentes bases de données : les valeurs de masse de graine et de surface foliaire proviennent de la base de données LEDA (Kleyer et al., 2008), les valeurs de début et de durée de floraison proviennent de la base de données Bioflor (Kühn et al., 2004) et les valeurs du taux de germination et de la hauteur proviennent de la base de donnée TRY (Kattge et al., 2020). Nous avons mis en place une procédure MICE suivant la méthodologie de Penone et al. (2014) pour estimer les valeurs manquantes de traits (> 2% des valeurs). Cette méthodologie permet de prédire les valeurs des traits manquantes à partir des traits d'histoire de vie observés en prenant en compte des informations phylogénétiques extraites de l'arbre phylogénétique de Zanne et al. (2014). A l'inverse, lorsque plusieurs valeurs étaient disponibles pour une seule espèce, nous avons gardé les valeurs ayant le plus grand nombre de répliques effectués pour estimer ces valeurs, et nous avons calculé la moyenne. Nous avons donc obtenu les valeurs des six traits fonctionnels sélectionnés pour les 207 espèces végétales identifiées au sein des relevés floristiques de prairies et de haies.

D. Mesure de la productivité des prairies

Etudier la biodiversité à grande échelle comme celle du paysage nécessite d'avoir des outils adaptés à ces enjeux. L'avènement de nouveaux outils amène l'écologie des paysages à remettre en question la façon dont elle caractérise et étudie ces paysages (Deconchat & Sirami, 2017). Les données écologiques sur le terrain sont généralement fastidieuses à récolter et sont souvent acquises à un instant t. L'échantillonnage des communautés végétales et de leurs fonctions ne permet pas de faire des suivis temporels réguliers. Dans ce contexte, l'imagerie satellitaire offre un panel d'outils très intéressants pour les écologistes.

Nous avons utilisé l'indice de végétation normalisée (NDVI) comme indicateur de la productivité des prairies. Cet indice est dérivé de données de télédétection des bandes rouge et proche infrarouge et constitue un bon indicateur de la photosynthèse (Pettorelli et al., 2005). Nous avons utilisé

les séries chronologiques annuelles des satellites Sentinel-2 (niveau 3A) fournies par le Centre français de données terrestres Theia. Le niveau 3A des images S-2 a une résolution de 10m dans les bandes rouge (b4 : 664 nm) et proche infrarouge (b8 : 835 nm). Ces images mensuelles (~40 jours) sont des composites sans nuages. Tout d'abord, nous avons acquis toutes les images des 2 tuiles couvrant notre zone d'étude d'Octobre 2019 à Septembre 2020. Au total, 13 images (i.e. 1 image pour chaque mois et 2 images pour Août 2020 en raison de conditions sans nuage) étaient disponibles. L'image d'Octobre 2019 a été exclue de l'analyse en raison de la grande couverture nuageuse sur les fenêtres paysagères étudiées. Douze images étaient donc disponibles pour l'évaluation de la productivité. Deuxièmement, avec une zone tampon interne de 10 m à partir du bord des parcelles pour éviter les valeurs aberrantes, nous avons calculé les valeurs NDVI médianes de chaque parcelle de prairie pour chaque mois (Veen et al., 2020). Nous avons basé nos analyses sur ces valeurs pour les articles 2 et 3.

Chapitre 2

Effet de la structure du paysage sur la diversité fonctionnelle des plantes

En résumé : La structure du paysage est l'un des principaux moteurs de la biodiversité, en particulier dans les paysages agricoles. Cependant, seules quelques études ont exploré son effet sur la diversité fonctionnelle gamma des plantes. Pourtant, les questions de recherche à cette échelle sont importantes pour mieux comprendre et préserver efficacement la biodiversité.

Trente fenêtres paysagères (1km²) ont été sélectionnées pour tester l'effet de la structure du paysage sur la diversité fonctionnelle des plantes des prairies permanentes et des haies à l'échelle gamma. Nos hypothèses étaient que (i) la quantité d'habitat et l'hétérogénéité du paysage augmentaient la diversité fonctionnelle gamma des assemblages de prairies et de haies et que (ii) la quantité d'habitat et l'hétérogénéité du paysage influençaient la contribution relative des traits fonctionnels à la diversité fonctionnelle de ces deux types de végétation.

L'hétérogénéité du paysage n'a affecté que la diversité fonctionnelle des plantes de haies. Parce qu'elles sont linéaires, les haies sont plus facilement influencées par les effets de lisière, notamment par l'immigration d'espèces provenant des autres occupations du sol du paysage ou par l'effet indirect des pratiques mises en place dans ces occupations du sol.

La quantité de prairies a eu un effet négatif sur la diversité fonctionnelle des assemblages de prairies alors que la quantité de haies a eu un effet positif sur la diversité fonctionnelle des assemblages de haies. Cet effet contrasté pourrait s'expliquer par des pratiques de gestion homogènes dans les prairies, mais aussi par les proportions des deux habitats dans le paysage : les haies étant un habitat rare, une augmentation de la quantité d'habitat serait plus favorable à leur diversité fonctionnelle que pour les prairies qui occupent déjà de grandes surfaces au sein des paysages.

La contribution des traits liés au processus de dispersion, de phénologie et d'établissement était influencée par la structure du paysage, soit par la quantité d'habitat pour les prairies, soit par l'hétérogénéité du paysage pour les haies. Nos résultats suggèrent notamment une baisse du filtre de dispersion dans les paysages avec une grande quantité de prairies, et un changement dans les assemblages de haies en fonction de leurs stratégies phénologiques et d'établissement le long du gradient d'hétérogénéité de composition.

Notre étude souligne la nécessité de poursuivre les efforts de recherche sur la réponse de la diversité fonctionnelle gamma en utilisant des gradients non corrélés de variables paysagères et des informations sur la gestion locale pour comprendre les règles d'assemblage de la biodiversité à l'échelle du paysage.

Investigating the effect of habitat amount and landscape heterogeneity on the gamma functional diversity of grassland and hedgerow plants

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Abstract

Landscape structure is one of the main drivers of biodiversity, especially in agricultural landscapes. However, only a few studies explored its effect on the gamma functional diversity of plants. Yet, research questions at this scale are important to better understand and effectively preserve biodiversity. Using a large-scale sampling design with 30 landscape windows, we investigated the effects of habitat amount (i.e. grassland and hedgerow amounts), compositional heterogeneity (i.e. land use diversity), and configurational heterogeneity (i.e. land use spatial complexity) on the gamma functional diversity of plants in two habitat types: hedgerows and grasslands. We also investigated the same effects on the contribution of each functional trait related to different stages of the plant regeneration cycle. Habitat amount had contrasted effects on the functional diversity of both habitat types, a negative effect on grassland plant assemblages and a positive effect on hedgerow plant assemblages. Landscape heterogeneity only affected the functional diversity of hedgerow plants: configurational heterogeneity favoured functional dispersion but reduced functional evenness, and compositional heterogeneity affected trait contribution especially by shifting phenological and establishment strategies. All stages of grassland and hedgerow plant regeneration cycle were influenced, but we found a stronger effect on traits related to establishment and dispersal. We discuss the contrasting results between plant assemblages of the two habitat types in light of the inherent characteristics of their habitat. We demonstrated that landscape components drive functional gamma plant diversity by altering the assemblage composition and by selecting particular trait syndromes. Our study highlights the need to continue research into the response of gamma functional diversity using uncorrelated gradients of landscape variables and information about local management to understand biodiversity assembly rules at the landscape scale.

Keywords

Functional diversity, gamma diversity, grasslands, habitat amount, hedgerows, landscape ecology, landscape heterogeneity, trait contribution

INTRODUCTION

Both theoretical and empirical ecological studies identify landscape structure as one of the main drivers of biodiversity, especially in agricultural landscapes (Billetter et al. 2008; Concepción et al. 2017). So far, most studies that investigated the impact of landscape structure on biodiversity focused either on the characteristics of one particular habitat (i.e. habitat amount and isolation; e.g. Sonnier et al. 2014; Newman et al. 2013; Haddad et al. 2017), or on the characteristics of all surrounding land uses (i.e. landscape heterogeneity; e.g. Lomba et al. 2011; Dufлот et al. 2014; Concepción et al. 2017). Studies that use both approaches to understand the response of plant diversity to landscape structure are still rare (but see Liu et al., 2018; Corro et al. 2019). Yet, habitat amount and landscape heterogeneity can influence processes driving the assemblages at the landscape scale, such as plant dispersal or niche availability (Poggio et al., 2010; Fahrig 2017). The habitat amount hypothesis (Fahrig 2013), which incorporates both patch size and isolation of one particular habitat, suggests that an increase in habitat amount in a given landscape window increases species richness in this particular habitat. The diversity of surrounding land uses (i.e. compositional heterogeneity; Fahrig et al. 2011) or the spatial complexity of these land uses (i.e. configurational heterogeneity; Fahrig et al. 2011) may also affect plant species richness and composition (e.g. Ekroos et al. 2013). Most authors who investigate plant responses to landscape structure conduct their research at the patch scale (e.g. Sonnier et al. 2014, Haddad et al. 2017), which corresponds to alpha diversity (Wagner et al., 2000). Yet, although patch-scale studies help understand processes including edge effects or local species interactions (Fletcher et al., 2018), we also need to investigate plant diversity at the landscape scale (i.e. gamma diversity; Crist and Veech 2006). Indeed, studying gamma plant diversity of several habitat types can help unravel global processes such as species dispersal or interspecies competition in a landscape (Fahrig, 2017).

One way to better understand the effect of landscape structure on plant gamma diversity is to not rely on biological indicators that assume all species are equal when facing an environmental variable (e.g. species richness) but rather to take into account the particular characteristics of each species (i.e. functional traits, Lavorel and Garnier 2002; Jonason et al., 2017). Indeed, the success or failure of plants to establish themselves in the landscape may depend on traits related to different stages of the plant regeneration cycle (Grubb, 1977). These stages include the production of viable seeds, dispersal in space and over time, and establishment. All traits related to these stages can be filtered by the landscape structure (Zambrano et al. 2019), and, as a result, the richness and composition of functional traits within the assemblages will change depending on whether the filter effect of the landscape increases or decreases. For example, an increase in habitat amount, compositional heterogeneity, or configurational heterogeneity is expected to increase plant species richness (Poggio et al. 2010; Fahrig 2017) and could therefore increase the total functional trait pool of gamma plant assemblages (i.e. functional richness; Villéger et al. 2008). Independently of its effect on the richness, landscape structure can also change the evenness of species distribution in a functional trait space by promoting the coexistence of multiple traits

(i.e. functional evenness; Villéger et al. 2008) or change the dominant strategies by promoting niche differentiation (i.e. functional dispersion; Villéger et al. 2008). These recently developed indices based on multidimensional space account for the inevitable trade-offs between traits (Grubb 1977; Wright et al. 2010) and can help understand gamma plant diversity. Further, the structure of the landscape can filter species according to a specific functional trait (e.g. Miller et al., 2018; Rocha-Santos et al., 2019). The filter effect, which narrows the range of the functional trait values (Keddy 1992; Diaz et al. 1998), would then result in the variation of the trait contribution to the overall functional indices. Either by its effect on species richness or by shifts in the assemblage composition, the landscape structure (i.e. landscape heterogeneity and habitat amount) is then hypothesised (i) to shape the multidimensional functional space of gamma plant diversity (Maire et al., 2015); and (ii) to affect the contribution of specific functional traits linked to different stages of the plant regeneration cycle.

In this study, we investigated the independent effects of habitat amount, compositional heterogeneity, and configurational heterogeneity on the gamma functional diversity of plant assemblages. We also investigated these effects on the contribution of each functional trait related to the different stages of the plant regeneration cycle. We used a large-scale sampling design with 30 landscape windows selected to distinguish the landscape components. The study was conducted in the agricultural landscapes of the Couesnon river watershed (France) which covers a wide range of landscape characteristics. To compare the response of two habitat types different in terms of structure, we studied herbaceous plant assemblages of permanent grasslands (i.e. surface habitat) and hedgerows (i.e. linear habitat). We tested the following hypothesis:

- (i) Both habitat amount and landscape heterogeneity increase the gamma functional diversity of grassland and hedgerow assemblages (i.e. functional richness, functional evenness, functional dispersion)
- (ii) Both habitat amount and landscape heterogeneity influence the relative contribution of functional traits to the functional diversity of grassland and hedgerow assemblages

METHODS

Study area and landscape window selection

The study was carried out in the Couesnon river watershed (France). The watershed covers 1,130 km² and is mostly agricultural land with both preserved bocage and intensively managed areas (i.e. crop-dominated landscapes). It is characterised by a low relief, predominantly granitic subsoils and a soil of good agronomic quality (SAGE Couesnon, 2021). We identified seven main land uses: grasslands, hedgerows, crops, fruit orchards, artificial surfaces, woodlands, and rare habitats (i.e. heathlands, water bodies). Thirty (1km x 1km) windows were selected to represent the landscape diversity across the watershed and four independent gradients: (i) compositional heterogeneity, (ii) configurational heterogeneity, (iii) grassland percentage, and (iv) hedgerow percentage (Fig. 1).

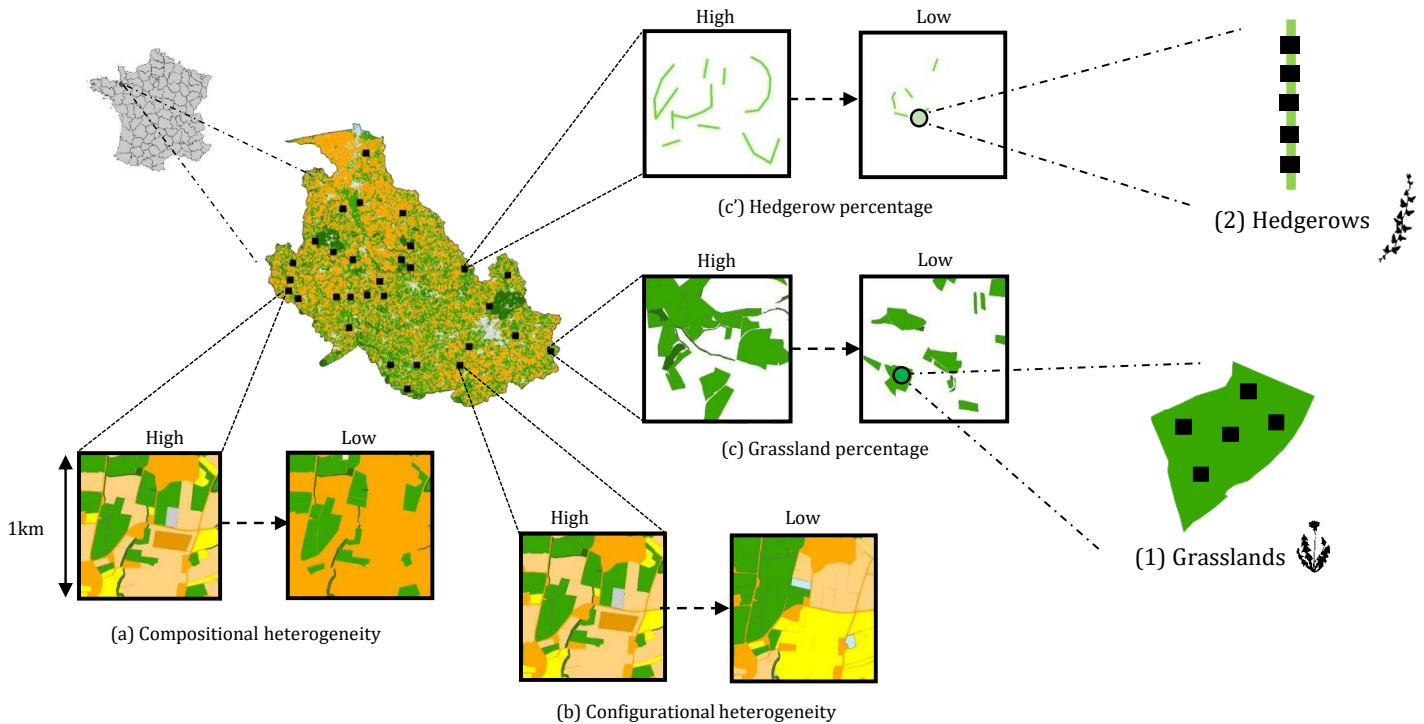


Figure 1: Representation of the four uncorrelated gradients of the 30 landscape windows selected in the Couesnon watershed and the floristics surveys conducted. Landscape variables: (a) Compositional heterogeneity (i.e. Shannon index), (b) Configurational heterogeneity (i.e. percentage of heterogeneous pairs of pixels with different land uses), and the habitat amount (percentage of grassland in grassland assemblages (c); or percentage of hedgerows in hedgerow assemblages (c')). For each gradient, the landscape window on the left represents a high value of the gradient considered and the landscape window on the right represents a low value of the gradient considered. Floristic surveys: in each landscape window, we selected 3 to 5 grassland parcels and 3 to 5 hedgerows. In each grassland parcel and each hedgerow, we conducted 5 floristic surveys. Each grassland survey corresponded to a 2m x 2m quadrat located at least at five metres from the edge of the plot (1). Each hedgerow survey corresponded to a quadrat 2m x the width of the hedgerow (2).

To be representative of the agricultural landscape in the Couesnon watershed, the 30 windows were selected based on other criteria which limit the probability of choosing atypical landscapes : in each window there had to be less than 2% of urbanised area or rare habitats, at least 5% grasslands, and 1% hedgerows. To ensure that the selected sites were representative of the surrounding landscape and to avoid any major edge effects, we compared the area per land-use type in the 1km x 1km landscape with a larger (2km x 2km) area and checked they presented less than 10% difference between each land use (following Dufлот et al., 2015). This selection process permitted to represent the landscape diversity across the watershed without selecting landscape window located at the extremes of the 4 gradients (e.g. 0.5% of grasslands vs. 100% of grasslands). In addition, we validated the homogeneity of the landscape windows selected concerning three ecological factors (i.e. humidity, pH, N score) through the calculation of community weighted means of Ellenberg indices (Please see Table and Fig. S1 for further information). Then, in each window, we analysed independently the herbaceous plant assemblages of two habitat types: hedgerows on one hand and grasslands on the other hand at the gamma diversity level (i.e. the total diversity of a habitat type - grasslands or hedgerows - within a given landscape window).

Landscape heterogeneity and habitat amount

We calculated landscape variables using detailed land-use maps with 5m resolution provided by the French Theia Land Data Centre and detailed hedgerow networks provided by the SAGE Couesnon. Landscape heterogeneity was characterised by two independent components quantified by taking all land-use classes into account: compositional heterogeneity and configurational heterogeneity (Fig. 1). Landscape compositional heterogeneity was characterized using the Shannon diversity index which equals minus the sum, across all land use types, of the proportional abundance of each land use type multiplied by that proportion (McGarigal et al., 2012). It ranged from 0.7 to 1.2 among the 30 landscape windows. The higher the Shannon index, the higher the compositional heterogeneity (i.e. the more land-use types and/or the most equitable the extent of the land-use types in the landscape). Configurational heterogeneity was characterised by the percentage of heterogeneous pairs in pixels including different land use types. It is a proxy of the amount of edges between different land use types which is considered as a variable quantifying configurational heterogeneity (Fahrig et al., 2011). It ranged from 4.7 to 10.3% among the 30 landscape windows. The higher the percentage of heterogeneous pairs, the higher the configurational heterogeneity. Hereafter, we refer to these two variables as compositional and configurational heterogeneity. The third landscape variable is the habitat amount, which was specific for grasslands and hedgerows and was characterized by their respective percentage in the landscape window. The grassland percentage ranged from 12.3 to 57.3% and the hedgerow percentage from 1.2 to 6.1%. All indices were computed using Chloe 3.1 software (Boussard & Baudry, 2014). All indices displayed correlations under 0.45 (Pearson tests, Supporting Information Table and Fig. S2).

Biological surveys

In each landscape window, we studied herbaceous plant assemblages of permanent grasslands (i.e. grassland that had been established at least 5 years previously) and herbaceous plant assemblages of hedgerows (i.e. linear element presenting at least the herbaceous and tree stratum) independently (Fig. 1). These ecosystems represent the two main semi-natural habitats in agricultural landscapes (Duflot et al., 2015) and fulfil many functions including that of refuges and corridors for plants. Moreover, these two habitats are very interesting to study separately as they have very different structures: hedgerows are linear wooded habitats whereas grasslands are habitats covering large areas. In each landscape window, we selected 3 to 5 grassland parcels and 3 to 5 hedgerows. In each grassland parcel and each hedgerow, we conducted 5 floristic surveys. Each grassland survey corresponded to a 2m x 2m quadrat located at least at five metres from the edge of the plot (i.e. 20m² per grassland parcel). Each hedgerow survey corresponded to a quadrat 2m x the width of the hedgerow (Fig. 1). Adapting the width of the survey permitted to capture all hedgerow species in the widest hedgerows and to avoid integrating the flora of other adjacent habitats in the narrower hedgerows. We did not include woody species in our surveys as most tree and shrub species in the hedgerows of the study area were planted by farmers and were consequently not spontaneous. Furthermore, we excluded from the sampling design permanent

grasslands and hedgerows with high level of humidity (i.e. *Juncus acutiflorus* grasslands, flood swards, and riparian hedgerows) to avoid surveys with atypical abiotic conditions. We also controlled partly for tree composition in hedgerows by avoiding hedgerows dominated by *Salix* species or coniferous species, or that were recently planted. Most sampled hedgerows were then dominated by oak and/or chestnut that are the species that were widely planted when bocage was set up. To ensure that the sampling design for both types of vegetation was adapted and sufficient to detect most species in the landscape assemblage, we calculated the species richness accumulation curves of grassland and hedgerow assemblages according to the number of floristic surveys conducted in each landscape window (Fig. S3). To study plant assemblages of both types of plant habitat at the gamma diversity level, the grassland surveys were pooled together on one hand and the surveys of hedgerows were pooled together on the other hand for each landscape window. The analyses were therefore based on the occurrence rate of species within the landscape window (i.e. the proportion of grassland parcels/hedgerows in which a given species was present). For the two types of plant habitat, we finally got a total of 30 gamma assemblages.

Functional traits

As recommended by Laughlin (2014), we selected six functional traits from multiple organs and corresponding to key functional aspects of the plant regeneration cycle (Table 1): seed mass and release height as traits related to the dispersal, onset and duration of flowering as traits related to phenology, and SLA and germination rate as traits related to establishment (Zambrano et al., 2019).

Table 1: Functional traits related to the different stages of the regeneration-cycle of plants of grasslands and hedgerows.

	Min	Max	Mean	SD	Stage of regeneration-cycle
Seed mass (mg)	0.01	46.65	2.51	5.92	Dispersal
Height (m)	0.08	7.63	0.55	0.63	
Onset of flowering (month)	1.00	9.00	5.40	1.30	Phenology
Flowering duration (month)	2.00	12.00	3.74	1.92	
SLA	8.90	57.85	25.67	7.45	Establishment
Germination rate (%)	41.00	100.00	91.33	11.66	

The values were extracted from the LEDA (Kleyer et al., 2008), Bioflor (Kühn et al., 2004), and TRY (Kattge et al., 2020) databases. Missing trait values (< 2% of all data analysed) were estimated using multivariate imputation by chained equation (MICE) following the methodology of Penone et al. (2014) with phylogenetic information extracted from the phylogenetic tree of Zanne et al. (2014). This methodology permits to predict missing trait values from observed life-history traits. Seed mass and plant height were first log-transformed to reduce skewness. All traits were scaled (mean = 0; SD = 1) before analysis, as recommended by Maire et al. (2015). To avoid redundancy in our analysis, we checked trait correlations. All traits were at most correlated with a coefficient of 0.51 (Spearman tests,

Supporting Information Table S4), which is under the 0.7 threshold recommended by Dormann et al. (2013) to detect redundant variables.

Functional diversity metrics and the contribution of individual traits

First, we assessed the gamma functional diversity of plant assemblages in each landscape window by taking the six traits we had selected into account. We measured functional diversity using three complementary multidimensional functional indices (Fig. 2): functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis; Cornwell et al. 2006; Villéger et al. 2008). The last two indices are weighted by the abundance of species and are not correlated with species richness (Fig. 2; Supporting Information Table S5). The quality of the functional space (i.e. the extent to which the functional space is a faithful representation of the initial functional trait values) using the mean squared deviation criterion (mSD) following Maire et al. (2015). Secondly, we investigated the importance of each trait in the calculation of the functional indices. We calculated the relative contribution of each trait to FRic, FEve, and FDis following the methodology of Bittebiere et al. (2019). The trait contribution is the ratio of the index calculated on the multidimensional space including all the functional traits to the index calculated on the multidimensional space that considers all traits except the trait of interest. An increase in the contribution of a given trait to FRic meant that the trait showed high variance and contributed substantially to shaping the index (Fig. 2). For FEve, it indicated that this trait improved the evenness of species distribution in the functional space. For FDis, it indicated that this trait helped disperse the species farther within the functional space. To avoid any mathematical artefact caused by species richness on trait contributions, we simulated 1,000 random assemblages for each landscape window by shuffling species labels across the matrix of functional trait values, and then calculated the expected contribution as the mean value of the 1,000 random assemblages. Then, to correct any mathematical effect of species richness, we calculated the difference between the observed and the expected contributions (Gardener, 2014). We analysed the effect of the landscape on the contribution of the trait to functional diversity using the contribution of the trait concerned corrected for the effect of species richness.

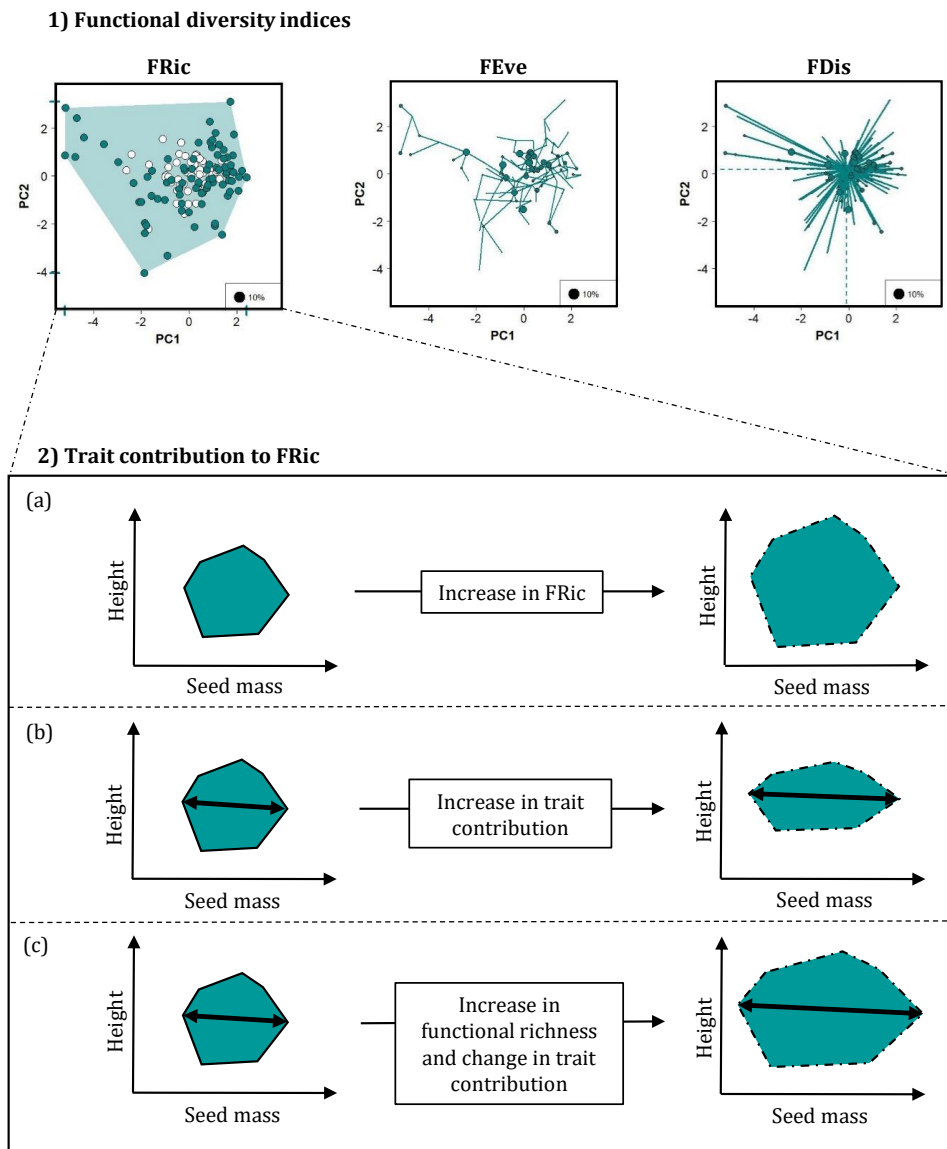


Figure 2: Representation of the three functional indices (FRic, FEve, FDis) and possible variations in trait contributions to FRic. 1) Species represented by circles are plotted in a 2-dimensions functional space according to their trait values on the 2 first axes of the PCoA built to construct the functional space. For FRic representation, blue circles are species present in more than 10% of the total samples and the white circles are species present in less than 10% of the total samples; for FEve and FDis, the size of the circle is proportional to the rate of occurrence of the species. These representation were created thanks to the script of Villéger et al. (2008). 2) Variations in the FRic index and the trait contribution to FRic are given here as examples: (a) the figure represents an increase in the overall FRic index with no change in trait contribution (i.e. greater hypervolume but the same shape), (b) the figure represents an increase in the contribution of seed mass to FRic with no impact on the overall FRic index (same hypervolume but a change in shape depending on the trait contribution); (c) the figure simultaneously represents an increase in FRic and an increase in the contribution of seed mass to FRic (change in both size and shape).

Data analysis

We first investigated the relationship between the functional diversity indices and the landscape structure. For each functional index (FRic, FEve, and FDis), we performed linear regressions with the functional index as the dependent variable and three explanatory variables: compositional heterogeneity

(i.e. the Shannon index), configurational heterogeneity (i.e. the percentage of heterogeneous pairs of pixels showing different land uses) and habitat amount (percentage grassland for grassland assemblages or percentage hedgerow for hedgerow assemblages). Second, we investigated the relationship between the relative contribution of each functional trait to each functional index and the landscape structure. For each functional index and each trait, we performed linear regressions with the relative contribution of the functional trait as the dependent variable and the three landscape variables (compositional heterogeneity, configurational heterogeneity, habitat amount) as explanatory variables. As our analyses were based on 30 landscape windows, we restricted the analysis to three landscape variables as 10 points per explanatory variable are necessary to ensure the validity of the statistical relationships (Peduzzi et al., 1996; Stoltzfus, 2011). For all regressions, the best model was selected by the Akaike information criterion with correction for small sample size (AICc; Burnham and Anderson 2002). The normality of the residuals of all models was tested with Shapiro tests. The maximum value of the variance inflation factor (VIFs) calculated for across the landscape variable was 1.16 and 1.45, for the grassland and hedgerow model respectively, which is well below the threshold of 10 described by Lindborg (2007). All landscape variables displayed indeed correlations below 0.45 (Pearson tests, Supporting Information Table and Fig. S2). The spatial autocorrelation of the residuals of all models was tested and was never significant. All analyses were performed using R software (R Core Team, 2020) with the MuMin (Bartoń, 2020), ncf (Bjornstad, 2020), and car (Fox & Weisberg, 2019) packages.

RESULTS

Functional richness, functional evenness, and functional dispersion of plant assemblages along the gradients

The functional diversity indices of grassland assemblages means were 0.10 +/- 0.06 for FRic, 0.76 +/- 0.04 for FEve, and 0.43 +/- 0.04 for FDis. All three indices were independent of compositional and configurational heterogeneity, whereas FRic and FDis were both significantly correlated with habitat amount. FRic and FDis decreased with an increase in the percentage of grassland (Fig. 3). For hedgerow assemblages, functional diversity indices means were 0.17 +/- 0.10 for FRic, 0.78 +/- 0.02 for FEve and 0.42 +/- 0.02 for FDis. Depending on the index, functional diversity was related to the configurational heterogeneity or the habitat amount. FEve decreased but FDis increased with an increase in configurational heterogeneity (Fig. 3). FRic increased with the percentage of hedgerows.

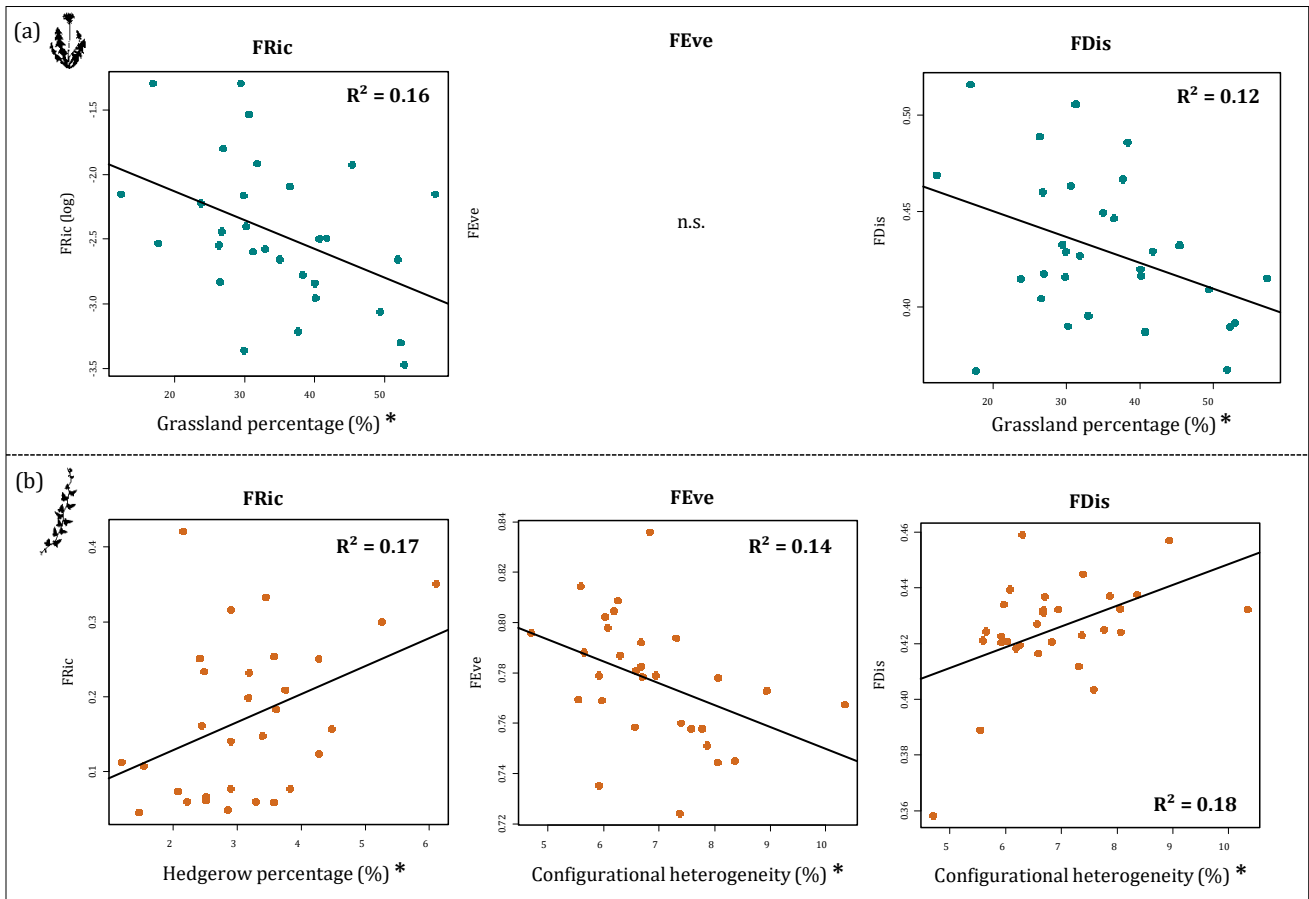


Figure 3: Results of linear models to test the effect of landscape variables on gamma functional diversity indices of grassland (a) and hedgerow (b) assemblages. Significance levels (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, non-significance (n.s.) and R^2 are indicated.



Trait contribution to functional indices along the gradients

The minimum, maximum and median relative contribution of each trait to each functional index are available in Supplementary materials (Table S6). None of the relative contributions of the functional traits predominated over others, whatever the functional index or the type of vegetation considered. However, a trait's relative contribution to the functional indices depended on landscape variables in three out of the six traits in grassland assemblages, and in two out the six traits in hedgerow assemblages. In grassland assemblages, trait relative contributions were not related to compositional or configurational landscape heterogeneity but some were related to habitat amount: two traits (seed mass and height) linked to dispersal and one (germination rate) linked to establishment. No trait contribution linked to phenology was influenced by landscape structure.

The increase in the percentage of grassland was linked to a decrease in the contribution of plant height and germination rate to FRic, and to an increase in the contribution of plant height to FEve and of seed mass to FDis (Table 2). In hedgerow assemblages, trait relative contributions were linked to the three landscape variables: one to phenology (i.e. onset of flowering) and one to establishment (i.e.

germination rate). No trait contribution linked to dispersal was linked to landscape structure. The contribution of the germination rate to FEve increased with the percentage of hedgerow and decreased with an increase in configurational heterogeneity. An increase in compositional heterogeneity was linked to a decrease in the contribution of the onset of flowering to FDis and an increase in the contribution of the germination rate to FDis and to FRic (Table 2).

Table 2: Results of linear models to test the effect of landscape predictors on trait contribution to gamma functional diversity indices of grassland (a) and hedgerow (b) assemblages. Significance levels of variables (**p < 0.01, ***p < 0.001, *p < 0.05), estimates, p-value of the model, R², and Shapiro tests of residuals are indicated.

	Trait	Variable	Intercept	Estimate	p-value	R ²	Shapiro
(a) 	Trait contribution to FRic	Height	0.195	-0.003**	0.002	0.32	0.84
		Configurational heterogeneity		-0.017			
	Germination rate	-0.067	-0.002*	0.04	0.11	0.45	
	Trait contribution to FEve	Height	-0.02	0.001*	0.048	0.10	0.49
Trait contribution to FDis	Seed mass	-0.019	0.001*	0.04	0.11	0.09	
(b) 	Trait contribution to FRic	Germination rate	-0.482	0.446*	0.01	0.17	0.51
	Trait contribution to FEve	Germination rate	0.031	-0.01*	0.02	0.19	0.84
		Percentage of hedgerows		0.01*			
	Trait contribution to FDis	Onset of flowering	0.025	-0.023*	0.048	0.10	0.36
Germination rate		-0.141	0.108***	< 0.001	0.32	0.45	

DISCUSSION

Habitat amount shaped the functional diversity of grassland and hedgerow assemblages

Habitat amount was assumed to increase the three indices describing the gamma functional diversity of our assemblages (i.e. FRic, FEve, FDis) due to the sample area effect (Fahrig, 2013) and the increase in the colonisation rate between patches (Macarthur & Levins, 1967). In the present work, we demonstrated a determining effect of habitat amount on the functional diversity of both vegetation types. However, the effect varied with the context, with a negative impact of habitat amount on the functional diversity of grassland assemblages but a positive impact on the functional diversity of hedgerow assemblages.

In grassland assemblages, the increase in habitat amount was found to be related to a decrease in FRic and FDis. In these assemblages, the increase in habitat amount did not increase the coexistence of functional strategies as predicted and could result from two possible mechanisms. The first mechanism possibly involved in the decrease of functional diversity with the habitat amount is a covariance between habitat amount and the agricultural management type. This assumption is supported by the exclusive or more frequent presence of species specifically related to mowing (e.g.

Arrhenatherum elatius Beauv., Presl. & Presl.; French Chamber of Agriculture, 2019) or intolerant to grazing (e.g. *Vicia hirsuta* Gray. or *Calystegia sepium* L., Kühn et al., 2004) in landscape windows with the highest functional richness values. However, this hypothesis needs to be confirmed with the precise local management data, which should be obtained by contacting all farmers managing the grassland fields in the studied landscape windows. The second mechanism possibly involved in the decrease of functional diversity with the habitat amount is the lower proportion of other land uses sheltering non-grassland species. In landscapes with a high proportion of grasslands, the immigration of sporadically occurring species such as *Glechoma hederacea* (L.), or *Calystegia sepium* (L.) is less likely to occur because of the smaller proportion of their native land uses (i.e. forest fragments; Supporting Information Table S7). Without these functionally original species (i.e. at the margin of the functional space), functional richness and functional dispersion decreased in landscapes with a high proportion of grasslands. By investigating the contribution of each trait, we highlighted the fact that the reduction in total FRic could be due to the decrease in the contribution of plant height and germination rate to this index. Interestingly, these traits are also involved in plant competition for establishment (Cheplick 1996; Gough et al. 2012). They might be selected by more intensive local competition through agricultural practices (Klimesova et al., 2008). In addition, the contribution of height to FEve and the contribution of seed mass to FDis increased with the habitat amount. This result indicates that the gamma plant assemblages were more regular in height and more diversified in seed mass in landscapes with a high habitat amount. The response of these two traits, both of which are related to seed dispersal distance (Thomson et al., 2011), suggests that landscapes dominated by grasslands do not filter dispersal movement and enable the coexistence of species with low or long-distance dispersal (Liao et al., 2013). Yet, seed mass is also an indicator for establishment success (Turnbull et al., 1999) and could also be impacted by the type of management practices. Further work is needed to unravel to which extent the landscape structure and the local management shape the gamma functional diversity of grassland plant assemblages.

In hedgerow assemblages, FRic increased with the habitat amount (i.e. hedgerow percentage). The lack of response by FEve or FDis to habitat amount suggests that this increase in functional richness was due to the presence of functionally original species at the margin of the functional space. In contrast to grasslands, hedgerows are by definition linear habitats that are very much subject to the edge effect due to their positioning at the interface among fields. Hedgerows are thus more likely to be influenced by nearby land uses (Schmucki et al., 2002), whether in terms of abiotic conditions or colonisation by adjacent flora. In landscapes with a dense hedgerow network, the probability of sampling different types of hedgerows associated with different land uses increases. For example, hedgerows adjacent to permanent grasslands are more likely to be semi-forested areas that could shelter species like *Melica uniflora* (Retz.), whereas hedgerows adjacent to crops are more likely to be drier and more frequently disturbed areas that could host species like *Luzula campestris* (DC.). These two species have a contrasted

germination rate: 55% and 100% respectively. As we investigated plant gamma diversity, this set of different local conditions and thus contrasted trait values increases functional richness at the landscape scale. In hedgerow assemblages, the contribution of only one trait, germination rate, was seen to depend on habitat amount. In landscapes with a low hedgerow amount, species functional overlap (i.e. lower contribution to FEve) was higher for this trait, suggesting that certain germination values predominate. These germination values may be related to the dominance of species with high germination rates, as these high germination rates promote their local abundance in the last remaining hedgerow habitats.

Landscape heterogeneity shaped the gamma functional diversity of hedgerows but not that of grasslands.

Landscape compositional and configurational heterogeneity were assumed to affect gamma functional diversity of plants by increasing potential niche availability and encounter rate of species (Poggio et al., 2010; Fahrig, 2017). In the present work, we showed a determining effect of landscape heterogeneity on the gamma functional diversity of hedgerow assemblages but not on grassland assemblages. Landscape configurational heterogeneity was linked to changes in functional diversity and trait contribution while landscape compositional heterogeneity only had an effect on trait contribution.

In hedgerow assemblages, increased configurational heterogeneity was linked to a decrease in FEve but an increase in FDis. This suggests that, in landscapes with high configurational heterogeneity, the functional space is less regularly occupied by species (i.e. some functional niches in landscapes remain vacant), and that this change is driven by a shift among dominant species with specific strategies that differ. An increase in configurational heterogeneity in landscape windows favours the probability of hedgerows being located at interfaces among different habitat types (Fahrig et al., 2011). This may promote the edge effect thereby increasing the probability of colonization by functionally different species. This may result in a shift in the competitive hierarchies among plant species (Zambrano et al., 2019). Thanks to our investigation of the contribution of each independent trait, we saw that the decrease in FEve was probably due to a decrease in the relative contribution of germination rate. This result underlines the role of functional traits in the establishment stage in the plant regeneration cycle. Indeed, functional traits related to establishment were recently shown to be particularly sensitive to edge effects that alter the abiotic conditions required for successful germination (Magnago et al. 2014; Zambrano et al. 2019).

Lastly, compositional heterogeneity affected the contribution of three hedgerow plant traits. The contribution of flowering onset to FDis decreased with increased compositional heterogeneity whereas the contribution of germination rate to FDis increased. Interestingly, compositional heterogeneity

affected the contribution of these traits without affecting the overall FDis index. The lack of effect suggests a stable overall functional dispersion along the compositional heterogeneity gradient but a shift in gamma plant assemblages in hedgerows depending on their phenological and establishment strategies. Indeed, compositional heterogeneity influences niche availability and can increase species turnover (Poggio et al., 2010). Therefore, landscapes with higher compositional heterogeneity could result in greater differentiation between establishment strategies (i.e. germination rate) than in phenology (i.e. onset of flowering). In addition to its higher contribution to FDis, the contribution of the germination rate to FRic also increased in landscapes with high compositional heterogeneity. This result shows that the above-mentioned increase in differentiation in establishment strategies also involved higher variance in this particular trait, with higher germination rates at the margins of the functional space.

Habitat amount versus landscape heterogeneity shape gamma functional diversity in plants

We underlined the usefulness of distinguishing between the independent effect of habitat amount and compositional and configurational heterogeneity by considering the statistically uncorrelated gradients of these components, as they do not influence the same underlying mechanisms. According to the habitat amount hypothesis (Fahrig, 2013), functional diversity was assumed to increase with the habitat amount at the landscape scale (Zambrano et al., 2019). Here we confirmed this hypothesis for hedgerow assemblages, but grassland assemblages displayed an opposite pattern. The contrasting response between the two habitat types could be due to homogeneous practices in grasslands as mentioned previously, but also to their respective proportions in the landscape: since the 1960's, the European agricultural policies implemented in the Couesnon watershed led to the cut down of many hedgerows (Burel & Baudry, 1995). Even in landscape windows where hedgerows were the most preserved, they only represent 6% of the total landscape window area. Any small increase in habitat amount can then be very beneficial to hedgerow assemblages, as opposed to grasslands that already occupy large areas within landscapes. In addition, grassland assemblages were only affected by habitat amount whereas hedgerow assemblages appeared to depend on both habitat amount and landscape heterogeneity. These contrasting results may be inherent to the characteristics of these habitats: because they are linear, hedgerows are more influenced by edge effects, including immigration of other species or by the indirect effect of management practices in adjacent land. Hedgerows are also more stable over time than grasslands (Forman and Baudry 1984; Schmucki et al. 2002) and are therefore more likely to be influenced by successive changes in land use in the surrounding landscape than grasslands, which subject to regular rotation.

Both habitat amount and landscape heterogeneity affected one trait (germination rate), whereas other traits responded specifically to one landscape component. This result underlines the importance of accounting for traits related to plant establishment, which are often overlooked in studies of the

functional response of biodiversity to landscape structure (Zambrano et al., 2019). Our study revealed that accounting for traits related to all stages of the plant regeneration cycle, including dispersal, phenology and establishment, will help understand the assembly rules of plant diversity, which agree with, but upscale, results of recent studies conducted at the patch scale (e.g. Provost et al., 2020; Solé-Senan, Juárez-Escario, Conesa, & Recasens, 2018). However, two traits (flowering duration and SLA) have never been shown to respond to landscape structure. Whether for grassland or hedgerow plants, it seems that reproduction duration and competition following establishment via germination do not play a role in the niche differentiation in either vegetation type. As landscape effect is known to affect biodiversity over long period (i.e. several decades Krauss et al., 2010), it would be interesting to include other traits characterizing the response of plants at a longer term such as seed bank persistence or plant longevity (Lindborg, 2007). Our study highlights the need for further research into the response of gamma functional diversity using uncorrelated gradients of landscape variables but also information about local management to understand the assembly rules of biodiversity at the landscape scale.

ACKNOWLEDGMENTS

We are grateful to Enora Salomon and Benjamin Besse for assistance in the field, to Léa Uroy for help with the collection of functional traits, and to Hugues Boussard for help with Chloé2012 software. This work was funded by the European project Interreg ALICE and Brittany region (France).

SUPPORTING INFORMATION

Table and Figure S1: Ecological description of the 30 landscape windows using community weighted means of Ellenberg humidity, pH and N score. Ellenberg indices describe the affinity of a species to an ecological factor. The humidity index varies from 1 to 12. The pH and N score indices vary from 1 to 9. Species values were collected in Julve (1998). For each landscape window, we calculated the community weighted means of the three indices based on the floristic surveys conducted in grassland assemblages. We chose grassland assemblages for this calculation because they better represent the general landscape window as they cover very large areas compare to the hedgerows. For each index, the standard deviation of the CWM never exceeded 0.26, thus illustrating the homogeneity of the 30 landscape windows.

	Humidity	pH	N score
Mean	5.58	5.34	5.79
SD	0.25	0.12	0.26

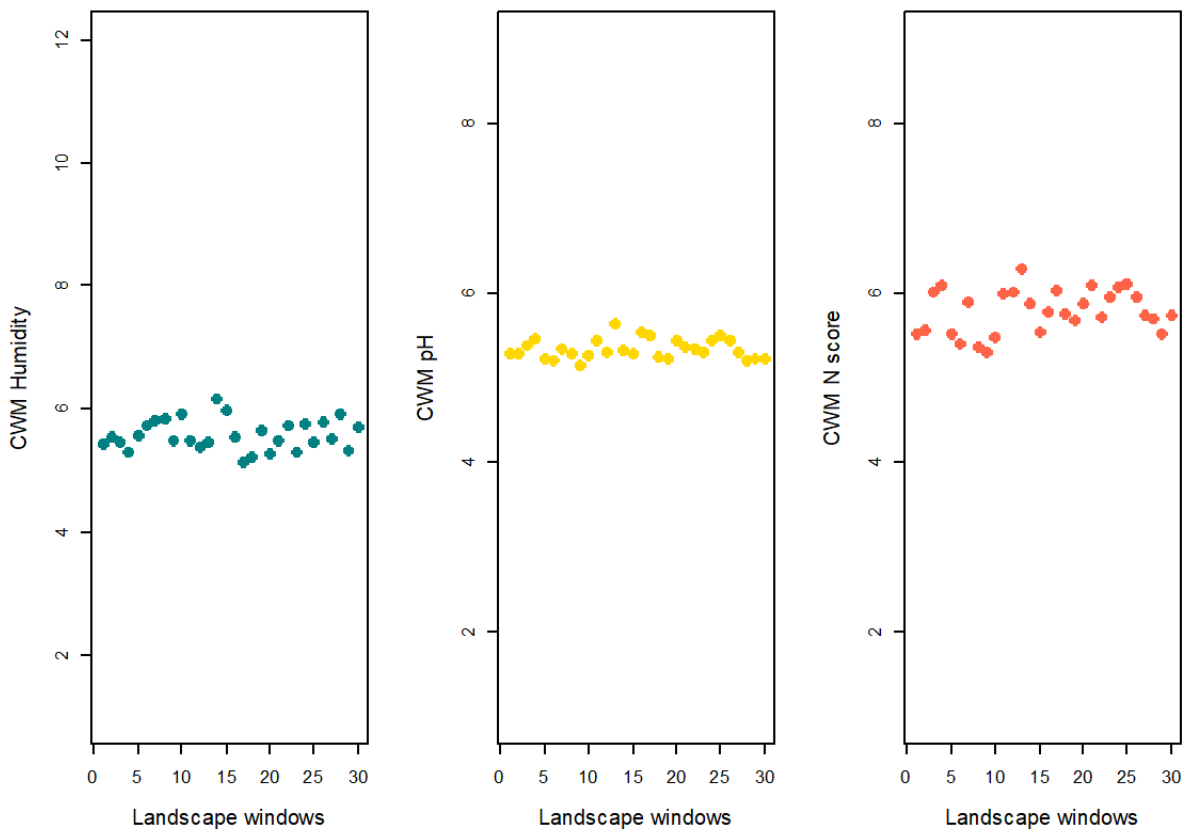


Table and Figure S2: Pearson correlations between the 4 gradients of landscape variables and plots of their ranges.

	Hedgerow percentage	Grassland percentage	Compositional heterogeneity	Configurational heterogeneity
Hedgerow percentage	1.00			
Grassland percentage	0.25	1.00		
Compositional heterogeneity	0.08	-0.08	1.00	
Configurational heterogeneity	0.44	-0.02	0.37	1.00

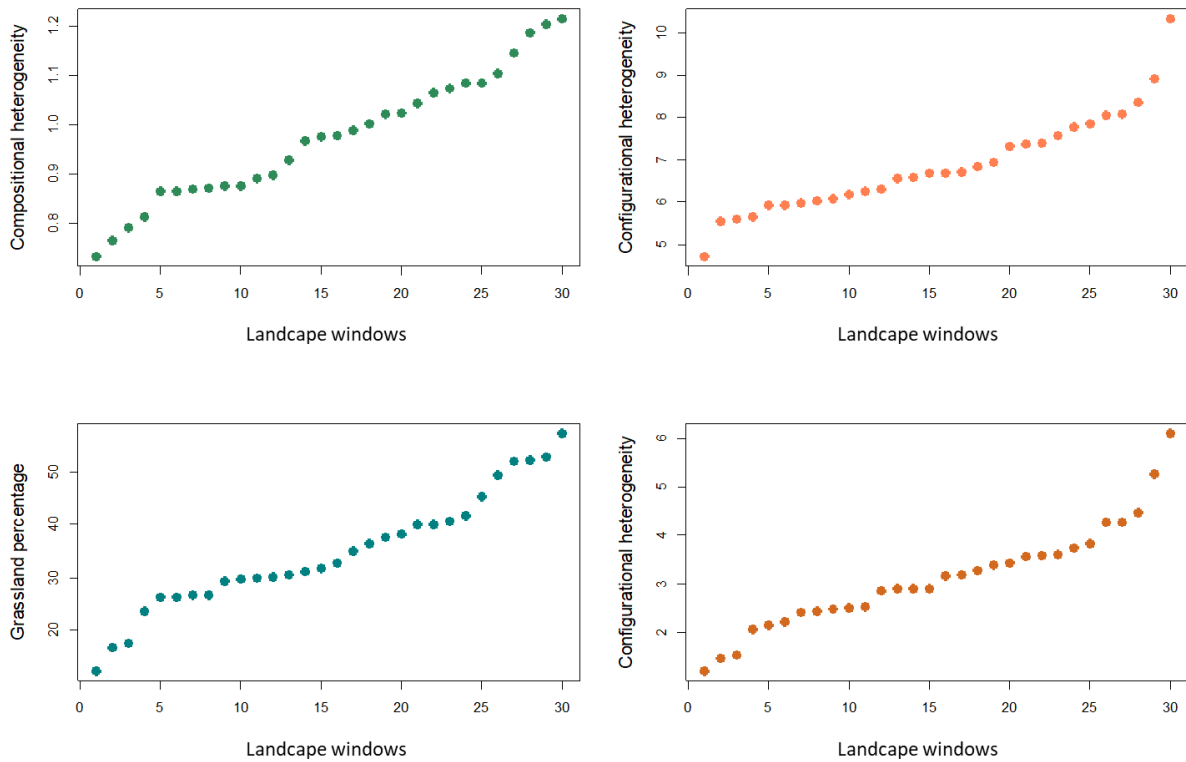


Figure S3: Species accumulation curves of grassland and hedgerow assemblages according to the number of floristic surveys conducted in the landscape windows.

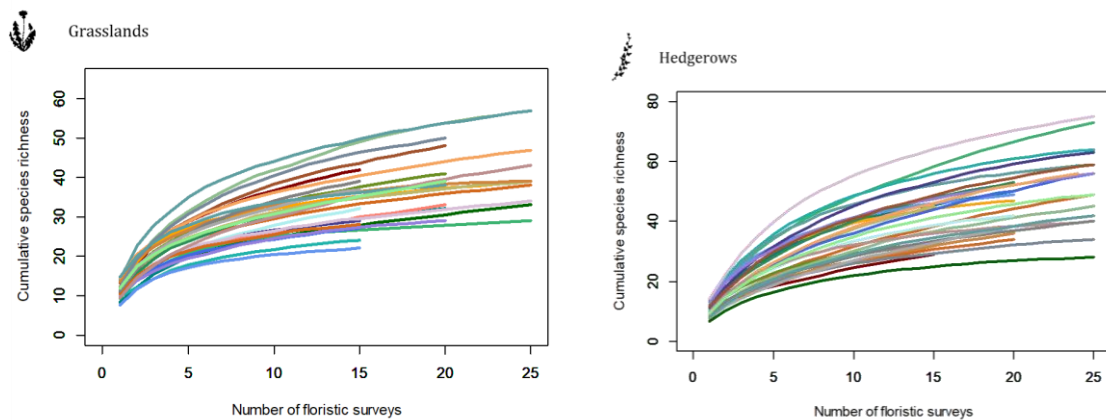


Table S4: Spearman's coefficients of correlation between functional traits.

	Onset	Duration	Seed mass	Height	SLA	Germination
Onset	1.00					
Duration	-0.26	1.00				
Seed mass	-0.03	-0.12	1.00			
Height	0.51	-0.24	0.30	1.00		
SLA	-0.30	0.30	-0.03	-0.18	1.00	
Germination	0.17	0.03	-0.09	0.16	-0.10	1.00

Table S5: Pearson's coefficients of correlation between species richness and the three functional indices for grassland (up) and hedgerow (down) assemblages.



		Species richness	FRic	FEve	FDis
	Species richness	1.00			
	FRic	0.79	1.00		
	FEve	-0.38	-0.35	1.00	
	FDis	-0.14	0.29	0.41	1.00
	Species richness	1.00			
	FRic	0.92	1.00		
	FEve	-0.19	-0.35	1.00	
	FDis	0.32	0.51	-0.30	1.00

Table S6: Minima, maxima, and medians of each trait contribution to each gamma functional index for grassland (a) and hedgerow (b) assemblages. Trait contributions varied from negative to positive because they correspond to the difference between the observed and the mean of expected contributions.



			Seed mass	Height	Onset	Duration	SLA	Germination
(a) 	FRic	Min	-0.170	-0.174	-0.174	-0.145	-0.121	-0.298
		Max	0.109	0.148	0.085	0.164	0.143	-0.021
		Median	-0.038	-0.049	-0.066	-0.052	-0.010	-0.159
	FEve	Min	-0.076	-0.044	-0.059	-0.026	-0.070	-0.040
		Max	0.088	0.056	0.066	0.067	0.102	0.086
		Median	-0.001	0.008	0.010	0.019	0.003	0.004
	FDis	Min	-0.039	-0.049	-0.032	-0.006	-0.045	-0.071
		Max	0.063	0.029	0.032	0.090	0.038	-0.014
		Median	0.016	-0.020	0.001	0.034	0.012	-0.051
(b) 	FRic	Min	-0.207	-0.086	-0.091	-0.174	-0.059	-0.241
		Max	0.235	0.121	0.098	0.109	0.223	0.184
		Median	0.010	-0.002	-0.001	-0.036	0.016	0.003
	FEve	Min	-0.046	-0.035	-0.051	-0.071	-0.033	-0.053
		Max	0.057	0.091	0.042	0.049	0.067	0.047
		Median	0.007	0.004	0.005	-0.012	0.006	-0.001
	FDis	Min	-0.036	-0.006	-0.014	-0.054	0.011	-0.075
		Max	0.094	0.049	0.019	-0.002	0.119	0.031
		Median	-0.001	0.019	0.002	-0.030	0.046	-0.039

Table S7: Pearson's coefficients of correlation between all percentages of land-uses across the 30 landscape windows of the Couesnon watershed.

	Water	Orchards	Other	Hedgerows	Grasslands	Crops	Forest	Artificial
Water	1							
Orchards	0.00	1.00						
Other	0.10	-0.18	1.00					
Hedgerows	0.09	-0.18	0.32	1.00				
Grasslands	-0.02	-0.28	-0.01	0.23	1.00			
Crops	0.08	0.06	-0.40	0.01	-0.58	1.00		
Forest	-0.09	0.04	0.46	-0.06	-0.28	-0.48	1.00	
Artificial	-0.28	-0.03	-0.34	0.23	0.22	0.10	-0.43	1

Chapitre 3

Effet de la structure du paysage sur la diversité fonctionnelle des prairies et leur productivité

En résumé : L'intensification de l'agriculture a entraîné la destruction progressive des habitats semi-naturels et la simplification des paysages du Nord-Ouest de l'Europe. Tous ces changements profonds ont des effets négatifs sur la diversité végétale et pourraient en avoir sur les fonctions écosystémiques associées, telles que la productivité primaire. À l'échelle du paysage, cette relation biodiversité-productivité doit encore être testée dans des systèmes réels.

Nous avons testé la relation paysage-biodiversité-productivité au sein de 30 fenêtres paysagères (1kmx1km). Nous avons mis en lien 4 variables paysagères (deux décrivant les quantités d'habitats semi-naturels et deux décrivant l'hétérogénéité du paysage), la diversité fonctionnelle des plantes de prairies et leur productivité. La diversité fonctionnelle a été calculée à partir de quatre traits fonctionnels pris en compte simultanément, et la productivité des prairies estimée grâce à une série temporelle d'images satellitaires Sentinel-2.

La diversité fonctionnelle des assemblages de plantes des prairies était influencée par les quantités d'habitats semi-naturels mais pas par l'hétérogénéité du paysage. Les trois indices décrivant la diversité fonctionnelle des assemblages de plantes diminuaient avec la quantité de prairies, et seule la régularité fonctionnelle augmentait avec la quantité de haies.

Les paysages abritant des communautés de plantes avec une régularité fonctionnelle plus élevée avaient une productivité annuelle moyenne plus élevée et moins variable dans l'espace. Ce résultat est en accord avec le principe de complémentarité des niches : des assemblages plus équilibrés sont plus efficaces dans l'exploitation des ressources, ce qui se traduit par une productivité plus élevée et moins variable dans l'espace.

L'effet positif des haies sur la régularité fonctionnelle des prairies et leur productivité indique que les paysages agricoles bénéficieraient de la préservation et de la restauration des haies pour assurer une grande diversité fonctionnelle végétale à l'échelle du paysage et pour maintenir une production efficace de fourrage dans le futur.

Landscape structure influences grassland productivity through plant functional diversity

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Agriculture intensification led to the gradual destruction of semi-natural habitats and landscape simplification in the landscapes of North-Western Europe. All these profound changes affected grassland plant assemblages. It could have negative effects on the plant diversity and the related ecosystem functions, such as primary productivity. At the landscape scale, this biodiversity-productivity relationship still have to be tested in real-world systems. It could have important economic implications concerning fodder production. We used a large-scale sampling design (30 landscape windows – 1km × 1km) to quantify landscape structure variables (semi-natural habitat amounts and landscape heterogeneity), grassland plant functional diversity calculated from multidimensional functional spaces (functional richness, evenness, dispersion), and grassland productivity (annual mean, temporal stability, spatial variability) derived from annual satellite time-series. Functional diversity of grassland plant assemblages was related to semi-natural habitat amounts but not to landscape heterogeneity. The overall functional diversity decreased with grassland amount whereas the functional evenness increased with hedgerow amount. Grassland plant assemblages with a higher functional evenness presented a higher annual mean productivity and lower spatial variability at the landscape scale. We demonstrated the effect of landscape structure on grassland productivity at the landscape scale, with a functional-mediated effect through the amount of semi-natural habitat and a direct effect through landscape heterogeneity. Agricultural landscapes would benefit from the preservation and restoration of hedgerows, to ensure high plant functional diversity at the landscape scale, and to maintain efficient and resilient production of fodder in the future.

Key words: landscape heterogeneity, habitat amount, grasslands, satellite, BES

INTRODUCTION

Since the first European agricultural policies implemented 60 years ago, the intensification of agriculture has been accompanied by a profound transformation of landscape structures (Tscharntke et al., 2005; Tieskens et al., 2017). For example, in the bocage landscapes of north-western Europe, this transformation occurred through the gradual destruction of semi-natural habitats such as hedgerows and permanent grasslands (Burel et al., 1998). It also occurred through a simplification of landscapes (Stoate et al., 2001), leading to homogeneous structures with enlarged fields and very few uncultivated areas (Tscharntke et al., 2005). All these profound changes resulted into a decline in biodiversity and an alteration of agroecosystem functioning (Burel et al., 1998; Sanaullah et al., 2020). It affected especially plant assemblages (e.g. Duflot et al., 2015), including grasslands that shelter a large range of plant species (Peyraud, 2017). These landscape structure changes can have negative effects on the plant diversity and the associated ecosystem functions such as primary productivity (Zirbel et al., 2019). Yet, maintaining and enhancing primary productivity, especially in grasslands, is an important issue in agroecosystems as grasslands are the major source of fodder that supports livestock (Isselstein et al., 2005). Understanding the relationship between the plant diversity and the productivity at in landscapes is crucial to maintain efficient ecosystem functioning in agrosystems.

The trait-based approach have been developed over the last years to better understand the diversity-ecosystem functioning relationship in plant assemblages (e.g. Cadotte et al., 2009; Lavorel, 2013). Indeed, beyond its usefulness to investigate the response of grassland assemblages to environmental conditions (i.e. response traits; Lavorel & Garnier, 2002), the trait-based approach also permits to investigate what effect these grassland plant assemblages have in turn on the ecosystem functioning (i.e. effect traits; Lavorel & Garnier, 2002). More recently, the development of indices based on multidimensional functional spaces (Villéger et al., 2008) better describe the presence, distribution, and diversity of traits within assemblages (Roscher et al., 2013) by considering the trade-offs between traits (Wright et al. 2010). It is possible to quantify the different facets of the functional diversity of assemblages by using complementary indices quantifying the functional richness (FRic), the functional evenness (FEve) or the functional dispersion (FDis). Although this trait-based approach is now well developed to study the biodiversity-productivity relationship in experimental grasslands (e.g. Roscher et al., 2013; Schittko et al., 2014), very few studies investigated this relationship in complex real-world grasslands where assemblages are influenced by the landscape structure (Hautier et al., 2018; Jochum et al., 2020).

Landscape structure is one of the main drivers of plant diversity in agricultural landscapes (Pfestorf et al., 2013). It can affect grassland plant diversity through several components: the grassland amount (Fahrig, 2013) and the amount of other semi-natural habitats that can serve as ecological shelters and way of dispersal (e.g. hedgerows; Burel & Baudry, 1995), but also through the diversity and the

spatial complexity of all land-uses in the landscape (i.e. compositional and configurational heterogeneity; Fahrig et al., 2011). All these landscape components are expected to independently influence processes such as dispersal (Fahrig, 2017) and niche availability (Poggio et al., 2010). Therefore, the effect of landscape structure on these processes might shape the trait-composition of grassland plant assemblages according to their response traits related to dispersal (e.g. height), establishment and persistence (e.g. SLA; Zambrano et al., 2019). Here we expected that landscapes with higher habitat amount and higher heterogeneity would favour the functional diversity of grassland plant assemblages by increasing its functional richness (i.e. higher FRic), evenness (i.e. higher FEve), and dispersion (i.e. higher FDis).

The trait-composition of grassland plant assemblages can have in turn an effect on ecosystem functions such as primary productivity (e.g. Yi et al., 2020; Zirbel et al., 2019). Indeed, traits related to dispersal (e.g. height), phenology (e.g. onset and duration of flowering), or establishment (e.g. SLA) can influence the mean, the temporal stability, and the spatial variability of the primary productivity (Weigelt et al., 2008; Zhao et al., 2010; Yi et al., 2020). According to the main theories developed for the biodiversity-productivity relationship, plant assemblages more diversified are expected to be more productive as they provide greater guarantees that some species will maintain functioning even if others fail (i.e. insurance hypothesis; Yachi & Loreau, 1999). More even plant assemblages are also expected to be more efficient at exploiting resources (i.e. niche complementarity; Tilman et al., 1997) which can also lead to enhance productivity. Here we expected that grassland plant assemblages with a wider (i.e. higher Fric), more balanced (i.e. higher FEve), and more diverse (i.e. higher FDis) trait-composition have higher, less spatially variable, and more temporally stable primary productivity at the landscape scale.

As highlighted above, the landscape structure can influence the trait-composition of grassland plant assemblages (i.e. response traits), and this trait-composition can in turn influence the primary productivity (i.e. effect trait). By considering traits that are both response and effect traits in indices describing the functional diversity of assemblages (i.e. FRic, FEve, FDis), we can expect to find a functional-mediated effect of the landscape structure on grassland productivity. Investigating this question is crucial in the current context of biodiversity loss in agricultural landscapes, as the results could have important economic issues for farmers who need to maintain a high level of fodder production (Oehri et al., 2017). Here, our work aimed to understand the relationships between the landscape structure, the functional diversity of grassland plant assemblages, and their primary productivity. We used a large-scale sampling design (30 landscape windows – 1×1km) to quantify several landscape structure variables related to the landscape heterogeneity and the amount of semi-natural habitats, grassland plant functional diversity calculated from multidimensional functional

spaces, and grassland productivity calculated using remote sensing tools. We tested the following hypothesis:

(i) The amount of semi-natural habitats (i.e. grasslands and hedgerows) and the landscape heterogeneity (i.e. compositional and configurational) shape the functional diversity of plant assemblages at the landscape-scale

(ii) A higher functional diversity of plants favours the annual mean and the temporal stability of productivity and reduces its spatial variability

(iii) The amount of semi-natural habitats and the landscape heterogeneity affect grassland productivity whether or not mediated by its effect on the functional diversity of plant assemblages

METHODS

Study area and landscape window selection

The study was carried out in the Couesnon river watershed (1130km², France). This study area is dominated by agricultural land and encompasses a large range of landscape structures. We selected thirty windows (1km x 1km; Fig. 1) to represent the landscape diversity across the watershed. They were selected along four independent landscape gradients: (i) grassland percentage, (ii) hedgerow percentage, (iii) compositional heterogeneity, (iv) configurational heterogeneity. (i) and (ii) characterised the amount of semi-natural habitats while (iii) and (iv) characterised the landscape heterogeneity. The 30 windows were selected based on additional criteria to limit the probability of choosing atypical landscapes: in each window, there had to be less than 2% of urban areas or rare habitats, at least 5% of grasslands, and 1% of hedgerows. To ensure that the selected windows were representative of the surrounding landscape and to avoid any major edge effects, we compared the area per land-use type in the 1km x 1km landscape with a larger 2km x 2km area and checked they presented less than 10% difference in each land use between the two scales (Duflot et al. 2015).

Amount of semi-natural habitats and landscape heterogeneity

We calculated landscape variables using a detailed 2017 land-use land cover (LULC) map with 10 m resolution provided by the French Theia Land Data Centre (overall accuracy 86%, Inglada et al., 2017), and a field-based map of hedgerow networks provided by the local manager. The LULC map was

subsampled to a 5m grid using the nearest neighbour approach and merge with the map of hedgerow networks. We obtain a map with 5m resolution where seven main LULC classes were identified: grasslands, hedgerows, crops, fruit orchards, artificial surfaces, woodlands, and rare habitats (i.e. heathlands, water bodies). We quantified the amount of the two main semi-natural habitats present in agricultural landscapes: grasslands and hedgerows. The grassland percentage ranged from 12.3 to 57.3% and the hedgerow percentage from 1.2 to 6.1% (Table 1). Two additional variables characterising the landscape heterogeneity were calculated by considering all LULC classes: compositional heterogeneity and configurational heterogeneity. Landscape compositional heterogeneity was characterized using the Shannon diversity index, which depends on the number of land-use types and their relative surface area (McGarigal et al., 2012). It ranged from 0.7 to 1.2 among the 30 landscape windows (Table 1). The higher the Shannon index, the higher the compositional heterogeneity (i.e. the more LULC classes and/or the most equitable the extent of the LULC classes in the landscape). Configurational heterogeneity was characterised by the percentage of heterogeneous pairs in pixels including different LULC classes (i.e. the percentage of interface among land-use patches). It ranged from 4.7 to 10.3% among the 30 landscape windows (Table 1). The higher the percentage of heterogeneous pairs, the higher the configurational heterogeneity. Hereafter, we refer to these two variables as compositional and configurational heterogeneity. All indices were computed using Chloe 3.1 software (Boussard & Baudry, 2014). All indices displayed correlations under 0.45 (Pearson tests, Supporting Information S1).

Biological surveys

In each landscape window, we collected in 2019 herbaceous plant assemblages of permanent grasslands (i.e. grasslands that have been established at least for 5 years). In each landscape window, between 3 to 5 grassland parcels were selected depending on the availability of grassland parcels within the landscape window. In each grassland parcel, 5 floristic surveys were conducted (Fig. 1). Each grassland survey corresponded to a 2m x 2m quadrat located at least at five meters from the edge of the plot to avoid any effect of adjacent land use. To characterize the species assemblage at the landscape scale, all surveys conducted in each landscape window were pooled and the analyses were based on the occurrence rate of species within the landscape window (i.e. the proportion of plots in which a given species was present).

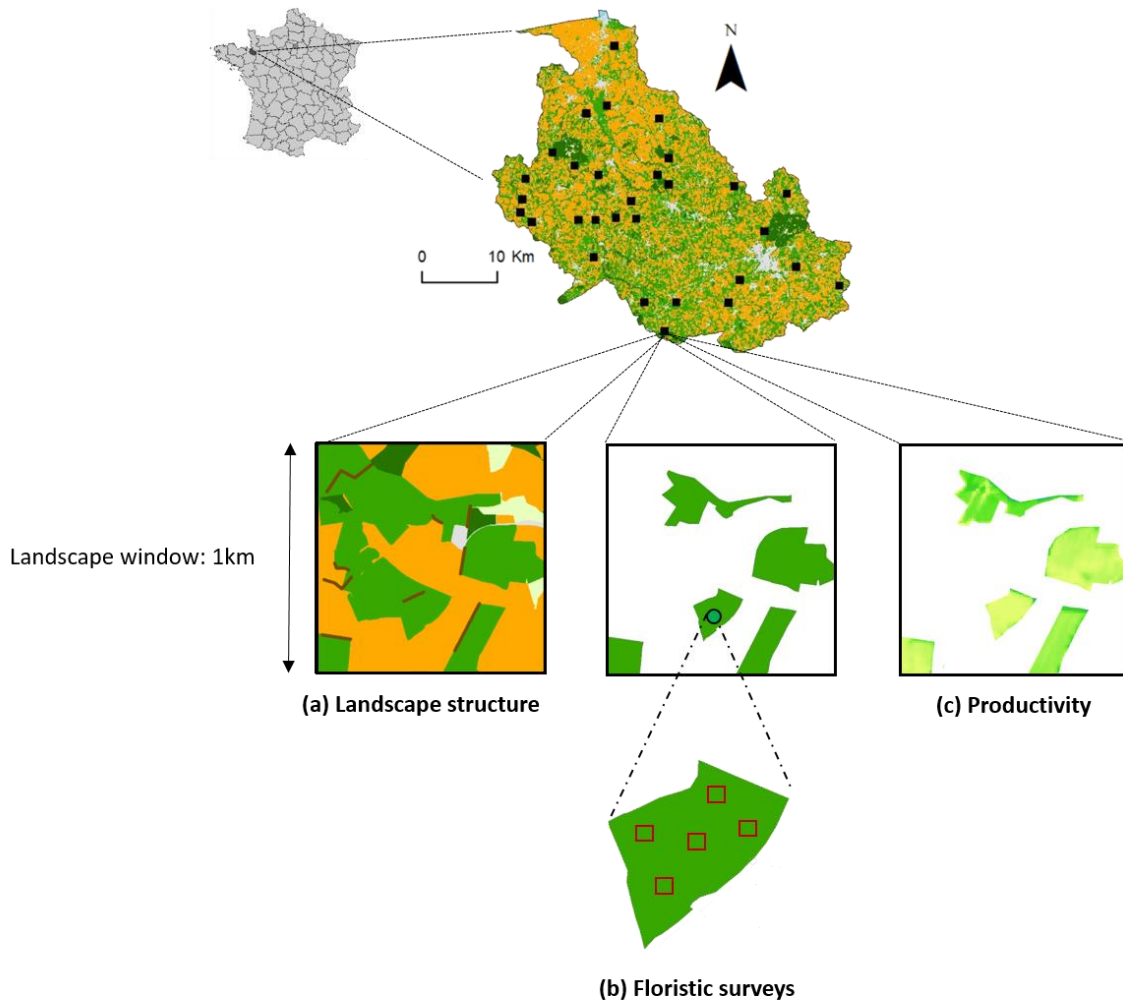


Figure 1: Overview of the protocol conducted to describe the landscape structure, the functional diversity, and the productivity of grasslands in the 30 landscape windows (black squares) distributed in the Couesnon watershed (France). In each landscape window, we quantified (a) the landscape variables (i.e. grassland amount, hedgerow amount, compositional heterogeneity, configurational heterogeneity). Land use classes are indicated by different colours. Dark green: woodlands; orange: crops; leaf green: grasslands; light green: orchards, brown: hedgerows; grey: artificial surfaces. (b) In each landscape window we conducted 5 floristic surveys (red squares) in 3 to 5 grassland parcels represented in green and (c) we calculated 3 productivity indices of the sampled grassland parcels using NDVI values derived from 2019-2020 annual satellite Sentinel-2 time-series. The pixel NDVI values are represented from yellow to blue colour: the more blue the higher the value.

Functional traits and indices

Four functional traits were selected to investigate both the response of plants to the landscape structure (i.e. response traits) and their effect on the primary productivity (i.e. effect traits): plant height, onset and duration of flowering, and SLA (Supporting Information S2). The values were extracted from the LEDA (Kleyer et al., 2008), Biolflor (Kühn et al., 2004), and TRY (Kattge et al., 2020) databases. Missing trait values (< 2% of all data analysed) were estimated using multivariate imputation by chained equation (MICE) following the methodology of Penone et al. (2014) with phylogenetic information extracted from the phylogenetic tree of Zanne et al. (2014). Plant height was first log-transformed to reduce skewness and all traits were scaled (mean = 0; SD = 1) before analysis, as recommended by Maire

et al. (2015). Furthermore, as recommended by Dormann et al. (2013), we checked the correlation between traits: all traits were at most correlated with a coefficient of 0.55 (Supporting Information S3). We assessed the functional diversity of plant assemblages in each landscape window by simultaneously considering the four selected traits. We measured functional diversity using three complementary multidimensional functional indices: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). FRic represents the amount of functional space filled by the assemblage within the convex hull volume (Cornwell et al. 2006; Villéger et al. 2008). This index is not weighted by the abundance of species but is correlated with species richness (Supporting Information S4). FEve represents the regularity of the distribution and the relative abundance of species within the functional space of the assemblage (Villéger et al. 2008). A high FEve implies a greater regularity of species distribution in the functional space. FDis represents the mean distance between each species and the centroid of all species in the functional space (Laliberté and Legendre 2010). A high FDis implies marked trait dissimilarity among species. The last two indices are weighted by the abundance of species and are not correlated with species richness (Supporting Information 4). Before calculating the functional indices, we checked the extent to which the functional space is a faithful representation of the initial functional trait values (i.e. quality of the functional space) using the mean squared deviation criterion (mSD) following Maire et al. (2015).

Grassland productivity data

We used the Normalized Difference Vegetation Index (NDVI) as a proxy of grassland productivity. This index is derived from remote sensing data in the red and the near-infrared bands and is a good indicator of photosynthesis (Pettorelli et al., 2005). We used annual satellite Sentinel-2 time-series (Level-3A) provided by the French Theia Land Data Centre. The level 3A of S-2 images has a resolution of 10m in the red (b4: 664 nm) and near-infrared (b8: 835 nm) bands. These monthly images (~40 days) are cloudless composite. First, we downloaded all images of the two tiles covering our study area from October 2019 to September 2020. In total, 13 images (i.e. 1 image for each month and 2 images for August 2020 due to cloud-free conditions) were available. The image of October 2019 was excluded from the analysis due to the large cloud cover on the studied landscape windows, leaving 12 images for the productivity assessment (i.e. from November 2019 to September 2020). Second, we digitalized the grassland parcels where floristic surveys were conducted, with an internal buffer of 10m from the edge to avoid outliers (Supporting Information S5). For each month, we calculated the median NDVI values of each grassland parcel (NDVI is hereafter referred as productivity). From these monthly data, we calculated the annual mean and standard deviation of each parcel. From the annual mean of each grassland parcel, we calculated two indices at the landscape window scale. To do so, we took all parcels included in each landscape window and we calculated the mean productivity, and the spatial variability of productivity (i.e. standard deviation of the annual means of the parcels over the window). From the

annual standard deviations of each grassland parcel, we calculated one additional index: the temporal stability of productivity (i.e. minus mean of annual standard deviations of the parcels over the window). None of the indices was correlated to the number of grassland parcels used for calculation (Pearson tests; Supporting Information S7).

Data analysis

To ensure appropriate comparisons of regression coefficients among models described hereafter, all variables were scaled before the analysis (mean = 0; SD = 1). To test our first hypothesis that the amount of semi-natural habitats and the landscape heterogeneity shape the functional diversity of plant assemblages at the landscape scale, we conducted linear regressions with each of the functional index (i.e. FRic, FEve, FDis) as dependent variables and the grassland amount, hedgerow amount, compositional heterogeneity, and configurational heterogeneity as independent variables (model A). To test our second hypothesis that a higher functional diversity of plants favours the grassland productivity, we conducted linear regressions with each of the productivity indices (i.e. mean productivity, spatial variability, temporal stability) as dependent variables and the 3 functional indices (i.e. FRic, FEve, FDis) as independent variables (model B). To test our third hypothesis that the amount of semi-natural habitats and the landscape heterogeneity affect grassland productivity, we conducted linear regressions with each of the productivity indices (i.e. mean productivity, spatial variability, temporal stability) as dependent variables and with the 4 landscape variables (i.e. grassland and hedgerows amounts, compositional and configurational heterogeneity) as independent variables. To further explore our third hypothesis that landscape structure has a mediated effect on grassland productivity, we performed a path analysis to calculate how the amount of semi-natural habitats and landscape heterogeneity affect the mean, spatial variability, and temporal stability of productivity through its effect on the functional assemblages of grassland plants. We multiplied (i) the standardized regression coefficient of model A with (ii) the standardized regression coefficient of model B. We thus obtained the mediated effect of the landscape structure on grassland productivity at the landscape scale. For all regressions, the best model was selected by the Akaike information criterion with correction for small sample size (AICc; Burnham and Anderson 2002). The normality of the residuals of all models was tested with Shapiro tests. Across all regressions, the maximal variance inflation factor (VIF) was 1.98 which is far below the threshold of 10 described by Lindborg (2007). The spatial autocorrelation of the residuals of all models was tested using spline correlograms and was never significant. All analyses were performed using R software (R Core Team, 2020) with the MuMIn (Bartoń, 2020), ncf (Bjornstad, 2020), and car (Fox & Weisberg, 2019) packages.

RESULTS

Across the 30 landscape windows selected, we found a total of 130 species of grassland plants. The grassland species richness within landscape windows ranged from 22 to 57 and was not related to any of the landscape variables. Ranges and means of all variables (i.e. landscape structure, functional diversity, productivity) included in the analysis before they were scaled are presented in Table 1.

Table 1: Minimum, maximum, and mean of landscape structure, functional diversity, and productivity variables included in the statistical analysis. These variables were calculated at the landscape window scale: landscape variables were quantified within each 1×1 km window, functional diversity variables were based on the species occurrence rate within each window, and productivity variables were calculated with monthly NDVI values of the sampled grassland plots within each landscape window.

	Min	Mean	Max
Landscape variables			
<i>Grassland amount (%)</i>	12.3	34.7	57.3
<i>Hedgerow amount (%)</i>	1.2	3.1	6.1
<i>Compositional heterogeneity</i>	0.7	1.0	1.2
<i>Configurational heterogeneity</i>	4.7	6.9	10.3
Functional diversity variables			
<i>FRic</i>	0.17	0.35	0.70
<i>FEve</i>	0.67	0.75	0.82
<i>FDis</i>	0.30	0.36	0.47
Productivity variables			
<i>Mean productivity</i>	0.75	0.81	0.94
<i>Spatial variability</i>	0.004	0.03	0.06
<i>Temporal stability</i>	-0.21	-0.14	-0.06

Effect of amount of semi-natural habitats and landscape heterogeneity on the functional diversity of grassland plant assemblages

The functional diversity indices of grassland assemblages ranged from 0.17 to 0.70 for FRic, from 0.67 to 0.82 for FEve, and from 0.30 to 0.47 for FDis before transformation (Table 1). All three indices were independent of the compositional and the configurational heterogeneity but were negatively related with the grassland amount. FRic, FEve, and FDis were lower in landscapes with higher grassland amount (Table 2; Fig. 2). This result indicates that a higher amount of grasslands resulted in a lower volume of the multidimensional functional space (FRic), but also a lower regularity of the distribution of species within the functional space (FEve), and a lower distance from the species to the centroid (FDis). In addition, FEve was positively correlated with the hedgerow amount: FEve was higher in landscape windows with higher hedgerow amount. This result indicates that plant species were more regularly distributed in the functional space when the hedgerow amount was high.

Table 2: Results of linear models conducted with landscape structure, functional diversity, and productivity variables. Each letter corresponds to one of the three hypotheses: (a) linear models conducted to test the link

between landscape structure and functional diversity variables (hyp. 1). (b) linear models conducted to test the link between functional diversity and productivity variables (hyp. 2). (c) linear models conducted to test the link between landscape structure and productivity variables (hyp. 3). Significance levels of variables (**p < 0.01, *p < 0.05), non-significance (n.s.), estimates, p-value of the model, R², and Shapiro tests of residuals are indicated.

		Variables	Intercept	Estimate	p-value	R ²	AICc	Shapiro
(a)	FRic	Grassland amount	2E-16	-0.42*	0.04	0.15	86.84	0.15
		Hedgerow amount		0.3				
	FEve	Grassland amount	6.00E-17	-0.39*	0.03	0.18	85.79	0.43
		Hedgerow amount		0.39*				
	FDis	Grassland amount	4E-16	-0.38*	0.03	0.12	86.15	0.65
(b)	Mean productivity	FEve	-3E-16	0.39**	0.004	0.28	81.78	0.32
	Spatial variability	FEve	-1E-16	-0.37*	0.04	0.11	86.54	0.07
	Temporal stability		n.s.					
(c)	Mean productivity	Configurational heterogeneity	-5E-16	-0.43*	0.01	0.15	84.97	0.13
	Spatial variability	Compositional heterogeneity	-3E-16	0.55**	0.002	0.31	80.06	0.31
		Grassland		0.27				
	Temporal stability		n.s.					

Effect of the functional diversity of grassland plant assemblages on the productivity

The productivity ranged from 0.75 to 0.94 for the mean, from 0.004 to 0.06 for the spatial variability, and from -0.21 to -0.06 for the temporal stability before transformation (Table 1). The mean productivity and the spatial variability were related to the functional evenness (i.e. FEve) of grassland plant assemblages (Table 2; Fig. 2) but not to the functional richness or dispersion. The mean productivity of grasslands was higher and the spatial variability of productivity was lower in landscape windows with a higher functional evenness of grassland plant assemblages. The temporal stability of productivity did not respond to any of the tested functional diversity variables.

Direct and mediated effects of landscape structure on grassland productivity

Two out of three productivity indices directly responded to landscape heterogeneity but any to habitat amount variables. Mean productivity was lower in landscape windows with higher configurational heterogeneity and spatial variability was higher in landscapes with higher compositional heterogeneity (Table 2; Fig. 2). As FEve (i) was driven by the grassland amount and the hedgerow amount and (ii) affected the mean and spatial variability of productivity, we obtained a mediated effect of the amount of semi-natural habitats on the mean and the spatial variability of grassland productivity. Specifically, the grassland amount within landscape windows caused the mean productivity to decline (-0.16) and the spatial variability of productivity to increase (0.15). Conversely, the hedgerow amount within landscape windows caused the mean productivity to increase (0.15) and the spatial variability of productivity to decline (-0.14).

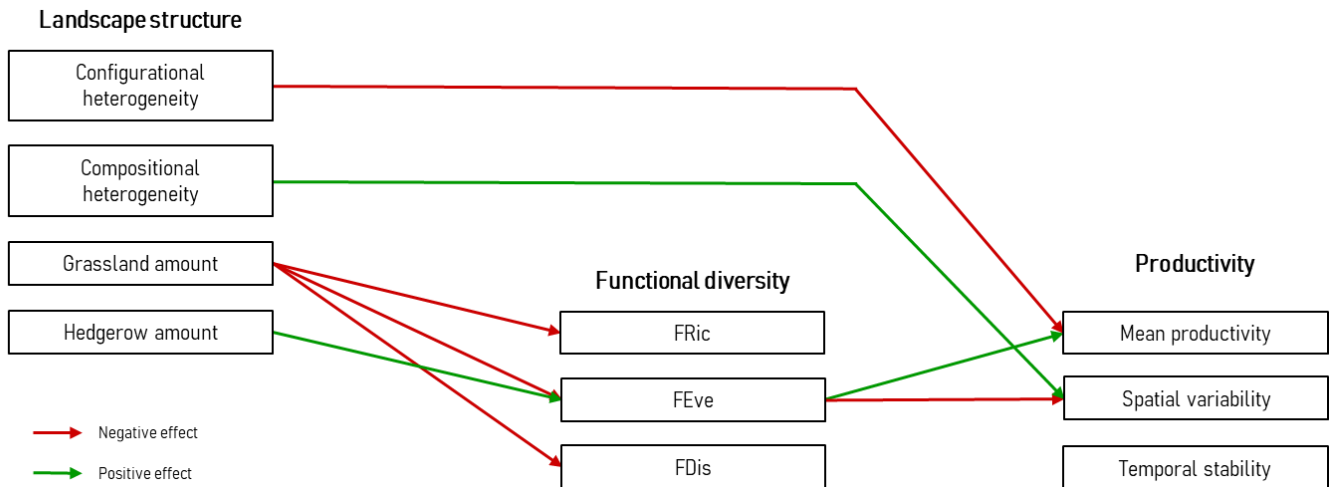


Figure 2: Representation of the significant relationships between landscape structure, functional diversity, and productivity variables. Red arrows represent negative effects, green arrows represent positive effects.

DISCUSSION

Effect of amount of semi-natural habitats on the functional diversity of grassland plant assemblages

Functional diversity of grassland plant assemblages were related to semi-natural habitat amounts but not to landscape heterogeneity, validating partially our first hypothesis. The functional diversity decreased with grassland amount (all metrics) and increased with hedgerow amount (FEve only).

Grassland amount was assumed to increase functional diversity at the landscape scale (Fahrig, 2013; Zambrano et al., 2019) because a higher habitat amount is supposed to increase the sample area effect (i.e. larger sample areas generally contain more species; MacDonald, Anderson, Acorn, & Nielsen, 2018) and the habitat availability (Gazol et al., 2012). Our results invalidated this hypothesis as landscapes with higher grassland amounts corresponded to grassland plant assemblages with lower FRic, FEve, and FDis. This lower functional diversity indicates a convergence of plants toward particular functional types. One possible explanation might be the covariation between high habitat amount and homogeneous agricultural practices, especially in this agricultural territory dominated by livestock production (47% of total agricultural production;). Grazing and mowing are indeed known for selecting specific strategies among plant assemblages according to their competitiveness and avoidance of disturbance (Díaz et al., 2007; Klimesova et al., 2008). This selection could result in a lower functional diversity in landscapes with a high amount of grasslands homogeneously managed. Further work is needed to unravel to which extent the amount but also the quality of the habitat are impacted by the agricultural practices conducted at the local scale.

Conversely, grassland plant assemblages presented species more regularly distributed in the functional space (higher FEve) when the hedgerow amount was high within landscapes. First, hedgerows are one of the semi-natural habitats that can serve as ecological shelters and corridors for plants in intensive agricultural landscapes (Burel & Baudry, 1999; Vanneste et al., 2020). With a higher hedgerow amount in a landscape window, species that are good dispersers but poor competitors can disperse and still establish in new grassland plots (i.e. mass effect, Shmida & Wilson 1985). Second, a high hedgerow amount may also favour the probability of species from other semi-natural habitats (e.g. woodlands, hedgerows), characterized by other functional traits, to immigrate and establish in grassland plots which can promote coexistence among plants. These two mechanisms might have promoted the complementarity of functional niches within grassland assemblages at the landscape scale, without affecting the total volume of the functional space (i.e. no response of FRic) or the dominance of specific dissimilar trait syndromes (i.e. no response of FDis).

Effect of the functional diversity of plant assemblages on grassland productivity

Our second hypothesis was that the functional diversity of plants favours the mean and temporal stability of productivity, and reduces the spatial variability. We demonstrated that only one functional index (i.e. FEve) was related to two productivity indices (i.e. mean and spatial variability). The temporal stability of productivity did not respond to any functional index.

Grassland plant assemblages with a higher FEve presented higher mean of productivity and lower spatial variability of productivity at the landscape scale. These results are in adequacy with the niche complementarity principle (Tilman et al., 1997): more functionally even assemblages are more efficient at exploiting resources, which resulted in higher and less spatially variable productivity. Although experimental studies found contrasted results concerning functional evenness and primary productivity (e.g. Roscher et al., 2013; Sonkoly et al., 2019), we bring new empirical evidence that increasing functional evenness favour *in situ* primary productivity at the landscape scale. The absence of a link between productivity and FRic do not validate the insurance hypothesis (Yachi & Loreau, 1999) but rather confirms that rare species are not determinant in the ecosystem productivity, following the mass ratio hypothesis of Grime (1998) (e.g. Sonkoly et al., 2019; Polley et al., 2020). The temporal stability of the productivity did not respond to any functional index. This could be due to the short period of productivity assessment as our remote-sensing data cover only one year. It would be interesting to further investigate this hypothesis by quantifying the temporal stability of grassland productivity over several years (e.g. García-Palacios et al., 2018; Oehri et al., 2017; Veen et al., 2020) as studies suggested that the plant diversity effects on productivity increase with time (Cardinale et al., 2011). Overall across the main possible explanations about the diversity-productivity relationship developed with

experimental designs (i.e. insurance hypothesis, niche complementarity), our results supported the niche complementarity at the landscape scale.

Effect of landscape structure on the productivity

Our third hypothesis was that an effect of the landscape structure on grassland productivity could be detected, whether or not mediated by the functional diversity of plant assemblages. We found both direct and indirect effects of the landscape structure but different landscape components were involved: landscape heterogeneity had a direct effect on grassland productivity whereas habitat amount had an effect mediated by the composition of plant assemblages. The configurational heterogeneity decreased mean productivity whereas compositional heterogeneity increased spatial variability of productivity. These relationships were not mediated by the functional diversity of plant assemblages, suggesting that landscape heterogeneity influences other processes independent of the plant composition. Indeed, landscape heterogeneity can also reflect the conducted agricultural practices such as the use of chemical pesticides and inorganic fertilisers (Norton et al., 2009). These practices could affect the level of productivity of the grasslands without influencing the trait composition of plant assemblages. Further work including information about the type and use of inputs might help to unravel the mechanisms explaining the direct effect of landscape heterogeneity on grassland productivity.

Applications and further research

We demonstrated that the landscape heterogeneity and the amount of semi-natural habitat both influenced the grassland productivity but not through the same processes. It highlights that disentangling uncorrelated gradients of landscape variables is today crucial to better understand which landscape component act on the plant diversity and the associated functions. The role of semi-natural habitats such as hedgerows in landscapes has long been considered as related to the support of biodiversity, wood production, control of soil erosion, and windbreak (Montgomery et al., 2020). Here we demonstrated that hedgerows can also affect the primary productivity of other LULC classes based on their effect on the diversity of grassland plant assemblages. Yet, the European agricultural policies implemented to facilitate agricultural work led to the cut down of many hedgerows in the north-western European landscapes (Carlier & Moran, 2019). These changes implemented to facilitate agricultural work could nevertheless prove to be counterproductive as they have negative effects on biodiversity and the related ecosystem functioning (Hooper et al., 2005; Montgomery et al., 2020). Agricultural landscapes would benefit from the preservation and the restoration of hedgerows to both shelter plant diversity and to maintain efficient and resilient production of fodder in the future.

The wide-scale multidisciplinary approach we developed in this study allowed us to investigate the effect of landscape structure on productivity through fine floristic surveys and remote sensing tools. So far, the rare studies investigating the effect of landscape variables on biodiversity-productivity

relationship quantified the grassland productivity by cutting and weighing all plant material at the end of the growing season (e.g. Zirbel et al., 2019). However, the recent development of remote sensing tools for investigating this type of research question is very promising because they allow a standardised, more regular, and complete spatial monitoring of the productivity (Pettorelli et al., 2018). The contribution of remote sensing to quantifying productivity on long and regular time scales offers new and highly stimulating research prospects that can be easily applied over large areas and thus contribute to decision-making in public policy.

Acknowledgments

We are grateful to Myriam Marsot, Olivier Jambon, Enora Salomon, and Benjamin Besse for assistance in the field. We are also grateful to the large network of farmers who gave access to their grassland fields and the SAGE Couesnon for the hedgerow network map. Sentinel-2 data were retrieved by CNES (<https://theia.cnes.fr/>) and the detailed 2017 LULC maps by CESBIO. This work was funded by the LTSER « ZA Armorique », the European project Interreg ALICE and the Brittany region (France).

Author's contribution

LL, AE, SR, and CM conceived the ideas and designed the methodology; EF helped to write the R scripts for remote sensing data acquisition; LL collected all data and did all analysis; LL, AE, and CM led the writing of the manuscript. All authors gave final approval for publication.

SUPPORTING INFORMATION

Table and figure S1: Pearson correlations between the 4 gradients of landscape variables and plots of their ranges.

	Hedgerow percentage	Grassland percentage	Compositional heterogeneity	Configurational heterogeneity
Hedgerow percentage	1.00			
Grassland percentage	0.25	1.00		
Compositional heterogeneity	0.08	-0.08	1.00	
Configurational heterogeneity	0.44	-0.02	0.37	1.00

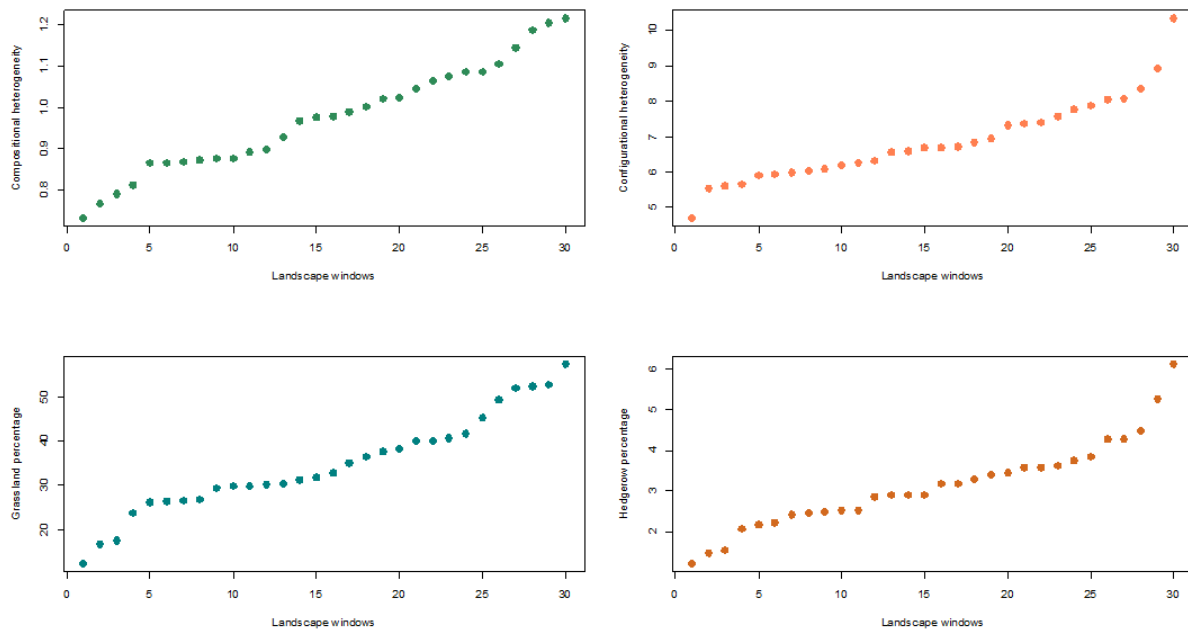


Table S2: Minimum, maximum, mean and standard deviation of functional traits.

	Min	Max	Mean	SD
Onset of flowering (month)	1.00	9.00	5.40	1.30
Flowering duration (month)	2.00	12.00	3.74	1.92
SLA	8.90	57.85	25.67	7.45
Height (m)	0.08	7.63	0.55	0.63

Table S3: Spearman’s coefficients of correlation between functional traits.

	Onset		Duration		Height		SLA	
	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value
Onset	1.00	0						
Duration	-0.34	< 0.001	1.00	0				
Height	0.55	<0.001	-0.30	<0.001	1.00	0.00		
SLA	-0.25	0.003	0.26	0.002	-0.17	0.04	1.00	0

Table S4: Pearson’s coefficients of correlation between species richness and the three functional indices for grassland assemblages.

	Species richness		FRic		FEve		FDis	
	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value
Species richness	1.00	0.00						
FRic	0.52	0.003	1.00	0.00				
FEve	-0.17	0.35	-0.19	0.3	1.00	0.00		
FDis	-0.14	0.47	0.57	0.001	0.24	0.19	1.00	0.00

Figure S5: Aerial image of a grassland parcel and the delimitation for productivity assessment. The crosshatched area is an example of the internal buffer conducted in each grassland parcel to avoid outliers.



Figure S6: Histogram of mean NDVI values per grassland plot calculated to test NDVI value saturation

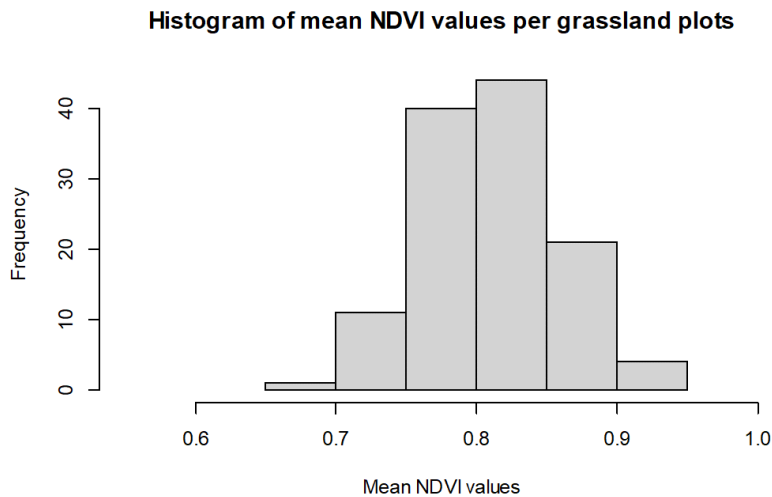


Table S7: Pearson's coefficients of correlation between productivity indices and number of grassland parcels.

	Number of plots	
	Coefficient	p-value
Mean	-0.38	0.04
Spatial variability	0.26	0.16
Max	0.50	0.004

Chapitre 4

Effet de la structure future du paysage du bassin versant du Couesnon sur les services écosystémiques

En résumé : Les politiques d'aménagement du territoire et de l'agriculture et les conséquences qui en découlent façonnent la structure du paysage au sein des régions. Cette structure paysagère peut avoir un impact sur les écosystèmes et sur la capacité de ces écosystèmes à fournir des services à l'Homme.

L'objectif de ce chapitre était de prédire les changements dans les services écosystémiques (diversité et productivité des plantes de prairies, régulation du climat) suivant différents scénarios d'aménagement du territoire du bassin versant du Couesnon. Nous avons estimé les relations entre la structure du paysage et les services écosystémiques directement à partir de relevés floristiques, d'images de télédétection et de la température de l'air mesurée dans 30 fenêtres paysagères (1kmx1km). Pour projeter ces relations dans le futur, nous nous sommes appuyés sur trois scénarios socio-économiques contrastés en termes de développement agricole et territorial : un tendanciel ('Business-as-usual') et deux contrastés, dont l'un axé sur un développement écologique ('Green attractivity') de l'agriculture et l'autre sur l'intensification agricole via la céréalisation ('Energy performance'). Les simulations ont été réalisées tous les 10 ans jusqu'à 2050.

Les fenêtres paysagères sélectionnées ont permis de capturer les différences d'évolution des occupations du sol entre les trois scénarios. Les différences dans l'hétérogénéité du paysage entre scénarios étaient faibles. Les paysages simulés différaient essentiellement par la quantité de prairies avec une grande augmentation pour le scénario 'Green attractivity', un maintien stable pour le scénario tendanciel et une perte drastique pour le scénario 'Energy performance'.

Les services de conservation de la diversité végétale des prairies étaient favorisés par le scénario tendanciel et le scénario le plus intensif en termes de développement agricole. Nous avons également démontré que ce scénario intensif était le plus favorable pour les services liés à la productivité, suggérant une absence de compromis entre les deux catégories de services. Cependant, la perte drastique de la quantité de prairies dans ce scénario intensif atténue ces résultats, car presque un quart des fenêtres paysagères sont passées sous un seuil de viabilité des prairies à la fin des pas de temps simulés.

L'effort de recherche sur les projections de l'évolution de l'occupation des sols est essentiel car les décisions que nous prenons actuellement conditionneront les structures futures du paysage et les services qu'elles fourniront.

Future impact of land-cover changes on grassland ecosystem services in a bocage landscape

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ABSTRACT

The territorial and agricultural planning policies and their resulting consequences shape the landscape structure within regions. This landscape structure can have an impact on the ecosystems and the ability of these ecosystems to provide services to humans. It is necessary to understand and project the relationships between the landscape structure and the ecosystem services in the future to assess the possible consequences of land-management policies on these services. The aim of this study was to predict the changes in ecosystem services (climate regulation and grassland plant diversity and productivity), in the bocage landscapes of the Couesnon watershed (France). We estimated the landscape structure-ecosystem services relationships directly from fine-grained values of floristic surveys, remote sensing images and air temperature measured in 30 landscape windows. To project these relationships in the future, we relied on three socioeconomic scenarios, one trend (Business-as-usual) and two contrasted in terms of agricultural and territorial development (Green attractivity and Energy performance), which simulated landscape maps based on a FORESCEM model. The current landscape structure did not influence the climate regulation services but influenced four grassland ecosystem services. Landscape changes depending on the scenario were related mostly to the modification in grassland and hedgerow amounts. We demonstrated that the services linked to grassland plant diversity were favoured by the Business-as-usual scenario and the most intensive scenario in terms of agricultural development. The latter scenario was also the most favourable for productivity-related services. However, the drastic loss of grassland amount in this scenario mitigates these results as almost a quarter of the landscape windows crossed under a grassland viability threshold at the end of the simulated time steps. The trend scenario Business-as-usual scenario finally ensures an intermediate level of services at the landscape level with a conservation of the grassland amount. Research effort on land cover change projections is essential as our currently made decisions will condition the future landscape structures and the services they will provide.

INTRODUCTION

Landscapes are constantly changing because they are under the pressure of human activities (Antrop 2005). Human activities generate rapid land cover changes, which are mostly responsible for the recent alteration of the Earth's land surface (Houet et al., 2010; Turner, 2010). Land cover and land use changes occur through the action of driving forces that are mostly endogenous to agricultural development (Mazzocchi et al., 2013) but also exogenous such as urban planning (Antrop, 2005; Mazzocchi et al., 2013). The different components of the landscape structure such as the heterogeneity of the landscape matrix (Fahrig et al., 2011) and the presence and abundance of semi-natural habitats (Duflot et al., 2015) are then changing over time. Changes in these components can then influence ecosystems functioning and the provision of services to humans (Grêt-Regamey et al., 2014). It is therefore important that land cover changes receive more and more attention from scientists and policymakers as they can have long-term consequences to human wellbeing (Turner, 2010).

Changes in landscape structure influence species assembly in semi-natural habitats (Sanaullah et al., 2020), particularly for plants (Zirbel et al., 2019). They influence notably dispersal processes (Shmida & Wilson, 1985; Fahrig 2017), niche availability (Poggio et al., 2010), and abiotic conditions distribution (e.g. energy flow, Ryszkowski & Kędziora, 1987; climate, Guyot & Seguin, 1976). For example, the amount of semi-natural habitats defines the availability for species to have their optimal environment within the landscape (Fahrig, 2013). In addition, the landscape composition and configuration of the surrounding matrix can facilitate dispersal through the presence of corridors, for example, or hinder it with the presence of barriers. Therefore, landscape structure changes can influence the taxonomic and functional diversity of plant assemblages within these habitats (e.g. Concepción et al., 2017; Jonason et al., 2017; Zambrano et al. 2019).

Species composition and their characteristics (i.e. functional traits) can in turn influence the ecosystem functioning and the services provided. For instance, several studies suggest that a high diversity of functional traits within plant communities may favour primary productivity (Oehri et al., 2017). Zirbel et al. (2019) highlighted that the functional diversity of grasslands was positively associated with multifunctionality, including above ground biomass, and was affected by the landscape context. Although the effects of the current landscape structure on plant assemblages and the associated services are increasingly recognised (e.g. Lavorel et al., 2011; Oehri et al., 2017), it appears important to investigate the potential effects of the future landscapes to predict the consequences of land management policies on ecosystem services in the medium and long term (Houet et al., 2016).

Among the different agricultural landscapes, the bocage is an important provider of various ecosystem services (Burel & Baudry, 1995). The bocage is defined as an agriculture-dominated

landscape characterised by the presence of networks of linear woody vegetation structures (i.e. hedgerows; Baudry & Jouin, 2003). Bocage landscapes are often also characterized by the presence of permanent grasslands and are typical of North-Western Europe (Burel et al., 1998). They are important providers of many ecosystem services: these services can be cultural and social as hedgerows and grassy environments fulfil an aesthetic function of the agricultural landscapes (van Zanten et al., 2014). Bocage landscapes support biodiversity conservation as hedgerows and grasslands shelter many species (Dufлот et al. 2015) and act as corridors for their dispersal (Mony et al., 2018). They also supply the production of fodder in grasslands (Isselstein et al., 2005) or wood in hedgerows (Montgomery et al. 2020), and regulate the climate through the bocage density. Hedgerow networks affect wind speed, air temperature and plant evapotranspiration (Guyot and Seguin 1976). Despite its potential interest in providing multiple ecosystem services, the bocage has been in sharp decline over the past 50 years due to land use changes induced by the implementation of European agricultural policies and urbanisation (Bazin & Schmutz, 1994; Bruhier et al., 2007). Because bocage is constituted of ecosystems that take a long time to be set up, its decline could slow down or accelerate in the future depending on territorial management decisions made currently (Morin et al., 2019), which may have consequences in several decades affecting the future provision of ecosystem services.

The aim of this study was to predict the changes in three types of ecosystem services (climate regulation and grassland plant diversity and grassland production) in the bocage landscapes of the Couesnon watershed (France). This small watershed encompasses a large range of landscape structures with a more or less dense network of hedgerows depending on the location. To assess the future impacts of land use changes on ecosystem services, we first selected 30 landscape windows across the watershed to represent the current landscape structure diversity. These 30 landscape windows allowed us to estimate the current values of ecosystem services (i.e. climate regulation, taxonomic and functional diversity and productivity of grassland plants) at the watershed scale. Second, we closely investigated the relationships between the current ecosystem services and the landscape structure in these landscape windows using floristic surveys and air temperature measured in the field, and productivity measurements through the analysis of Sentinel-2 images. Finally, we tested three socioeconomic scenarios constructed by Palka et al. (submitted) reflecting contrasted trajectories of agricultural and territorial development to project the possible consequences of land-use changes on the ecosystem services.

METHODS

1. Study area and selection of sites

Study area

The study was carried out in the Couesnon river watershed located in North-Western France (Figure 1). This small watershed (1130km²) is dominated by agricultural land and encompasses a large range of landscape structures. The agricultural production is mainly allocated to livestock and dairy production. This type of production is reflected in the landscape by a large proportion of grasslands (temporary and permanent, 33% in the watershed), with also large areas allocated to maize, and other crops (46 % in the watershed). Forest areas are concentrated in two main forests and the rest of the woodland areas are small post-agricultural woodland patches (10% in the watershed). The Couesnon watershed is also characterized by a network of hedgerows more or less dense according to the location (4% in the watershed).

Site selection

We used a detailed land-cover map done in 2018 (Kermap database) and the hedgerow network (SAGE Couesnon, 2021). Both maps were converted to 5 m resolution raster and merged together. We identified seven main land uses: grasslands, hedgerows, crops, artificial surfaces, woodlands, water bodies and rare habitats (i.e. heathlands, recolonisation). We selected thirty windows (1km x 1km) to represent the landscape diversity across the watershed. They displayed four main independent landscape gradients: (i) grassland percentage, (ii) hedgerow percentage, (iii) landscape compositional heterogeneity, (iv) landscape configurational heterogeneity. Landscape compositional heterogeneity was characterized using the Shannon diversity index (Supplementary S1). The higher the Shannon index, the higher the compositional heterogeneity. Configurational heterogeneity was characterised by the percentage of heterogeneous pairs in pixels including different land-use types (Supplementary S1). The higher the percentage, the higher the configurational heterogeneity. All indices were computed using Chloe 3.1 software (Boussard & Baudry, 2014). All indices displayed correlations under 0.46 (Pearson tests, Supplementary Table S2).

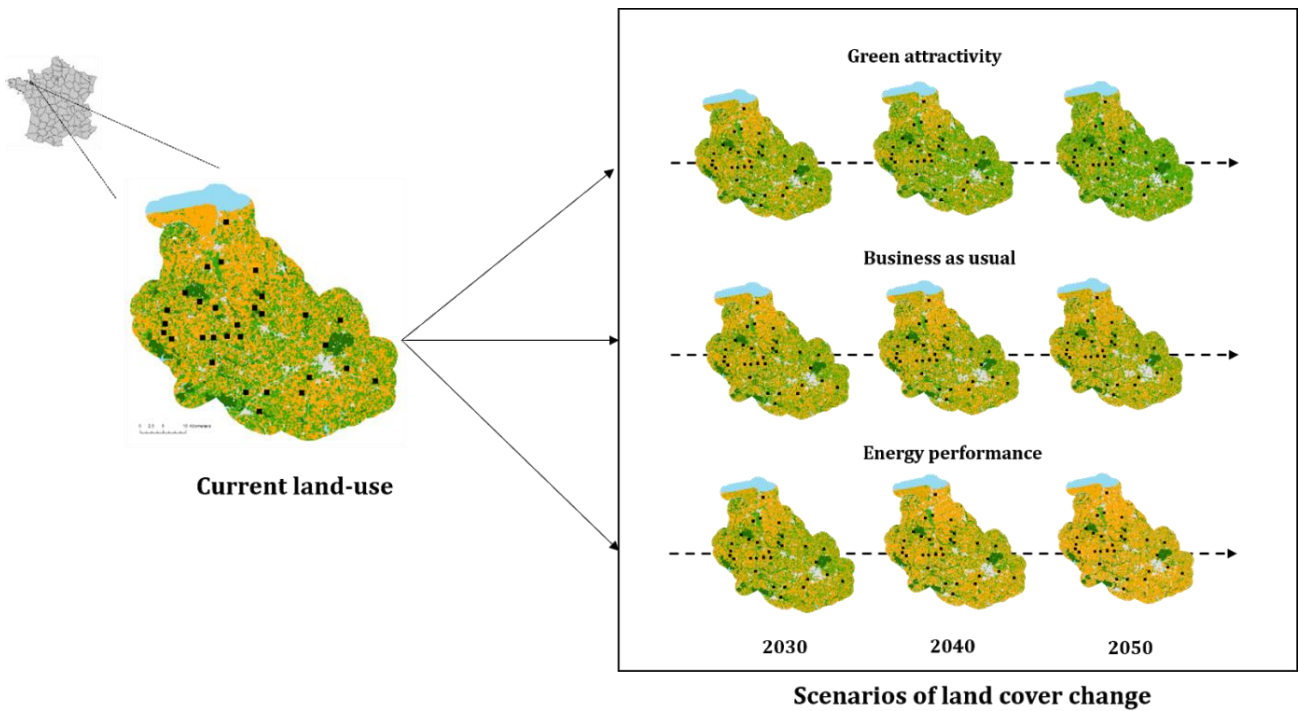


Figure 1: Study area location and schematic representation of the protocol set up to estimate the bocage services under three land use changes scenarios. The black squares are the 30 landscape windows selected across the watershed. We kept one trend scenario and two contrasted scenarios among the eight possible used in Palka et al. (submitted), namely (i) Business as usual, (ii) Green attractivity, and (iii) Energy performance.

2. Establishing the relationships among current landscape variables and bocage services

Climate regulation

We quantified climate regulation services that can be influenced by the landscape structure, especially by the hedgerow network of the bocage (Guyot and Seguin 1976; Forman & Baudry, 1984). Two air temperature loggers were placed in each landscape window. These loggers (Tinytag Plus 2 - TGP-4017, © Tinytag) were placed in shelters (ACS-5050, © Tinytag) and fixed at 2m above the ground on wooden poles adjacent to grassland parcels. Before and after the recording experiment, we conducted tests to check for potential logger effects: all loggers were placed in the same room for 24h and we checked that the recorded values were similar. The 60 loggers located across the watershed recorded the air temperature every hour from October 2019 to September 2020. From these values, we calculated three climate regulation indices: (i) the annual mean temperature, (ii) the sum of degree-days (Supplementary S3), and (iii) the number of frost days (i.e. days that crossed below 0°C) per landscape window.

Grassland ecosystem services

Biological surveys

In each landscape window, we focused on the herbaceous plant assemblages of permanent grasslands, which correspond to grasslands that have been established at least for 5 years. In each landscape window,

from 3 to 5 grassland parcels were selected depending on the availability of grassland parcels comparable in terms of ecological conditions. Indeed, to avoid the selection of grassland parcels with atypical abiotic conditions, we excluded from the sampling design permanent grasslands with high level of humidity or grasslands assumed recently over-seeded. In each grassland parcel selected, we conducted five floristic surveys. Each grassland survey corresponded to a 2m x 2m quadrat located at least at five meters from the edge of the plot to avoid any edge effect from the adjacent land cover. The five surveys within a parcel were pooled together to match the minimal area suggested by Mueller-Dombois & Ellenberg (1974): 20m² per grassland were thus surveyed. Finally, to characterize the species assemblage at the landscape scale, all surveys conducted in each landscape window were pooled and the analyses were based on the occurrence rate of species within the landscape window (i.e. the proportion of parcels in which a given species was present).

Taxonomic and functional diversity of grasslands.

For each landscape window, we quantified the taxonomic and functional diversity of grassland plant assemblages by calculating six indices. Three indices were related to taxonomic diversity: the species richness (SR), the Shannon diversity and Pielou's evenness indices. Three indices were related to functional diversity: the functional richness (FRic), the functional evenness (FEve) and the functional dispersion for the functional diversity (FDis). To calculate the functional diversity indices, we selected four functional traits: plant height, onset and duration of flowering, and SLA (Supplementary Table S4.). The values were extracted from the LEDA (Kleyer et al., 2008), Bioflor (Kühn et al., 2004), and TRY (Kattge et al., 2020) databases. Missing trait values (< 2% of all data analysed) were estimated using multivariate imputation by chained equation (MICE; Penone et al., 2014). Before calculating the functional indices, plant height was log-transformed and all traits were scaled (mean = 0; SD = 1). From the floristic surveys and the functional traits, we assessed the functional diversity of grassland plant assemblages by simultaneously considering the four selected traits. All functional indices were calculated using the script of Villéger et al. (2008). Finally, we checked the correlation coefficient between the six indices and we then keep only the three least correlated indices: species richness, FEve and FDis values for the 30 landscape windows (Supplementary Table S5).

Grassland productivity

For each landscape window, we quantified the grassland productivity services. To do so, we calculated the Normalized Difference Vegetation Index (NDVI) as a proxy of grassland productivity. We used Sentinel-2 images at the 3A-Level provided by the French Theia Land Data Centre (10m resolution). We used 12 images (i.e. from November 2019 to September 2020) from which we extracted the median NDVI values of each grassland parcel (i.e. the 3 to 5 grassland parcels selected per landscape window). From these median values of NDVI calculated for each month (NDVI is hereafter referred to as productivity), we then calculated the three productivity services at the landscape window scale. We

calculated: (i) the annual mean productivity, (ii) the spatial variability (i.e. standard deviation of annual means of the grassland parcels included in a landscape window), and (iii) the temporal stability (i.e. minus the mean of standard deviations of the grassland parcels included in a landscape window) for each landscape window.

3. Current bocage services and their relationship with the landscape structure

We aimed at analysing the effect of landscape structure (i.e. compositional heterogeneity, configurational heterogeneity, grassland amount and hedgerow amount) on the three ecosystem services selected (climate regulation, biodiversity conservation in grasslands, grassland productivity). For each service, we investigated the shape of possible relations in order to (i) best explain the observed relationships between landscape structure and ecosystem services, (ii) and make the extrapolation of these relationships biologically plausible under different scenarios (please see next paragraph for the scenarios description). We used each service as the dependent variable and the four landscape structure variables as the independent variables. To do so, we fitted linear and logistic regressions (Supplementary Figure S6) using the `lm`, `nls` and `SSlogis` functions in R (R Core Team, 2020). For each service, the model selected was the model displaying the best R^2 . For climate regulation, as climate is primarily influenced by geographic and topographic factors (Kang et al., 2000), we first performed linear regressions with the climate regulation indices as dependent variables and the topography and distance to the sea as independent variables. We extracted the residuals of these first models and used them as dependent variables in second linear regressions with the landscape structure variables as independent variables. We did not find any relationship between landscape structure and the climate indices, the functional dispersion of plant assemblages, and the temporal stability of productivity. The equations linking each service to the landscape structure variables are presented in Table 1.

Table 1: Models developed to quantify the ecosystem grassland services based on the current values of services and landscape structure.

Grassland services	Indicator	Equation	p-value	R ²
Biodiversity	SR	$SR = 0.3310 \cdot (50 / (1 + \exp((5 - \text{Configuration}) / 1)))) + 30.7319$	0.009	0.19
	FEve	$FEve = (0.0116931 \cdot \text{Hedgerows}) + (-0.0014315 \cdot \text{Grasslands}) + 0.7546498$	0.004	0.28
Productivity	Mean	$\text{Mean} = -0.15742 \cdot (0.7 / (1 + \exp((7 - \text{Configuration}) / 1))))$	0.007	0.2
	Spatial	$\text{Spatial} = (0.0005141 \cdot \text{Grasslands}) + (0.0425608 \cdot \text{Composition}) - 0.0240778$	> 0.001	0.42

4. Land-use scenarios

Land-use scenarios construction

To project the possible consequences of land-use changes on future ecosystem services of grassland across the Couesnon watershed, we used the land-use changes scenarios developed in Palka et al. (submitted) at 3 dates (i.e. 2030, 2040, 2050). To construct these scenarios, three independent and contrasted agricultural assumptions were cross-combined with three independent and contrasted

territorial development assumptions (Table 2). The three agricultural assumptions were (i) the “Cerealization” assumption which favored the major development of cereal productions, (ii) the “Dairy intensification” assumption which favored the intensification of local livestock/dairy production, and (iii) the “Greening” assumption which promoted an ecological transition and agrifood protection. The three territorial assumptions were (i) the “Business as Usual” assumption which followed the past-trends of peri-urbanisation, (ii) the “Energy transition” assumption which is oriented to the construction of eco-neighbourhoods and buildings renovation, and (iii) the “Ecological citizen” assumption which is driven by citizens' research for a better quality of life away from cities and more food independence (more details about the assumptions will be available in Palka et al., submitted). The cross-combination of these 3x3 assumptions led to eight scenario possibilities (one excluded as not plausible; Table 2). These scenarios were discussed during two participatory workshops with local farmers and stakeholders who helped to locate where the probable land-use changes related to each scenario could occur. In a second step, these scenarios were translated into quantitative spatially explicit LUCC maps thanks to a FORESCEM model developed by Palka et al. (Submitted). It aimed to simulate LUCC at a fine scale and to make as transparent and direct as possible the translation of scenarios into input parameters of the model (Houet et al., submitted). Furthermore, as highlighted by Albert et al. (2020), linear elements are often overlooked in the modelling of land-use changes. Therefore, a model to estimate hedgerow losses across the Couesnon watershed was also developed in parallel. Each hedgerow had a probability of being preserved or removed based on the number of occurrences of an adjacent land use type over a 10 year time step (i.e. 10 years being a time step consistent with the dynamics of the hedge network in the Couesnon watershed). For example, for the “Energy performance” scenario, if a parcel adjacent to the hedgerow was used as a crop for more than 5 years on a 10-year time step, the hedgerow was removed as we considered that direct proximity to a parcel often exploited increases the risk of hedgerow removal. All decision rules regarding the preservation or removal of hedgerows under each scenario will be available in Palka et al. (submitted). This model allowed estimating the loss of hedgerows according to the three scenarios at three dates (2030, 2040, 2050). Then, we rasterized the hedgerow network at 5 meter resolution and integrated it to the land-use maps previously constructed with the FORESCEM model. We thus obtained three land use maps (i.e. 2030, 2040, 2050) for each scenario that take into account land use changes and hedgerow removal. As traditionally advised to facilitate comparison of results (Voiron-Canicio, 2012), we kept only 3 scenarios among the 8 possible scenarios. We kept one trend scenario and two contrasted scenarios, namely (i) Business as usual, (ii) Green attractivity, and (iii) Energy performance (Table 2).

Table 2: Agricultural and territorial development assumptions leading to eight possible scenarios. We selected three scenarios, one trend (i.e. Business-as-usual) and two contrasted (i.e. Green attractivity and Energy performance). They are indicated in bold font.

		Territorial development assumptions		
		<i>Business as usual</i>	<i>Energy tranistion</i>	<i>Eco-citizen</i>
Agricultural development assumptions	<i>Cerealisation</i>	Cereal desert	Energy performance	Conflicts
	<i>Dairy intensification</i>	Business-as-usual	Diversified biomass	Double performance
	<i>Energy transition</i>	∅	Optimized BGINs	Green attractivity

Bocage services estimation under the three scenarios

Future ecosystem services were modelled accounting for land use changes and hedgerow loss for the three scenarios. We did not take into account potential climate changes as the changes expected at the medium term (i.e. 2050) are assumed negligible due to species adaptation potential, phenotypic plasticity, and nonlinear shifts (Schirpke et al., 2017). For each scenario and for each date, we calculated the four landscape variables selected (i.e. compositional heterogeneity, configurational heterogeneity, hedgerow percentage, grassland percentage) within the 30 landscape windows based on the maps obtained from the scenarios. We tested whether landscape variables differed between the scenarios at each date using covariance analysis with scenario type and initial value in 2018 of the landscape variable tested as independent variables.

We predicted future ecosystem services based on the simulated values of landscape variables 2030, 2040 and 2050. We used the equations calculated in Table 1. For each date, we tested whether the ecosystem values differed among scenarios using a covariance analysis with the initial value of the service considered in 2018 and (ii) the scenario type as independent variables. In some landscape windows, the grassland percentage simulated was too low (i.e. below 5%) to confidently use the models linking landscape variables and ecosystem services. When the percentage of grassland was below 5%, the landscape windows concerned were not included in the calculations of the mean value of the service at the watershed scale. To further discuss this issue, we quantified an extra bocage service: the habitat availability. For each scenario, we calculated the number of landscape windows where the percentage of grassland was still above a viability threshold of 5% at the end of the simulated time steps.

RESULTS

Current bocage services of and relationships with the landscape structure

The minimum mean annual temperature found in landscape windows was 11.9°C and the maximum was 12.7°C. The mean annual temperature across the 30 landscape windows was 12.3°C +/- 0.21. The minimum sum of growing degree days found in landscape windows was 2568 and the maximum was 2936. The mean growing degree days across the 30 landscape windows was 2770 +/- 88. The minimum frost days found in landscape windows was 9 and the maximum was 42. The mean frost days across the 30 landscape windows was 22 +/- 7.7.

The minimum species richness found in landscape windows was 22 and the maximum was 57. The mean species richness across the 30 landscape windows was 37.5 +/- 8.6. The minimum Shannon index found in landscape windows was 4.3 and the maximum was 5.6. The mean Shannon index across the 30 landscape windows was 4.9 +/- 0.3. The minimum Pielou's evenness found in landscape windows was 1.35 and the maximum was 1.4. The mean Pielou's evenness across the 30 landscape windows was 1.4 +/- 0.01. The functional richness varied from 0.17 to 0.69, and the mean across the 30 landscape windows was 0.34 +/- 0.12. The functional evenness varied from 0.67 to 0.82, and the mean across the 30 landscape windows was 0.75 +/- 0.04. The functional dispersion varied from 0.29 to 0.47, and the mean across the 30 landscape windows was 0.36 +/- 0.04.

The mean annual productivity varied from 0.74 to 0.93, and the mean across the 30 landscape windows was 0.81 +/- 0.04. The spatial variability of productivity varied from 0.004 to 0.06, and the mean across the 30 landscape windows was 0.31 +/- 0.01. The temporal stability of productivity varied from -0.06 to -0.20, and the mean across the 30 landscape windows was -0.13 +/- 0.03.

As mentioned in the Methods, we did not find any relationship between landscape structure and the climate indices, the functional dispersion in plants, and the temporal stability of productivity. These data were then not presented in the rest of the manuscript. The two indices related to the conservation of grassland biodiversity responded to landscape heterogeneity and amounts of semi-natural habitat. The species richness increased with the configurational heterogeneity following a logistic regression (Table1, Supplementary Figure S6). The functional evenness was positively related to the hedgerow amount and negatively related to the grassland amount following a linear regression (Table 1). The two productivity indices responded to both components of landscape heterogeneity and grassland amount. The mean productivity increased with the configurational heterogeneity following a logistic regression (Table1, Supplementary Figure S6). The spatial variability was positively correlated to the compositional heterogeneity and the grassland amount following a linear regression (Table 1).

Land cover changes under the three scenarios

The 30 landscape windows selected captured the overall land cover changes according to the narratives and spatial modelling of the three scenarios. The heterogeneity of composition displayed a low variation for the Green attractivity scenario, increased slightly for the Business-as-usual scenario and decreased for the Energy performance scenario. The heterogeneity of configuration increased for the Green attractivity and Business-as-usual scenarios but decreased for the Energy performance scenario (Figure 2). Differences among scenarios were significant only in 2050. The amount of grassland increased more strongly in the Green attractivity scenario (increase of 58%), remained almost constant in the Business-as-usual scenario and decreased very strongly in the Energy performance scenario (loss of 56%). These differences among scenarios were significant in 2040 and 2050. The amount of hedgerows decreased in all three scenarios, with a greater decrease in the Energy performance scenario (27%) than the Business-as-usual (15%) and the Green attractivity (6%). The differences between scenarios were significant at all dates.

At the end of the simulated time steps in 2050, the scenario Business-as-usual presented a mean of compositional heterogeneity of 0.94 +/- 0.16, a mean of configurational heterogeneity of 5.6 +/- 1.5, a mean of grassland percentage of 34.2 +/- 11, an a mean of hedgerow percentage of 3.3 +/- 1.1. The scenario Green attractivity presented a mean of compositional heterogeneity of 0.88 +/- 0.17, a mean of configurational heterogeneity of 5.4 +/- 1.5, a mean of grassland percentage of 55.3 +/- 14, an a mean of hedgerow percentage of 3.6 +/- 1.3. The scenario Energy performance presented a mean of compositional heterogeneity of 0.80 +/- 0.3, a mean of configurational heterogeneity of 4.7 +/- 1.8, a mean of grassland percentage of 15.4 +/- 11, an a mean of hedgerow percentage of 2.8 +/- 1.

Future ecosystem services of grasslands under the three scenarios

The habitat availability quantified via the calculation of the number of landscape windows with a minimum of 5% of grasslands, varied mainly between the Energy performance scenario and the other two scenarios: in 2050, only 23 out of 30 landscape windows still had a percentage of grassland above 5% in the Energy performance scenario, while the Green attractivity and Business-as-usual scenario still had 30 and 29 windows respectively (Figure 3).

Concerning the services of the biodiversity conservation of grassland, the species richness of grassland plants increased for all three scenarios in 2030 and then decreased in 2040 (Figure 3). In 2050, the Business-as-usual scenario had a higher species richness than the Green attractivity scenario, which in turn had a higher species richness than the Energy performance scenario. However, these differences were not statistically significant. Functional evenness decreased in all scenarios in 2030, then increased for the Energy performance scenario, remained stable for Business-as-usual and decreased sharply for

the Green attractivity scenario. The difference between the scenarios was significant for all three dates but the residuals of the models showed non-normal distribution for 2030 and 2050 (Figure 3).

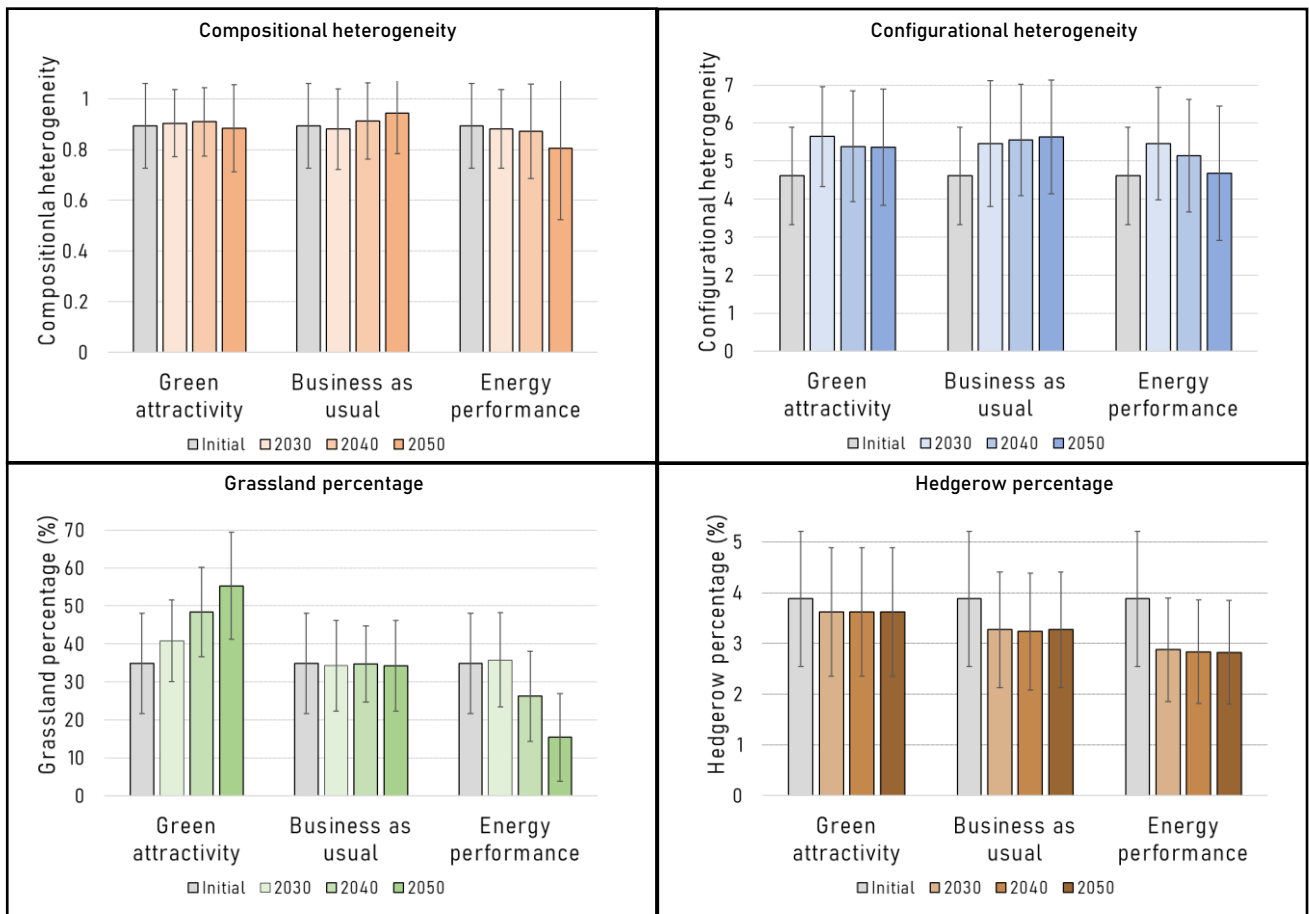


Figure 2: The mean values +/- sd of the four landscape structure variables for each date for the three scenarios selected.

Concerning the productivity services, the mean productivity decreased drastically for all three scenarios in 2030 and then increased in 2040. In 2050, the Energy performance scenario had a higher mean productivity than the Green attractivity scenario, which itself had a higher productivity than the Business-as-usual scenario. However, these differences were not statistically significant. Spatial variability in productivity increased steadily for the Green attractivity scenario from 2030 to 2050. It increased slightly for the Business-as-usual scenario and decreased for the Energy performance scenario (Figure 3). The difference between the scenarios was significant for all three dates but the residuals of the models showed non-normal distribution for 2030 and 2050.

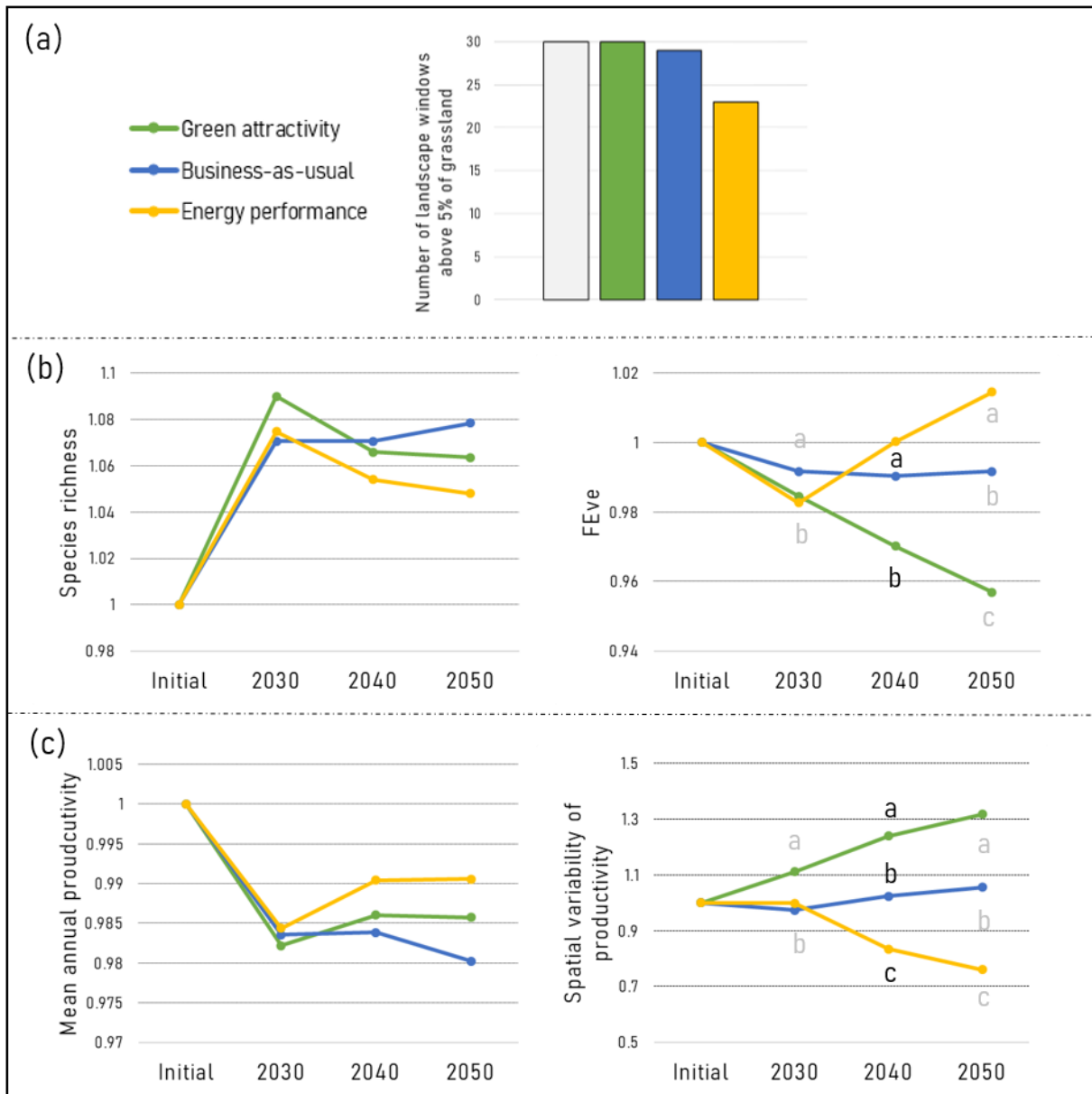


Figure 3: Future trends of ecosystem services of grasslands under the three scenarios. All services were normalised by their initial values in 2018. Black letters represent a significant effect of the scenarios tested through covariance analysis. Grey letters represent a significant effect of the scenario tested through covariance analysis although the condition of normality of residuals was not fulfilled.

DISCUSSION

In this study we used three scenarios, one trend (i.e. Business-as-usual) and two contrasted (i.e. Green attractivity and Energy performance) to estimate the possible impacts of land cover changes on ecosystem services. The 30 landscape windows selected in the Couesnon watershed allowed us to quantify the current values of services and to estimate the changes according to the scenario type, thus providing a basis for land-use policies and decision making (Fisher et al., 2009). All selected landscape variables had at least one relationship with an ecosystem service, demonstrating the importance of taking into account both the amount of semi-natural habitat in agricultural landscapes (Duflot et al. 2015), and the structure of the surrounding matrix (Fahrig et al. 2011; Laterra et al., 2012).

Land cover changes under the three scenarios

The 30 landscape windows selected in the Couesnon watershed captured the differences in land use changes among the three scenarios. However, these changes were highlighted more strongly by the amount of semi-natural habitats than by the landscape heterogeneity components.

The two landscape heterogeneity components developed similarly over time and the differences between scenarios were low. At the end of the simulated time steps (i.e. 2050), the Energy performance scenario was the scenario with the lowest compositional and configurational heterogeneity across the three scenarios. This result is in line with the agricultural development narrative of this scenario that focused on the assumption of a “Cerealisation”, characterised by an expansion of farms and specialization in cereals cultivation. These characteristic of landscape changes are part of the main changes described by landscape ecologists as agricultural intensification: a simplification of the mosaic, with an increase in the size of parcels and a decrease in the diversity of land use types due to the farming specialisation (Burel & Baudry, 1999; Tschamtker et al., 2005). Although, the two other scenarios, supposed to be less driven by agricultural intensification, displayed non-significant differences of landscape heterogeneity.

The most marked land use changes between the scenarios concerned the amount of semi-natural habitats: the amount of grasslands increased strongly in the Green attractivity scenario, stayed stable in the Business-as-usual scenario, and decreased strongly in the Energy performance scenario. These changes are in adequacy with the narratives, as the Green attractivity scenario is mostly driven by an agricultural development oriented towards the development of grassy forages supporting livestock, whereas the Energy performance is oriented toward the cultivation of cereals. The drastic loss of grasslands in the Energy performance scenario fits with the current trend occurring across Europe as grasslands are reduced to a low percentage of the agriculturally utilised area (Isselstein et al. 2005). Yet, grasslands provide a high number of services as they are the primary source of livestock support, and control the soil erosion (Zhao et al., 2020). It is therefore crucial to quantify the changes in grassland supply in the future. The hedgerow amount decreased in all scenarios but decreased more drastically in the Energy performance scenario, meaning that there is a decrease in the bocage landscapes across the Couesnon watershed. Yet, the bocage landscapes are very important in North-Western Europe as providers of cultural and social services as they fulfil an aesthetic function of the agricultural landscapes (van Zanten et al. 2014). Therefore, beyond the loss of regulation, provision and support services fulfilled by hedgerows (i.e. wind-breakers, wood production, corridors for fauna and flora; Montgomery et al. 2020), the loss of bocage landscapes could also have impacts on cultural services (de Groot, 2006). This impact would be possible to quantify by setting up social questionnaire campaigns to assess the extent to which the aesthetic value of the landscapes is of interest to the inhabitants of the region (e.g. Fagerholm et al., 2016; Moreno et al., 2018). Here, we included these linear elements (i.e. hedgerows),

land covers that are too often neglected in studies using land cover changes projections (Albert et al. 2020). Although, the model used in this study for hedgerows did not allow the addition of new hedgerows. Yet, hedgerows planting is currently supported in France by several institutions such as the French Chamber of Agriculture (French Chamber of Agriculture, 2016). Further work is needed to develop models that will widen disparities between scenarios by removing but also adding linear of hedgerows according to the narratives.

Most of the changes in the landscape variables occurred between the initial state of the landscape (i.e. 2018) and the first simulated time step (i.e., 2030) and followed relatively the same direction for all three scenarios. This result can be explained by two elements: first, this first time step is the longest (12 years vs. 10 years); there was more changes accumulated during this time step than for the other time steps. Second, in the narratives of the scenarios used in this study, the year 2030 is the pivotal year from which the three scenarios really take territorial and agricultural developments in contrasting directions. These two elements therefore induced similar but marked changes during the first time step, then contrasting changes thereafter between scenarios. This will induce changes in the services related to these landscape variables following the same trends.

Future values of ecosystem services

During the simulated time steps, the ecosystem services developed in contrasted directions depending on the scenario. First, the overall habitat availability service remained stable or decreased across the three scenarios. The major change is the drastic loss of this availability in the Energy performance scenario, where seven landscape windows crossed under a 5% threshold of viability (Aavik & Helm, 2018). As described above, this result resulted from the narrative of this scenario oriented toward the cultivation of cereals at the expense of grasslands. The changes in the service values provided by grasslands thereafter should therefore be interpreted in the context of an overall loss of grassland amount for this scenario.

The species richness of grassland plants tended to increase for all scenarios, with a stronger increase for the Business-as-usual scenario. This increase is due to the overall increase in configurational heterogeneity, which is assumed to be favourable to biodiversity through its effect on dispersal and niche availability (Fahrig et al. 2011; Poggio et al. 2010). However, these differences were not sufficiently marked to be statistically significant suggesting that land-use changes did not drastically affect the ecosystem values for this time-scale simulation. The functional evenness drastically decreased in the Green attractivity scenario, slightly decreased in the Business-as-usual scenario and increased in the Energy performance scenario. This result can seem to be counterintuitive, as we would expect an improvement of taxonomic and functional facets of plant diversity within the increase of grassland

amount in the Green attractivity scenario. This result can be explained by the negative relationship found between the grassland amount and the functional evenness in 2018: in our study area, landscapes with a high amount of grassland are often managed using similar agricultural practices and are mostly grazed as pasture. Pasture can select specific functional strategies in plant communities (Gilhaus et al., 2017). In a landscape window, if all parcels are managed the same way, the difference of diversity between the grassland parcels is then low (i.e. more similar functional traits), which leads to a lower diversity at the landscape scale. Continuous large areas of grassland could thus lead to a functional homogenisation, mechanism already highlighted with a too high connectivity between habitat patches of plant communities (Tschardt et al., 2012; Arroyo-Rodríguez et al., 2013).

The results are particularly interesting for land-management policies : the overall increase of species richness via the increase of heterogeneity of configuration implies to focus more on the spatial arrangement of land covers than on the diversity of land covers (Fahrig, 2017). However, this configurational heterogeneity needs to be combined with sufficient maintenance of habitat availability to ensure population viability (Flather & Bevers, 2002), especially since the response of biodiversity to changes in landscape structure is not always immediate (Kuussaari et al., 2009). It is therefore interesting to consider that the diversity of land uses and practices could benefit biodiversity in the future, information that can be useful for land use planning decisions in the Couesnon watershed.

We observed an overall decrease in grassland productivity for all scenarios. However, the decrease in productivity is however less marked for the Energy performance scenario as this scenario had the lowest configurational heterogeneity in 2050. The positive effect of the decrease in landscape heterogeneity on productivity still needs to be fully understood. One possible explanation could be that the low heterogeneity reflects the intensive agricultural practices conducted in the landscape windows, such as the use of chemical pesticides and inorganic fertilisers (Norton et al., 2009; Tschardt et al., 2012). These agricultural practices could explain the increased productivity at the landscape scale. Moreover, the Energy performance scenario had the lowest spatial variability of productivity and is therefore the most favourable scenario for productivity-related services. However, this result must be interpreted in conjunction with the drastic loss of grassland amount for this scenario: the decrease of 56% of grassland amount across the 30 landscape window suggests that the overall result for this scenario would be a lower productivity due to the lower area allocated to grasslands, even if the remaining grassland parcels are highly productive. Yet, the production of fodder is one of the main issues for the future (Oehri et al., 2017), especially in watersheds where the dairy production represents 47% of the production (SAGE Couesnon, 2021). Current public policies seem to be moving in the right direction in the study area as they aim to restore and maintain hedgerows (CC Couesnon, 2018), and to diversify agricultural practices within the territory in the future (Brittany region, 2019).

We found no link between landscape structure and the climate regulation services, we therefore were not able to predict how future landscape changes could affect the local climate. This lack of results does not necessarily indicate that the landscape does not influence the climate within the landscape windows : it may be necessary to look at finer landscape variables (e.g. hedgerow height, orientation, or tree composition), or to acquire climatic data over a longer time step, to highlight an effect of the landscape structure on climate. In addition, we did not take into account for potential climate change in the scenarios due to the intermediate time step simulated (i.e. 2050), which still permits to restrain the uncertainties compare to simulations at broader time scales (e.g. 2080, Schroter, 2005; 2100, Schirpke et al. 2017). However, climate change may have a large impact on ecosystem services and could exacerbate or improve the effect of land cover changes on biodiversity (de Chazal & Rounsevell, 2009).

Conclusion and main prospects

In this study, we chose to investigate the fine relationships between the landscape structure and the bocage ecosystem services to quantify the future values of services. We focused on the biodiversity and productivity services of grasslands to include key ecological processes influencing their assemblage at the landscape scale. Across the three scenarios studied, the one assumed the least favourable for biodiversity (i.e. Energy performance) seemed to have the highest level of services for three out of five at the end of the simulated time steps. However, this scenario led to a large loss of habitat. Therefore, our results showed that the trend scenario Business-as-usual might be a compromise for maintaining a multitude of services in the bocage landscapes without leading to a functional homogenisation of the grassland plant assemblages or a drastic loss of habitat availability.

Our study aimed to estimate the mean value of services across the watershed across the simulated time steps. However, the Couesnon watershed is an area divided in several sub-areas with different landscape characteristics: large-scale crops and vegetable crops currently characterize the North of the watershed, whereas the rest of the watershed is represented by a dominant system of polyculture-dairy farming. Therefore, some landscape structures and the associated services could be very localised, and could represent 'hot' or 'cold' spots of services delivery (Lavorel et al., 2011). These spots could be impacted differently according to the scenarios: for example, some landscape windows located in a specific sub-area could be more favoured by the Green attractivity scenario whereas the other windows could be favored by the Business-as-usual. Taking into account the sub-areas would allow to identify a possible coexistence of ideal scenarios more finely territorialised. The orientation of public policies would therefore be towards more territorialised decisions, but with coherence on a regional scale to ensure that services are maintained over the watershed.

Overall, the territorial and agricultural development and their interactions leading to scenarios greatly drive the land cover changes in the future. In the current context of biodiversity loss, especially

in agricultural landscapes, the research effort on land cover change projections is essential, as our currently made decisions will condition the future landscape structures and the services they will provide.

Acknowledgments

We are grateful to Myriam Marsot, Enora Salomon, and Benjamin Besse for assistance in the field. We are also grateful to the large network of farmers who gave access to their grassland fields and the SAGE Couesnon for the hedgerow network map. Sentinel-2 data were retrieved by CNES (<https://theia.cnes.fr/>) and the detailed 2017 LULC maps by CESBIO. This work was funded by the LTSER « ZA Armorique », the European project Interreg ALICE and the Brittany region (France).

SUPPLEMENTARY MATERIALS

Supplementary S1: Calculation of compositional and configurational heterogeneity.

Landscape compositional heterogeneity was characterized using the Shannon diversity index. This index is defined as:

$$SHDI = - \sum_{i=1}^n P_i \times \ln(P_i)$$

where n is the number of land use types in the landscape window, and P_i the proportion of the landscape occupied by the land use type i (McGarigal et al., 2012). The higher the Shannon index, the higher the compositional heterogeneity (i.e. the more land-use types and/or the most equitable the extent of the land-use types in the landscape).

Landscape configurational heterogeneity was characterised by the percentage of heterogeneous pairs in pixels including different land use types. It is a proxy of the amount of edges between different land use types which is considered as a variable quantifying configurational heterogeneity (Fahrig et al., 2011). The higher the percentage of heterogeneous pairs, the higher the configurational heterogeneity.

Table S2: Pearson correlations between the 4 gradients of landscape variables.

	Hedgerow percentage		Grassland percentage		Compositional heterogeneity		Configurational heterogeneity	
	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value
Hedgerow percentage	1.00	0						
Grassland percentage	0.25	0.17	1.00	0				
Compositional heterogeneity	0.08	0.68	-0.08	0.67	1.00	0		
Configurational heterogeneity	0.44	0.01	-0.02	0.92	0.37	0.04	1.00	0

Supplementary S3: Calculation of growing degree days

The growing degree day is an empirical measure used to calculate the heat accumulation which is used to estimate the duration of a biological development such as the growth of a plant taking into account the temperature. To calculate the value of the number of degree days, we used a base temperature of 5°C for the grasslands (Tautenhahn et al., 2019). Then we noted the maximum and minimum temperatures of a day and calculated the degree day for each day following the formula:

$$GDD = \frac{T_{max} + T_{min}}{2} - T_{base}$$

with Tmax is the maximal temperature of the day, Tmin is the minimal temperature of the day and Tbase is the temperature established previously according to the plant development.

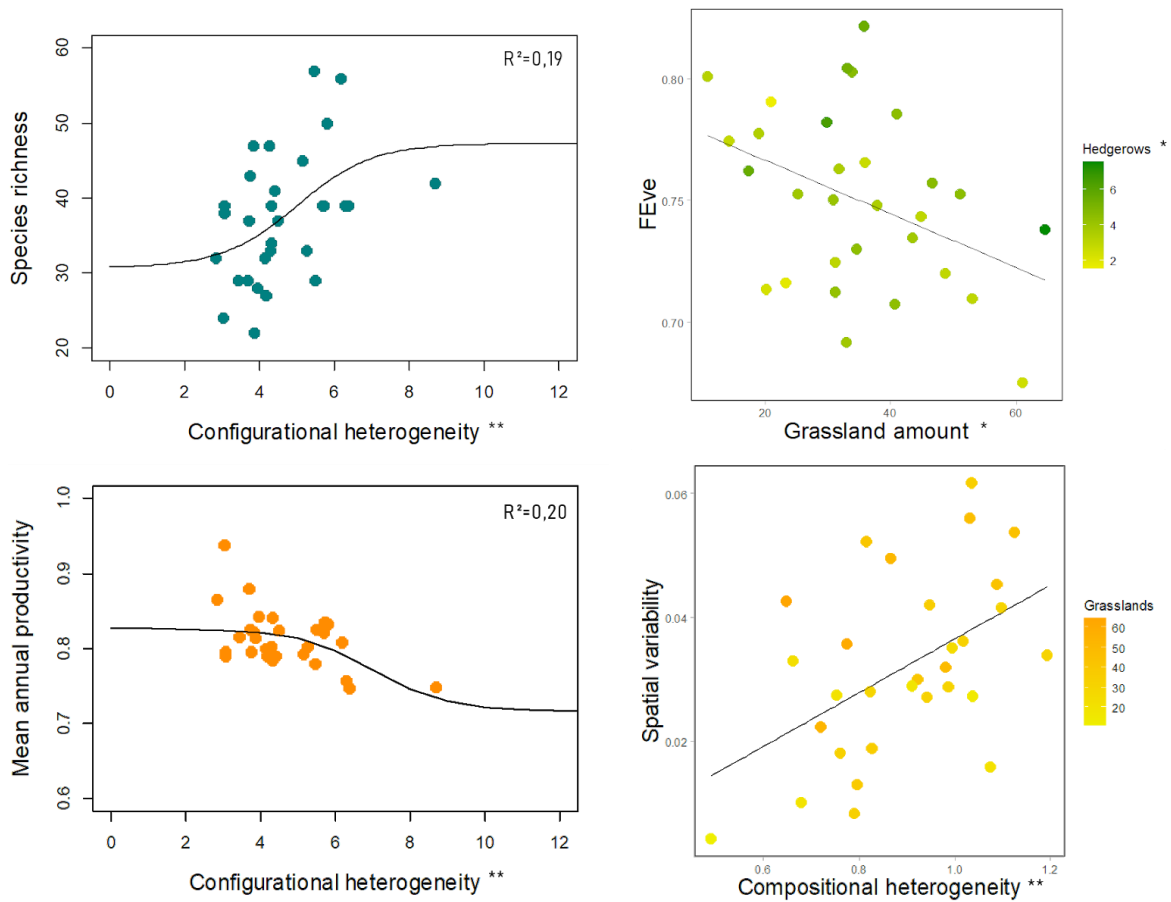
Table S4: Minimum, maximum, mean and standard deviation of functional traits before transformation.

	Min	Max	Mean	SD
Onset of flowering (month)	1.00	9.00	5.40	1.30
Flowering duration (month)	2.00	12.00	3.74	1.92
SLA (m ² .kg ⁻¹)	8.90	57.85	25.67	7.45
Height (m)	0.08	7.63	0.55	0.63

Table S5: Correlation between the three biological indices selected.

	SR		FEve		FDis	
	Coefficient	p-value	Coefficient	p-value	Coefficient	p-value
SR	1	0	-0.15	0.43	-0.05	0.79
FEve			1	0	0.30	0.1
FDis					1	0

Figure S6: Plots of the logistic regressions linking the species richness of grassland plants and the configurational heterogeneity, and the mean productivity and the configurational heterogeneity.



Discussion générale

1. Apports des recherches au cadre théorique de l'effet de la structure du paysage sur les communautés végétales

- A. Le paysage, un filtre agissant sur la diversité fonctionnelle des plantes et les fonctions écologiques
- B. L'importance de dissocier les composantes du paysage
 - 1. La quantité d'habitat: un effet contrasté suivant le type de végétation
 - 2. L'hétérogénéité du paysage: l'importance de dissocier les deux composantes
- C. La télédétection offre un panel d'outils pour les écologues
- D. Applications pour l'aménagement du territoire

2. Perspectives de recherches

- A. Le paysage et le climat, encore une question en suspens
- B. La prise en compte des pratiques locales
- C. La diversité hiérarchisée pour comprendre les processus d'assemblages des plantes à l'échelle du paysage
- D. La prise en compte du temps dans la réponse des plantes aux changements du paysage

L'objectif général de cette thèse était de déterminer l'effet de la structure du paysage sur la diversité fonctionnelle des communautés de plantes et les fonctions écologiques associées. Nous avons démontré dans le premier article que les composantes du paysage déterminent la diversité fonctionnelle des plantes à l'échelle gamma. Ces modifications sont issues de changements dans la composition des communautés conduisant à la sélection de syndromes particuliers de traits. Dans le deuxième article, nous avons montré que l'effet du paysage sur la diversité fonctionnelle des prairies pouvait en retour influencer des fonctions de l'écosystème prairial comme le niveau de productivité et la variabilité spatiale de cette productivité. Par l'intermédiaire ou non d'un effet sur les assemblages de plantes, le paysage joue un rôle sur la productivité des prairies. Finalement, nous avons montré que ces effets de la structure du paysage sur la biodiversité et la productivité pourraient varier dans le futur en fonction de différents scénarios d'aménagement du territoire amenant à des évolutions différentes du paysage.



Apports des recherches au cadre théorique de l'effet de la structure du paysage sur les communautés végétales

A. Le paysage, un filtre agissant sur la diversité fonctionnelle des plantes et les fonctions écologiques

Nos résultats soutiennent la théorie selon laquelle le paysage agit bien comme un filtre écologique sélectionnant les espèces selon leurs traits fonctionnels au sein des communautés végétales (ARTICLES 1 à 3). Dans un premier temps, nous avons montré que les traits fonctionnels, qu'ils soient liés au processus de dispersion, de phénologie ou d'établissement, étaient influencés par la structure du paysage (ARTICLE 1 et 2). Dans la théorie des filtres écologiques (voir Introduction 1.A.1), le filtre du paysage est classiquement associé au processus de dispersion et donc aux traits liés à cette dispersion. Ici, nous avons montré que les traits supposés liés à d'autres processus tels que la phénologie ou la compétition étaient également influencés (ARTICLE 1). Nos recherches rejoignent donc les études récentes qui soulignent le besoin de prendre en compte des traits liés à toutes les étapes du cycle de vie des plantes lorsqu'on s'intéresse à leur réponse face à la structure du paysage (Zambrano et al., 2019). Cette démarche permet de mettre en évidence d'éventuels *trade-offs* entre ces traits et entre les processus de dispersion, d'établissement et de persistance liés à ces traits, processus qui régissent l'assemblage des plantes à l'échelle du paysage (Wright et al., 2010; Saatkamp et al., 2019).

Dans un second temps, nous avons montré que la diversité fonctionnelle des plantes de prairies pouvait avoir en retour un effet sur les fonctions écologiques (ARTICLE 2) : l'augmentation de la régularité fonctionnelle était positivement liée à la productivité annuelle et la réduction de la variabilité spatiale. Ces résultats soutiennent plusieurs théories tentant d'expliquer l'effet bénéfique de la

biodiversité sur la productivité des communautés végétales (Jochum et al., 2020). L'augmentation de la régularité fonctionnelle au sein des assemblages de plantes permettrait d'utiliser plus efficacement les ressources limitantes de l'environnement, correspondant au concept de partition de niches (i.e. utilisation différentielle des ressources pour la coexistence des espèces, (Tilman et al., 1997)). Ce résultat soutient également l'hypothèse de l'assurance (Yachi & Loreau, 1999) qui stipule que le maintien de la productivité dans les assemblages végétaux est plus probable lorsque le pool d'espèces est diversifié car il offre de plus grandes garanties que certaines espèces maintiendront leur fonctionnement au cours du temps quand d'autres échoueront (voir Introduction Encadré 2). Ici, ces théories se traduisent dans nos communautés de prairies par une productivité plus élevée à l'année et moins variable dans l'espace lorsque celles-ci sont plus fonctionnellement régulières. Nos recherches apportent donc de nouvelles preuves empiriques qu'une régularité fonctionnelle croissante favorise la productivité primaire, théorie présentant encore des résultats contrastés à l'heure actuelle (Roscher et al., 2013; Sonkoly et al., 2019). De plus, nos travaux soulignent que ces différents processus expliquant le lien biodiversité-productivité, classiquement démontrés à l'échelle de la communauté locale (i.e. alpha), peuvent aussi s'exprimer à l'échelle des paysages (i.e. diversité gamma). Cependant, il reste à démontrer si ces résultats observés à l'échelle gamma sont la résultante d'une addition d'effets locaux, ou une réelle possibilité de transposition des théories biodiversité-productivité à l'échelle du paysage. Nos résultats suggèrent que ces théories développées pour la diversité alpha doivent être plus amplement testées sur la diversité gamma, car elles permettraient de mieux comprendre les processus d'assemblage des plantes à l'échelle paysagère mais aussi de plus efficacement conserver et restaurer la diversité végétale et les services associés au sein des paysages.

Que ce soit dans le cas des réponses des assemblages de plantes ou de leurs effets sur le fonctionnement de l'écosystème, nous n'avons pas mesuré directement les processus de convergence et de divergence des traits au sein des communautés de plantes (voir Introduction 1.B.2.): nous les avons inférés via la structure fonctionnelle des communautés. Pour tester la présence de ces processus, il serait possible de construire des modèles nuls (voir ARTICLE 4) qui permettent de tester si ce sont des processus déterministes (i.e. filtres successifs abiotiques et biotiques) qui influencent la présence et la coexistence des plantes, ou si finalement leur assemblage est principalement lié à des processus non-déterministes et neutres tels que les événements probabilistes de spéciation et d'immigration (Hubbell, 2001; Mittelbach & Schemske, 2015).

B. L'importance de dissocier les différentes composantes du paysage

Dans ce manuscrit, nous avons montré que les deux visions, celle habitat centrée (i. e. tache-matrice, Hanski & Gilpin, 1991) et celle de la matrice globale (i.e. tache-mosaïque ; Wiens, 1995) sont importantes car elles n'influencent pas les mêmes processus lors de l'assemblage des communautés végétales.

1. *La quantité d'habitat: un effet contrasté suivant le type de végétation*

Nous avons mis en avant que la quantité d'habitat incluse dans une fenêtre paysagère influençait la composition floristique pour les deux types de végétation étudiés, les prairies permanentes et les haies (ARTICLE 1). La quantité d'habitat avait un effet positif sur la diversité fonctionnelle des haies, ce qui appuie la théorie de l'*habitat amount* (Fahrig, 2013) pour la facette fonctionnelle des assemblages de plantes. Cependant, la quantité d'habitat avait un effet négatif pour la diversité fonctionnelle des assemblages de prairies, et ce quel que soit le nombre de traits fonctionnels pris en compte pour quantifier la diversité fonctionnelle (ARTICLE 1 et 2). La réponse contrastée entre les deux types d'habitats pourrait notamment être due à leurs proportions respectives dans le paysage : même dans les fenêtres paysagères les plus préservées, les haies ne représentaient que six pourcents de la surface totale. Une toute petite augmentation de la quantité d'habitat peut donc être favorable à la diversité fonctionnelle des assemblages de haies, contrairement aux prairies qui occupent déjà de grandes surfaces au sein des paysages (i.e. théorie du seuil d'extinction, Ewers & Didham, 2006).

2. *L'hétérogénéité du paysage: l'importance de dissocier les deux composantes*

En mettant en place un protocole à large échelle qui minimise la corrélation entre les composantes du paysage, nous avons démontré que l'hétérogénéité de la matrice affectait aussi la diversité fonctionnelle des assemblages de haies indépendamment de la quantité d'habitat (ARTICLE 1). L'évaluation des effets indépendants des composantes de l'hétérogénéité a permis de mettre en avant l'importance de l'hétérogénéité de configuration sur la structuration des assemblages de plantes de haies, plus que celle de l'hétérogénéité de composition. De par son effet sur la longueur des interfaces avec les taches d'occupation du sol adjacentes et ses effets sur les processus de dispersion (Poggio et al., 2010), l'hétérogénéité de configuration influence les taux de rencontre entre espèces et donc les interactions biotiques qui sont reconnues d'importance dans l'assemblage des plantes (voir Introduction 1.A.1.)

Nous avons démontré un effet direct de l'hétérogénéité du paysage sur les fonctions de l'écosystème (ARTICLE 2) : l'hétérogénéité de configuration et de composition influençait les indices de productivité des prairies, sans être médiée par un effet sur les communautés prairiales. La compréhension des processus expliquant les liens entre l'hétérogénéité et la productivité doit encore être renforcée mais une piste prometteuse est la possible co-variation entre hétérogénéité et pratiques agricoles. Les modifications dans la structure du paysage et dans les pratiques associées pourraient avoir des effets sur le long terme sur la capacité des territoires à fournir des services dans le futur (ARTICLE 3).

Une question subsiste quant à la manière de quantifier ces différentes composantes de l'hétérogénéité. En effet, les plantes n'ont probablement pas une perception binaire ou catégorielle du paysage, mais répondent plutôt à des gradients de qualité des ressources et d'interactions biotiques

(Murphy & Lovett-Doust, 2004). Quantifier les composantes du paysage à travers des cartes catégorielles peut donc s'avérer peu réaliste du point de vue de l'écologie des organismes étudiés. De plus, de nombreuses plantes dépendent d'agents de dispersion (i.e. vent, animaux, eau) qui peuvent eux aussi être influencés par la structure du paysage (Murphy & Lovett-Doust, 2004). Pour prendre en compte des gradients plutôt que des catégories, il est possible de développer des cartes d'hétérogénéité fonctionnelle qui prennent en compte les différences entre occupations du sol selon si elles sont plus ou moins favorables au groupe biologique étudié (Fahrig et al., 2011). Au sein de ces cartes, l'insertion d'éléments paysagers linéaires autres que les haies, comme les bordures de route (Vanneste et al., 2020) ou les fossés (Favre-Bac et al., 2014) qui peuvent servir de corridors, pourrait permettre d'affiner la description des paysages. Cependant, cette description ne doit pas se complexifier outre mesure et doit rester à la fois exploitable pour les scientifiques et biologiquement pertinente pour les organismes d'intérêts.

C. La télédétection offre un panel d'outils pour les écologues

Nous avons utilisé des images satellitaires pour quantifier les fonctions de l'écosystème telle que la productivité des prairies (ARTICLE 2 et 3). Depuis plus de 15 ans, les données satellitaires sont couramment utilisées dans le domaine de l'agriculture, notamment pour la modulation des intrants, l'estimation des rendements ou encore la détection des adventices (Bockstaller et al., 2021). Elles sont également de plus en plus utilisées par les écologues afin de quantifier des processus écologiques s'opérant sur des grandes échelles spatio-temporelles (e.g. Oehri et al., 2017). En effet, bien qu'il existe actuellement une multitude de méthodes de quantification des fonctions des écosystèmes reposant sur la collecte de données sur le terrain (e.g. mesure de la productivité par fauche et pesage, Yi et al., 2020; Zirbel et al., 2019), aucune d'entre elles n'est facilement transposables à grande échelle de façon réaliste et régulière (Pettorelli et al., 2018). Jusqu'à récemment les images satellitaires permettaient de quantifier les fonctions de l'écosystème mais à une résolution spatiale ou temporelle relativement grossière (voir reviews de Araujo Barbosa et al., 2015, et Pettorelli et al., 2018). Le développement récent d'outils de plus en plus précis en résolution à la fois spatiale et temporelle vont donc permettre de quantifier une multitude de services écosystémiques de manière fine et sur de grandes étendues, comme ici où nous avons quantifié la productivité mensuelle des prairies à l'échelle parcellaire sur tout un bassin versant. Cette quantification peut s'avérer pertinente pour des services dans d'autres types d'habitats semi-naturel comme par exemple la production de bois dans les linéaires de haies (e.g. Van Den Berge et al., 2021).

Une autre application des outils de télédétection est de caractériser et de cartographier finement les communautés végétales (e.g. (Rapinel et al., 2018). Par exemple, dans une étude annexe à nos travaux présentés ici, nous avons utilisé des séries temporelles pour cartographier différentes communautés végétales dans les prairies se ségréant par leur résistance à l'inondation ou au pâturage (Article Annexe

1). Cependant, bien que la télédétection soit de plus en plus utilisée pour cartographier les communautés végétales, certains habitats telles que les prairies humides restent difficiles à cartographier en raison de la variabilité spectrale, spatiale et temporelle de la couverture végétale (Alvarez-Vanhard et al., 2020). Les cartes produites ne sont pas suffisamment précises pour répondre aux exigences de la gestion des milieux (Rapinel et al., 2018), et actuellement, aucune constellation de satellites ne possède les résolutions requises pour cartographier les habitats assez finement (Alvarez-Vanhard et al., 2020). L'avènement de nouveaux outils comme les drones permettent de s'approcher de plus en plus de la réalité biologique des écosystèmes (voir Article Annexe 2) mais reste encore aujourd'hui tributaire des données de validations acquises *in situ*. L'utilisation combinée des outils de télédétection tels que les drones et les satellites, et les relevés floristiques de terrain sont des outils prometteurs pour permettre aux écologues de caractériser les communautés végétales et les fonctions écologiques associées à grande échelle.

D. Applications pour l'aménagement du territoire

Nos recherches présentent des résultats suggérant que les différents éléments du paysage sont à prendre en compte dans le contexte actuel de la conservation de la biodiversité et des services utiles à l'Homme. Nous avons par exemple montré un effet positif de la quantité de haies i) sur leur propre diversité fonctionnelle mais aussi ii) sur la régularité fonctionnelle des prairies permanentes et leur productivité (ARTICLES 1 et 2). Les linéaires de haies ont drastiquement diminué depuis les années 60 suite à la mise en place du remembrement dans les politiques agricoles européennes (Burel & Baudry, 1995). Cette suppression de nombreuses haies dans les paysages du Nord-Ouest de l'Europe a été mise en œuvre pour faciliter le travail agricole (Carlier & Moran, 2019). La suppression des haies dans les paysages agricoles pourrait donc s'avérer à terme contre-productive car elle pourrait avoir des effets négatifs sur la biodiversité et le fonctionnement des écosystèmes qui y sont liés (Hooper et al., 2005; Montgomery et al., 2020). Les paysages agricoles bénéficieraient de la préservation et de la restauration des haies pour à la fois abriter la diversité végétale et maintenir une production efficace de fourrage à l'avenir.

Nos résultats ont également mis en avant un effet plus important de l'hétérogénéité de configuration sur les communautés végétales (i.e. complexité spatiale des différentes occupations du sol) que celui de l'hétérogénéité de composition (i.e. diversité en type d'occupations du sol). Ces résultats sont particulièrement intéressants car ils montrent qu'il est primordial de continuer les efforts de recherches en séparant les deux composantes de l'hétérogénéité car elles n'ont pas les mêmes répercussions en termes d'aménagement du territoire actuel et futur (ARTICLE 3). En effet, nos résultats suggèrent que les prises de décisions sur l'aménagement du territoire devront tout aussi bien concerner la conservation des habitats et des éléments semi-naturels que l'arrangement spatial des occupations du sol (i.e. hétérogénéité de configuration) afin de soutenir la provision de services écosystémiques dans le futur.

2

Perspectives de recherches

Les recherches menées dans cette thèse apportent de nouvelles preuves empiriques de l'effet de la structure du paysage sur l'assemblage des plantes et les fonctions écologiques associées. Cependant, plusieurs questions restent en suspens et le protocole à large échelle mis en place va permettre de développer plusieurs perspectives de recherches, qu'elles soient liées à la compréhension de l'assemblage des espèces végétales mais également à l'effet du paysage sur le climat local.

A. Le paysage et le climat local, encore une question en suspens

Au cours de nos recherches, nous n'avons pas mis en évidence de lien direct entre la structure du paysage, et plus particulièrement la densité du réseau de haie, et le climat. A notre connaissance, aucune étude portant sur l'effet du réseau de haies en Bretagne sur le climat local n'a été conduite récemment. Or, l'effet des haies sur le régime du vent et les températures de l'air peuvent avoir des effets contrastés, voir opposés suivant la zone géographique et le climat qui lui est associé, ou suivant si la température est mesurée au sol ou en hauteur (e.g. Sánchez et al., 2010). De plus, la variabilité du climat est une donnée pouvant s'échelonner dans le temps : le protocole mis en place dans cette thèse est donc toujours en place et continuera d'enregistrer les données climatiques pendant encore 5 ans. Grâce à ce suivi sur le long terme, des recherches plus approfondies sur le lien paysage-climat-biodiversité pourront être conduites dans le futur.

B. La prise en compte des pratiques locales

Dans cette thèse, nous nous sommes concentrés sur les effets des différentes composantes du paysage sur l'assemblage des communautés végétales à l'échelle de la diversité gamma. Nous n'avons pas pris en compte les effets potentiels de l'intensité et de la nature des pratiques locales, que ce soit pour les prairies ou pour les haies. Dans la suite de ces recherches, les pratiques agricoles devront être prises en compte car ce sont des facteurs importants dans la structuration des communautés végétales. En effet, les plantes peuvent être soumises à des perturbations locales plus ou moins régulières comme la fauche ou à des stress plus continus comme le pâturage (Socher et al., 2012) qui ont pour effet de sélectionner certaines stratégies fonctionnelles. Plusieurs études ont démontré que les différents régimes de fauche (date et/ou fréquence, Blüthgen et al., 2012) et les critères de pâturage (chargement, type d'animaux, Gaujour et al., 2012), peuvent avoir des effets sur la diversité des plantes de prairies. Ces différents régimes ont d'ailleurs été montrés comme pouvant être corrélés à la structure du paysage. Plusieurs études ont mis en lumière un lien entre une faible hétérogénéité du paysage et une plus grande intensité des pratiques agricoles tel que l'utilisation d'engrais et de pesticides artificiels (Norton et al., 2009). Pour

intégrer les effets des pratiques agricoles locales à nos recherches, une large campagne d'enquêtes est en cours afin d'obtenir les informations de pratiques des parcelles de prairies échantillonnées.

C. La diversité hiérarchisée pour comprendre les processus d'assemblage des plantes à l'échelle du paysage

Dans le contexte de l'étude de la biodiversité via une vision additive (voir Introduction 2.B.1.), étudier la diversité beta (i.e. diversité entre les différentes communautés au sein d'une même fenêtre paysagère) pourrait permettre de comprendre plus finement les patterns observés de diversité gamma. La diversité beta peut en effet refléter deux phénomènes différents: la différenciation spatiale des espèces et l'imbrication des assemblages (Baselga, 2010). La différenciation spatiale implique le remplacement de certaines espèces par d'autres en raison d'un tri environnemental ou de contraintes spatiales et historiques au sein des parcelles. Chaque parcelle incluse dans un paysage présente donc une communauté distincte d'espèces. L'imbrication des assemblages quant à elle, implique que certaines des parcelles incluses dans un paysage ne soient simplement que des sous-ensembles de la parcelle la plus riche, reflétant un processus non aléatoire de perte d'espèces. Appliqué aux traits fonctionnels, étudier ces deux mécanismes pourrait permettre de savoir si une faible diversité gamma au sein d'un paysage est finalement la résultante de la présence de communautés spatialement distinctes et peu différenciées en termes de stratégie fonctionnelles (i.e. différenciation spatiale), ou si finalement le paysage est composé d'une seule parcelle très riche fonctionnellement avec d'autres parcelles qui sont des sous-ensembles moins riches (i.e. imbrication des assemblages). L'analyse des effets de la structure du paysage sur la diversité beta pourrait donc s'avérer très utile pour comprendre plus finement l'assemblage des plantes à l'échelle du paysage.

D. La prise en compte du temps dans la réponse des plantes aux changements du paysage

Dans les recherches présentées précédemment (ARTICLES 1, 2 et 3), nous avons tenté d'expliquer la distribution des assemblages de plantes en réponse au paysage actuel et de prédire les éventuels changements dans le futur. Cependant, une autre composante du paysage encore trop souvent négligée dans les études en écologie est l'aspect historique et les impacts qu'il peut avoir sur l'assemblage actuel des communautés. En effet, les paysages sont dynamiques et la réponse des organismes aux changements environnementaux n'est pas nécessairement immédiate. Les assemblages peuvent présenter une i) réponse décalée dans le temps et ii) peuvent inclure un certain nombre d'espèces dont on prévoit l'extinction. Ces deux processus sont décrits sous le nom de temps de relaxation (Diamond, 1972) et dette d'extinction respectivement (Hanski & Ovaskainen, 2002). Ils décrivent le temps et le nombre d'espèces allant être perdues entre les changements environnementaux et le retour à l'équilibre dans les communautés. Ces deux processus sont aujourd'hui reconnus mais peu d'études ont examiné la question à la lumière des traits fonctionnels. Pourtant, certains traits peuvent augmenter ou diminuer le

temps de relaxation, comme la durée de vie (Lindborg, 2007), le taux de reproduction (Kuussaari et al., 2009), ou encore la capacité de dispersion (Hendrickx et al., 2009). Il est possible que certaines modifications dans la structure du paysage soient toutefois considérées comme favorables pour la biodiversité. On considère alors que ces modifications offrent de nouvelles tâches d'habitat colonisables, augmentent leur accessibilité ou favorisent l'hétérogénéité de la matrice. Sur le même principe que le temps de relaxation, le temps pour les espèces d'immigrer et le nombre d'espèces immigrantes sont reconnues comme délai à l'immigration et le crédit à l'immigration (Jackson & Sax, 2010). Théoriquement, les mécanismes de dette d'extinction (i.e. disparition d'espèces) et crédit de colonisation (i.e. arrivée de nouvelles espèces) peuvent coexister au sein des assemblages à la suite de modifications dans la structure du paysage (Jackson & Sax 2010). L'enjeu est de comprendre ces mécanismes car ils peuvent être d'importance dans l'explication de la composition actuelle des assemblages, mais également future.

Nous avons inclus dans ce chapitre une étude empirique qui montre l'effet de la structure du paysage passée sur les plantes de prairies et de haies mais également les oiseaux (ARTICLE 4). Cette étude a été réalisée dans une zone d'étude différente des trois premiers chapitres: la vallée de la Seine. Nous avons utilisé une approche basée sur les traits pour comprendre la réponse des plantes et des oiseaux à la simplification du paysage et à la fragmentation de l'habitat. Contrairement aux articles 1, 2 et 3, nous nous sommes appuyés ici sur des indices fonctionnels uni-traits (i.e. qui prennent en compte un seul trait fonctionnel à la fois). Nous avons quantifié la structure du paysage à trois années différentes (1963, 1985, 2000) et nous nous sommes appuyés sur un échantillonnage des assemblages de plantes et d'oiseaux dans vingt fenêtres paysagères de 1 km x 1 km situées le long de la vallée de la Seine (France). L'échantillonnage des taxons considérés a été effectué en 2002 et correspond à la biodiversité dite actuelle. Dans chaque fenêtre paysagère, nous avons calculé la richesse en espèces de plantes et d'oiseaux, la variance pondérée de la communauté (CWV) et la moyenne pondérée de la communauté (CWM) de cinq traits fonctionnels liés à la capacité de dispersion, à la reproduction et au cycle de vie. Nous avons étudié les effets de la structure du paysage actuelle et passée sur ces indices taxonomiques et fonctionnels. Le résultat principal à souligner ici est que les assemblages de plantes et d'oiseaux ont répondu préférentiellement aux paysages passés plutôt qu'aux paysages actuels. Les oiseaux présentaient d'ailleurs une réponse encore plus retardée que les plantes (i.e. 1963 vs. 1985). Les résultats de cet article suggèrent que les assemblages de plantes et d'oiseaux dans les paysages de la vallée de la Seine sont encore en état de transition et qu'ils pourraient, au-delà du nombre d'espèces qui devraient être perdues, être confrontés à une dette d'extinction fonctionnelle.

Dans le contexte actuel de perte de biodiversité et des fonctions écologiques associées, cet article parmi d'autres présents dans la littérature scientifique souligne que l'effet des changements dans la structure des paysages sur la biodiversité ne sera pas visible immédiatement (e.g. Provost et al., 2020).

A la suite de cette thèse, nous nous appuyerons sur des cartes anciennes d'occupations du sol afin de tester si les assemblages de plantes observés actuellement au sein du bassin versant du Couesnon sont eux aussi en transition ou s'ils ont déjà atteint un nouvel équilibre. Les résultats pourraient alors permettre d'affiner la compréhension actuelle de la distribution des plantes, mais aussi de prédire plus finement les conséquences des changements d'occupation du sol futurs sur les communautés végétales et leurs fonctions écologiques associées.

Article 4: Past landscape structure drives the functional assemblages of plants and birds

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Scientific Reports (2021), 11, 3443

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Abstract

Landscape structure is a major driver of biodiversity in agricultural landscapes. However, the response of biodiversity can be delayed after landscape changes. This study aimed to determine the effect of current and past landscape structure on plant and bird assemblages. We used a trait-based approach to understand their responses to landscape simplification and habitat fragmentation. We quantified landscape structure at three different years (1963, 1985, 2000) and sampled current plant and bird assemblages in twenty 1km² landscape windows located along the Seine Valley (France). For each window, we calculated plant and bird species richness, Community Weighted Variance (CWV), and Community Weighted Mean (CWM) of five functional traits related to dispersal capacity, reproduction, and life-cycle. We detected non-random patterns of traits for both taxa. Plant and bird species richness was lower in simple landscapes. The functional variance of plant traits was higher in landscapes simple in configuration. Both plant and bird assemblages strongly responded to past landscapes, especially their traits related to reproduction and life-cycle. It suggests that landscapes of the Seine valley will face a functional extinction debt. Further research is needed to better predict the delayed response of biodiversity expected to occur after landscape structure changes.

Keywords

Past landscape, functional variance, null models, environmental filters

INTRODUCTION

Biodiversity loss is increasing at an unprecedented rate at the global scale and agricultural intensification is known to be a major driver of this process in human-dominated regions (Tscharrntke et al., 2012; Fahrig et al., 2011). Agricultural intensification is not only reflected by an increasing use of phytosanitary products and higher mechanization, but also in alteration of the structure of the landscape through two processes: landscape simplification and habitat fragmentation (Fig. 1). The alteration of the landscape structure influences the assembly of plants or animals (Rundlöf et al., 2008; Wamser et al., 2012; Sonnier et al., 2014). At the landscape level, landscape simplification implies a decrease in both components of heterogeneity (i.e. compositional and configurational heterogeneity), generally resulting in reduced species richness within landscapes (Rundlöf et al., 2008). At the habitat level, habitat fragmentation implies a decrease in the amount and/or the increase of the degree of isolation of the habitat concerned (Wilcove & McLellan, 1986), generally resulting in a decrease in the richness of species specific to this habitat (Wilcox & Murphy, 1985; Leibold et al., 2004). The importance of distinguishing landscape simplification and habitat fragmentation when investigating the response of biodiversity to the landscape structure has recently been underlined by the debate over their conceptualization and the appropriate scale at which they should be studied (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019). Therefore, it appears essential to choose gradients at both landscape and habitat level, to better understand the impact of alteration to the landscape structure on biodiversity.

Both landscape simplification and habitat fragmentation can affect biodiversity and an increasing number of studies have attempted to understand the species-related mechanisms underlying the observed response of assemblages (Gámez-Virué et al., 2015; Perović et al., 2015; Concepción et al., 2017; Rocha-Santos et al., 2019; Provost et al., 2020). In particular, using trait-based approaches offers promising avenues to better understand the effects of the landscape structure on the composition of assemblages (Rocha-Santos et al., 2019; Solé-Senan et al., 2017). The trait-based approach allows biological assemblages to be characterized no longer through distinct taxonomic groups but through continuous quantitative measurements of trait values. For example, it is possible to quantify the dispersion of trait values around the mean (e.g. Community Weighted Variance) to investigate the assembly processes driving species assemblages (Concepción et al., 2017): the decrease of the dispersion (i.e. convergence) is usually attributed to the effect of environmental filtering (Grime, 2006), while an increase of the dispersion (i.e. divergence) is usually attributed to the limiting similarity (MacArthur & Levins, 1967), or more recently to the environmental heterogeneity of microhabitats (de Bello et al., 2013). It is also possible to quantify the mean within an assemblage (e.g. Community Weighted Mean) to identify toward which optimal value the convergence occurs (Muscarella & Uriarte, 2016). In a context of a filtering effect of the landscape structure, the observed assemblages might then present values of trait significantly different from randomly selected species in the regional pool: either under-dispersed trait values, indicating a convergence of strategies toward a specific trait value, or over-

dispersed trait values indicating a divergence (de Bello et al., 2009). The indices based on functional traits and used to describe biodiversity aim to be independent of species richness. These indices, by taking the different characteristics of each species into account, are complementary to traditional measures of biodiversity that are based on the assumption that all species are equal facing environmental conditions (Mouchet et al., 2010).

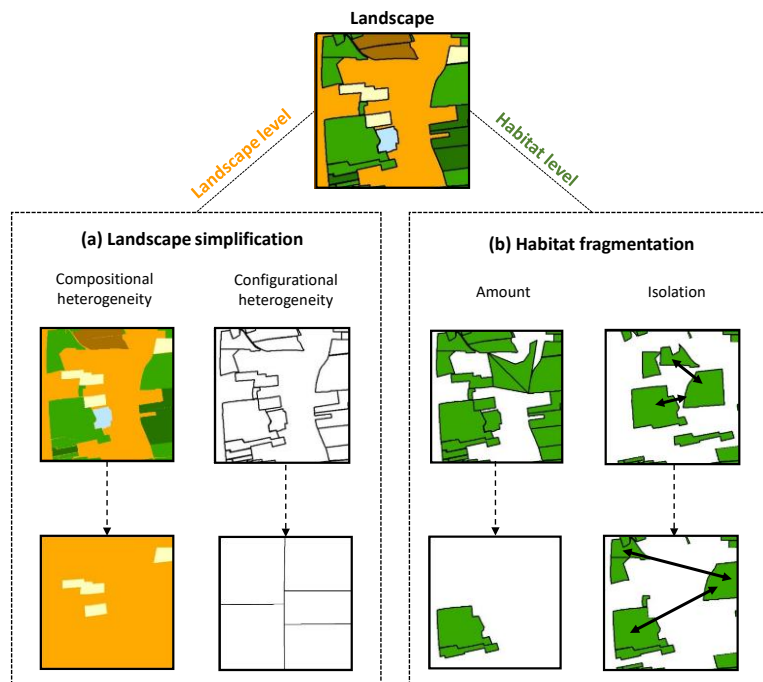


Figure 1: The two processes involved in the definition of landscape structure in the agricultural intensification context. (a) Landscape simplification is a process that is measured at the landscape level, where all classes of land use are taken under consideration. It is defined as the reduction in compositional heterogeneity (i.e. habitat diversity) and/or the reduction in configurational heterogeneity (i.e. complexity of the spatial pattern, Fahrig et al., 2011). (b) Habitat fragmentation is a process that is measured at the habitat level, where only one class of land use is taken into consideration. It is defined as a reduction in habitat amount and/or an increase in the isolation of habitat patches (Fahrig, 2003). The four dotted arrows represent the direction of an increase in landscape simplification and habitat fragmentation. This figure was created using ArcGIS Software (v. 10.6.1, URL: <https://desktop.arcgis.com>).

Low compositional or configurational heterogeneity has been shown to reduce functional variance (i.e. reduce the range of dispersion trait values around the mean) by selecting for specific strategies (Gámez-Virués et al., 2015, Provost et al., 2020). A decrease in heterogeneity (i.e. landscape covered by few land-use types and/or with very large patch area) in agricultural landscapes could lead to a convergence of trait values toward high dispersal potential, whether in space or time, or a high reproduction rate resulting in a greater mass effect (Shmida & Wilson, 1985, i.e. a higher rate of propagule influx that allows species to establish in sites where they cannot maintain viable populations). In addition, low agricultural landscape heterogeneity, reflecting intensive land management (Baudry & Papy, 2001), could filter traits related to the timing of reproduction. Species could be selected to reproduce before too intense disturbances occur (Duflot et al., 2014) or to synchronize their period of

reproduction with resource abundance peaks to feed their offspring (Cleland et al., 2007). Habitat fragmentation can also reduce functional variance of assemblages by favouring species that are able to survive in a small patch and/or able to disperse over longer distances. In landscapes with small amounts of habitat or high isolation, species with a high dispersal capacity (Hendrickx et al., 2009) could be selected, especially organisms that need several patches of the same habitat throughout their lifetime (i.e. supplementation, Dunning et al., 1992). Landscape simplification and habitat fragmentation could then filter species according to specific strategies, regardless of the taxon under consideration.

Interest in the functional structure of assemblages in relation to landscape metrics is currently growing (Concepción et al., 2017; Jonason et al., 2017). However, one overlooked component of the landscape is its variability over time. Indeed, landscapes are dynamic and the response of organisms to environmental changes is not necessarily immediate (Kuussaari et al., 2009). Assemblages can display a time-lagged response (i.e. relaxation time, Diamond, 1972) and can include a certain number of species predicted to become extinct (i.e. extinction debt, Hanski & Ovaskainen, 2002) as the assemblage reaches a new equilibrium after these environmental changes. These two processes have been identified across several taxa (Helm et al., 2005; Sang et al., 2010) but few studies have investigated the question in the light of functional traits (but see Lindborg, 2007; Saar et al., 2017; Yamanaka et al., 2015). The trait-based approach is a promising method to understand the mechanisms underlying relaxation time. Indeed, some functional traits could promote a delay in the organism's response by maintaining them for a period of time before they become extinct. In plants for example, this could be a high investment in clonality as it provides the opportunity for species that are no longer able to disperse to survive at the local level over a more or less long term (Piqueray et al., 2011). For birds, traits related to breeding parameters can indicate a higher sensitivity to habitat fragmentation (Barbaro & van Halder, 2009) and can affect their response delay. For instance, a longer lifespan associated with a low reproductive capacity (e.g. *Buteo buteo*, L. 1758), can imply a slower response to changes in the environment than more productive short-lived species. Analyzing the relationship between the current and past landscape structure and the distribution of traits within assemblages can help to detect delayed responses by organisms and predict the long-term effects of changes in agricultural landscapes.

This study aimed to determine the effects of current and past landscape structures on the functional assemblages of two contrasting taxa in terms of dispersal capacity: plants and birds. The study was conducted in the agricultural landscape of the Seine valley in Normandy (France), which is characterized by a gradient of landscape simplification and habitat fragmentation. Its temporal dynamics are mainly due to agricultural intensification that resulted from the implementation of the Common Agricultural Policy (CAP) in the 1960s. We quantified landscape structure at three different periods: before the implementation of the CAP (i.e. 40 years ago, 1963), after it was first implemented (i.e. 15 years ago, 1985) and after several successive reforms (i.e. current, 2000). We sampled current plant and

bird assemblages in twenty 1 km² square landscape windows. To extend the reach of our results, we studied plant assemblages in two different types of semi-natural habitat - grasslands and hedgerows. We first evaluated the randomness of the functional variance of assemblages through two null models: one based on the presence/absence of species (NM1), the other one on the occurrence rate of species (NM2). These two null models allowed us to highlight a possible convergence or divergence of trait values within assemblages. We then examined the independent effects of landscape simplification characterized by compositional and configurational heterogeneity (i.e. Shannon index and mean patch area respectively) and habitat fragmentation characterized by habitat amount and isolation of both plant habitat types (grassland percentage or length of hedgerows, and mean nearest distance between grassland patches or the number of disconnected networks of hedgerows; please see Methods for further information) on species richness, trait ranges (CWV) and mean values (CWM). To investigate the potential delayed response of plant and bird assemblages, we developed one linear model for each year (current, 15 years ago, 40 years ago). For each taxon, we focused on 5 traits related to dispersal, reproduction, and life-cycle (Table 1). Specifically, we tested the following hypotheses: (i) Functional variance of traits within plant and bird assemblages is not randomly distributed at the landscape scale; (ii) An increase of the landscape simplification and habitat fragmentation act as environmental filters and leads to lower species richness and convergence of trait values within assemblages; (iii) Functional assemblages of plants and birds are determined by past rather than present landscape structure, due to the relaxation time occurring after changes in landscape structure.

RESULTS

A total of 241 species of hedgerow plants, 173 species of grassland plants, 84 species of birds from all habitats were identified across the 20 landscape windows surveyed. In each landscape window, hedgerow plant species richness varied from 58 to 108, grassland plant species richness varied from 32 to 78, and bird species richness varied from 5 to 37.

Non-random patterns of trait values

Our first hypothesis was that the functional variance of traits within plant and bird assemblages is not randomly distributed at the landscape scale. The two null models constructed tested if trait values influenced the presence of species (i.e. NM1), or the dominance of species within assemblages (i.e. NM2). To highlight a convergence or divergence of traits, we calculated the effect size (i.e. ES; please see Methods for further information): negative ES values indicate functional convergence while positive values indicate divergence. Considering the first null model based on the presence/absence of species (NM1), only one trait - flowering duration of hedgerow plant assemblages – across the three species groups (i.e. hedgerow plants, grassland plants, birds) was not randomly distributed and showed a convergence of its values ($ES < 0$; Supplementary Fig. S1). Considering the second null model based on the occurrence rate of species (NM2), all traits of hedgerow plant assemblages were not randomly

distributed except the allocation to clonal reproduction. With the null model NM2, onset of flowering, flowering duration and lifespan showed convergence (negative ES) whereas seed mass was divergent (positive ES; Fig. 2). For grassland plant assemblages, all traits were not randomly distributed except the flowering duration. With the null model NM2, seed mass, onset of flowering and lifespan showed convergence while allocation to clonal reproduction showed divergence (Fig. 3). Within bird assemblages, body mass, onset of breeding and the number of breeding events were not randomly distributed and showed significant convergence (Fig. 4). As the null model based on the occurrence rate of species (NM2) for plants and birds showed significant results, only the community weighted variances (CWV) and community weighted means (CWM) based on species occurrence rate were tested against past and current landscape structure.

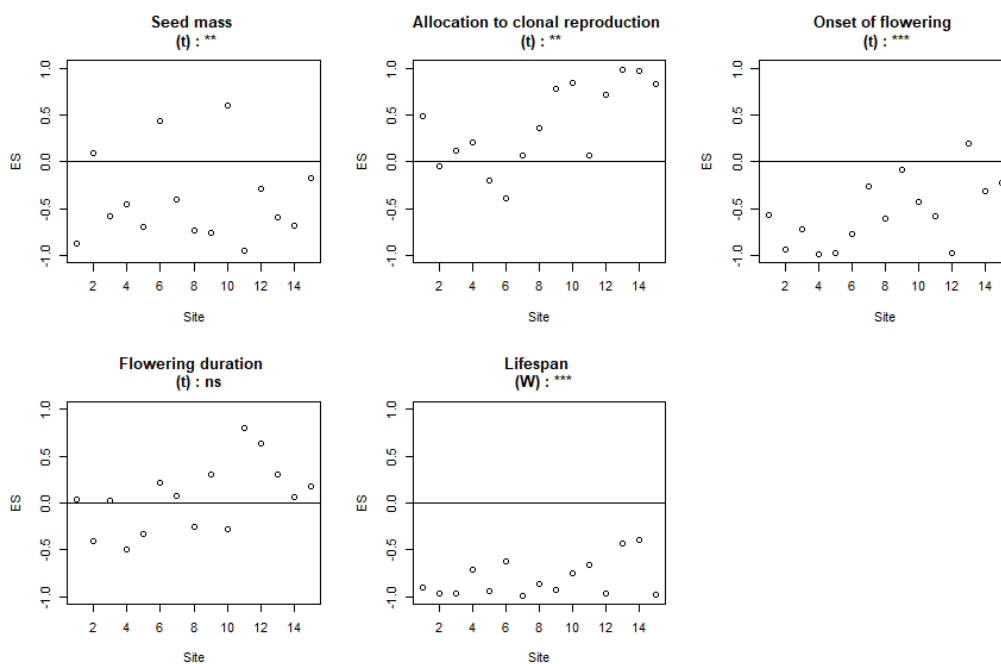


Figure 2: Effect size (ES) of hedgerow plant assemblages obtained using the “species occurrence rate model” (NM2) for each of the five traits: seed mass, allocation to clonal reproduction, onset of flowering, flowering duration and lifespan. Significance levels (***) $p < 0.001$, (**) $p < 0.01$, (*) $p < 0.05$ and non-significance (ns) of the Wilcoxon tests (W) or Student’s t tests (t) are presented on top of each graph. $Df = 17$. This figure was created using R Software (R Core Team, 2020) (v. 4.02, URL: <https://www.r-project.org>).

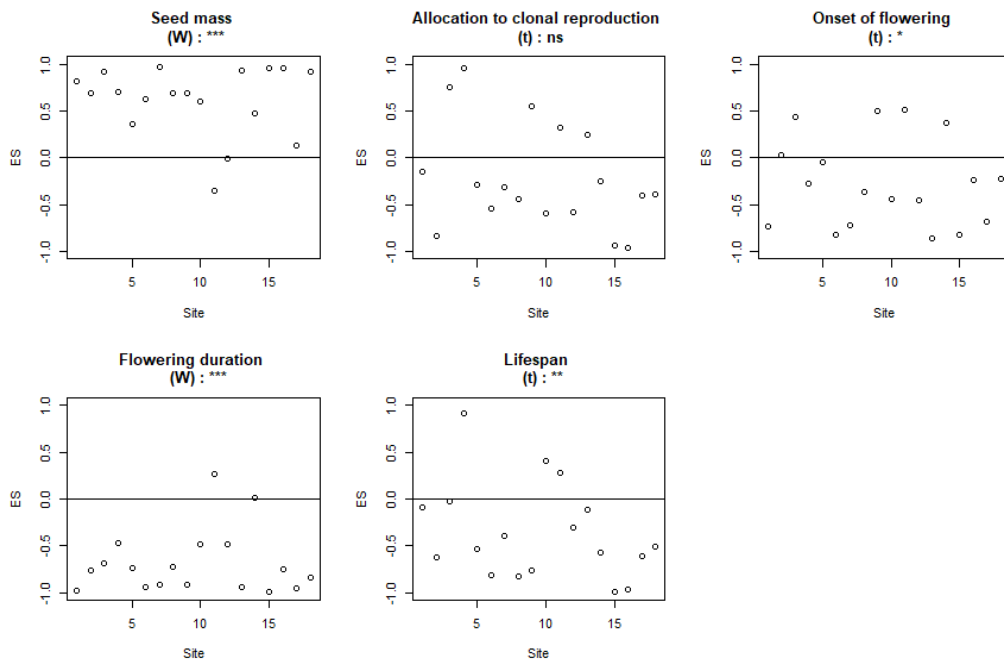


Figure 3: Effect size (ES) of grassland plant assemblages obtained using the “species occurrence rate model” (NM2) for each of the five traits: seed mass, allocation to clonal reproduction, onset of flowering, flowering duration and lifespan. Significance levels (** $p < 0.001$, * $p < 0.01$, * $p < 0.05$) and non-significance (ns) of the Wilcoxon tests (W) or Student’s t tests (t) are presented on top of each graph. Df = 14. This figure was created using R Software (R Core Team, 2020) (v. 4.02, URL: <https://www.r-project.org>).

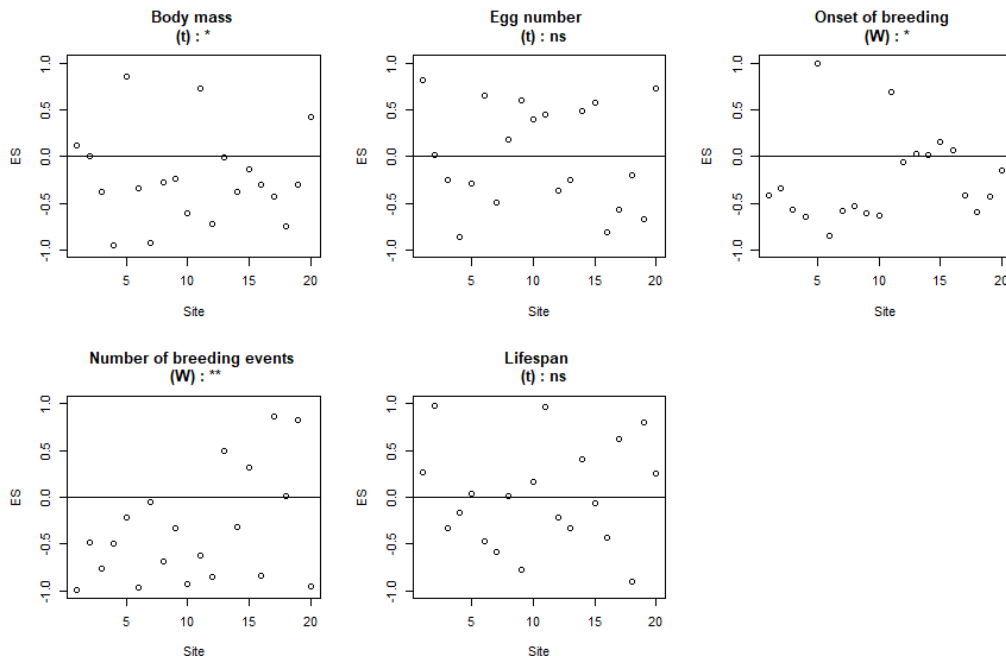


Figure 4: Effect size (ES) of bird assemblages obtained using the “species occurrence rate model” (NM2) for each of the five traits: body mass, egg number, onset of breeding, number of breeding events and lifespan. Significance levels (** $p < 0.001$, * $p < 0.01$, * $p < 0.05$) and non-significance (ns) of the Wilcoxon tests (W) or Student’s t tests (t) are presented on top of each graph. Df = 19. This figure was created using R Software (R Core Team, 2020) (v. 4.02, URL: <https://www.r-project.org>).

Influence of landscape simplification and habitat fragmentation on species richness and functional assemblages of plants and birds

Our second hypothesis is that an increase of landscape simplification and habitat fragmentation act as environmental filters and leads to lower species richness and convergence of trait values within assemblages. When a trait was found to be randomly distributed following the null model NM2, the effects of the landscape structure were not tested on CWVs and CWMs. Within hedgerow plant assemblages, the species richness depended only on compositional heterogeneity: species richness was lower in landscapes with a low compositional heterogeneity (Table 2). Species richness was thus lower in simple landscapes. Considering the functional composition of these hedgerow plant assemblages, CWV of flowering duration and CWV of lifespan were higher in landscapes with a low configurational heterogeneity (Table 2). CWV of hedgerow plant assemblages for these traits were thus higher in simple landscapes. CWM of flowering duration was higher whereas CWM of lifespan was lower in landscapes with a low configurational heterogeneity (Table 2). This result indicates that simplified landscapes favour long-flowering and short-lived assemblages. Within grassland plant assemblages, species richness depended on the compositional heterogeneity and the habitat amount. Species richness was lower in landscapes with a low compositional heterogeneity or a low grassland amount (Table 3). CWV of allocation to clonal reproduction was higher in landscapes with a low configurational heterogeneity or a low grassland amount (Table 3). CWV of onset of flowering was higher in landscapes with a low grassland amount. Within grassland plant assemblages, no response of CWM was detected (Table 3). The species richness of birds was higher in landscapes with high compositional heterogeneity (Table 4). Within bird functional composition, only one trait out of the four non-random traits depended on landscape variables. CWV of number of breeding events was lower in landscapes with a high hedgerow amount. The CWM of this trait was higher in landscapes with higher grassland isolation.

Influence of past and current landscape structure on species richness and functional assemblages of plants and birds

Our third hypothesis is that species richness and functional assemblages of plants and birds are determined by the past rather than present landscape structure, due to the relaxation time occurring after changes in landscape structure. Species richness of hedgerow plant assemblages responded to the current landscape structure and the landscape structure observed 15 years ago (Table 2). Within these hedgerow plant assemblages, CWV of flowering duration responded to the landscape structure observed 15 years ago and 40 years ago. CWM of flowering duration responded only to the landscape structure observed 40 years ago. CWV and CWM of lifespan responded to the current landscape structure and the landscape structure observed 15 years ago (Table 2). Species richness of grassland plant assemblages only responded to the landscape structure observed 15 years ago (Table 3). Within these grassland plant assemblages, CWV of allocation to clonal reproduction responded to the current landscape structure whereas CWV of onset of flowering responded to the landscape structure observed 15 years ago.

Therefore, plant assemblages found in hedgerows and grasslands mostly responded to the current landscape structure (4 significant relations) and the landscape structure observed 15 years ago landscapes (6 significant relations) rather than the landscape structure observed 40 years ago (2 significant relations). Species richness, CWV and CWM of the number of breeding events of bird assemblages only responded to the landscape structure observed 40 years ago (Table 4).

Table 2: Results of linear models testing the effect of landscape predictors on species richness, community weighted variance (CWV) and community weighted mean (CWM) of each trait, calculated from the occurrence rate of plant assemblages in hedgerows. AICc, intercept, R² and Shapiro test for normality of residuals of each significant model are indicated. Estimates of the landscape predictors and their significance levels (***p<0.001, **p<0.01, *p< 0.05) are indicated. Non-significance of models and landscape predictors (-) are indicated. Selected best-fitting models meeting the conditions of lowest AICc ($\Delta AICc < 2$) and normal residuals are indicated by bold font. Models in normal font are included to illustrate the $\Delta AICc$ between significant models. The trait ‘allocation to clonal reproduction’ was not considered because the CWVs were found randomly distributed with the null model NM2. The trait ‘seed mass’ in the CWM section is colored in grey because CWMs for this trait were not calculated as the CWV was found divergent with the null model NM2.

	Species richness	CWV				CWM			
		Seed mass	Onset of flowering	Flowering duration	Lifespan	Seed mass	Onset of flowering	Flowering duration	Lifespan
40 years ago									
AICc	-	-	-	30.29	12.17		-	-22.05	-11
Intercept	-	-	-	0.71	1.25		-	2.93	3.42
R ²	-	-	-	0.32	0.16		-	0.64	0.18
Shapiro test for normality	-	-	-	0.14	0.63		-	0.43	0.13
Compositional heterogeneity	-	-	-	-	-		-	-	-
Configurational heterogeneity	-	-	-	-0.8**	-		-	-0.34	-
Hedgerow amount	-	-	-	-	-		-	-	-
Hedgerow isolation	-	-	-	-	-0.01		-	-	0.008
15 years ago									
AICc	138	-	-	30.56	6.67		-	-14.06	-18.68
Intercept	67.7	-	-	0.84	0.54		-	3.4	3.82
R ²	0.33	-	-	0.3	0.39		-	0.43	0.47
Shapiro test for normality	0.16	-	-	0.07	0.35		-	0.01	0.8
Compositional heterogeneity	26.4**	-	-	-	-		-	-	-
Configurational heterogeneity	-	-	-	-0.81*	-0.49**		-	-0.3**	0.29**
Hedgerow amount	-	-	-	-	-		-	-	-
Hedgerow isolation	-	-	-	-	-		-	-	-
Current landscape									
AICc	139	-	-	33.05	7.42		-	-12.32	-17.3
Intercept	73.2	-	-	2.09	0.56		-	3.5	3.08
R ²	0.29	-	-	0.2	0.36		-	0.37	0.42
Shapiro test for normality	0.41	-	-	0.1	0.61		-	0.02	0.98
Compositional heterogeneity	20*	-	-	-	-		-	-	-
Configurational heterogeneity	-	-	-	-	-0.45**		-	-	0.26**
Hedgerow amount	-	-	-	-0.0004	-		-	-	-
Hedgerow isolation	-	-	-	-	-		-	-0.006**	-

Table 3: Results of linear models testing the effect of landscape predictors on species richness, community weighted variance (CWW) and community weighted mean (CWM) of each trait, calculated from the occurrence rate of plant assemblages in grasslands. AICc, intercept, R² and Shapiro test for normality of residuals of each significant model are indicated. Estimates of the landscape predictors and their significance levels (**p<0.01, *p<0.05) are indicated. Non-significance of models and landscape predictors (-) are indicated. Selected best-fitting models meeting the conditions of lowest AICc ($\Delta AICc < 2$) and normal residuals are indicated by bold font. Models in normal font are included to illustrate the $\Delta AICc$ between significant models. The trait ‘flowering duration’ was not considered here because the CWWs were found randomly distributed with the null model NM2. The trait ‘allocation to clonal reproduction’ in the CWM section is colored in grey because CWMs for this trait were not calculated as the CWW was found divergent with the null model NM2.

	Species richness	CWW				CWM			
		Seed mass	Allocation to clonal reproduction	Onset of flowering	Lifespan	Seed mass	Allocation to clonal reproduction	Onset of flowering	Lifespan
40 years ago									
AICc	117.53	-	-8.62	-	-	-		-	-
Intercept	113.8	-	0.33	-	-	-		-	-
R ²	0.4	-	0.27	-	-	-		-	-
Normality	0.03	-	0.09	-	-	-		-	-
<i>Compositional heterogeneity</i>	-	-	-	-	-	-		-	-
<i>Configurational heterogeneity</i>	-	-	-	-	-	-		-	-
<i>Grassland amount</i>	-0.75**	-	0.008	-	-	-		-	-
<i>Grassland isolation</i>	-	-	-	-	-	-		-	-
15 years ago									
AICc	117.48	-	-10.54	3.48	-	-		-	-
Intercept	-20.1	-	2.76	1.47	-	-		-	-
R ²	0.5	-	0.57	0.32	-	-		-	-
Normality	0.22	-	0.007	0.3	-	-		-	-
<i>Compositional heterogeneity</i>	57.2**	-	-1.002**	-	-	-		-	-
<i>Configurational heterogeneity</i>	-	-	-	-	-	-		-	-
<i>Grassland amount</i>	0.37*	-	-0.13**	-0.01*	-	-		-	-
<i>Grassland isolation</i>	-	-	-0.001*	-	-	-		-	-
Current landscape									
AICc	119.4	-	-15.86	4.88	-	-		-	-
Intercept	72.19	-	1.15	1.28	-	-		-	-
R ²	0.32	-	0.62	0.26	-	-		-	-
Normality	0.35	-	0.05	0.01	-	-		-	-
<i>Compositional heterogeneity</i>	-	-	--	-	-	-		-	-
<i>Configurational heterogeneity</i>	24*	-	-0.34**	-	-	-		-	-
<i>Grassland amount</i>	-	-	-0.006**	-0.008*	-	-		-	-
<i>Grassland isolation</i>	-	-	--	-	-	-		-	-

Table 4: Results of linear models testing the effect of landscape predictors on species richness, community weighted variance (CWV) and community weighted mean (CWM) of each trait, calculated from the occurrence rate of bird assemblages. AICc, intercept, R² and Shapiro test for normality of residuals of each significant model are indicated. Estimates of the landscape predictors and their significance levels (***p<0.001, **p<0.01, *p<0.05) are indicated. Non-significance of models and landscape predictors (-) are indicated. Selected best-fitting models meeting the conditions of lowest AICc ($\Delta AICc < 2$) and normal residuals are indicated by bold font. Models in normal font are included to illustrate the $\Delta AICc$ between significant models. The traits ‘egg number’ and ‘lifespan’ were not considered here because the CWVs were found randomly distributed with the null model NM2.

	Species richness	CWV			CWM		
		Body mass	Onset of breeding	Number of breeding events	Body mass	Onset of breeding	Number of breeding events
40 years ago							
AICc	130.3	-	-	-57.5	-	-	-46.7
Intercept	15.2	-	-	0.3	-	-	1.94
R ²	0.47	-	-	0.5	-	-	0.3
Normality	0.23	-	-	0.5	-	-	0.71
<i>Compositional heterogeneity</i>	17.4***	-	-	-7.43	-	-	-
<i>Configurational heterogeneity</i>	-	-	-	-	-	-	-
<i>Hedgerow amount</i>	-	-	-	-1.1e-05**	-	-	-
<i>Hedgerow isolation</i>	-	-	-	-	-	-	-
<i>Grassland amount</i>	-	-	-	-	-	-	-
<i>Grassland isolation</i>	-	-	-	-	-	-	0.001**
15 years ago							
AICc	-	-	-	-58	-	-	-
Intercept	-	-	-	0.3	-	-	-
R ²	-	-	-	0.47	-	-	-
Normality	-	-	-	0.01	-	-	-
<i>Compositional heterogeneity</i>	-	-	-	-	-	-	-
<i>Configurational heterogeneity</i>	-	-	-	-	-	-	-
<i>Hedgerow amount</i>	-	-	-	-1.6e-05***	-	-	-
<i>Hedgerow isolation</i>	-	-	-	-	-	-	-
<i>Grassland amount</i>	-	-	-	-	-	-	-
<i>Grassland isolation</i>	-	-	-	-	-	-	-
Current landscape							
AICc	-	-	-	-55	-	-	-43.8
Intercept	-	-	-	0.3	-	-	2.04
R ²	-	-	-	0.39	-	-	0.2
Normality	-	-	-	0.12	-	-	0.17
<i>Compositional heterogeneity</i>	-	-	-	-	-	-	-
<i>Configurational heterogeneity</i>	-	-	-	-	-	-	-
<i>Hedgerow amount</i>	-	-	-	-1.3e-05**	-	-	-
<i>Hedgerow isolation</i>	-	-	-	-	-	-	-
<i>Grassland amount</i>	-	-	-	-	-	-	-0.001*
<i>Grassland isolation</i>	-	-	-	-	-	-	-

DISCUSSION

Functional strategies can determine the dominance of species at the landscape scale

To test our first hypothesis, we investigated the distribution of the functional variance of traits within plant and bird assemblages. We demonstrated that most traits were not randomly distributed for both plant and bird assemblages at the landscape scale when the occurrence rate of species was shuffled (i.e. NM2) rather than when species identity was modified (i.e. NM1). This suggests that trait values do not influence the presence of species but their dominance within assemblages. This result is interesting to highlight because it is recognised that the trait values of dominant species influence the ecosystem functioning (i.e. mass-ratio hypothesis, Grime, 1998). Therefore, functional strategies of species at the landscape scale will not only determine their dominance within assemblages but will also influence the ecosystem functioning (Concepción et al., 2017). We demonstrated that most of these functional traits displayed convergence in both taxonomic groups. At the landscape scale, one of the first processes expected to drive the species assembly is dispersal (Lortie et al., 2004; Leibold et al., 2004). The convergence of dispersal-related traits within our assemblages thus demonstrated this paradigm and validated that these traits must be taken into account in landscape-scale studies. However, two functional traits within plant assemblages showed a divergence: seed mass of plant species in hedgerows and allocation to clonal reproduction of plant species in grasslands. These two traits are also considered as traits related to the competition process (Turnbull et al., 1999; Kleunen et al., 2001). Competition, theoretically acting on species assembly at a more local scale than dispersal (Lortie et al., 2004), can lead to more local convergences within assemblages. The multitude of local convergences gives rise to patterns of divergence, which is in agreement with previous studies that demonstrated similar mixed patterns of convergence and divergence at the landscape scale (e.g. de Bello et al., 2013; Concepción et al., 2017). We believe that further work is needed to clearly identify the key traits that mediate species response at the landscape scale by including a wider range of traits related to all stages of the regeneration-cycle of organisms (Zambrano et al., 2019), such as plant establishment or bird resource-acquisition (Concepción et al., 2017; Provost et al., 2020).

Landscape simplification and habitat fragmentation

According to our second hypothesis, higher landscape simplification and higher habitat fragmentation leads to lower species richness and convergence of trait values within assemblages. This hypothesis was verified for the species richness of both plants and birds: species richness of hedgerow plants, grassland plants, and birds were lower in landscapes with low compositional heterogeneity, which is in agreement with the results of previous studies (Atauri & de Lucio, 2001; Weibull et al., 2003; Smith et al., 2010; Sirami et al., 2019). Indeed, low compositional heterogeneity, which corresponds to low diversity and/or evenness in land-uses, hinders the coexistence of both species linked to a specific habitat, and generalist species which are generally the ones benefiting from landscape simplification (Redon et al., 2014). In addition, the species richness of grassland plants was higher in landscapes with a high grassland

percentage. It supports the recent habitat amount hypothesis (Fahrig, 2013) suggesting that an increase in habitat amount in a given landscape window increases species richness. This increase is attributed to the sample area effect (i.e. larger sample areas generally contain more species, MacDonald et al., 2018) and to the increase in the colonization rate between patches (MacArthur & Levins, 1967). However, contrary to our expectation, a higher landscape simplification did not lead to the convergence of trait values within assemblages: in landscapes with simple spatial configuration, the functional variance of plant assemblages was higher, especially for plant assemblages observed in hedgerows. A low configurational heterogeneity decreases the probability of hedgerows being located at interfaces among different land-use types (Fahrig et al., 2011). The reduced interfaces between hedgerows and other land-uses limits the edge effect by reducing the probability of colonization by species and can impact *in fine* the competitive hierarchies among plant species (Zambrano et al., 2019). Therefore, in a simplified landscape, the reduced competition with incoming species could allow hedgerow plant assemblages to relax the convergence toward a specific functional strategy and thus to present higher functional variances.

Furthermore, we demonstrated that higher habitat fragmentation did not lead to the convergence of trait values either: the functional variance of grassland assemblages was higher in landscapes with low grassland amount. This result is not due to an indirect effect of higher species richness as we previously demonstrated that species richness was lower in this type of landscape. It means that in landscapes with a lower habitat amount, fewer plant species were present in grasslands but they presented more variable trait values. This result can be explained by the characteristics of the study area: in this agricultural but preserved study area, landscapes with a lower grassland amount were not characterized by homogeneous intensive agricultural practices as usually described in fragmented European agrosystem (Smart et al., 2002) but by more diverse, heterogeneous practices (e.g. pasture, mowing). This diversity of local agricultural practices can lead to the selection of local trait syndromes (Klimesova et al., 2008) which resulted in higher functional variance of trait values related to the phenology (i.e. onset of flowering) or local competition (i.e. allocation to clonal reproduction) at the landscape scale.

Finally, within bird assemblages only the number of breeding events was influenced by the landscape structure: the functional variance of this trait was lower in landscapes with higher hedgerow amount. In landscapes with higher hedgerow amount, bird communities may be more represented by birds specialized in this type of wooded habitat, like greenfinches *Carduelis chloris* or dunnocks *Prunella modularis* (Fuller et al., 2001), that have a high number of breeding events (2 and 2.5 respectively whereas the mean of the regional pool is 1.7). Wooded environments may have specific constraints related to the type of resources (Hinsley & Bellamy, 2000) which might have repercussions on the number of breeding events. Landscapes with higher hedgerow amount thus favour species with

similar values of this trait which resulted in lower functional variance. However, this convergence did not seem to occur toward one specific strategy as no significant effect of the hedgerow amount on CWMs of this trait was detected. We demonstrated that including variables at both landscape level (compositional and configurational heterogeneity) and habitat level (habitat amount and isolation) can allow to highlight different mechanisms. However, the correlation between our variables was sometimes high which could have hidden some relations between the landscape structure and the functional assemblages. Future research should investigate this type of question using a large-scale sampling design that minimizes *a priori* the correlation between variables. This approach could help to disentangle the independent effect of landscape simplification and habitat fragmentation still widely discussed today. (Fahrig, 2017; Fletcher et al., 2018; Fahrig et al., 2019)

The plant and bird functional traits are related to the past landscape structure

As predicted in our third hypothesis, taxonomic and functional structures of both plant and bird assemblages were driven by past landscape structure. Plants responded to both current and past landscapes whereas birds only responded to past landscapes. The time-lagged response, known as relaxation time (Diamond, 1972), has been demonstrated for species richness and composition of assemblages (see review of Kuussaari et al., 2009) and is also highlighted here with the delay found for species richness. However, only a few studies investigated this question using a trait-based approach (but see Saar et al., 2017; Provost et al., 2020). Within the studied functional assemblages, responses to past landscapes were not related to organism dispersal capacity but rather to the reproduction and the organism's life-cycle. Our study thus provides new empirical evidence for the paradigm suggesting that delayed extinctions are especially linked to the characteristics of organisms related to turnover rates (Kuussaari et al., 2009). Indeed, both theoretical and empirical studies suggested that delayed extinctions are more likely to occur in assemblages represented by species with low turnover rates (e.g. Lindborg, 2007; Kuussaari et al., 2009; Noh et al., 2019), mostly because they display slower responses to environmental changes (Lindborg, 2007; Saar et al., 2012). Furthermore, as highlighted by Figueiredo et al. (2019), the plants' level of allocation to clonality can also delay extinctions, which was demonstrated in our assemblages of grassland plants. Bird response was even more delayed than plant response within our assemblages: bird assemblages responded to the landscape structure observed 40 years ago whereas plant assemblages mostly responded to the current landscape structure and the landscape structure observed 15 years ago. This delayed response of birds may be due to two reasons. First, bird assemblages in our study area have a longer mean lifespan than herbaceous plants: 14 years and less than 5 years respectively. According to Kuussaari et al. (2009), long-lived species are likely to show slower relaxation to a new equilibrium than short-lived species. Our results are therefore consistent with this theory and with the results of other studies conducted across several taxa highlighting a long relaxation time in long-lived species (Krauss et al., 2010). Secondly, bird delayed response could also result from high plasticity in their behaviour (With, 2015). Indeed, some species can increase their

territory and their food search radius to compensate for habitat loss (Andrén, 1994), or can adapt to unfamiliar food sources when there are alternative habitats in the surroundings if increasing mobility is too costly (Kavelaars et al., 2020). This behavioral plasticity thus allows them to survive for some time in an unfavorable environment before going extinct.

Beyond the interest in understanding the assembly rules of biodiversity at the landscape scale, our findings may also be useful in the context of landscape management. Indeed, we highlighted that bird assemblages still responded to the landscape structure observed 40 years ago, i.e. before the implementation of the Common Agricultural Policy (CAP). Though, this policy implemented at the European scale has profoundly changed the structure of agricultural landscapes in the last 50 years (van Zanten et al., 2014). Our results therefore suggest that the extinction debt of bird assemblages has not yet been paid following the implementation of the CAP and that more impacts are expected to come in the future. Moreover, the trait-based approach validates that the delayed response of biodiversity can depend on specific species' characteristics and that, beyond the number of species that are expected to be lost, agricultural landscapes of the Seine valley could also face a "functional extinction debt" (Ramalho et al., 2018). In the current context of biodiversity loss and the associated ecological functions, it is thus important to emphasize that the effect of landscape changes, whether expected to be harmful (i.e. extinction debt, Hanski & Ovaskainen, 2002) or beneficial (i.e. immigration credit, Jackson & Sax, 2010) for biodiversity, will not be visible immediately. Moreover, the difference in response delay between the plant assemblages (primary producers) and bird assemblages (herbivorous and predatory vertebrates) can exacerbate this problem by generating temporal mismatches between trophic levels (Provost et al., 2020). These trophic mismatches already observed in response to climate change (Renner & Zohner, 2018; Damien & Tougeron, 2019) can occur in response to changes in landscape structure over a longer time scale and could *in fine* alter the entire ecosystem functioning. We believe that additional empirical studies as presented here are needed and that, combined with simulation-based investigations (e.g. Lalechère et al., 2019), they could be used to predict delayed response of biodiversity expected to occur after perturbations or restoration measures.

CONCLUSION

This paper provides new insights into the response of organisms to past and current landscape structure. First, we demonstrated that patterns of convergence and divergence of traits coexist at the landscape scale as suggested by previous studies (de Bello et al., 2013). Second, we highlighted an effect of landscape structure on functional traits, especially those related to reproduction and life-cycle. These functional responses are not due to changes in species richness, indicating a direct filter effect of the landscape on the functional structure of assemblages. Third, we highlighted the major importance of the temporal component of the landscape: both plants and birds responded to past landscapes, suggesting that the biodiversity of the Seine Valley alluvial plain is still in a transitional state following the CAP

implementation. Relaxation time should therefore be considered as a key process in the context of landscape management and should be taken into account when considering the long-term consequences of land-use changes. The trait-based approach can be particularly useful to identify traits that make species sensitive to response delay and thus can help to better predict the consequences of land management policies for biodiversity in the current context of global change.

METHODS

Study site and sampling design

The study was carried out on the alluvial plain of the Seine valley in Normandy (France) and relies on the biological data collected by Ernoult et al. (2006) in 2003. This region is characteristic of the enclosed *bocage* landscape found in north-western Europe (Meeus et al., 1990). Agricultural activities are restricted mainly by floods linked to the sub-surface alluvial groundwater along the Seine (Ernoult et al., 2006). Twenty (1km x 1km) landscape windows were specifically selected to represent the range of landscape simplification and habitat fragmentation found within the Seine valley. In the 20 landscape windows, we characterized landscape parameters both at the landscape and habitat level. To take landscape dynamic into account, we analyzed these parameters at three distinct years selected based on the introduction of the common agricultural policy (CAP), which mainly consisted of an increase in field areas by merging sets of small fields into larger fields to adapt to the use of mechanical machinery: before (1963), after it was first implemented (1985) and after several successive reforms (2000). We thus analyzed three sets of land-cover data representing: (i) the current landscape structure, i.e. observed in 2000, (ii) the landscape structure observed 15 years ago, i.e. in 1985, (iii) the landscape structure observed 40 years ago, i.e. in 1963. Major changes in land-uses within the study area took place between 1963 and 1985, with a major conversion of grasslands to crops and a loss in the total hedgerow length (Supplementary Fig. S2).

Landscape structure analysis

Land-use within each of the 20 landscape windows was characterized using aerial photographs. We identified seven main land-use types: grasslands, hedgerows, crops, fruit orchards, artificial surfaces (i.e. roads, buildings), woodlands and water bodies. Land-use types and hedgerow networks were identified from black and white IGN (i.e. French national institute of geographical and forestry information) aerial photographs (1/20 000) for 1963 and 1985, and from colour IGN aerial photographs (1/25 000) for 2000 (Supplementary Fig. S3). The landscape structure in each of the 20 landscape windows was characterized at the three years studied. Landscape simplification was characterized by the landscape compositional and configurational heterogeneity. Shannon diversity index was chosen as a measure of the compositional heterogeneity (McGarigal et al., 2012). This index integrates both the diversity of land-use types present within each landscape window and their evenness. A high value indicates a high number of land-uses and/or an even distribution of land-uses within the landscape. A

value of 0 indicates that the landscape is constituted of a single land-use type. This index is independent from the patches spatial configuration (Supplementary Tables S1 and S2). In the other sections of this manuscript, we referred to this index as the compositional heterogeneity. The mean patch area was chosen as a measure of the configurational heterogeneity. This index characterizes the complexity of the spatial pattern of all land-use patches within each landscape window (Fahrig et al., 2011). A small value represents a high configurational heterogeneity. To reduce skewness, this indice was log-transformed prior to any analysis. In the other sections of this manuscript, we referred to this index as the configurational heterogeneity. Therefore, the sign of this index has been reversed, as a small value of mean patch area represents a high configurational heterogeneity. Habitat fragmentation was characterized based on two specific plant habitat types: hedgerows and grasslands (Dufлот et al., 2015). We selected the amount of habitat and the degree of isolation between patches. Habitat amount was measured as the percentage of the landscape window occupied by grasslands, and as the total length of hedgerows. In the other sections of this manuscript, we referred to these indices as the grassland amount and the hedgerow amount respectively. Habitat isolation of grasslands was quantified by the mean nearest Euclidean distance between grassland patches. The isolation of hedgerows was quantified by the number of disconnected networks of hedgerows. In the other sections of this manuscript, we referred to these indices as the grassland isolation and the hedgerow isolation respectively. All indices were calculated using Fragstat software (McGarigal et al., 2012), except total length and the number of hedgerow networks that were calculated using the ‘calculate geometry tool’ in ArcGis software. Correlations (Spearman) between landscape variables were under 0.87 at each year (Supplementary Tables S1 and S2).

Biodiversity surveys

Within each landscape window, we surveyed plant assemblages (floristic surveys of herbaceous plants in hedgerows and grasslands) and bird assemblages (point count data). Among the plant groups, we studied two independent habitats: grasslands and hedgerows. Biological data were sampled in one session by Ernoult et al. (2006) in 2003. Within each landscape window, from 12 to 27 floristic surveys of grasslands were conducted, corresponding to 294 surveys, due to the absence of grasslands in five landscape windows and inaccessible fields in other windows. In each sampled grassland, a 4m x 4m plot was delimited at the center of the patch and divided into 16 quadrats. In each quadrat, a sample of 0.20 x 0.20m was conducted (Supplementary Fig. S4). Within each landscape window, from 8 to 20 floristic surveys of hedgerows were conducted, corresponding to 274 surveys, due to the absence of hedgerows in 2 landscape windows and inaccessible hedgerows in other windows. In each sampled hedgerow, a 10m² section was selected and divided into 10 quadrats of 1m x 1m on each side of the hedgerow (Supplementary Fig. S4). Plant species were identified and their abundance was defined as the number of occurrences in each plot. Within each landscape window, four bird surveys spaced 500 meters apart were carried out with a total of 80 sampling points. Bird surveys were conducted in May and June 2003

using the point-count method (Bibby et al., 2000): all nesting species from any land-uses detected visually and acoustically over a 20-minute listening period were recorded. To study bird and plant assemblages at the landscape-scale diversity, all surveys were pooled per landscape window (Supplementary Table S3, Supplementary Fig. S4 and S5). For both birds and plants, the analyses of these data were based on the presence/absence of species, and on the occurrence rate of species.

Functional traits and indices

Five functional response traits were selected for plants and birds to reflect key functional aspects of their life-history: dispersal, reproduction and life-cycle (Table 1). For plants, values were extracted from the Bioflor (Kühn et al., 2004) and LEDA (Kleyer et al., 2008) databases. For birds, trait values were collected in Duquet (2015). In rare cases (< 2% of the species analyzed) when data were not available at the species level, trait values were determined by calculating the mean trait value of species belonging to the same genus. For species with several values for the same trait, the mean of the available data was calculated. To avoid redundancy in our analysis, we checked that trait correlations were under 0.7 (Dormann et al., 2013). Traits were at most correlated with a Spearman coefficient of 0.7 (Supplementary Table S4).

Table 1: Functional response traits selected for plants and bird

Functional traits <i>Description</i>	Process	Trait value			
		Min	Max	Mean	SD
Plants					
Seed mass (mg) <i>Mean seed mass</i>	Dispersal capacity	0.01	47.6	2.6	6
Allocation to clonal reproduction <i>Index from 1 to 5, the value 5 representing a strictly vegetative reproduction</i>		1	5	2.3	1
Beginning of flowering (month) <i>Mean value at the beginning of flowering by species</i>	Phenology	1	9	5.7	1.2
Flowering duration (month) <i>Mean flowering duration measured by species</i>		1	12	3.6	1.7
Lifespan <i>Index ranging from 1 to 4, with the value 1 representing species with a maximum cycle of one year and the value 4 representing species with more than one generative phase in their lives</i>	Life-cycle	1	4	3.3	1.2
Birds					
Body mass (g) <i>Mean body mass measured by species</i>	Dispersal capacity	8.5	10950	331.8	1256
Egg number <i>Number of eggs per average brood per species</i>		2	12	5.6	2.1
Beginning of breeding (months) <i>Mean value of the beginning of breeding by species</i>	Phenology	4	7	5.3	1
Brood number <i>Mean number of broods per year measured by species</i>		1	3.5	1.7	1
Lifespan (years) <i>Maximum lifespan per species recorded per banding</i>	Life-cycle	5	39	14.8	6.8

For each trait, we calculated two functional indices: the community weighted mean (CWM) and the community weighted variance (CWV) to characterize independently the functional structure of each biological model. These functional indices were measured for each landscape window. First, we quantified CWM which corresponds to the mean value of the functional trait considered, weighted by the relative abundances of the different species in each site (Garnier et al., 2004). Secondly, we calculated the functional variance within communities as CWV to quantify the deviation of trait values from the mean (Sonnier et al., 2010). These two indices are defined as:

$$CWM_{jk} = \sum_{i=1}^n P_{ik} \times (trait_{ij})$$

$$CWV_{jk} = \sum_{i=1}^n P_{ik} \times (trait_{ij})^2 - (CWM_{jk})^2$$

where n is the total number of species in site k , P_{ik} is the presence/absence or the occurrence rate of species i in site k and $trait_{ij}$ is the value of trait j for species i . CWV and CWM were calculated using R software (R Core Team, 2020).

Data analysis

We first analyzed trait phylogenetic signals to ensure that the information obtained in our analyses was not related to the evolutionary history of the species. The phylogenetic signal is defined as the tendency of related species to resemble each other more than randomly selected species in the phylogenetic tree (Blomberg et al., 2003). This signal was tested for each functional trait using Blomberg's K (Blomberg & Garland, 2002) with the phylogenetic tree of Zanne et al. (2014) for plants, and the tree of Jetz et al. (2012) for birds using the "phytools" package (Revell, 2012). Of all the species sampled, 82% of plants and 98% of birds were included in phylogenetic trees. All the functional traits of plant species (except flowering duration) and bird species showed a significant phylogenetic signal (Supplementary Table S5). However, the phylogenetic signals of the traits studied were lower than expected in a Brownian model ($K < 1$). Furthermore, as our question focused on the landscape filtering effect operating at the human time scale and not at the scale of an evolutionary process, phylogenetic information was not included in statistical models as recommended by de Bello et al. (2015)

Our first hypothesis is that the functional variance of traits within plant and bird assemblages is not randomly distributed at the landscape scale. To test this hypothesis, the observed CWV values of each assemblage were compared to the values of the same index calculated from random assemblages. This method tested for a possible convergence of trait values towards a single strategy (i.e. landscape

filter effect) or a possible divergence of strategies (i.e. landscape-scale divergence or local convergences): if the observed assemblages present values of trait significantly under-dispersed, it indicates a convergence of strategies toward a specific trait value; if the observed assemblages present values of trait significantly over-dispersed trait values it indicates a divergence (de Bello et al., 2009). Thus, two null models adapted from the scripts of Bernard-Verdier et al. (2012) were constructed: one to test if trait values influence the presence of species, and the second to test if trait values influence the dominance of species within assemblages. The species selection model (NM1) was based on the presence-absence of species in each assemblage and aimed to test the null hypothesis that species identity is randomly distributed from the regional species pool. In this first model, only the identity of the species was modified, the total species richness of each assemblage was fixed. The probability of a species to be drawn was weighted by its relative abundance in the regional pool (i.e. abundant species have a higher probability of being drawn than rare species). The species occurrence rate model (NM2) was based on the species occurrence rate and aimed to test the null hypothesis that the proportion of each species within assemblages is random. In this model, the species richness and identity of each species remained fixed, while occurrence rate values of species within each landscape window were randomly shuffled. For each biological models (i.e. hedgerow plants, grassland plants, and birds), 5 traits and 2 null models, 999 null assemblages were simulated and CWV was calculated for each. To highlight a convergence or divergence of traits, the observed CWV values were compared to those under the null hypothesis via the calculation of the effect size (i.e. ES). ES was preferred to Standardized Effect Size (SES) due to the non-normal distribution of null values (Bernard-Verdier et al., 2012). The ES is defined as:

$$ES = \left(\frac{\text{Number}(null < obs) + \frac{\text{Number}(null = obs)}{2}}{1000} - 0.5 \right) \times 2$$

ES varies between -1 and 1: negative ES values indicate functional convergence while positive values indicate divergence. For each trait and model, we used Student's t-tests (when distributions were normal) and Mann-Whitney tests (when distributions were non-normal) to test the significant difference of ES compared to zero.

When the CWV of the assemblages differed from random, we tested our second hypothesis: we expected that landscape simplification (i.e. decrease in compositional and configurational heterogeneity) and habitat fragmentation (i.e. decrease in habitat amount and increase in isolation) act as environmental filters and lead to the convergence of trait values within assemblages. We thus analyzed the effect of landscape variables on the CWV. The observed CWVs were preferred over ES because the models had better coefficients of determination, the results of the two methods being relatively similar. Furthermore, when null models showed a convergence of values for a given trait, the CWVs were also studied in

response to landscape variables following the same models as CWV. In addition, to have keys of understanding concerning possible indirect functional responses related to taxonomic richness (i.e. increase in functional variance due to an increase in species richness), we analyzed the effect of landscape variables on the species richness of each taxon. Very few CWVs were significantly correlated with species richness (Supplementary Table S6). For plant assemblages, we performed linear regression with four explanatory variables. For both hedgerow plant and grassland plant assemblages, the variables describing landscape simplification were the compositional heterogeneity and the configurational heterogeneity. At the habitat level, we included (i) the hedgerow amount and isolation for hedgerow plant assemblages and (ii) the grassland amount and isolation for grassland plant assemblages, as variables describing habitat fragmentation. For bird species assemblages, we performed linear regression with the six above explanatory variables because the sampling of assemblages was not focused on a single habitat type. The percentage of crops was not included in these regressions as it was correlated with the grassland amount over 0.60 (Spearman test; Supplementary Table S7).

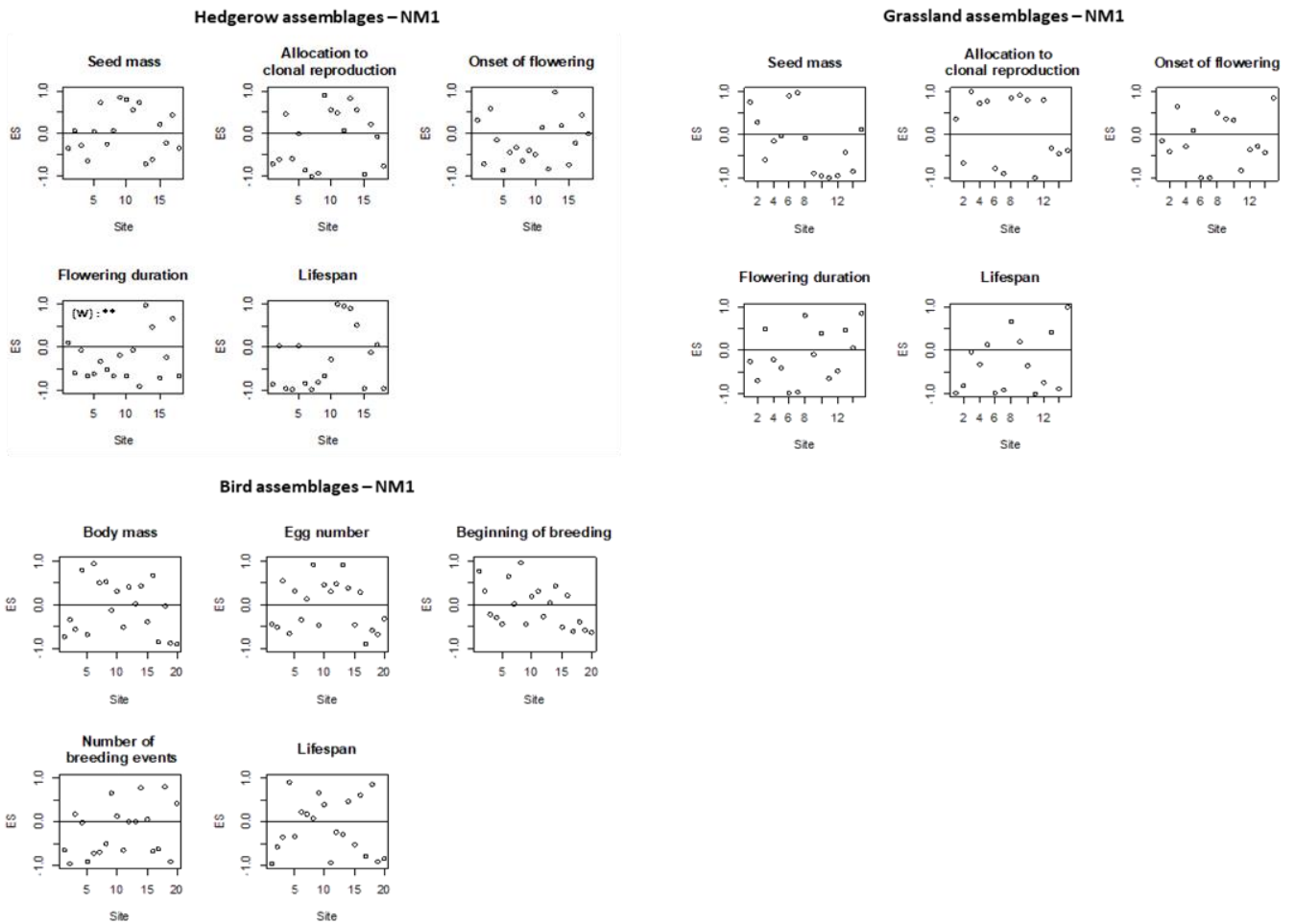
To test our third hypothesis that functional assemblages of plants and birds depend on past landscape structure rather than present landscape structure, we relied on the methodology conventionally used in articles investigating the response of organisms to the past: we confronted current biological data with past and current landscape variables. However, due to the important multicollinearity with all predictors included in a single model per trait (Supplementary Table S8), we choose to develop one model for each year (current, 15 years ago, 40 years ago). For each trait, the best model was selected by the Akaike information criterion with correction for small sample size (AICc (Burnham & Anderson, 2002)). We selected the best-fitting model with lower AICc ($\Delta AICc < 2$). All analyses were performed using R software with the 'MASS'⁵², and 'car'(Fox & Weisberg, 2019) packages.

Author contributions: All authors contributed to the methodology of the study. AE collected the biological data. LL 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.

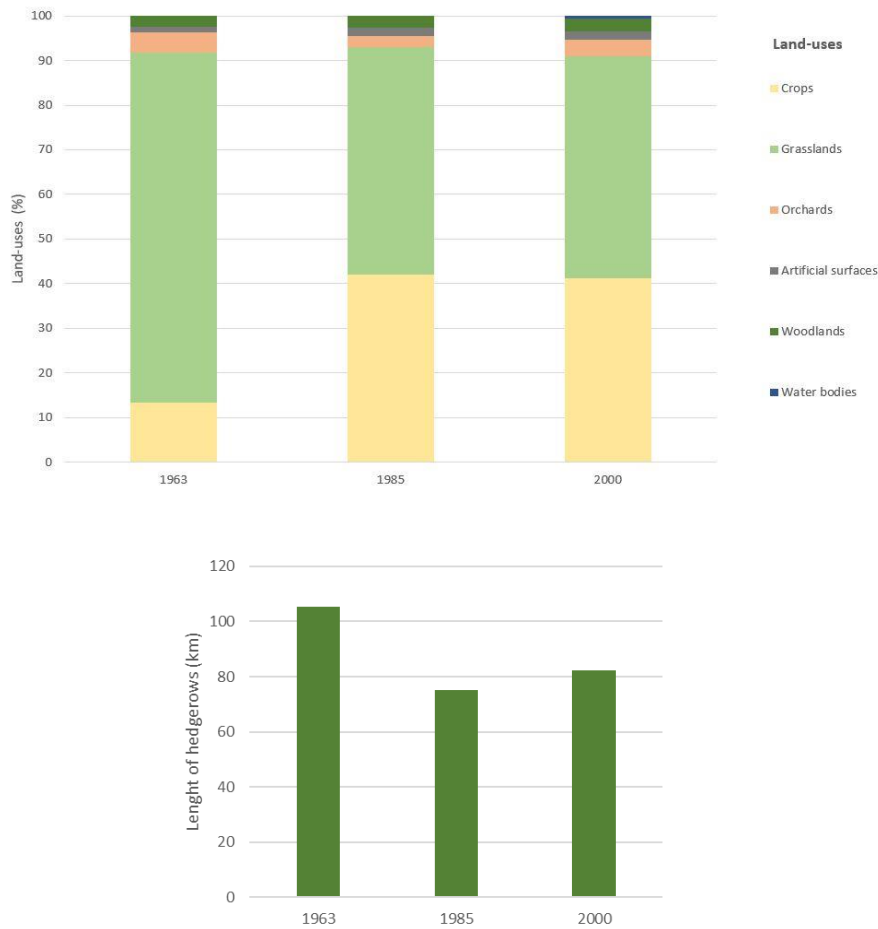
SUPPLEMENTARY MATERIALS

Supplementary Figure S1: Results of the null models NM1 of each biological model

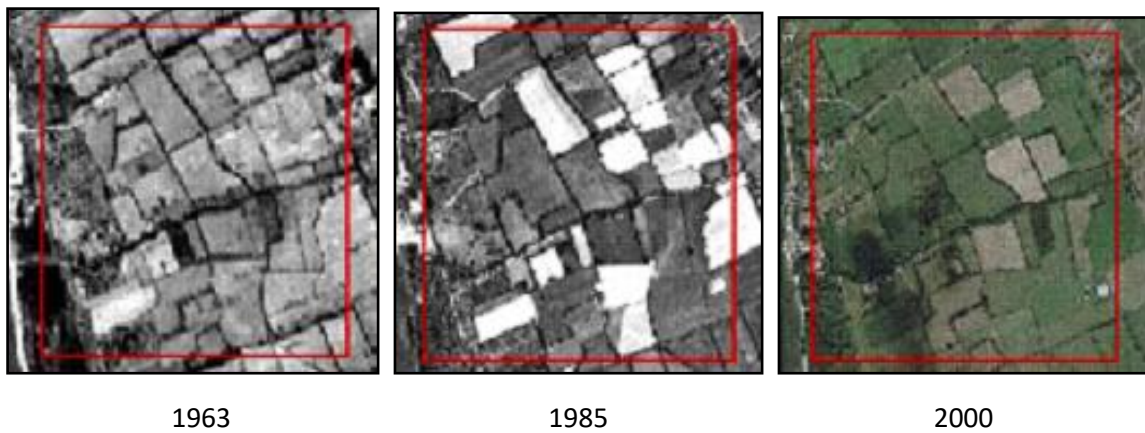
The species selection model (NM1) was based on the presence-absence of species in each assemblage and aimed to test the null hypothesis that species identity is randomly distributed from the regional species pool. In this first model, only the identity of the species was modified, the total species richness of each assemblage was fixed. The probability of a species to be drawn was weighted by its relative abundance in the regional pool (i.e. abundant species have a higher probability of being drawn than rare species). Significance level (** $p < 0.01$) of the only significant Wilcoxon test (W) is presented on the figure of flowering duration of hedgerow assemblages. This figure was created using R Software (v. 4.02, URL: <https://www.r-project.org>).



Supplementary Figure S2: Percentages of land-uses (up) and total length of the hedgerow network (down) of each year within the study area (20 sites along the Seine valley).



Supplementary Figure S3: Aerial images of one landscape window at each year (1963, 1985, 2000). This figure was created using ArcGIS Software (v. 10.6.1, URL: <https://desktop.arcgis.com>). Aerial images were bought in 2002 from the French National Institute of Geographic and Forestry Information (IGN, URL: <https://www.ign.fr/>).



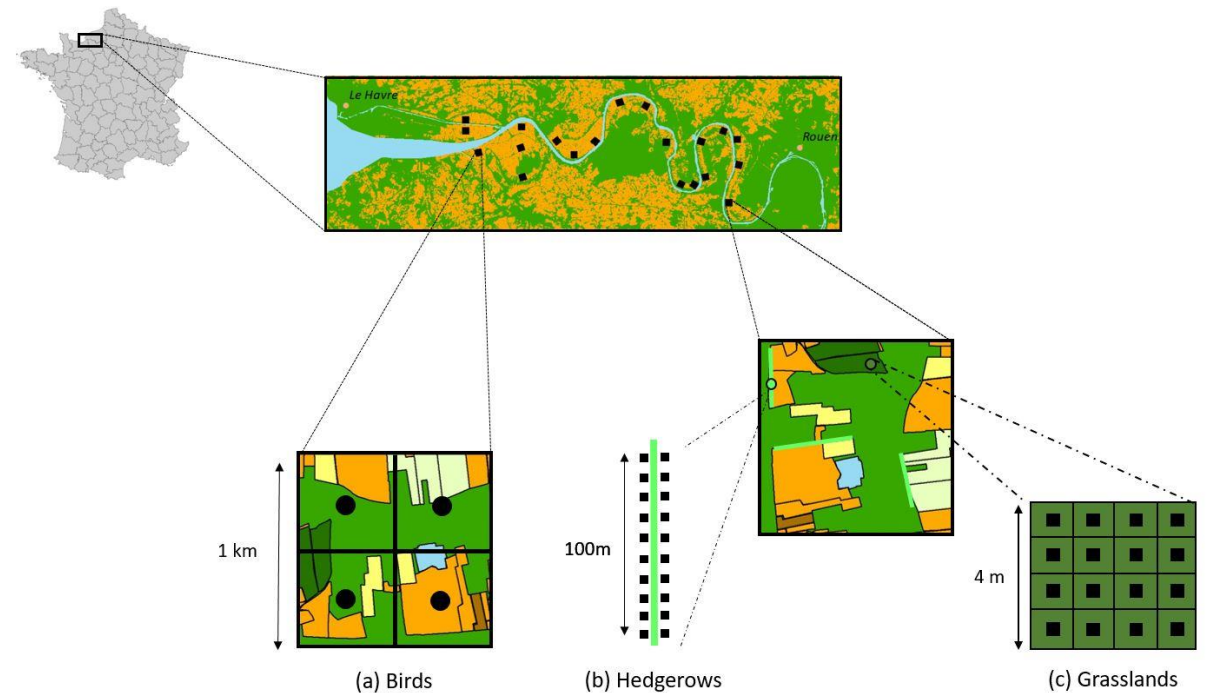
Supplementary Table S1: Results of Spearman tests (coefficient and p-value) between landscape variables of each year used in linear models for hedgerows and grasslands

Hedgerows								
2000	Mean patch area		Shannon diversity index		Hedgerow length		Number of disconnected networks of hedgerows	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean patch area	1	0						
Shannon diversity index	-0.85	<0.001	1	0				
Hedgerow length	-0.76	<0.001	0.61	0.007	1	0		
Number of disconnected networks of hedgerows	-0.81	<0.001	0.67	0.002	0.8	<0.001	1	0
1985	Mean patch area		Shannon diversity index		Hedgerow length		Number of disconnected networks of hedgerows	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean patch area	1	0						
Shannon diversity index	-0.87	<0.001	1	0				
Hedgerow length	-0.74	<0.001	0.67	0.002	1	0		
Number of disconnected networks of hedgerows	-0.75	<0.001	0.62	0.005	0.75	<0.001	1	0
1963	Mean patch area		Shannon diversity index		Hedgerow length		Number of disconnected networks of hedgerows	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean patch area	1	0						
Shannon diversity index	-0.59	0.01	1	0				
Hedgerow length	-0.58	0.01	0.12	0.63	1	0		
Number of disconnected networks of hedgerows	-0.8	<0.001	0.39	0.11	0.52	0.02	1	0
Grasslands								
2000	Shannon diversity index		Mean nearest Euclidean distance between grassland patches		Mean patch area		Grassland percentage	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Shannon diversity index	1	0						
Mean nearest Euclidean distance between grassland patches	-0.14	0.6	1	0				
Mean patch area	-0.85	<0.001	0.068	0.8	1	0		
Grassland percentage	-0.27	0.3	-0.027	0.9	0.22	0.4	1	0
1985	Mean patch area		Grassland percentage		Shannon diversity index		Mean nearest Euclidean distance between grassland patches	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean patch area	1	0						
Grassland percentage	0.22	0.42	1	0				
Shannon diversity index	-0.84	<0.001	-0.54	0.03	1	0		
Mean nearest Euclidean distance between grassland patches	-0.084	0.77	-0.28	0.3	0.034	0.9	1	0
1963	Mean patch area		Grassland percentage		Shannon diversity index		Mean nearest Euclidean distance between grassland patches	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean patch area	1	0						
Grassland percentage	0.85	<0.001	1	0				
Shannon diversity index	-0.82	<0.001	-0.88	<0.001	1	0		
Mean nearest Euclidean distance between grassland patches	-0.59	0.02	-0.78	<0.001	0.6	0.02	1	0

Supplementary Table S2: Results of Spearman tests (coefficient and p-value) between landscape variables of each year used in linear models for birds

Birds												
	2000											
	Mean nearest Euclidean distance between grassland patches		Mean patch area		Grassland percentage		Shannon diversity index		Hedgerow length		Number of disconnected networks of hedgerows	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Mean nearest Euclidean distance between grassland patches	1	0										
Mean patch area	0.4	0.08	1	0								
Grassland percentage	-0.35	0.13	-0.26	0.28	1	0						
Shannon diversity index	-0.47	0.03	-0.86	<0.001	0.21	0.38	1	0				
Hedgerow length	-0.32	0.17	-0.74	<0.001	0.26	0.26	0.58		1	0		
Number of disconnected networks of hedgerows	-0.51	0.02	-0.81	<0.001	0.14	0.54	0.66	0.001	0.82	<0.001	1	0
1985												
	Mean nearest Euclidean distance between grassland patches		Mean patch area		Grassland percentage		Shannon diversity index		Hedgerow length		Number of disconnected networks of hedgerows	
Mean nearest Euclidean distance between grassland patches	1	0										
Mean patch area	0.086	0.7	1	0								
Grassland percentage	-0.26	0.26	-0.27	0.2	1	0						
Shannon diversity index	-0.093	0.7	-0.87	<0.001	0.078	0.7	1	0				
Hedgerow length	-0.2	0.4	-0.66	0.002	0.23	0.3	0.63	1	1	0		
Number of disconnected networks of hedgerows	-0.25	0.29	-0.72	<0.001	0.29	0.2	0.61	0.004	0.8	<0.001	1	0
1963												
	Grassland percentage		Mean patch area		Hedgerow length		Number of disconnected networks of hedgerows		Mean nearest Euclidean distance between grassland patches		Shannon diversity index	
Grassland percentage	1	0										
Mean patch area	0.57	0.009	1	0								
Hedgerow length	-0.1	0.6	-0.54	0.01	1	0						
Number of disconnected networks of hedgerows	-0.27	0.2	<0.001	<0.001	0.51	0.02	1	0				
Mean nearest Euclidean distance between grassland patches	-0.61	0.004	-0.46	0.04	0.45	0.04	0.2	0.3	1	0		
Shannon diversity index	-0.8	<0.001	-0.68	0.001	0.15	0.5	0.49	0.02	0.45	0.04	1	0

Supplementary Figure S4: Protocol of biological surveys conducted in the Seine valley in 2003. All biological surveys were conducted by Ernout et al. in 2003. At each site : (a) 4 bird surveys spaced 500 meters apart were carried out with a total of 80 sampling points using the point-count method (Bibby et al. 2000). (b) 20 floristic surveys of hedgerows were conducted. A survey corresponds to 2 sections of 10m² divided into 10 quadrats of 1m x 1m on each side of the hedgerow. (c) 20 floristic surveys of grasslands were conducted. A survey corresponds to a 4m x 4m plot delimited at the center of the patch and divided into 16 quadrats where a sample of 0.20 x 0.20m was conducted. For both birds and plants, the analyses were based on one hand on the presence/absence of species and on the other hand the occurrence rate of species. This figure was created using ArcGIS Software (v. 10.6.1, URL: <https://desktop.arcgis.com>). The shapefile of the departments and the raster of land-uses were downloaded on the French government website (<https://www.data.gouv.fr>) and on the French Theia Land Data Centre (<https://www.theia-land.fr>) respectively.



Supplementary Table S3: List of all plant and bird species found across the 20 landscape windows along the Seine valley

Hedgerows	Grasslands	Birds
<i>Achillea millefolium</i>	<i>Achillea millefolium</i>	<i>Acrocephalus palustris</i>
<i>Agrimonia eupatoria</i>	<i>Aegopodium podagraria</i>	<i>Acrocephalus schoenobaenus</i>
<i>Agropyrum caninum</i>	<i>Aethusia cynapium</i>	<i>Acrocephalus scirpaceus</i>
<i>Agropyrum repens</i>	<i>Agropyrum repens</i>	<i>Aegithalos caudatus</i>
<i>Agrostis canina</i>	<i>Agrostis capillaris</i>	<i>Alauda arvensis</i>
<i>Agrostis stolonifera</i>	<i>Agrostis stolonifera</i>	<i>Alcedo atthis</i>
<i>Alisma plantago aquatica</i>	<i>Alopecurus bulbosus</i>	<i>Anas crecca</i>
<i>Alliaria petiolata</i>	<i>Alopecurus geniculatus</i>	<i>Anas platyrhynchos</i>
<i>Allium triquetrum</i>	<i>Angelica sylvestris</i>	<i>Anthus pratensis</i>
<i>Allium vineale</i>	<i>Anthoxanthum odoratum</i>	<i>Anthus trivialis</i>
<i>Alopecurus geniculatus</i>	<i>Anthriscus sylvestris</i>	<i>Athene noctua</i>
<i>Anagallis arvensis</i>	<i>Anthyllis vulneraria</i>	<i>Buteo buteo</i>
<i>Angelica sylvestris</i>	<i>Apium nodiflorum</i>	<i>Carduelis cannabina</i>
<i>Anthoxanthum odoratum</i>	<i>Arabis hirsuta</i>	<i>Carduelis carduelis</i>
<i>Anthriscus sylvestris</i>	<i>Arrhenatherum elatius</i>	<i>Carduelis chloris</i>
<i>Arctium lappa</i>	<i>Atriplex prostrata</i>	<i>Certhia brachydactyla</i>
<i>Arrhenatherum elatius</i>	<i>Avenula pratensis</i>	<i>Cettia cetti</i>
<i>Artemisia vulgaris</i>	<i>Bellis perennis</i>	<i>Charadrius dubius</i>
<i>Arum maculatum</i>	<i>Brachypodium sylvaticum</i>	<i>Ciconia ciconia</i>
<i>Aster lanceolatus</i>	<i>bromus erectus</i>	<i>Circus cyaneus</i>
<i>Atriplex prostrata</i>	<i>Bromus mollis</i>	<i>Cisticola juncidis</i>
<i>Atropa bella donna</i>	<i>Bromus racemosus</i>	<i>Columba oenas</i>
<i>Avena fatua</i>	<i>Bromus sp</i>	<i>Columba palumbus</i>
<i>Barbarea vulgaris</i>	<i>Bromus sterilis</i>	<i>Corvus corone</i>
<i>Bellis perennis</i>	<i>Calystegia sepium</i>	<i>Coturnix coturnix</i>
<i>Berula erecta</i>	<i>Campanula rapunculus</i>	<i>Cuculus canorus</i>
<i>Bidens tripartita</i>	<i>Capsella bursa pastoris</i>	<i>Cygnus olor</i>
<i>Brachypodium sylvaticum</i>	<i>Cardamine pratensis</i>	<i>Dendrocopos major</i>
<i>Brassica nigra</i>	<i>Carduus crispus</i>	<i>Dendrocopos minor</i>
<i>Brassica olearaceaeX.colza.</i>	<i>Carex acutiformis</i>	<i>Dryocopus martius</i>
<i>Bromus inermis</i>	<i>Carex binervis</i>	<i>Emberiza cirius</i>
<i>Bromus mollis</i>	<i>Carex diandra</i>	<i>Emberiza citrinella</i>
<i>Bromus racemosus</i>	<i>Carex distans</i>	<i>Emberiza schoeniclus</i>
<i>Bromus sterilis</i>	<i>Carex disticha</i>	<i>Erithacus rubecula</i>
<i>Bryona cretica</i>	<i>Carex flacca</i>	<i>Falco tinnunculus</i>
<i>Buddleja davidii</i>	<i>Carex hirta</i>	<i>Fringilla coelebs</i>
<i>Butomus umbellatus</i>	<i>Carex muricata</i>	<i>Fulica atra</i>
<i>Calamintha sylvatica</i>	<i>Carex ovalis</i>	<i>Gallinula chloropus</i>
<i>Caltha palustris</i>	<i>Carex otrubae</i>	<i>Garrulus glandarius</i>
<i>Calystegia sepium</i>	<i>Carex riparia</i>	<i>Hippolais polyglotta</i>
<i>Campanula rapunculus</i>	<i>Carex sp</i>	<i>Hirundo rustica</i>
<i>Capsella bursa.pastoris</i>	<i>Carex spicata</i>	<i>Larus ridibundus</i>
<i>Cardamine pratensis</i>	<i>Centaurea jacea</i>	<i>Locustella naevia</i>
<i>Carduus crispus</i>	<i>Centaurea nigra</i>	<i>Luscinia megarhynchos</i>
<i>Carex acutiformis</i>	<i>Cerastium arvense</i>	<i>Luscinia svecica</i>
<i>Carex diandra</i>	<i>Cerastium fontanum</i>	<i>Miliaria calandra</i>
<i>Carex disticha</i>	<i>Cerastium conglomeratus</i>	<i>Motacilla alba</i>
<i>Carex flacca</i>	<i>Cirsium arvense</i>	<i>Motacilla flava</i>
<i>Carex hirta</i>	<i>Cirsium vulgare</i>	<i>Muscicapa striata</i>
<i>Carex otrubae</i>	<i>convolvulus arvensis</i>	<i>Numenius arquata</i>
<i>Carex pseudocyperus</i>	<i>Crepis biennis</i>	<i>Parus caeruleus</i>
<i>Carex remota</i>	<i>Cynosurus cristatus</i>	<i>Parus major</i>
<i>Carex riparia</i>	<i>Dactylis glomerata</i>	<i>Parus montanus</i>
<i>Carex sp</i>	<i>Daucus carota</i>	<i>Parus palustris</i>
<i>Carex spicata</i>	<i>Deschampsia cespitosa</i>	<i>Passer domesticus</i>
<i>Centaurea jacea</i>	<i>Eleocharis palustris</i>	<i>Passer montanus</i>
<i>Centaurea nemoralis</i>	<i>Epilobium augustifolium</i>	<i>Perdix perdix</i>
<i>Centaurea nigra</i>	<i>Epilobium hirsutum</i>	<i>Phasianus colchicus</i>
<i>Centaureum pulchellum</i>	<i>Epilobium parviflorum</i>	<i>Phoenicurus ochruros</i>
<i>Cerastium fontanum</i>	<i>Epilobium tetragonum</i>	<i>Phoenicurus phoenicurus</i>
<i>Chenopodium album</i>	<i>Equisetum palustris</i>	<i>Phylloscopus collybita</i>
<i>Chenopodium polyspermum</i>	<i>Eupatorium cannabinum</i>	<i>Phylloscopus trochilus</i>
<i>Cirsium arvense</i>	<i>Euphorbia palustris</i>	<i>Pica pica</i>
<i>Cirsium acaule</i>	<i>Festuca arundinacea</i>	<i>Picus viridis</i>
<i>Cirsium palustre</i>	<i>Festuca ovina</i>	<i>Prunella modularis</i>

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<i>Cirsium vulgare</i>	<i>Festuca pratensis</i>	<i>Pyrrhula pyrrhula</i>
<i>Cladium mariscus</i>	<i>Festuca rubra</i>	<i>Rallus aquaticus</i>
<i>Clematis vitalba</i>	<i>Festulolium</i>	<i>Saxicola rubetra</i>
<i>convolvulus arvensis</i>	<i>Ficaria ranuncoloides</i>	<i>Saxicola torquata</i>
<i>Crepis biennis</i>	<i>Fillipendula ulmaria</i>	<i>Serinus serinus</i>
<i>Cynosurus cristatus</i>	<i>Fraxinus excelsior</i>	<i>Sitta europaea</i>
<i>Dactylis glomerata</i>	<i>Galium aparine</i>	<i>Streptopelia decaocto</i>
<i>Daucus carota</i>	<i>Galium mollugo</i>	<i>Streptopelia turtur</i>
<i>Deschampsia cespitosa</i>	<i>Galium palustre</i>	<i>Sturnus vulgaris</i>
<i>Dipsacus fullonum</i>	<i>Galium verum</i>	<i>Sylvia atricapilla</i>
<i>Echinochloa crus galli</i>	<i>Gaudinia fragilis</i>	<i>Sylvia borin</i>
<i>Eleocharis palustris</i>	<i>Geranium dissectum</i>	<i>Sylvia communis</i>
<i>Epilobium hirsutum</i>	<i>Geranium molle</i>	<i>Tadorna tadorna</i>
<i>Epilobium palustre</i>	<i>Geranium pusillum</i>	<i>Troglodytes troglodytes</i>
<i>Epilobium parviflorum</i>	<i>Geranium robertianum</i>	<i>Turdus merula</i>
<i>Epilobium tetragonum</i>	<i>Glechoma hederacea</i>	<i>Turdus philomelos</i>
<i>Epipactis helleborine</i>	<i>Glyceria fluitans</i>	<i>Turdus viscivorus</i>
<i>Equisetum arvense</i>	<i>Glyceria maxima</i>	<i>Tyto alba</i>
<i>Equisetum palustris</i>	<i>Hedera helix</i>	<i>Vanellus vanellus</i>
<i>Equisetum pratense</i>	<i>Heracleum sphondylium</i>	
<i>Eupatorium cannabinum</i>	<i>Holcus lanatus</i>	
<i>Euphorbia palustris</i>	<i>Hordeum murinum</i>	
<i>Festuca arundinacea</i>	<i>Hordeum secalinum</i>	
<i>Festuca pratensis</i>	<i>Humulus lupulus</i>	
<i>Festuca rubra</i>	<i>Hydrocotyle vulgaris</i>	
<i>Ficaria ranuncoloides</i>	<i>Hypochaeris radicata</i>	
<i>Filipendula ulmaria</i>	<i>Iris pseudacorus</i>	
<i>Fragaria vesca</i>	<i>Juncus acutiflorus</i>	
<i>Galinsoga parviflora</i>	<i>Juncus articulatus</i>	
<i>Galium aparine</i>	<i>Juncus effusus</i>	
<i>Galium mollugo</i>	<i>Juncus gerardii</i>	
<i>Galium palustre</i>	<i>Juncus inflexus</i>	
<i>Galeopsis angustifolia</i>	<i>Juncus subnodulosus</i>	
<i>Galeopsis tetrahit</i>	<i>Juncus sp</i>	
<i>Geranium dissectum</i>	<i>Lathyrus pratensis</i>	
<i>Geranium molle</i>	<i>Lolium multiflorum</i>	
<i>Geranium robertianum</i>	<i>Lolium perenne</i>	
<i>Geum urbatum</i>	<i>Lotus corniculatus</i>	
<i>Glechoma hederacea</i>	<i>Lotus pedunculatus</i>	
<i>Glyceria fluitans</i>	<i>Lychnis flo cuculi</i>	
<i>Gnaphalium uliginosum</i>	<i>Lycopus europaeus</i>	
<i>Hedera helix</i>	<i>Lysimachia numularia</i>	
<i>Heracleum sphondylium</i>	<i>Lysimachia vulgaris</i>	
<i>Holcus lanatus</i>	<i>Lythrum salicaria</i>	
<i>Hordeum secalinum</i>	<i>Medicago lupulina</i>	
<i>Humulus lupulus</i>	<i>Medicago sativa</i>	
<i>Hypericum perforatum</i>	<i>Mentha aquatica</i>	
<i>Hypericum quadrangulum</i>	<i>Mentha pulegium</i>	
<i>Impatiens capensis</i>	<i>Mentha sp</i>	
<i>Inula conyzae</i>	<i>Mentha spicata</i>	
<i>Iris foetidissima</i>	<i>Moehringia trinervia</i>	
<i>Iris pseudacorus</i>	<i>Myosotis arvensis</i>	
<i>Juncus acutiflorus</i>	<i>Myosotis discolor</i>	
<i>Juncus articulatus</i>	<i>Myosotis scorphioides</i>	
<i>Juncus bufonius</i>	<i>Oenanthe fistulosa</i>	
<i>Juncus effusus</i>	<i>Oenanthe salaifolia</i>	
<i>Juncus inflexus</i>	<i>Persicaria maculosa</i>	
<i>Lamiastrum galeobdolon</i>	<i>Phalaris arundinacea</i>	
<i>Lamium album</i>	<i>Pheum pratense</i>	
<i>Lamium purpureum</i>	<i>Phragmites australis</i>	
<i>Lapsana communis</i>	<i>Plantago lanceolata</i>	
<i>Lathyrus pratensis</i>	<i>Plantago major</i>	
<i>Leontodon hispidus</i>	<i>Plantago minor</i>	
<i>Leucanthemum vulgare</i>	<i>Poa pratensis</i>	

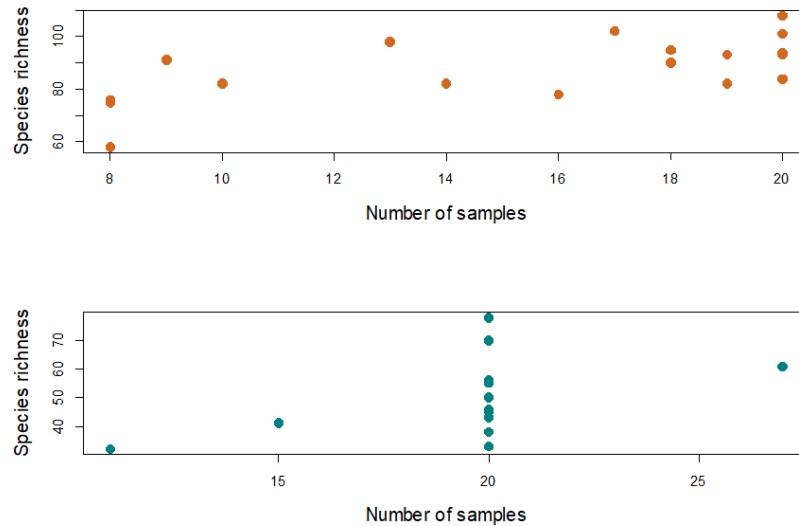
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Lolium multiflorum	Poa trivialis	
Lolium perenne	Polygonum amphibium	
Lonicera periclymenum	Polygonum aviculare	
Lotus corniculatus	Polygonum hidropiper	
Lotus pedunculatus	Polygonum sp	
Lychnis flos cuculi	Potentilla anserina	
Lycopus europaeus	Potentilla reptans	
Lysimachia nummularia	Prunella vulgaris	
Lysimachia vulgaris	Quercus petraea	
Lythrum salicaria	Ranunculus acris	
Matricaria chamomilla	Ranunculus flammula	
Matricaria discoidea	Ranunculus repens	
Medicago arabica	Ranunculus sardus	
Medicago lupulina	Rubus fruticosus	
Melilotus altissimus	Rubus sp	
Melilotus officinalis	Rumex acetosa	
Mentha aquatica	Rumex conglomeratus	
Mentha arvensis	Rumex crispus	
Mercurialis perennis	Rumex obtusifolius	
Moehringia trinervia	Samolus valerandi	
Mycelis muralis	scrophularia auriculata	
Myosotis arvensis	Senecio vulgaris	
Myosotis scorphioides	Silene latifolia	
Myosoton aquaticum	Solanum dulcamaria	
Oenanthe fistulosa	Sonchus arvensis	
Ononis spinosa	Sonchus asper	
Papaver rhoeas	Sonchus sp	
Persicaria persicaria	Stellaria media	
Petasites hybridus	Symphitum officinale	
Phalaris arundinacea	Taraxacum sp.	
Phleum pratense	Thalictrum aquilegifolium	
Phragmites australis	Thalictrum flavum	
Picris hieracioides	Tragopogon sp	
Plantago lanceolata	Trifolium campestre	
Plantago major	Trifolium dubium	
Poa nemoralis	Trifolium pratense	
Poa pratensis	Trifolium repens	
Poa trivialis	Urtica dioica	
Polygonum aviculare	Veronica hederifolia	
Polygonum hydropiper	Veronica sp	
Polygonum persicaria	Veronica verna	
Polygonum sp	Vicia cracca	
Potentilla anserina	Vicia sativa	
Potentilla reptans	Vicia sepium	
Primula veris		
Prunella vulgaris		
Pulicaria dysenterica		
Ranunculus acris		
Ranunculus aquatilis		
Ranunculus flammula		
Ranunculus repens		
Rorippa amphibia		
Rorippa nasturtium aquaticum		
Rorippa palustris		
Rosa sp		
Rubus fruticosus		
Rubus sp		
Rumex acetosa		
Rumex conglomeratus		
Rumex crispus		
Rumex hydrolaphatum		
Rumex obtusifolius		
Rumex sp		

Discussion générale

Samolus valerandi		
Scirpus maritimus		
scrophularia auriculata		
Scrophularia nodosa		
Scutellaria galericulata		
Senecio erucifolius		
Senecio vulgaris		
Setaria verticillata		
Silene latifolia		
Silene vulgaris		
Sisymbrium officinale		
Solanum dulcamaria		
Solanum nigrum		
Sonchus arvensis		
Sonchus asper		
Stachys palustris		
Stachys sylvatica		
Stellaria graminea		
Stellaria media		
Symphitum officinale		
Synapsis arvensis		
Tamus communis		
Taraxacum officinale		
Thalictrum aquilegifolium		
Thalictrum flavum		
Torilis japonica		
Tragopogon pratensis		
Trifolium dubium		
Trifolium pratense		
Trifolium repens		
matricaria maritima inodora		
Trisetum flavescens		
Triticum aestivum		
Urtica dioica		
Valeriana officinalis		
Verbena officinalis		
Veronica anagalis aquatica		
Veronica beccabunga		
Veronica catenata		
Veronica chamaedrys		
Veronica scutellata		
Veronica hederifolia		
Veronica serpyllifolia		
Veronica persica		
Veronica sp		
Vicia cracca		
Viola canina		
Viola reichenbachiana		
Viola sp		

Supplementary Figure S5: Rarefaction curves of hedgerow and grassland assemblages. Within each landscape window, from 12 to 27 floristic surveys of grasslands, and from 8 to 20 floristic surveys of hedgerows were conducted. These plots represent the number of species of hedgerow and grassland plants as a function of the number of samples. They were represented to ensure that number of samples did not have a major influence on the species richness quantified in each landscape window. This figure was created using R Software (v. 4.02, URL: <https://www.r-project.org>).



Supplementary Table S4: Results of Spearman tests (coefficient and p-value) on functional traits of hedgerows, grasslands and birds.

Hedgerows	Seed mass		Allocation		Beginning of flowering		Flowering duration		Lifespan	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Seed mass	1	0								
Allocation to clonal reproduction	-0.24	<0.001	1	0						
Beginning of flowering	-0.02	0.81	-0.04	0.59	1	0				
Flowering duration	-0.14	0.04	-0.19	<0.01	-0.26	<0.001	1	0		
Lifespan	-0.14	0.04	0.52	<0.001	-0.03	0.70	-0.34	<0.001	1	0

Grasslands	Seed mass		Allocation		Beginning of flowering		Flowering duration		Lifespan	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Seed mass	1	0								
Allocation to clonal reproduction	-0.18	0.02	1	0						
Beginning of flowering	-0.044	-0.044	-0.22	<0.01	1	0				
Flowering duration	-0.035	0.66	0.11	0.16	-0.3	<0.001	1	0		
Lifespan	-0.17	0.03	0.38	<0.001	-0.38	<0.001	0.22	<0.01	1	0

Birds	Body mass		Egg number		Beginning of breeding		Number of breeding events		Lifespan	
	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p
Body mass	1	0								
Egg number	-0.14	0.22	1	0						
Beginning of breeding	-0.23	0.04	-0.19	0.1	1	0				
Number of breeding events	-0.29	0.01	-0.3	<0.01	0.32	<0.01	1	0		
Lifespan	0.7	<0.001	-0.09	0.43	-0.29	<0.01	-0.27	0.02	1	0

Supplementary Table S5: Significance of the phylogenetic signals of the 5 continuous traits of plants and birds. Blomberg's K values vary from 0 (no signal) to infinity. P-values estimated from randomization testing, while shuffling 999 times the names of the species on the phylogenetic tree.

Traits	Hedgerows		Grasslands	
	Blomberg	p-value	Blomberg	p-value
Seed mass	0.1	0.003	0.7	0.001
Allocation to clonal reproduction	0.01	0.03	0.01	0.2
Beginning of flowering	0.02	0.009	0.02	0.04
Flowering duration	0.007	0.3	0.007	0.7
Lifespan	0.01	0.08	0.02	0.07

Traits	Birds	
	Blomberg	p-value
Body mass	0.5	0.001
Egg number	0.9	0.001
Beginning of breeding	0.3	0.05
Number of breeding events	0.5	0.001
Lifespan	0.9	0.001

Supplementary Table S6: Results of Spearman tests (coefficient and p-value) between species richness and CMVs of each biological model.

	Species richness	
	Coefficient	p
<i>Hedgerows</i>		
- CWV of seed mass	0.52	0.02
- CWV of onset of flowering	-0.32	0.19
- CWV of flowering duration	-0.19	0.46
- CWV of lifespan	-0.21	0.4
<i>Grasslands</i>		
- CWV of seed mass	0.66	0.007
- CWV of allocation to clonal reproduction	-0.72	0.002
- CWV of onset of flowering	-0.14	0.6
- CWV of lifespan	-0.003	0.9
<i>Birds</i>		
- CWV of body mass	0.43	0.053
- CWV of beginning of breeding	0.4	0.08
- CWV of number of breeding events	-0.28	0.22

Supplementary Table S7: Results of Spearman tests (coefficient and p-value) between the percentage of crops and the percentage of grasslands for the three date studied.

	Current	1985	1963
Correlation coefficient	-0.84	-0.78	-0.61
p-value	<0.001	<0.001	0.004

Supplementary Table S8: Results of the variance inflation factor (VIFs) of all linear models conducted.

	Models	VIF
Hedgerows	Functional indices of hedgerow ~ Current Shannon + Current Area mean + Current hedgerows lenght + Current Networks + 15 years ago Shannon + 15 years ago Area mean + 15 years ago hedgerows lenght + 15 years ago Networks 40 years ago Shannon + 40 years ago Area mean + 40 years ago hedgerows lenght + 40 years ago Networks	54
	Functional indices of hedgerows ~ Current Shannon + Current Area mean + Current hedgerows lenght + Current Networks	8.24
	Functional indices of hedgerows ~ 15 years ago Shannon + 15 years ago Area mean + 15 years ago hedgerows lenght + 15 years ago Networks	7.04
	Functional indices of hedgerows ~ 40 years ago Shannon + 40 years ago Area mean + 40 years ago hedgerows lenght + 40 years ago Networks	5.95
Grasslands	Functional indices of grasslands ~ Current Shannon + Current Area mean + Current grassland percentage + Current mean distance + 15 years ago Shannon + 15 years ago Area mean + 15 years ago grasslands percentage + 15 years ago mean distance + 40 years ago Shannon + 40 years ago Area mean + 40 years ago hedgerows lenght + 40 years ago Networks	103
	Functional indices of grasslands ~ Current Shannon + Current Area mean + Current grassland percentage + Current mean distance	4.3
	Functional indices of grasslands ~ 15 years ago Shannon + 15 years ago Area mean + 15 years ago grasslands percentage + 15 years ago mean distance	4.79
	Functional indices of grasslands ~ 40 years ago Shannon + 40 years ago Area mean + 40 years ago grasslands percentage + 40 years ago mean distance	7.63
Birds	Functional indices of birds ~ Current Shannon + Current Area mean + Current grassland percentage + Current mean distance + Current hedgerows lenght + Current Networks + 15 years ago Shannon + 15 years ago Area mean + 15 years ago grasslands percentage + 15 years ago mean distance + 15 years ago hedgerows lenght + 15 years ago Networks + 40 years ago Shannon + 40 years ago Area mean + 40 years ago grasslands percentage + 40 years ago mean distance + 40 years ago hedgerows lenght + 40 years ago Networks	2971
	Functional indices of birds ~ Current Shannon + Current Area mean + Current grassland percentage + Current mean distance + Current hedgerows lenght + Current Networks	10
	Functional indices of birds ~ 15 years ago Shannon + 15 years ago Area mean + 15 years ago grasslands percentage + 15 years ago mean distance + 15 years ago hedgerows lenght + 15 years ago Networks	6.98
	Functional indices of birds ~ 40 years ago Shannon + 40 years ago Area mean + 40 years ago grasslands percentage + 40 years ago mean distance + 40 years ago hedgerows lenght + 40 years ago Networks	8.4

Annexes

Article A1: Evaluation of Sentinel-2 time-series for mapping floodplain grassland plant communities

Article A2: Can UAVs fill the gap between in situ surveys and satellites for habitat mapping?

Listes des publications

Article A1: Evaluation of Sentinel-2 time-series for mapping floodplain grassland plant communities

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Remote Sensing of Environment (2019), 223, 115-129

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Abstract

Monitoring grassland plant communities is crucial for understanding and managing biodiversity. Previous studies indicate that mapping these natural habitats from single-date remotely sensed imagery remains challenging because some communities have similar physiognomy. The recently launched Sentinel-2 satellites are a promising opportunity for monitoring vegetation. This article assesses the advantages of Sentinel-2 time-series for discriminating plant communities in wet grasslands. An annual Sentinel-2 time-series was compared respectively to single-date and single-band datasets derived from this time-series for mapping grassland plant communities in a temperate floodplain located near Mont-Saint-Michel Bay, which is included in the long-term ecological research network “ZA Armorique” (France). At this 475 ha site, 123 vegetation relevés were collected and assigned to seven plant communities to calibrate and validate the Sentinel-2 data. Satellite images were classified using support vector machine (SVM) and random forest (RF) classifiers. Results show that the SVM classifier performs slightly better than the RF classifier (overall accuracy 0.78 and 0.71, respectively). They highlight that accuracy is lower when using single-date (0.67) or single-band images (0.70). The results also reveal that discrimination of plant communities is more sensitive to temporal resolution ($\Delta=0.34$ in overall accuracy) than spectral resolution ($\Delta=0.12$ in overall accuracy).

Keywords: Vegetation, Wetlands, Natural habitats, Phytosociology, EUNIS

Article A2: Can UAVs fill the gap between in situ surveys and satellites for habitat mapping?

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Remote Sensing of Environment (2020), 243, 111780

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Habitat mapping is an essential descriptor to monitor and manage natural or semi-natural ecosystems. Habitats integrate both the environmental conditions and the related biodiversity. However, it remains challenging to map certain habitats such as inland wetlands due to spectral, spatial and temporal variability in the vegetation cover. Currently, no satellite constellations optimize the spectral, spatial and temporal resolutions required to map wetlands according to the habitats discriminated from in situ surveys. Our approach aims to combine satellite and unmanned aerial vehicle (UAV) data to exceed their respective limitations. Both data sources were combined through a spectral unmixing algorithm with the hypothesis that endmembers from UAV data are pure enough to enhance plant community abundances estimated from satellite data. The experiment was conducted on the regional preserve of the Sougéal marsh, a wet grassland of 174 ha located upstream of the Mont-Saint-Michel Bay. Two satellite data sources - Sentinel-2 and Pleiades - and three acquisition periods - November 2017, April 2018 and May 2018 - were considered. A reference map of plant community distribution was produced from UAV multitemporal data and floristic surveys to validate the unmixing of satellite data. This study shows innovative results and perspectives: while UAV can improve habitat discrimination, results vary among acquisition periods and habitats. Results illustrate well the great potential of combined UAV and satellite data but also demonstrate the influence of endmembers on the unmixing process and technical limitations (e.g. spectral mismatches between sensors), which can be overcome using domain adaptation.

Keywords: Unmanned aerial vehicle, Sensor synergy, Endmember, Wetlands, Spectral unmixing, Habitat mapping, LTSER Armorique

Liste des publications

1. Publiées dans des journaux à comité de lecture

L. Lecoq, A. Ernoult, C. Mony (2021). Past landscape structure drives the functional assemblages of plants and birds, *Scientific Reports*, 11, p. 1-15.

E. Alvarez-Vanhard, T. Houet, C. Mony, **L. Lecoq**, T. Corpetti (2020). Can UAVs fill the gap between in situ surveys and satellites for habitat mapping? - *Remote Sensing of Environment*, 243, p. 111780.

S. Rapinel, C. Mony, **L. Lecoq**, B. Clement, A. Thomas, L. Hubert-Moy (2019). Evaluation of Sentinel-2 time-series for mapping floodplain grassland plant communities - *Remote Sensing of Environment*, 223, p.115-129

2. Soumis (ou à soumettre) dans des journaux à comité de lecture

L. Lecoq, C. Mony, H. Saiz, M. Marsot, A. Ernoult (en révisions dans *Journal of Ecology*). Investigating the effect of habitat amount and landscape heterogeneity on the gamma functional diversity of grassland and hedgerow plants.

L. Lecoq, A. Ernoult, E. Fabre, S. Rapinel, C. Mony (à soumettre dans *Journal of Applied Ecology*). Landscape structure influences grassland productivity through plant functional diversity.

M. Biget, T. Wang, C. Mony C, Q. Xu, **L. Lecoq**, K. Theis, S. Bordenstein, N. Ling, P. Vandenkoornhuyse (en preparation pour PNAS). Evaluating the Hologenome theory from chimeric plants.

L. Lecoq, C. Mony, G. Palka, T. Houet, O. Jambon, H. Quénot, A. Ernoult (en préparation). Future impact of land-cover changes on grassland ecosystem services in a bocage landscape.

T. Houet, G. Palka, R. Rigo, H. Boussard, J. Baudry, X. Poux, J-B. Narcy, J.M. Alvarez Martinez, S. Balbi, C. Mony, **L. Lecoq**, J. Ballé-Béganton, J. Barquin (en préparation). A scenario-based assessment of land use changes on the Blue and Green Infrastructure Networks (BGINs) strategy: the case of Couesnon watershed (Brittany, France).

3. Communications dans des conférences nationales et internationales

* : présentatrice/présentateur

L. Lecoq*, A. Ernoult, E. Fabre, S. Rapinel, C. Mony. Landscape structure influences grassland productivity through plant functional diversity. Journées scientifiques de l'ED EGAAL, July 1 2021.

L. Lecoq*, A. Ernoult, C. Mony. Impact of current and past landscape structures on plant and bird functional assemblages. *10th IALE World Congress*, Milano, Italy, July 1-5 2019.

Alvarez-Vanhard*, **L. Lecoq**, T. Houet, T. Corpetti, C. Mony - Satellite multispectral unmixing by drone data for wet grassland habitats classification - 4th Open Science Meeting of the Global Land Programme, Apr 2019, Berne, Switzerland.

L. Lecoq*, A. Ernoult, C. Mony. Impact of current and past landscape structures on plant and bird functional assemblages. 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.

4. Vulgarisation scientifique

Video

R. Causse-Védrines, **L. Lecoq.**, 2019. Simplification du paysage et services écosystémiques. <https://www.youtube.com/watch?v=XYcO0zSM8AU>

Medias

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Titre : Effet de l'hétérogénéité du paysage sur la diversité fonctionnelle des communautés végétales et les fonctions écologiques associées

Mots clés : prairies, haies, traits fonctionnels, diversité, productivité, climat, télédétection, scénarios.

Résumé : La structure du paysage, de par la quantité d'habitat semi-naturels et par l'hétérogénéité de la matrice qu'elle présente, est l'un des principaux facteurs influençant la biodiversité, en particulier dans les paysages agricoles. Cette diversité, notamment la diversité végétale, conditionne le fonctionnement des écosystèmes actuels et futurs. L'objectif général de cette thèse était de déterminer l'effet de la structure du paysage sur la diversité fonctionnelle des communautés de plantes et les fonctions écologiques associées. Menée au sein du bassin versant du Couesnon, cette étude se concentre sur deux types de végétation semi-naturelle : les prairies permanentes et les haies. Nous avons démontré que les composantes du paysage déterminent la diversité fonctionnelle des plantes à l'échelle gamma. Ces modifications sont issues de changements dans la composition des assemblages conduisant à la sélection de syndromes particuliers de traits. Nous avons également montré que l'effet du paysage sur la diversité fonctionnelle de prairies pouvait en retour influencer des fonctions de l'écosystème prairial comme le niveau de productivité et la variabilité spatiale de cette productivité. Par l'intermédiaire ou non de son effet sur les assemblages de plantes, le paysage joue donc un rôle sur la productivité des prairies. Finalement, nous avons montré que ces effets de la structure du paysage sur la biodiversité et la productivité pourraient varier dans le futur suivant différents scénarios concernant des décisions prises pour l'aménagement du territoire. Ces travaux suggèrent que ces prises de décisions devront s'orienter vers une préservation des linéaires de haies et un maintien de la complexité spatiale de la matrice paysagère afin de conserver efficacement la biodiversité et les fonctions écologiques associées.

Title: Effect of the landscape heterogeneity on the functional diversity of plant communities and the associated ecological functions

Key words: Grasslands, hedgerows, productivity, climate, remote sensing, scenarios.

Abstract: Landscape structure, through the amount of semi-natural habitat and matrix heterogeneity, is one of the main drivers of biodiversity, particularly in agricultural landscapes. This diversity, especially plant diversity, conditions the functioning of the current and future ecosystems. The overall objective of this thesis was to determine the effect of landscape structure on the functional diversity of plant communities and associated ecological functions. Conducted within the Couesnon watershed (France), this study focused on two types of semi-natural habitats: permanent grasslands and hedgerows. We demonstrated that landscape components determine the functional diversity of plants at the gamma scale. These changes are driven by changes in assemblage composition leading to the selection of particular trait syndromes. We also showed that the effect of the landscape on the functional diversity of grasslands could in turn influence grassland ecosystem functions such as the level of productivity and the spatial variability of this productivity. Mediated or not by the effect on plant assemblages, the landscape thus plays a role on the productivity of grasslands. Finally, we showed that these effects of landscape structure on biodiversity and productivity could vary in the future under different scenarios of land-use decisions. This work suggests that these decisions will have to be oriented towards the preservation of hedgerows and the maintenance of the spatial complexity of the landscape matrix, in order to effectively conserve biodiversity and the associated ecological functions.