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

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Abstract

1. 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.

2. 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 to the overall functional diversity of plants.

3. 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. Because they are linear habitats, hedgerows are indeed more likely to be influenced by edge effects than grasslands and thus displayed a strong response to landscape heterogeneity. Landscape variables influenced all stage of regeneration, and especially had a strong effect on traits related to establishment and dispersal.

4. *Synthesis.* We demonstrated that landscape structure can both affect functional diversity and select particular trait syndromes related to plant dispersal, phenology and competitiveness. These results are important because they highlight that functional diversity must be studied at the gamma scale, to better understand the effects of land management and to preserve more effectively the ecosystem functioning associated.

Keywords

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

Résumé

1. 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 ses effets 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.

2. Grâce à un plan d'échantillonnage à grande échelle utilisant 30 fenêtres paysagères, nous avons étudié les effets indépendants de la quantité d'habitat, de l'hétérogénéité de composition et de configuration sur la diversité fonctionnelle gamma des plantes de deux types d'habitat : les haies et les prairies. Nous avons également étudié ces effets sur la contribution de chaque trait lié aux différentes étapes du cycle de régénération des plantes sur la diversité fonctionnelle globale.

3. La quantité d'habitat a eu un effet contrasté sur la diversité fonctionnelle des deux types de végétation, avec un effet négatif sur les assemblages de prairies mais un effet positif sur les assemblages de haies. L'hétérogénéité du paysage n'a affecté que la diversité fonctionnelle des plantes de haies : l'hétérogénéité de configuration a favorisé la dispersion fonctionnelle mais a réduit l'équitabilité fonctionnelle, et l'hétérogénéité de composition a affecté la contribution des traits en modifiant les stratégies phénologiques et d'établissement. La structure du paysage a eu un effet très important sur les différentes étapes du cycle de régénération des plantes, en particulier sur les traits liés à l'établissement et à la dispersion.

4. *Synthèse.* Nous avons démontré que la structure du paysage peut à la fois affecter la diversité fonctionnelle et sélectionner des syndromes de traits particuliers liés à la dispersion, la phénologie et la compétitivité des plantes. Ces résultats sont importants car ils soulignent que la diversité fonctionnelle doit être étudiée à l'échelle gamma, afin de mieux comprendre les effets de la gestion des terres et de préserver plus efficacement le fonctionnement des écosystèmes associés.

Mots-clefs

Diversité fonctionnelle, diversité gamma, prairies, quantité d'habitat, haies, écologie du paysage, hétérogénéité du paysage, contribution des traits

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). However, the impacts of the landscape structure on biodiversity are still widely debated among landscape ecologists mostly because the concept of “landscape” differs among studies. In studies using the “patch-matrix” landscape model (sensu Sirami et al., 2016), which considers landscape as a set of habitat versus non habitat patches, biodiversity has for long been seen as dependent on patch size and patch isolation (Island biogeography theory; MacArthur and Wilson, 1967), while the amount of a given habitat type was considered recently as an integrative measure of both parameters (Habitat amount hypothesis; Fahrig, 2013). Habitat amount is assumed to increase species richness by favouring species colonization and providing a higher resource availability, while little support was provided yet to these predictions (Martin, 2018). In studies using the “landscape mosaic” model (Wiens, 1995), which takes into account the heterogeneity of landscape matrix, biodiversity was assumed to depend on the diversity in all surrounding land-uses (i.e. compositional heterogeneity; Fahrig et al., 2011) and on the spatial complexity of land-uses patches (i.e. configurational heterogeneity; Fahrig et al., 2011). Both components of heterogeneity may impact the potential species turnover (Poggio et al., 2010) or the dispersal movements (Duflot et al., 2014; Fahrig, 2017). So far, most studies (but see Liu et al., 2018; Corro et al., 2019) investigated the impact of landscape structure on biodiversity focusing 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 the landscape mosaic (i.e. landscape heterogeneity; e.g. Lomba et al., 2011; Duflot et al., 2014; Concepción et al., 2017), while both drivers may act simultaneously. In addition, 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

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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 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. Considering changes in trait contribution in functional diversity in response to landscape structure enable to more precisely consider the mechanisms involved in species assembly, while taking into account the dependency among traits. Response to changes in habitat amount and landscape heterogeneity might involve tight adjustment of traits related to different stages of plant regeneration, though precise predictions remain difficult.

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. We analyzed the response for grasslands and hedgerows – that constitute two semi-natural habitat types of the landscapes. 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 to shape the multidimensional functional space of gamma plant diversity (Maire et al., 2015). More specifically, 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. We expect that some specific traits might contribute more in certain situations through tight adjustment of trait syndromes.

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 (i.e. landscape characterised by the presence of networks of linear woody vegetation structures; Baudry and Jouin, 2003) 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). To describe the landscape structure with gradients as uncorrelated as possible, we did a preselection of 90 sites on which we calculated four gradients: (i) compositional heterogeneity, (ii) configurational heterogeneity, (iii) grassland percentage, and (iv) hedgerow percentage. Then we selected 30 landscape windows among the 90 pre-selected to (i) maximize the uncorrelation of each gradient, (ii) characterize a wide range of values for these four gradients (Fig. 1).

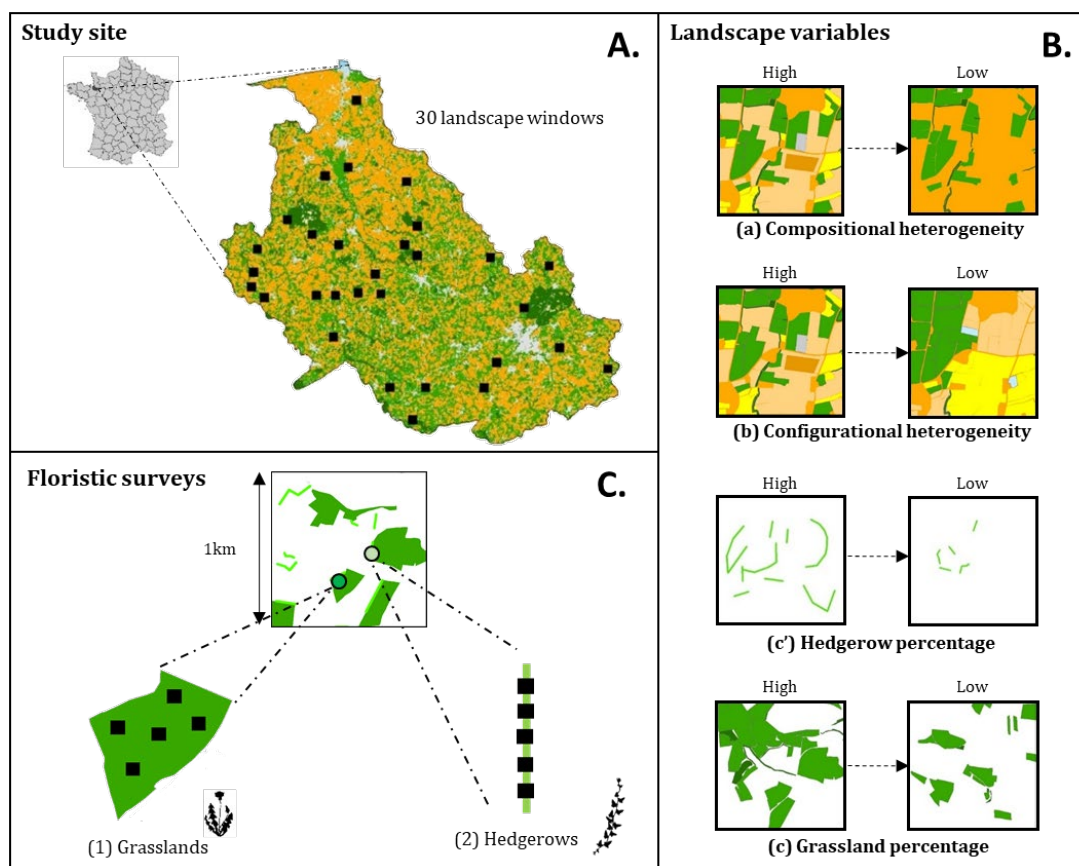


Figure 1: Representation of the four uncorrelated gradients of the 30 landscape windows selected in the Couesnon watershed (A.) and the floristic surveys conducted. B. Landscape variables: (a) Compositional heterogeneity (i.e. Shannon index) – High compositional heterogeneity corresponds to a higher diversity in land-cover types (5 in the example) while low composition heterogeneity corresponds to a low diversity in land-cover types (2 in the example), (b) Configurational heterogeneity (i.e. percentage of heterogeneous pairs of pixels with different land uses) – High configurational heterogeneity correspond to numerous small patches while low configurational heterogeneity correspond to few large patches, and the habitat

amount (percentage of grassland in grassland assemblages (c); or percentage of hedgerows in hedgerow assemblages (c')) – High habitat amount corresponds to high percentage of grassland and/or hedgerow. 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. C. 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 parcel (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 based on the plant grassland surveys (Please see Supporting Information Table and Fig. S1 for further information).

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 (Syndicat d'Aménagement et de Gestion des Eaux) 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

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pairs, the higher the configurational heterogeneity. Hereafter, we refer to these two variables as compositional and configurational heterogeneity. For the third landscape variable, we limited our choice to one variable habitat focused (i.e. either grassland or hedgerows). According to Fahrig et al. (2013), the habitat amount can summarize two predictor variables, patch size and isolation. We thus selected the habitat amount as habitat-focused variable 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 Chloé 3.1 software (Baudry et al., 2006). All indices displayed correlations under 0.45 (Pearson tests, Supporting Information Table and Fig. S2). Furthermore, to ensure that these landscape variables were not correlated with environmental factors that could influence our analyses, we conducted Spearman's correlation tests between these landscape variables and the CWM of the Ellenberg indices of i) humidity, ii) pH, iii) N score, and iv) the mean grassland age, and v) the percentage of grazed grassland parcels within the landscape windows. These tests revealed no significant correlations between the landscape variables and the environmental factor information collected (Supporting Information Table S3).

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 (Dufloy 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 meters from the edge of the parcel (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 restrict our sampling to hedgerows dominated by oak and/or chestnut that are the species that were widely planted when bocage was set up. 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 (i.e. not spontaneous) and the tree and shrub composition was equivalent between landscape windows. We ensure 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 extreme abiotic conditions and hedgerows dominated by *Salix* species or coniferous species, or that were recently planted. 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 (Supporting Information Fig. S4). 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), 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). 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 S5), 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 S6). 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). The interest of analysing trait individual contribution in the multidimensional functional indices is to take into account trait dependencies when looking at trait variance along landscape gradients. 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.

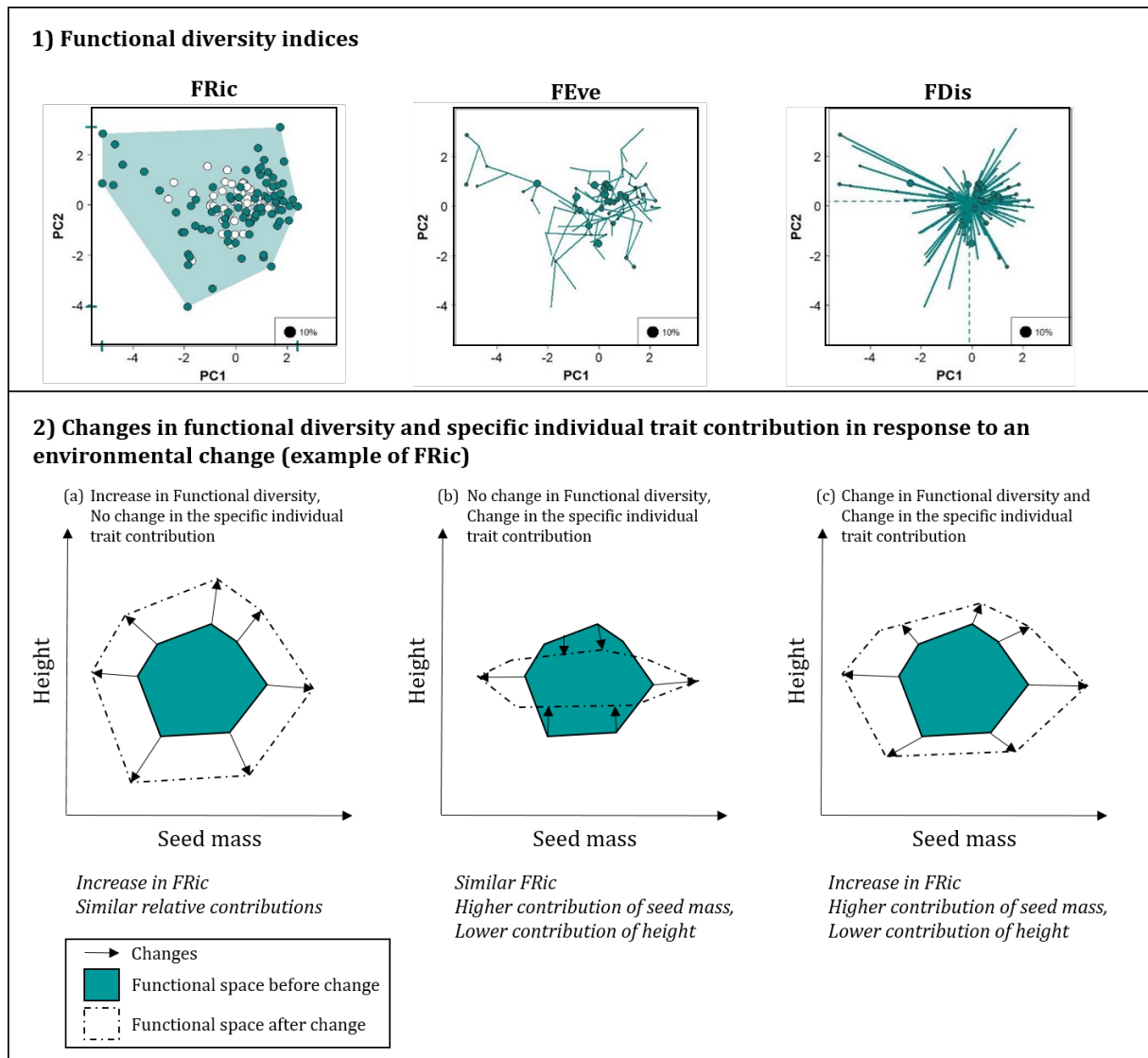


Figure 2: Representation of the three functional indices (FRic, FEve, FDis) and possible variations in trait contributions to FRic. 1) Species represented by circles are plotted in a 2-dimensions functional space according to their trait values on the 2 first axes of the PCoA built to construct the functional 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). Arrows represent the sense of the change of the functional space limits before and after the change

Data analysis

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). 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 and Weisberg, 2019) packages.

RESULTS

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

For grassland assemblages, 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 was related to the

configurational heterogeneity or the habitat amount depending on the index. FEve decreased but FDis increased with an increase in configurational heterogeneity (Fig. 3). FRic increased with the percentage of hedgerows.

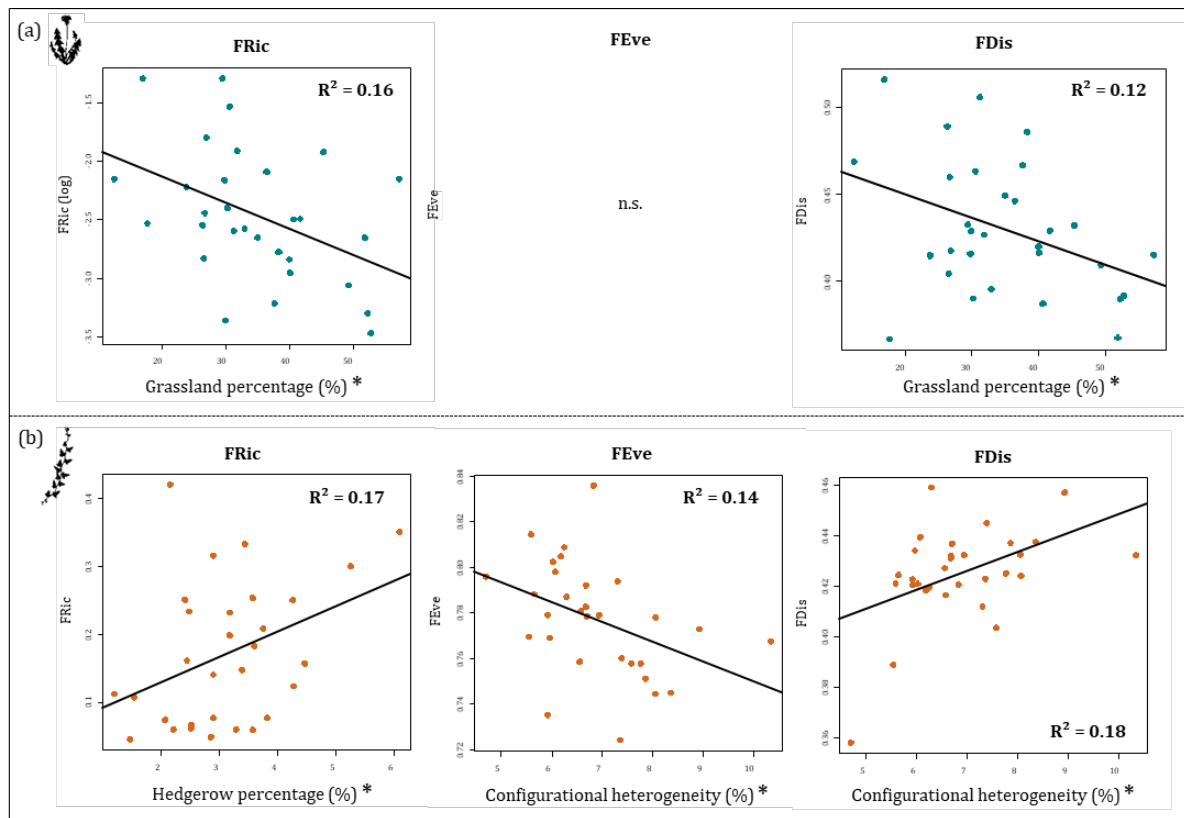


Figure 3: Results of linear models to test the effect of landscape variables on gamma functional diversity indices of grassland (a) and hedgerow (b) assemblages. Significance levels (** $p < 0.001$, * $p < 0.01$, $p < 0.05$), non-significance (n.s.) and R^2 are indicated.



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 Supporting Information (Table S7). 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. Seed mass contributed more to FDis, while plant height contributed more to FEve in landscape with high grassland amount (higher contribution of dispersal traits). Germination rate contributed less to FRic in such landscapes, i.e.

higher convergence of trait values for this trait involved in plant 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 | Percentage of grasslands | -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 | Percentage of grasslands | -0.019 | 0.001* | 0.04 | 0.11 | 0.09 | |
| (b)  | Trait contribution to FRic | Germination rate | Compositional heterogeneity | -0.482 | 0.446* | 0.01 | 0.17 | 0.51 |
| | Trait contribution to FEve | Germination rate | Compositional heterogeneity | 0.031 | -0.01* | 0.02 | 0.19 | 0.84 |
| | Trait contribution to FDis | Onset of flowering | Percentage of hedgerows | 0.025 | 0.01* | 0.048 | 0.10 | 0.36 |
| | | Germination rate | Compositional heterogeneity | -0.141 | -0.023* | < 0.001 | 0.32 | 0.45 |

DISCUSSION

Habitat amount shaped the functional diversity of grassland and hedgerow assemblages

We demonstrated that functional diversity of hedgerow assemblages increased with an increase of habitat amount, while its decreased for grassland assemblages, validating only partially the first prediction of a positive effect of habitat amount on gamma functional diversity.

In grassland assemblages, an increase in habitat amount in the landscape (i.e. increase in grassland cover percentage) was related to a decrease in FRic and FDis. This negative effect on functional diversity could result

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from two non-exclusive explanations. Firstly, landscapes with high amount of grasslands display lower proportions of other land uses. Such other land uses may shelter non-grassland species that are able to establish in grasslands. For instance, there is a higher probability of immigration in grasslands of sporadically occurring species such as *Glechoma hederacea* (L.), or *Calystegia sepium* (L.) when their native land uses (i.e. forest fragments; Supporting Information Table S8) are abundant in the landscapes. Because such species are functionally original (i.e. at the margin of the functional space), their occurrence in grassland assemblages increases functional richness and functional dispersion for assemblages of landscapes with a low proportion of grasslands. Secondly, habitat amount may covary with the agricultural management type. Grasslands in landscape with high habitat amount may be managed through the homogeneous practices - here through grazing - due to the spatial arrangement of fields within farm spatial limits. This assumption is supported by the exclusive or more frequent presence of species characteristic of mown grasslands (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. In addition, the reduction in FRic in response to higher grassland amount in the landscape was related to a decrease in contribution of plant height and germination rate to FRic. Both traits are involved in plant competitive abilities and have an important role in plant establishment (Cheplick, 1996; Gough et al., 2012). A lower variance of these traits may result from a stronger filtering process, likely due to plant local adaptation to competition as a result of intensive agricultural practices (Klimesova et al., 2008). In addition, we observed a higher contribution of height to FEve and of seed mass to FDis in landscapes with high amount of grasslands suggesting a relaxing process of the dispersal-filter and the coexistence of species with low or long-distance dispersal (Liao et al., 2013). Further refinement of this hypothesis could be done integrating the precise local management data into analyses. Such data could be acquired by contacting all farmers managing the grassland fields in the studied landscape windows.

In hedgerow assemblages, an increase in habitat amount in the landscape (i.e. increase in hedgerow cover percentage) was related to an increase in FRic. 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. Because of their linear form, hedgerows are very much subject to the edge effect (sensu Ries et al., 2004) 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 hedgerows located at the interface of various land uses increases, resulting in a higher diversity of local habitat conditions and/or composition of

colonizing species originating from the adjacent habitats. 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.). This diversity of hedgerow characteristics could promote contrasted trait values at the landscape scale and increase the functional richness. In hedgerow assemblages, the contribution of only one trait, germination rate, was related to habitat amount. In landscapes with a high hedgerow amount, species with contrasted germination trait values coexist at the gamma scale, while a high functional overlap was found in landscape with few remaining hedgerows. In these latter landscapes, assemblages may be dominated by species with particular germination rates, likely characterised by strong values, as a result of increased isolation among habitat patches which may select for species having a high establishment capacity.

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

In the present work, we demonstrated that the landscape heterogeneity influenced the gamma functional diversity of hedgerow assemblages but not of grassland assemblages, validating partially our second prediction of a positive effect of landscape heterogeneity on functional diversity. In addition, the functional diversity of hedgerow assemblages was influenced by landscape configurational heterogeneity but not compositional heterogeneity, while trait contribution depended on both.

In hedgerow assemblages, landscapes with high configurational heterogeneity (i.e. landscapes with more numerous and smaller habitat patches) corresponded to functional spaces that were less regularly occupied by plant species (i.e. decrease in FEve) indicating that some functional niches in landscapes remain vacant. In addition, assemblages are characterized by species that differ in their specific strategies at the landscape scale (i.e. increase in FDis). In such landscapes, there is a higher probability of hedgerows being located at interfaces between different habitat types (Fahrig et al., 2011). This may promote the edge effect thereby increasing the probability of colonization by functionally different species coming from nearby habitats, and result in a shift in local competitive hierarchies among plant species (Zambrano et al., 2019). In addition, the decrease in the relative contribution of germination rate in response to higher configurational heterogeneity might stress the importance of establishment traits for adapting to the abiotic conditions altered by the edge effects (Magnago et al., 2014; Zambrano et al., 2019). Surprisingly, compositional heterogeneity did not influence plant functional diversity but rather affected the relative contribution of traits into it. More specifically, increased compositional heterogeneity within the landscapes increased the contribution of germination rate but decreased the contribution of the flowering

onset to FDis, suggesting a shift in the filtering process of plant assemblages in hedgerows depending on their phenological (higher similarity among plants in landscapes with a high diversity in land-use types) and establishment strategies (higher similarity among plants in landscapes with a low diversity in land-use types). These changes might be related to modifications in niche availability and a greater differentiation of assemblages at the landscape level in response to a higher diversity in habitat types (Poggio et al., 2010). The occurrence of a higher number of species at the margins of the functional space (increased contribution in FRic) for germination rate in landscape with high compositional heterogeneity indicates also the colonization of species with atypical values, likely originated from the other land-uses.

Habitat amount versus landscape heterogeneity shape gamma functional diversity in plants

We demonstrated that both habitat amount and landscape heterogeneity influenced the functional structure of plant assemblages, with contrasting effects for the two habitat types under study. Grassland assemblages were only affected by habitat amount whereas hedgerow assemblages appeared to depend on both habitat amount and landscape heterogeneity.

The validation of the habitat amount hypothesis in hedgerow assemblages (positive effect on functional diversity), but its rejection for grassland assemblages (negative effect on functional diversity) might be due to the possible dependency of high habitat amount with the homogeneity/heterogeneity of local habitat conditions. Landscapes with high habitat amount might correspond to landscapes with more homogeneous agricultural practices for grasslands, and reversely with a higher diversity of hedgerow contexts. The contrasted response patterns between both assemblage types can also be related to the respective proportions in the landscape of the two habitats: grasslands are abundant in the landscape matrix (16 to 57% of cover percentage), while hedgerows represent at most 6% of the cover percentage (1 to 6% of cover percentage). The low cover of hedgerows in the landscape result from the successive European agricultural policies that have been implemented in the Couesnon watershed since 1960's and led to massive hedgerow removal (Burel and Baudry, 1995). Therefore, the habitat amount effect may be more pronounced for hedgerows than for grasslands because of a higher dispersal limitation of plant species among hedgerow fragments, and a lower carrying capacity of the remaining hedgerow fragments, while these assumptions need to be confirmed.

The validation of the landscape heterogeneity hypothesis in hedgerow assemblages (positive effect on functional diversity) but its invalidation for grassland assemblages (neutral effect) indicates a strong importance of edge effects in hedgerows, because of their linear form. Edge effects might include immigration of species from

adjacent land, or the indirect effect of management practices done in adjacent lands on the environmental characteristics of hedgerows. 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. These results suggest then major differences in the mechanisms underlying functional diversity in plants for these two habitat types. However to be totally comparable between both habitat types, plant surveys in hedgerows would benefit from larger quadrats to effectively detect all species, especially forest-species, but also ensure that the plateau of the species accumulation curve is reached (Figure S4).

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). Indeed, accounting for traits related to all stages of the plant regeneration cycle, including dispersal, phenology and establishment, was necessary to fully understand the mechanisms underlying plant assembly. Such result was already demonstrated with recent studies conducted at the patch scale (e.g. Provost et al., 2020; Solé-Senan et al., 2018), and can therefore be upscaled at the gamma scale where all species do not necessarily interact locally. 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 species coexistence at the landscape scale.

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Data availability: Data used for this study are available on Figshare:

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Conflict of Interest: The authors declare that they have no conflict of interest.

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