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Configurational crop heterogeneity increases within-field plant diversity

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Abstract

1. Increasing landscape heterogeneity by restoring semi-natural elements to reverse farmland biodiversity declines is not always economically feasible or acceptable to farmers due to competition for land. We hypothesized that increasing the heterogeneity of the crop mosaic itself, hereafter referred to as crop heterogeneity, can have beneficial effects on within-field plant diversity.

2. Using a unique multi-country dataset from a cross-continent collaborative project covering 1451 agricultural fields within 432 landscapes in Europe and Canada, we assessed the relative effects of compositional and configurational crop heterogeneity on within-field plant diversity components. We also examined how these relationships were modulated by the position within the field.

3. We found strong positive effects of configurational crop heterogeneity on within-field plant alpha and gamma diversity in field interiors. These effects were as high as the effect of semi-natural cover. In field borders, effects of crop heterogeneity were limited to alpha diversity. We suggest that a heterogeneous crop mosaic may overcome the high negative impact of management practices on plant diversity in field interiors, whereas in field borders, where plant diversity is already high, landscape effects are more limited.

4. Synthesis and applications. Our study shows that increasing configurational crop heterogeneity is beneficial to within-field plant diversity. It opens up a new effective and complementary way to promote farmland biodiversity without taking land out of agricultural production. We therefore recommend adopting manipulation of crop heterogeneity as a specific, effective management option in future policy measures, perhaps adding to agri-environment schemes, to contribute to the conservation of farmland plant diversity.

Keywords: biodiversity conservation, crop mosaic, diversity partitioning, farmland, field border, landscape composition, landscape configuration, weed

Résumé

1. Accroître l'hétérogénéité du paysage en restaurant les éléments semi-naturels pour enrayer le déclin de la biodiversité agricole n'est pas toujours économiquement faisable ou socialement acceptable pour les agriculteurs étant donné la compétition pour les terres. Nous faisons l'hypothèse qu'accroître l'hétérogénéité de la mosaïque de cultures, ci-après désignée par l'hétérogénéité des cultures, peut aussi avoir des effets bénéfiques sur la diversité des plantes au sein des parcelles.

2. Par l'utilisation d'un jeu de données multi-pays issu d'un projet collaboratif trans-continental rassemblant 1451 parcelles agricoles distribuées dans 432 paysages d'Europe et du Canada, nous avons estimé les effets de la composition et la configuration de l'hétérogénéité des cultures sur les composantes de la diversité des plantes au sein des parcelles.

3. Nous avons mis en évidence un fort effet positif de l'hétérogénéité de configuration des cultures sur la diversité alpha et beta des plantes, à l'intérieur des parcelles. Ces effets sont aussi importants que l'effet des éléments semi-naturels. Au niveau des bords de champs, l'effet de le hétérogénéité des cultures se limite à la diversité alpha. Nous suggérons qu'une mosaïque de cultures hétérogène peut atténuer l'effet négatif des pratiques de gestion sur la diversité des plantes à l'intérieur des parcelles, tandis qu'au niveau des bords de champs, où la diversité en plantes est plus élevée, les effets du paysage sont plus limités.

Synthèse et applications. Notre étude montre qu'accroître l'hétérogénéité de configuration des cultures est bénéfique pour la diversité des plantes au sein des parcelles. Elle ouvre de nouvelles perspectives quant au maintien et à la restauration de la biodiversité agricole sans empiéter sur les surfaces de production agricole. C'est pourquoi nous recommandons de considérer la manipulation de l'hétérogénéité des cultures dans l'élaboration des mesures politiques, en complément des mesures agri-environnementales, pour contribuer à la conservation de la diversité des plantes en milieu agricole.

Mots-clés : adventice, bordure de champ, composition du paysage, configuration du paysage, conservation de la biodiversité, milieu agricole, mosaïque de cultures, partition de biodiversité

Introduction

Since the mid-20th century, agricultural intensification has led to the conversion of complex mosaic agricultural landscapes into highly productive arable land, through field enlargement, expansion of crop areas and simplified crop rotations (Foley et al., 2011). The resulting landscape homogenization and increasing use of chemical inputs are recognized as major drivers of dramatic losses of farmland biodiversity and associated ecosystem services (Norris, 2008; Newbold et al., 2015). To stop or to reverse farmland biodiversity declines, several studies have recommended the restoration of landscape heterogeneity (Benton et al., 2003; Roschewitz et al., 2005). Increasing landscape heterogeneity by increasing the amount of semi-natural elements may, however, not be economically feasible or acceptable to farmers (Burton et al., 2008). Therefore, an alternative management strategy would be to consider whether increasing the heterogeneity of the crop mosaic itself in the landscape can provide equivalent benefits (Fahrig et al., 2011).

Within-field plants, here defined as wild, unsown plants in agricultural fields, are an important component of farmland biodiversity. They play a crucial role in supporting biological diversity by providing food and shelter for a wide variety of animals such as auxiliary insects e.g. carabids, pollinators and birds (Marshall et al., 2003; Storkey, 2006; Bretagnolle and Gaba, 2015). While a large body of literature has focused on the effects of farming practices on within-field plant diversity, an increasing number of empirical studies suggest that landscape-scale factors should also be considered (Roschewitz et al., 2005; Solé-Senan et al., 2014; Alignier et al., 2017).

The heterogeneity of the crop mosaic, hereafter referred to as crop heterogeneity, can be decomposed into two distinct components: compositional and configurational crop heterogeneity. Compositional crop heterogeneity refers to the composition of the crop mosaic, i.e. the diversity of crop cover types. Configurational crop heterogeneity refers to the shape and spatial arrangement of crop fields which can be measured as the mean size of fields or edge density (Fahrig et al., 2011). The effects of compositional and configurational crop heterogeneity on species diversity are rarely disentangled because they are typically highly correlated (Kareiva et al., 2007).

The few attempts to tease apart the effects of crop heterogeneity components on species diversity have found positive effects of compositional crop heterogeneity, i.e. Shannon crop diversity and/or configurational crop heterogeneity, i.e. edge density or mean field size, on predatory arthropods (Palmu et al., 2014; Fahrig et al., 2015; Bertrand et al., 2016; Bosem Baillod et al., 2017; Martin et al., 2019), butterflies (Perović et al., 2015) and wild bees (Hass et al., 2018). Studies addressing this issue for the diversity of plants within agricultural fields are rarer (but see Fahrig et al., 2015).

Both components of crop heterogeneity may theoretically benefit within-field plant diversity. Studies at the national scale in Europe have identified crop type as the most determinant factor of plant species composition within fields (Lososová et al., 2004; Fried et al., 2009). Therefore, diversifying crop types at the landscape scale, i.e. increasing compositional crop heterogeneity, should increase the plant species pool in the landscape by creating more niche opportunities (Benton et al., 2003; Marshall, 2009). By extension, the probability that new plant species (i.e. plant species that were not present already) immigrate into a field would be greater when the proportion and the diversity of alternative crop habitats in the landscape is increased, leading to higher local species richness (Auerbach and Shmida, 1987). Decreasing mean field size, i.e. increasing configurational crop heterogeneity, should promote the migration of short-distance dispersal plant species, facilitate their access to field interiors from neighbouring non-crop features or adjacent crop fields (i.e. cross-habitat spillover; Tscharntke et al., 2012; Henckel et al., 2015) and increase local species richness in agricultural fields.

In this paper, we assess the relative effects of compositional and configurational crop heterogeneity on within-field diversity of plants. We use a unique dataset from a cross-continent collaborative project (http://www.farmland-biodiversity.org/) covering 1451 agricultural fields, located in Europe and Canada, along uncorrelated gradients of compositional and configurational crop heterogeneity.

To our knowledge, this is the first multi-country study investigating how landscape heterogeneity of the crop mosaic is modulating alpha, beta and gamma diversity of plants in agricultural fields. We predicted that increasing compositional and configurational crop heterogeneity would increase within-field plant diversity. Field borders and field interiors may differ in non-crop plant diversity due to spatial differences in the impact of farming practices which is higher towards field interiors, and the limited plant seed dispersal from adjacent crop and non-crop features (José-María et al., 2010; Poggio et al., 2013). The spatial differences in plant diversity within fields can indeed be attributed to the higher efficacy of farming practices (crop sowing, fertilization and weed control) that may limit non-crop species occurrence in field interiors compared to field borders. Moreover, the importance of the surrounding landscape which is a source of species seed pool, is expected to decrease with increasing distance to field borders (José-María et al., 2010; Petit et al., 2013). We thus examined how relationships between crop heterogeneity and plant diversity were modulated by the position within the field. We predicted that the effect of compositional crop heterogeneity on alpha, beta and gamma plant diversity would be identical in field borders and interiors. Conversely, we predicted that the effect of configurational crop heterogeneity would be stronger on alpha, beta and gamma plant diversity in field borders than in field interiors due to higher probability of seed dispersal events from adjacent crop and non-crop features.

Materials and methods

Region and landscape selection

The study was conducted in eight agricultural regions comprising seven regions in Europe and one region in eastern Canada (near *Ottawa*; Fig. 1). The European regions followed a south-to-north gradient, with four regions in France (near *Arles*, *Niort*, *Rennes*, *Toulouse*), one in England (centred on *Ely*, Cambridgeshire), one in Germany (near *Goettingen*) and one in Spain (near *Lleida*; Fig. 1). Within these agricultural regions, we selected a total of 432 1 km × 1 km landscapes, with 60 to 90 % of crop cover in each. These landscapes represented, by design, uncorrelated gradients of compositional crop heterogeneity, assessed by the Shannon diversity index of the crop cover types, and of configurational crop heterogeneity, assessed by the total length of crop field borders (see Pasher et al., 2003 and Sirami et al., 2019 for details). The landscape selection process used the most recent remotely sensed data or land cover map available for each agricultural region (see Table S1 in Supporting Information).

While land cover maps were adequate for landscape selection, their coarse spatial resolution did not allow for the accurate delineation of narrow strips of non-crop covers between fields. Thus, all landscapes were digitized from aerial photos to create detailed maps delineating all fields managed for agricultural production (including crops, and temporary and permanent grasslands), linear semi-natural boundaries between crop fields and non-crop patches. Non-crop cover types included woodland, open land, wetland and built-up areas. Linear semi-natural boundaries included hedgerows, grassy strips and watery boundaries such as ditches. These maps were visually validated by field crews within each agricultural region before the sampling of the vegetation in a given landscape.

Based on these more accurate and recent maps, several landscape variables were calculated. Compositional crop heterogeneity was assessed using the Shannon diversity index of agricultural cover types as $SHDI = -\sum_{i=1}^{n} p_i \ln p_i$ where p_i is the proportion of crop cover type *i* (including grasslands) in the agricultural mosaic. Configurational crop heterogeneity was measured as the total field border length (*TBL*). *TBL* was the sum of perimeters of all fields within the 1 x 1 km landscape minus the length of perimeters artificially created by intersection with the limits of the 1 km × 1 km landscape. The percentage of semi-natural cover types (*SemiNatCover*) was calculated as the sum of the proportions of woodland, open land and wetland in the landscape. The length of semi-natural boundaries (*SemiNatBound*) was calculated as half of the sum of the perimeter of woody, grassy and watery boundaries in the landscape. We checked for correlations among landscape variables to avoid distortion in models caused by multi-collinearity. There was no collinearity between *SHDI* and *TBL* (Pearson correlation test, r = 0.01, *P* = 0.62; Fig. S1). Due to strong correlation between

SemiNatBound and *TBL* (r = 0.70, $P < 0.01$; Table S2), only *TBL* was kept in further analyses. We used a subset of our dataset for which *SemiNatBound* and *TBL* were not strongly correlated, to verify that this correlation did not affect our conclusions (see Appendix S1 in Supporting Information). The average value and range of the four landscape variables are presented in Table 1.

Sampling site selection

Within each landscape, we selected three to four sampling sites. Sampling sites were fields managed for agricultural production including crops, temporary and permanent grasslands. Fields were selected such that at least one contained the dominant crop type in the region, the other fields being representative of crops present within the focal landscape (Table S3). Fields were at least 200 m apart, at least 50 m away from the border of the 1 km × 1 km landscape and at least 50 m away from large non-crop cover type patches such as woodland. We selected fields bordered by a similar boundary types within each region, i.e. only grassy strips or hedgerows, wherever possible. In total, 1451 agricultural fields were sampled.

Vegetation sampling

Within each sampling site, we surveyed within-field plant species along two parallel, 1 m wide and 50 m long transects, one located on the field border, the other within the field interior resulting in 2788 transects surveyed. Transects were about 25 m distant from each other. We sampled five plots (4 m × 1 m) along each transect, i.e. 20 m² per transect (Fig. 2). Note that in *Ottawa*, transects were 2 m wide and the field border transect encompassed part of the boundary vegetation. We verified that this slight difference in sampling protocol did not affect our conclusions (Appendix S2). Percentage cover of all vascular plant species was recorded. We conducted these plant surveys over two years between 2011 and 2014, each sampling site being sampled only within a single year. Surveys were conducted once before crop harvesting, except in *Ely*, *Goettingen* and *Ottawa* where surveys were conducted twice (Table S4). In those regions, we pooled within-field plant data from the two visits per year and retained the total number of plant species for each sampled plot. Plant nomenclature followed TaxRef (Gargominy et al., 2014).

Data analysis

Following Whittaker (1972), we used the multiplicative diversity partitioning method to assess plant species diversity components where β = γ/α. Gamma diversity (γ) was the total number of species across all plots sampled in a given transect and alpha (α) diversity was the number of within-field plant species present in each plot averaged across the five plots per transect (Fig. 2). This measure of beta diversity (β) describes variation in plant species composition in the whole transect by comparison with an average plot.

We analysed variations in alpha, beta and gamma plant diversity using linear mixed-effects models (LMMs). Compositional and configurational crop heterogeneity (*SHDI* and *TBL*), and their interaction with within-field position (field border versus field interior, *POS*) and the proportion of semi-natural cover types (*SemiNatCover*) were included as fixed effects. To allow for direct comparison of the estimated coefficients and for rigorous treatment of interactions (Grueber et al., 2011), all response variables (alpha, beta and gamma diversity) and explanatory variables were centred and scaled across all regions. The partially cross-nested random structure (due to transects being sampled in the same field and different crop types being sampled in different regions, as well as different crop types being sampled in landscapes of the same region) was taken into account in the random structure of the models. The model formula was:

$$Model\ 1: y \sim SHDI + TBL + POS + SemiNatCover + SHDI{:}TBL + SHDI{:}POS + TBL{:}POS + SemiNatCover{:}SHDI + SemiNatCover{:}TBL + SemiNatCover{:}POS + (1|Region/Landscape) + \ (1|Region/Crop\ type)) + (1|IDfield)$$

Visual inspection of residual plots reveal no large deviations from homoscedasticity or normality. We then performed a multi-model inference procedure based upon the bias-corrected Akaike information criterion (AICc). We built all possible alternative candidate models based on the linear additive functions of explanatory variables. We averaged the parameters of all models for which the respective variables were present. We considered variables as significant when confidence intervals did not include zero (Burnham and Anderson 2002). Finally, we estimated variance explained by models using the marginal and conditional pseudo-R^2 statistic (Nakagawa and Schielzeth, 2013). Statistical analyses were carried out using the “lme4” package for mixed models (Bates et al., 2015) and “MuMIn” for multimodel inference (Barton, 2017) in R 3.2.3 (R Core Team, 2015).

Results

We recorded a total of 899 plant species across the eight agricultural regions. Each region contained 16 – 33 % of the total species richness.

Alpha diversity ranged from 0.4 to 42 and averaged 10.5 (SE 6.5) in field border transects. Alpha diversity ranged from 0.2 to 30.6 and averaged 5.8 (SE 5.2) in field interior transects. Within-field position (*POS*) had a strong independent effect on alpha diversity (Table 2). Alpha diversity was twice as high in field borders as in field interiors. Configurational crop heterogeneity (*TBL)* had a significant effect through an interaction with within-field position (*POS*). *TBL* had a strong positive effect on alpha diversity in field interiors but no effect on alpha diversity in field borders (Fig. 3; Appendix S3). *SemiNatCover* also had a positive effect on alpha diversity, alone or in interaction with *POS* (Table 2; Appendix S3).

Beta diversity ranged from 1 to 5 and averaged 1.95 (SE 0.44) in field border transects and 2.13 (SE 0.85) in field interior transects. Within-field position (*POS*) had a strong independent effect on beta diversity (Table 2). The only landscape variable to have a significant effect on beta diversity was configurational crop heterogeneity (*TBL)*, through an interaction with within-field position (*POS*). However, when separating field border transects and field interior transects, the effects of *TBL* were no longer significant (Appendix S3). *SHDI* and *SemiNatCover,* alone or in interaction, had no significant effect on beta diversity (Table 2).

Gamma diversity ranged from 1 to 65 in field border transects and from 1 to 50 in field interior transects. Gamma diversity was on average twice as high in field borders (mean 19.4 SE 10.7) as in field interiors (mean 10.8 SE 9.2). Configurational crop heterogeneity (*TBL)* had significant interacting effects with *POS* on gamma diversity (Table 2). *TBL* had strong positive effects on gamma diversity in field interior transects but no effect on gamma diversity in field border transects (Fig. 5; Appendix S3). *SemiNatCover*, alone or in an interaction with *POS*, had a significant and positive effect on gamma diversity (Table 2; Appendix S3).

Discussion

This study provides the first multi-country evidence that crop heterogeneity drives plant diversity within agricultural fields. As hypothesized, we showed that responses of within-field plant diversity to crop heterogeneity were modulated by the position within the field.

Alpha and gamma plant diversity increased with increasing configurational crop heterogeneity in field interior transects. Because of their high disturbance levels compared to natural ecosystems, agricultural fields are usually seen as depauperate features sheltering only a small proportion of the regional plant species pool (Landis and Marino, 1999). Heterogeneous agricultural landscapes contain a diversity of crop types which can enlarge the landscape-level plant species pool from which local communities are drawn (Tscharntke et al., 2005), resulting in higher local species richness. The strong positive effect of increasing configurational crop heterogeneity on alpha and gamma plant diversity in field interior transects is consistent with the findings of Fahrig et al. (2015) and Sirami et al. (2019). In landscapes with higher field border length, the probability of short-distance dispersal events being successful is enhanced. Thus, immigration towards the inner field from the neighbourhood is facilitated through mass effect (Schmida et al., 1985; Henckel et al., 2015). However, this result questions the viability of plant populations in the inner field if viable source populations were not maintained in the neighbourhood. The fact that beta diversity decreased with increasing configurational crop heterogeneity in field interior transects suggests that landscape effects override the effects of spatial variability in within-field management practices classically resulting in high spatial variability in plant communities in field interiors (Gaméz-Virués et al., 2015). However, when separating field border and field interior transects, this effect was no longer significant.

In contrast, we observed no effect of configurational crop heterogeneity on plant diversity (alpha and gamma) in field borders. However, we detected a positive effect of compositional crop heterogeneity on alpha diversity, about half the effect of semi-natural cover when focusing only on field borders (Appendix S3). This suggests that landscape effects are more limited where plant richness is already high. Indeed, field borders are known to act as reservoir and corridor from and by which plant species may disperse (Marshall and Moonen 2002). Therefore, the maintenance of landscape connectivity through high field border length in agricultural landscapes is important to conserve diverse plant communities.

The discrepancy in the response of within-plant diversity to configurational crop heterogeneity between field borders and field interiors can be seen as a compensation for disturbances (through intensive management practices) by complex, high diversity crop mosaics (Tscharntke et al., 2005). Previous work suggested differences in impacts of farming practices within fields (Poggio et al., 2013) with lower intensity of farming practices such as herbicide applications near field borders (Marshall and Moonen, 2002). We thus propose that, in field interiors where disturbance level is higher and colonization by short-distance dispersal events from surrounding patches more limited, increasing configurational crop heterogeneity would be more effective in enhancing species richness and diversity. Conversely, in field borders where disturbance level is lower and short-distance seed dispersal events are facilitated, increasing configurational crop heterogeneity would not result in locally enhanced plant diversity because plant diversity is already high. We could not properly test this hypothesis as spatial information about management practices was not available. However, assuming spatial heterogeneity in management impact between field borders and field interiors, our results are important for agri-environment schemes. They confirm that conservation of plant biodiversity in agricultural systems requires a landscape perspective (Tscharntke et al., 2005).

Besides the influence of configurational crop heterogeneity, we also detected a significant and positive effect of the amount of semi-natural cover types in the landscape on alpha and gamma diversity. This effect was slightly stronger than the effect of crop configurational heterogeneity (Table2). This result provides additional evidence that increasing the amount of semi-natural cover in the landscape enhances local diversity in agroecosystems (Tscharntke et al., 2005; Concepción et al., 2012).

Finally, we showed that main relationships between crop heterogeneity and plant diversity hold true when accounting for crop type identity, or when focusing only on cereal fields, the most dominant crop type across our eight regions, or on grasslands (Appendix S4). However, the crop heterogeneity component differed with crop type, with a positive effect of crop compositional heterogeneity in cereals but a positive effect of configurational crop heterogeneity in grasslands. Further research is needed to identify the conditions (pedo-climatic context, crop type) and mechanisms involved, to understand under when, increasing crop heterogeneity benefits plant diversity.

Conclusions and management implications

Our study provides the first multi-country evidence that heterogeneity of the crop mosaic itself can provide additional benefits to semi-natural elements for the maintenance of plant diversity within agricultural fields. Our findings support the importance of adopting a landscape perspective in policy measures, perhaps adding to agri-environmental schemes, to preserve within-field plant diversity and by extension, associated ecosystem services (Tscharntke et al., 2005).

The length of field borders benefits plant diversity as much as semi-natural cover. Thus, managing configurational crop heterogeneity opens new effective and complementary approaches to farmland biodiversity conservation (Fahrig et al., 2015; Batáry et al., 2017; Solé-Senan et al., 2018; Martin et al.

2019; Sirami et al., 2019). By increasing plant diversity within-field, the increase of field border length may also contribute to increase the provisioning and spatial continuity of floral resource for organisms ensuring ecological functions beneficial to agricultural production, such as pollination and pest regulation (Vialatte et al., 2017). To do so will require the development of policy measures aiming at increasing configurational crop heterogeneity such as changing field shape to increase field border length, restoring margins or sowing in-field strips while maintaining habitats for viable source plant populations. Such policies could be favourably perceived by farmers and constitute a valuable alternative to agri-environmental schemes as they do not require taking land out of agricultural production and as machinery efficiency does not decrease significantly in smaller fields (Rodríguez and Wiegand, 2009). Isolating economic effects of landscape fragmentation, Latruffe and Piet (2014) showed that decreasing field size reduces productivity as well as total technical efficiency (that is to say whether farmers operate their farm efficiently and whether the farm's production scale is optimal) but increases gross product and profitability.

We are aware that these recommendations may have trade-offs. We recognize that reversing the trend of the loss of plant diversity in agro-ecosystems is not usually within the farmers' top objectives and that there may be a conflict between weed management and biodiversity conservation. We argue that the choice of cropping systems (which includes crop rotation) and specific management strategies can help determine the pool of non-crop species present in each field (Smith and Mortensen, 2017). Furthermore, the maintenance of higher crop diversity can help prevent the development of single, problematic weed species in the long term (Melander et al., 2005, Blackshaw et al., 2007, Smith and Mortensen, 2017). We also recognize that increasing the amount of field borders (to increase configurational crop heterogeneity) might have negative side effects on natural areas. Despite extensive research showing that vegetated field borders contribute to reduce pesticide transport by run-off, some authors reported that field borders might also consitute a source of pollutant run-off (e.g. Sheppard et al., 2006). Biodiversity in natural areas may then be at significant ecotoxicological risk from drift nearby such borders. In conclusion, managing heterogeneity of the crop mosaic itself appears as a promising alternative way to preserve farmland biodiversity even in landscapes dominated by intensively cultivated lands.

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Authors' contribution

LF, JLM, GS, VB, LB, FB, BP, TT and PB conceived the idea and designed methodology within the FarmLand project; AA, XOSS, IR, BB, DG, NG, JR, CS, GS, ABB, CB, RC, AH, LH, PM, IB, GB, FC, YC, RG, JG, KL, JM, SM, NP, AV and NY collected data. AA, XOSS, IR, BP, LF, DG, NG, JLM, JR, CS, GS and PB analysed the data. AA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Average and range of landscape explanatory variables across all regions.

Code	Variable	Mean ± SE	Min	Max
SHDI	Shannon crop diversity index	1.02 ± 0.39	0	2.03
TBL	Total length of crop borders (in kilometers)	19.25 ± 7.71	5.76	60.13
SemiNatCover	Proportion of semi-natural cover types (in %)	12.72 ± 9.03	0	49.52
SemiNatBound	Length of semi-natural boundaries (in kilometers)	5.63 ± 3.82	0	29.79

Table 2 : Model-averaged standardized estimates and *P* values from LMMs of alpha, beta and gamma within-field plant diversity in relation to compositional and configurational crop heterogeneity, within-field position and the amount of semi-natural cover. Data are from 2788 transects pertaining to 432 1 km x 1 km landscapes in eight agricultural regions. Six transects were sampled in each landscape, one at the edge and one in the interior of each of three agricultural fields. Each transect contained five plots, over which the diversity measures were calculated (see Fig 1). *SHDI* : Shannon crop diversity index, *TBL*: Total length of crop borders, *SemiNatCover*: Proportion of semi-natural cover types in the landscape, *POS*: within-field position, ns: not significant, *: *P* < 0.05, **: *P* < 0.01, ***: *P* < 0.001.

	Alpha diversity			Beta diversity			Gamma diversity		
	Estimate	SE	P value	Estimate	SE	P value	Estimate	SE	P value
Intercept	0.358	0.142	*	-0.113	0.102	ns	0.401	0.143	**
SHDI	0.031	0.027	ns	0.017	0.027	ns	0.043	0.027	ns
TBL	-0.022	0.036	ns	0.045	0.040	ns	0.007	0.036	ns
SemiNatCover	0.303	0.030	***	-0.035	0.028	ns	0.292	0.029	***
POS [interior]	-0.790	0.025	***	0.267	0.034	***	-0.842	0.025	***
SHDI x TBL	0.001	0.022	ns	0.036	0.023	ns	0.010	0.021	ns
SHDI x POS	0.043	0.026	ns	0.012	0.035	ns	0.048	0.025	ns
TBL x POS	0.213	0.026	***	-0.125	0.034	***	0.170	0.026	***
SemiNatCover x SHDI	0.017	0.022	ns	-0.020	0.022	ns	0.016	0.021	ns
SemiNatCover x TBL	-0.025	0.023	ns	0.008	0.023	ns	-0.026	0.022	ns
SemiNatCover x POS	-0.346	0.026	***	-0.018	0.039	ns	-0.337	0.026	***
Conditional R²		0.57			0.18			0.57	
Marginal R²		0.22			0.02			0.24	

Figure captions

Figure 1. Location (nearest big city) of the eight study sites in a) Europe and b) eastern Ontario, Canada (sample landscapes spread through the shaded region of Ontario, with arrow pointing at the largest city, Ottawa, at the north edge of the region for context). c) Illustration of the location of 1 km x 1 km sample landscapes in one of the eight regions (near Rennes in Brittany, France).

Figure 2. Illustration of the sampling design and within-field plant diversity components. Within each sampling site, we surveyed within-field plant species along two transects, one located on the field border, the other within the field interior. Gamma diversity (γ) was the total number of species across all plots sampled in a given transect and alpha (α) diversity was the number of within-field plant species present in each plot averaged across the five plots per transect. Beta diversity (β) describes how many more species are present in the whole transect than at an average plot.

Figure 3. Interaction plot of the effect on alpha diversity (i.e. mean plot species diversity) of within-field plants with configurational crop heterogeneity measured as the total crop border length (*TBL*), according to within-field position. The dotted line fits field interior transects whereas the solid line fits field border transects. Grey zones delimit the confidence intervals at 95%. Note that variables are centred and scaled.

Figure 4. Interaction plot of the effect on beta diversity (i.e. ratio between gamma and alpha diversity) of within-field plants with configurational crop heterogeneity measured as the total crop border length (*TBL*), according to within-field position. The dotted line fits field interior transects whereas the solid line fits field border transects. Grey zones delimit the confidence intervals at 95%. Note that variables are centred and scaled.

Figure 5. Interaction plot of the effect on gamma diversity (i.e. total number of species across all five plots sampled in a transect) of within-field plants with configurational crop heterogeneity measured as the total crop border length (*TBL*), according to within-field position. The dotted line fits field

interior transects whereas the solid line fits field border transects. Grey zones delimit the confidence intervals at 95%. Note that variables are centred and scaled.

List of figures

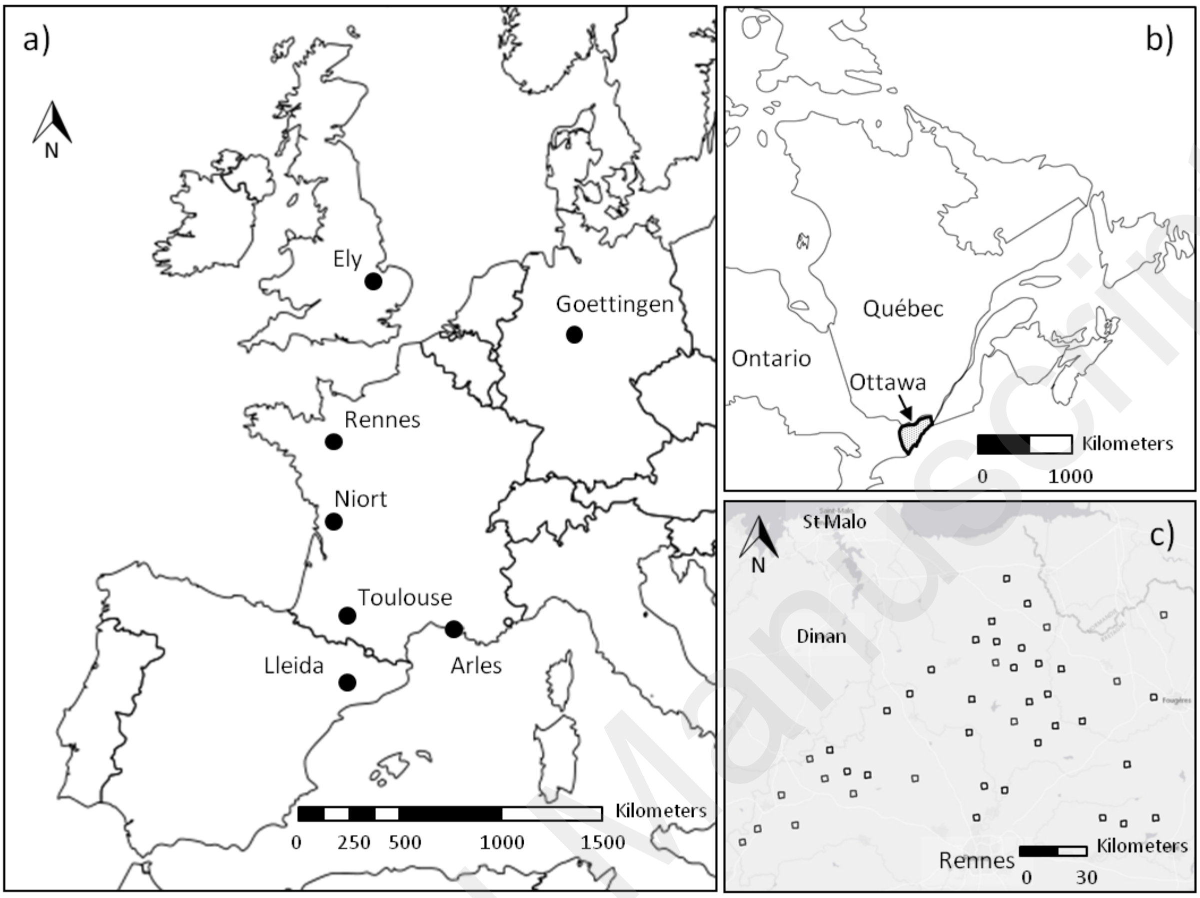


Figure 1.

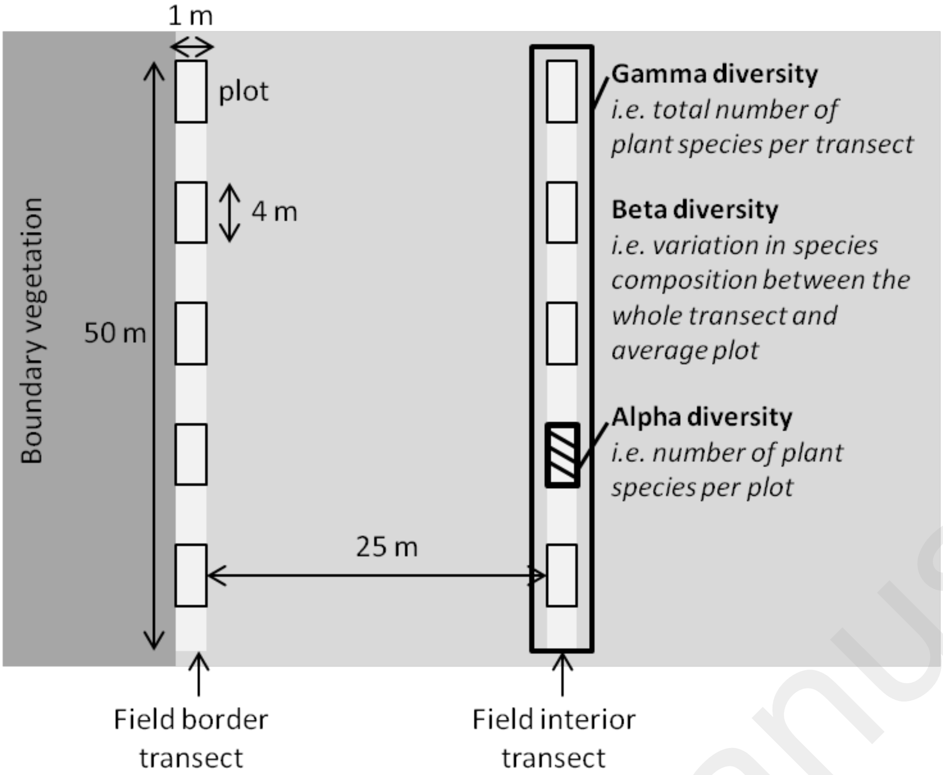
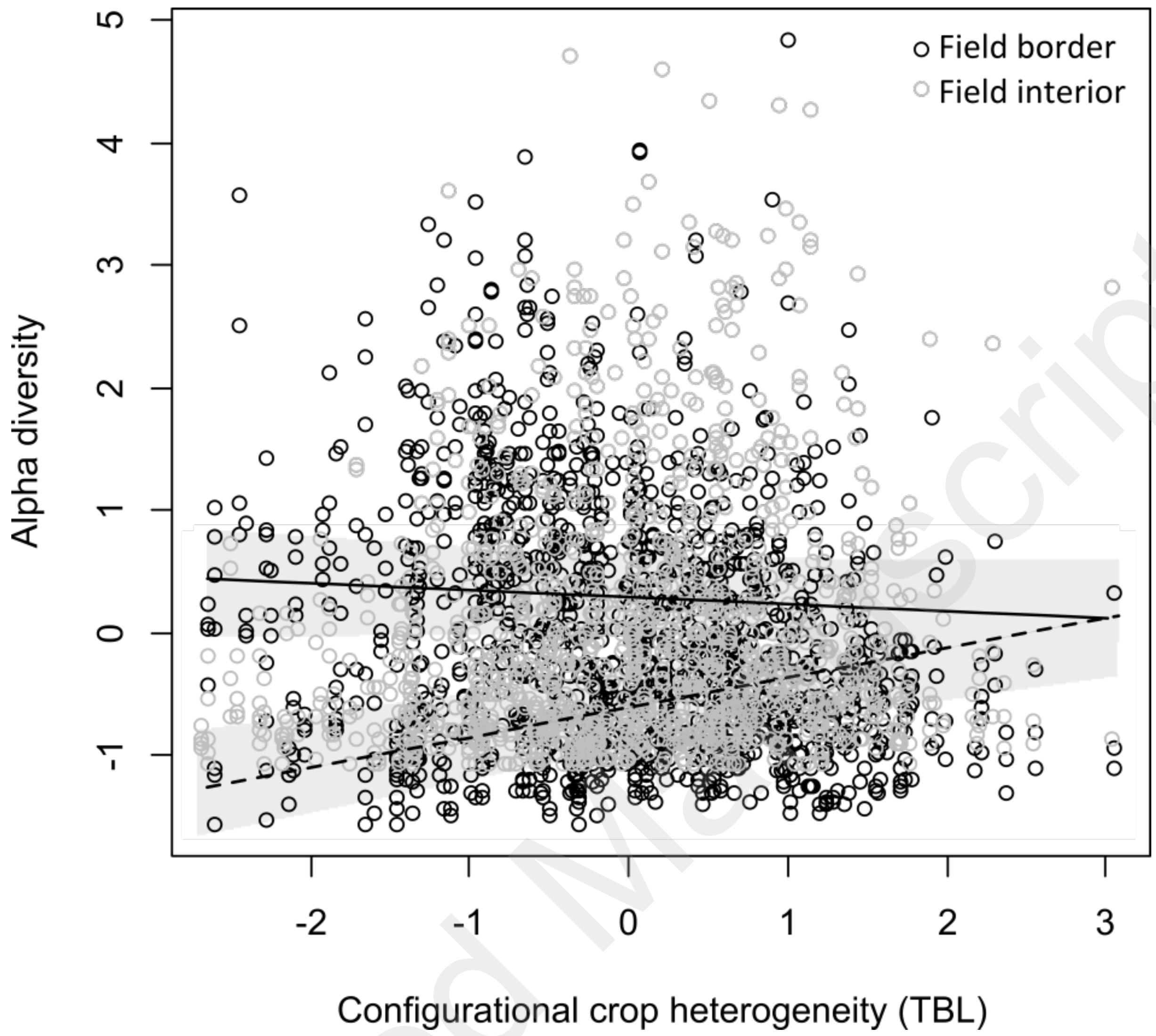

1 m
plot
4 m
50 m
Boundary vegetation
25 m
Gamma diversity
i.e. total number of plant species per transect
Beta diversity
i.e. variation in species composition between the whole transect and average plot
Alpha diversity
i.e. number of plant species per plot
Field border transect
Field interior transect

Figure 2.



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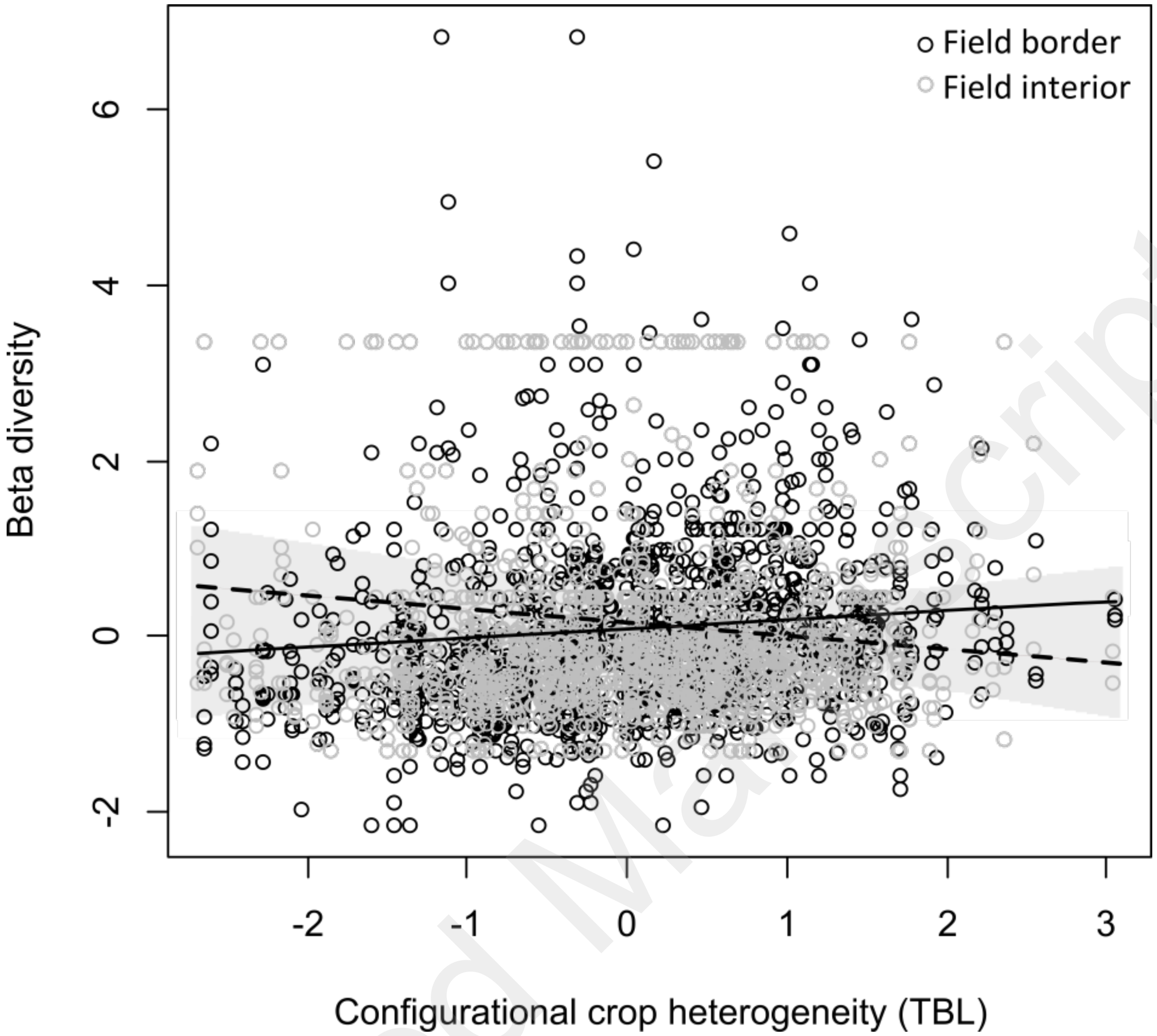
588 Figure 3.



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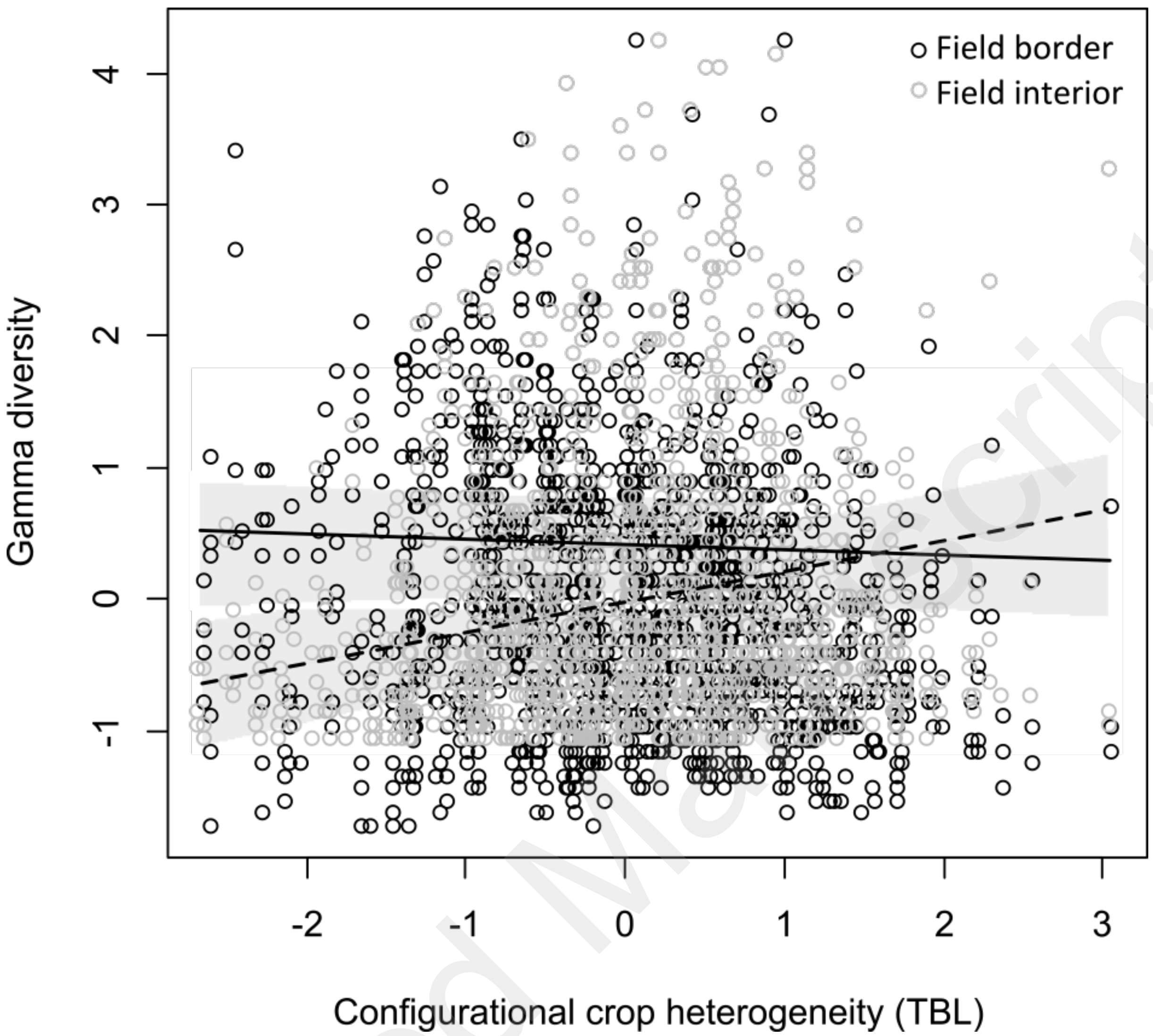
590 Figure 4.



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592 Figure 5.