



Configurational crop heterogeneity increases within-field plant diversity

Audrey Alignier, Xavier Solé-senan, Irene Robleño, Bàrbara Baraibar, Lenore Fahrig, David Giralt, Nicolas Gross, Jean-Louis Martin, Jordi Recasens, Clélia Sirami, et al.

► To cite this version:

Audrey Alignier, Xavier Solé-senan, Irene Robleño, Bàrbara Baraibar, Lenore Fahrig, et al.. Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, 2020, 57 (4), pp.654-663. 10.1111/1365-2664.13585 . hal-02518943

HAL Id: hal-02518943

<https://hal.inrae.fr/hal-02518943>

Submitted on 27 May 2020

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

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

1 **Configurational crop heterogeneity increases within-field plant diversity**

2 Audrey Alignier^{1,2*}, Xavier O. Solé-Senan³, Irene Robleño³, Bàrbara Baraibar^{3,4}, Lenore Fahrig⁵, David
3 Giralt⁶, Nicolas Gross^{7,8,9}, Jean-Louis Martin¹⁰, Jordi Recasens³, Clélia Sirami^{10,11}, Gavin Siriwardena¹²
4 Alette Bøsem Baillod^{13,14}, Colette Bertrand^{1,15}, Romain Carrié^{11,16}, Annika Hass^{13,17}, Laura Henckel^{7,8,18},
5 Paul Miguët^{7,8,18}, Isabelle Badenhäusser^{7,8,19}, Jacques Baudry¹, Gerard Bota⁶, Vincent Bretagnolle^{7,18},
6 Lluís Brotons^{20,21,22}, Françoise Burel¹⁵, François Calatayud¹¹, Yann Clough^{13,16}, Romain Georges^{2,15},
7 Annick Gibon¹¹, Jude Girard⁵, Kathryn Lindsay⁵, Jesus Minano²⁰, Scott Mitchell⁵, Nathalie Patry²³,
8 Brigitte Poulin²³, Teja Tscharntke¹³, Aude Vialatte¹¹, Cyrille Violle¹⁰, Nicole Yaverscovski²³, Péter
9 Batáry²⁴

10 ¹ UMR 0980 BAGAP, INRAE - Institut Agro - ESA, 65 Rue de Saint-Brieuc CS 84215, 35042 Rennes
11 Cedex, France

12 ² LTSE « Zone Atelier Armorique », 35042 Rennes Cedex, France

13 ³ ETSEA. Agrotecnio. Dept HBJ. Universitat de Lleida. Alcalde Rovira Roure 191, 25198, Lleida, Spain

14 ⁴ The Pennsylvania State University. University Park, State College, 16802, Pennsylvania, USA

15 ⁵ Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, 1125
16 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

17 ⁶ CTFC Forest Science and Technology Centre of Catalonia, 25280 Solsona, Catalonia, Spain

18 ⁷ Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS - Université de La Rochelle, 79360 Villiers
19 en Bois, France

20 ⁸ USC 1339 Station d'Ecologie de Chizé - La Rochelle, INRA, Villiers en Bois, 79360 Niort, France

21 ⁹ UCA, INRAE, VetAgro Sup, UMR Ecosystème Prairial, 63000 Clermont-Ferrand, France.

22 ¹⁰ UMR 5175 CEFE, CNRS – Université de Montpellier – EPHE - IRD, 1919 route de Mende, 34293
23 Montpellier Cedex 5, France

24 ¹¹ UMR 1201 Dynafor, Université de Toulouse – INRAE - INPT - EI PURPAN, 31326 Castanet-Tolosan,
25 France

26 ¹² British Trust for Ornithology, Thetford, Norfolk IP24 2PU, UK

27 ¹³ Agroecology, Department for Crop Sciences, University of Goettingen, Grisebachstr. 6, 37077

28 Göttingen, Germany

29 ¹⁴ Agroscope, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland

30 ¹⁵ UMR 6553 ECOBIO, CNRS, 35042 Rennes, France

31 ¹⁶ Centre for Environmental and Climate Research, Lund University, Sölvegatan 37, SE-22362 Lund,

32 Sweden

33 ¹⁷ Functional Agrobiodiversity, Department for Crop Sciences, University of Goettingen, Grisebachstr.

34 6, 37077 Göttingen, Germany

35 ¹⁸ LTSE « Zone Atelier Plaine & Val de Sèvre », 79360 Villiers en Bois, France

36 ¹⁹ URP3F, INRAE, 86600 Lusignan, France

37 ²⁰ InForest Joint Research Unit (CTFC-CREAF), 25280 Solsona, Spain

38 ²¹ CREAF, 08193 Bellaterra, Spain

39 ²² CSIC, 08193 Cerdanyola del Vallès, Spain

40 ²³ Tour du Valat Research Institute for the conservation of Mediterranean wetlands, Le Sambuc,

41 13200 Arles, France

42 ²⁴ MTA Centre for Ecological Research, Institute of Ecology and Botany, “Lendület” Landscape and

43 Conservation Ecology, Alkotmány u. 2-4, 2163 Vácrátót, Hungary

44

45 * Corresponding author : INRAE, UMR 0980 BAGAP, 65 Rue de Saint-Brieuc CS 84215, 35042 Rennes

46 Cedex, France ; Tel : +33 (0)2 23 48 57 70 ; Fax : +33 (0)2 23 48 56 20 ; audrey.alignier@inrae.fr

47 Manuscript word count (without supplementary material): 7070

48 Number of tables and figures: 2 tables and 5 figures (4 additional tables and 1 additional figure in

49 supplementary material)

50 Number of references : 54

51 **Data availability statement**

52 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.t76hdr7xh> (Alignier et
53 al., 2020).

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

78 **Résumé**

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

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

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

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

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

Accepted Manuscript

104 Introduction

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

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

123 The heterogeneity of the crop mosaic, hereafter referred to as crop heterogeneity, can be
124 decomposed into two distinct components: compositional and configurational crop heterogeneity.
125 Compositional crop heterogeneity refers to the composition of the crop mosaic, i.e. the diversity of
126 crop cover types. Configurational crop heterogeneity refers to the shape and spatial arrangement of
127 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; Boserup 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; Tcharntke 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 x 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 \times 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 \times 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 $\beta = \gamma/\alpha$. 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

302 effects override the effects of spatial variability in within-field management practices classically
303 resulting in high spatial variability in plant communities in field interiors (Gaméz-Virués et al., 2015).
304 However, when separating field border and field interior transects, this effect was no longer
305 significant.

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

314 The discrepancy in the response of within-plant diversity to configurational crop heterogeneity
315 between field borders and field interiors can be seen as a compensation for disturbances (through
316 intensive management practices) by complex, high diversity crop mosaics (Tscharntke et al., 2005).
317 Previous work suggested differences in impacts of farming practices within fields (Poggio et al., 2013)
318 with lower intensity of farming practices such as herbicide applications near field borders (Marshall
319 and Moonen, 2002). We thus propose that, in field interiors where disturbance level is higher and
320 colonization by short-distance dispersal events from surrounding patches more limited, increasing
321 configurational crop heterogeneity would be more effective in enhancing species richness and
322 diversity. Conversely, in field borders where disturbance level is lower and short-distance seed
323 dispersal events are facilitated, increasing configurational crop heterogeneity would not result in
324 locally enhanced plant diversity because plant diversity is already high. We could not properly test
325 this hypothesis as spatial information about management practices was not available. However,
326 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 constitute 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.

Acknowledgments

This work was funded by the ERA-Net BiodivERsA, with the national funders French National Research Agency (ANR-11-EBID-0004), German Ministry of Research and Education, German Research Foundation and Spanish Ministry of Economy and Competitiveness, part of the 2011 BiodivERsA call for research proposals. The contribution from the UK was funded by the UK Government Department of the Environment, Food and Rural Affairs (Defra), as project WC1034. The Canadian component of this research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Strategic Project grant, the Canada Foundation for Innovation, Environment Canada (EC), and Agriculture and Agri-Foods Canada (AAFC). We thank Yann Fillatre, Bastien Lamouroux, Annie Ouin and Jérôme Willm for field assistance. We thank all farmers and farm owners who graciously permitted us to work in their fields as well as all people and technical staff involved in geomatic analyses, plant surveys and species identification. We are grateful to all FarmLand partners for stimulating discussions. Finally, we would like to thank the associate editor, Pieter De Frenne, and two anonymous reviewers for their very constructive comments on an earlier version of the manuscript.

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.

References

- Alignier, A., Petit, S., & Bohan, D. A. (2017). Relative effects of local management and landscape heterogeneity on weed richness, density, biomass and seed rain at the country-wide level, Great Britain. *Agriculture, Ecosystems and Environment*, **246**, 12-20.
- Alignier A., Solé-Senan X., Robleño I., Baraibar B., Fahrig L., ... & Batáry, P. (2020) *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.t76hdr7xh>
- Auerbach, M., & Shmida, A. (1987). Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution*, **2**, 238-242.
- Barton, K. (2017). MuMIn: Multi-Model Inference. R package version 1.40.0. <https://CRAN.R-project.org/package=MuMIn>
- Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C. F., Mußhoff, O., ... & Tschardtke, T. (2017). The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. *Nature Ecology and Evolution*, **1**, 1279-1284.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, **67**, 1-48.
- Benton, T.G., Vickery, J.A., & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182–188.
- Bertrand, C., Burel, F., & Baudry, J. (2016). Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, **31**, 451–466.
- Blackshaw, R. E., Anderson, R. L., & Lemerle, D. (2007). In M. K. Upadhyaya & R.E. Blackshaw (Eds.), *Non-Chemical Weed Management. Principles, concepts and technology* (pp. 35-47). Wallingford, UK: CAB International (www.cabi.org).

422 Bøsem Baillod, A., Tscharrntke, T., Clough, Y., & Batáry, P. (2017). Landscape-scale interactions of
 423 spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of*
 424 *Applied Ecology*, **54**, 1804-1813.

425 Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable*
 426 *Development*, **35**, 891-909.

427 Burnham, K.P., & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical*
 428 *Information-Theoretic Approach*, second ed. Springer Verlag, New York.

429 Burton, R.J.F., Kuczera, C., & Schwarz, G. (2008). Exploring farmers' cultural resistance to voluntary
 430 agri-environmental schemes. *Sociologia Ruralis*, **48**, 16–37.

431 Concepción, E. D., Fernández-González, F., & Díaz, M. (2012). Plant diversity partitioning in
 432 Mediterranean croplands: effects of farming intensity, field edge, and landscape context. *Ecological*
 433 *Applications*, **22**, 972-981.

434 Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., ... & Martin, J.-L. (2011).
 435 Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology*
 436 *Letters*, **14**, 101–112.

437 Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., ... & Tischendorf, L. (2015). Farmlands
 438 with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems and*
 439 *Environment*, **200**, 219-234.

440 Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., ... & Zaks, D. P.
 441 M. (2011). Solutions for a cultivated planet. *Nature*, **478**, 337.

442 Fried, G., Petit, S., Dessaint, F., & Reboud, X. (2009). Arable weed decline in Northern France: crop
 443 edges as refugia for weed conservation? *Biological Conservation*, **142**, 238-243.

444 Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H., ... &
 445 Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization.
 446 *Nature Communications*, **6**, 8568.

447 Gargominy, O., Terceire, S., Régnier, C., Ramage, T., Schoelinck, C., Dupont, P., ... & Poncet, L. (2014).
 448 *TAXREF v8. 0, référentiel taxonomique pour la France: méthodologie, mise en œuvre et diffusion*.
 449 Muséum National d'Histoire Naturelle, Paris. Rapport SPN 2014-42, 126 pp.

450 Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology
 451 and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699-711.

452 Hass, A. L., Kormann, U. G., Tschardt, T., Clough, Y., Baillod, A. B., Sirami, C., ... & Batáry, P. (2018).
 453 Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains
 454 pollinators and plant reproduction in western Europe. *Proceedings of the Royal Society B*, **285**,
 455 20172242.

456 Henckel, L., Börger, L., Meiss, H., Gaba, S., & Bretagnolle, V. (2015). Organic fields sustain weed
 457 metacommunity dynamics in farmland landscapes. *Proceedings of the Royal Society B*, **282**,
 458 20150002.

459 José-María, L., Armengot, L., Blanco-Moreno, J.M., Bassa, M., & Sans, F.X. (2010). Effects of
 460 agricultural intensification on plant diversity in Mediterranean dry-land cereal fields. *Journal of*
 461 *Applied Ecology*, **47**, 832–840.

462 Kareiva, P., Watts, S., McDonald, R., & Boucher, T. (2007). Domesticated nature: shaping landscapes
 463 and ecosystems for human welfare. *Science*, **316**, 1866-1869.

464 Kleijn, D., Baquero, R. A., Clough, Y., Diaz, M., De Esteban, J., Fernández, F., ... & Yela, J. L. (2006).
 465 Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*,
 466 **9**(3), 243-254.

467 Landis, D. A., & Marino, P. C. (1999). Landscape structure and extra-field processes: impact on
 468 management of pests and beneficials. In *Handbook of pest management* (pp. 101-126). CRC Press.

469 Latruffe, L., & Piet, L. (2014). Does land fragmentation affect farm performance? A case study from
 470 Brittany, France. *Agricultural Systems*, **129**, 68-80.

471 Lososová, Z., Chytrý, M., Cimalova, S., Kropáč, Z., Otýpková, Z., Pyšek, P., & Tichý, L. (2004). Weed
 472 vegetation of arable land in Central Europe: Gradients of diversity and species composition. *Journal*
 473 *of Vegetation Science*, **15**, 415-422.

474 Marshall, E.J.P. (2009). The impact of landscape structure and sown grass margin strips on weed
 475 assemblages in arable crops and their boundaries. *Weed Research*, **49**, 107–115.

476 Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R., & Ward, L.K. (2003). The
 477 role of weeds in supporting biological diversity within crop fields. *Weed Research*, **43**, 77–89.

478 Marshall, E. J. P., & Moonen, A. C. (2002). Field margins in northern Europe: their functions and
 479 interactions with agriculture. *Agriculture, Ecosystems and Environment*, **89**, 5–21.

480 Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., ... & Steffan-Dewenter, I.
 481 (2019). The interplay of landscape composition and configuration: new pathways to manage
 482 functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, **22**, 1083-1094.

483 Melander, B., Rasmussen, I.A., & Barberi, P. (2005) Integrating physical and cultural methods of weed
 484 control-examples from European research. *Weed Science*, **53**(3), 369-381

485 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from
 486 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-142.

487 Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R.A.,...& Purvis, A. (2015). Global
 488 effects of land use on local terrestrial biodiversity. *Nature*, **520**(7545), 45-50.

489 Norris, K. (2008). Agriculture and biodiversity conservation: opportunity knocks. *Conservation Letters*,
 490 **1**, 2-11.

491 Palmu, E., Ekroos, J., Hanson, H.I., Smith, H.G., & Hedlund, K. (2014). Landscape-scale crop diversity
 492 interacts with local management to determine ground beetle diversity. *Basic and Applied Ecology*,
 493 **15**, 241–249.

494 Pasher, J., Mitchell, S.W., King, D.J., Fahrig, L., Smith, A.C., & Lindsay, K.E. (2013). Optimizing
 495 landscape selection for estimating relative effects of landscape variables on ecological responses.
 496 *Landscape Ecology*, **28**, 371–383.

497 Perović, D., Gámez-Virués, S., Börschig, C., Klein, A. M., Krauss, J., Steckel, J., ... & Westphal, C. (2015).
 498 Configurational landscape heterogeneity shapes functional community composition of grassland
 499 butterflies. *Journal of Applied Ecology*, **52**, 505-513.

500 Petit, S., Alignier, A., Colbach, N., Joannon, A., Le Cœur, D., & Thenail, C. (2013). Weed dispersal by
 501 farming at various spatial scales. A review. *Agronomy for Sustainable Development*, **33**, 205-217.

502 Poggio, S. L., Chaneton, E. J., & Ghersa, C. M. (2013). The arable plant diversity of intensively
 503 managed farmland: effects of field position and crop type at local and landscape scales. *Agriculture,*
 504 *Ecosystems and Environment*, **166**, 55-64.

505 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
 506 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

507 Rodríguez, C., & Wiegand, K. (2009). Evaluating the trade-off between machinery efficiency and loss
 508 of biodiversity-friendly habitats in arable landscapes: The role of field size. *Agriculture, Ecosystems*
 509 *and Environment*, **129**, 361-366.

510 Roschewitz, I., Gabriel, D., Tschardt, T., & Thies, C. (2005). The effects of landscape complexity on
 511 arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, **42**,
 512 873–882.

513 Sheppard, S. C., Sheppard, M. I., Long, J., Sanipelli, B., & Tait, J. (2006). Runoff phosphorus retention
 514 in vegetated field margins on flat landscapes. *Canadian Journal of Soil Science*, **86**, 871-884.

515 Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of*
 516 *Biogeography*, **12**, 1–20.

517 Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... & Fahrig, L. (2019). Increasing
 518 crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the*
 519 *National Academy of Sciences*, **116**(33), 16442-16447.

520 Smith, R. G., & Mortensen, D. A. (2017). A disturbance-based framework for understanding weed
 521 community assembly in agroecosystems: challenges and opportunities for agroecological weed
 522 management. In A. Wezed (Ed.), *Agroecological practices for sustainable agriculture: Principles,*
 523 *applications, and making the transition* (pp. 127-153). Lyon, France: World Scientific.

524 Solé-Senan, X. O., Juárez-Escario, A., Conesa, J. A., Torra, J., Royo-Esnal, A., & Recasens, J. (2014).
 525 Plant diversity in Mediterranean cereal fields: unraveling the effect of landscape complexity on rare
 526 arable plants. *Agriculture, Ecosystems and Environment*, **185**, 221-230.

527 Solé-Senan, X. O., Juárez-Escario, A., Conesa, J. A., & Recasens, J. (2018). Plant species, functional
 528 assemblages and partitioning of diversity in a Mediterranean agricultural mosaic landscape.
 529 *Agriculture, Ecosystems and Environment*, **256**, 163-177

530 Storkey, J., 2006. A functional group approach
 531 to the management of UK arable weeds to support biological diversity. *Weed Research*, **46**, 513–522.

532 Storkey, J. (2006). A functional group approach to the management of UK arable weeds to support
 533 biological diversity. *Weed Research*, **46**, 513-522.

533 Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape
534 perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology*
535 *Letters*, **8**, 857–874.

536 Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batary, P., ... & Westphal, C.
537 (2012). Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological*
538 *Reviews*, **87**, 661-685.

539 Vialatte, A., Tsafack, N., Al Hassan, D., Duflot, R., Plantegenest, M., Ouin, A., ... & Ernoult, A. (2017).
540 Landscape potential for pollen provisioning for beneficial insects favours biological control in crop
541 fields. *Landscape Ecology*, **32**, 465-480.

542 Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

543 **List of tables**

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

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

545

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 R ²		0.57			0.18			0.57	
Marginal R ²		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.

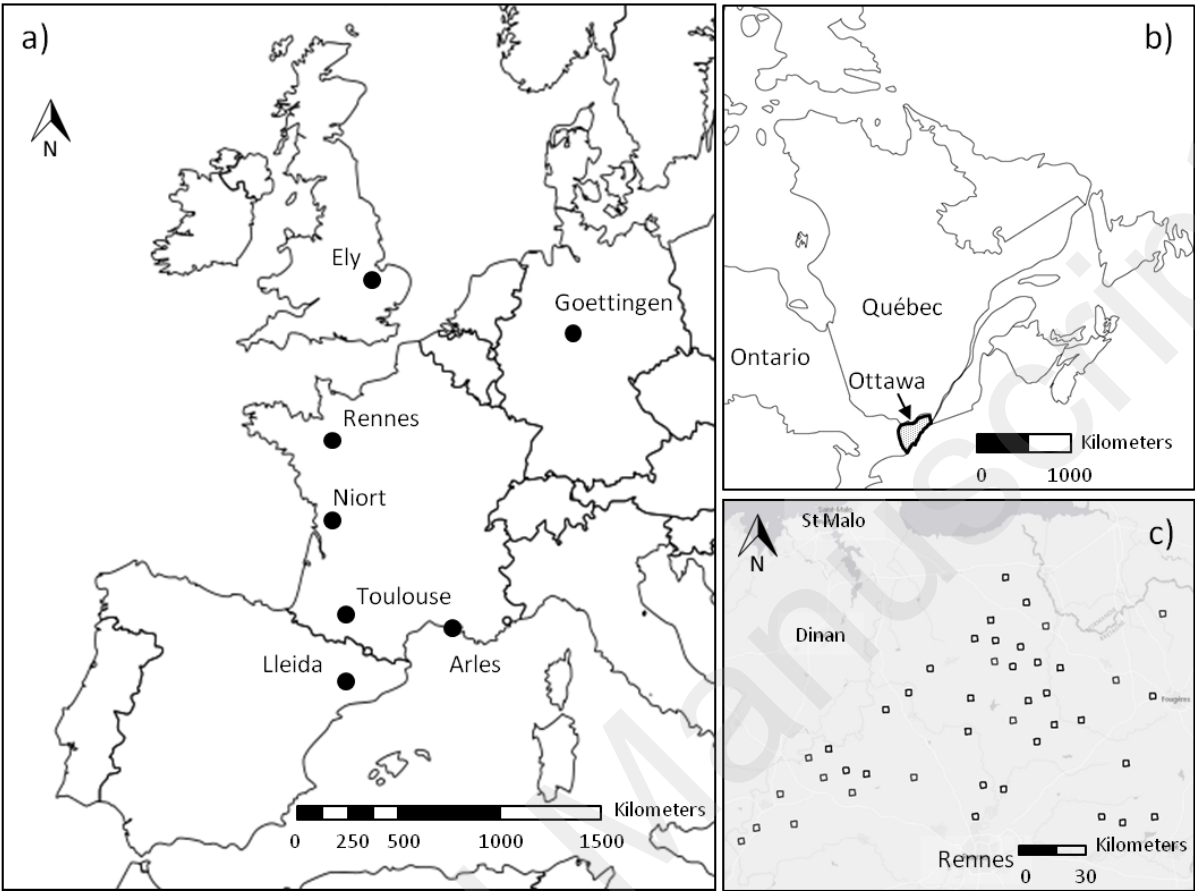
Figure 4. Interaction plot of the effect on beta diversity (i.e. ratio between gamma and alpha diversity) of within-field plants with configurational crop heterogeneity measured as the total crop border length (*TBL*), according to within-field position. The dotted line fits field interior transects 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

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

581

Accepted Manuscript



584 **Figure 1.**

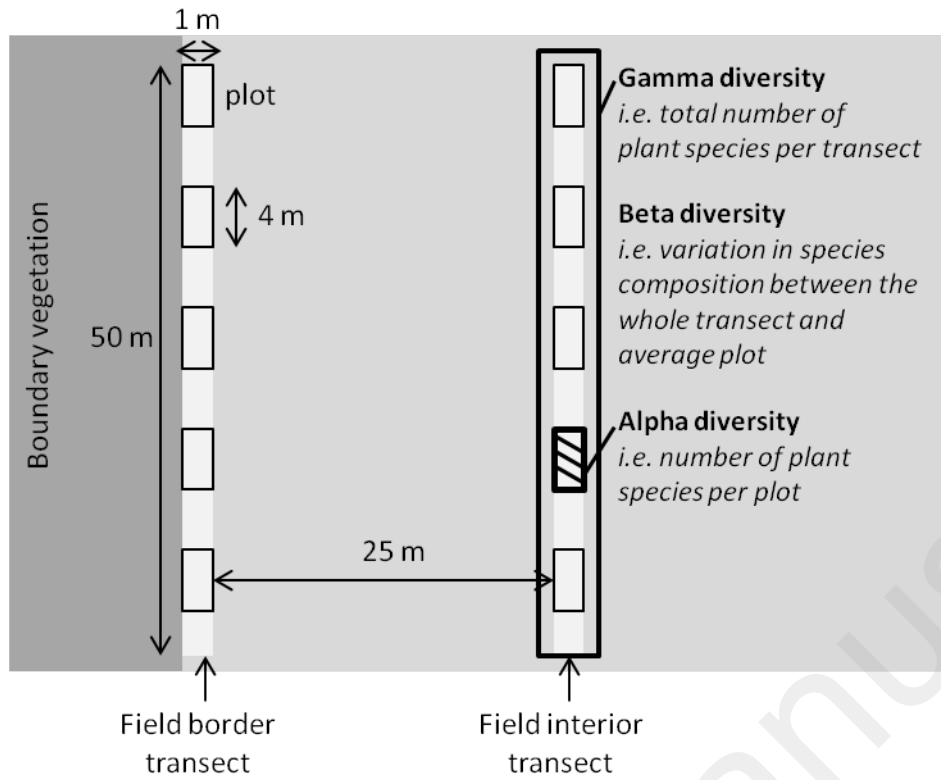
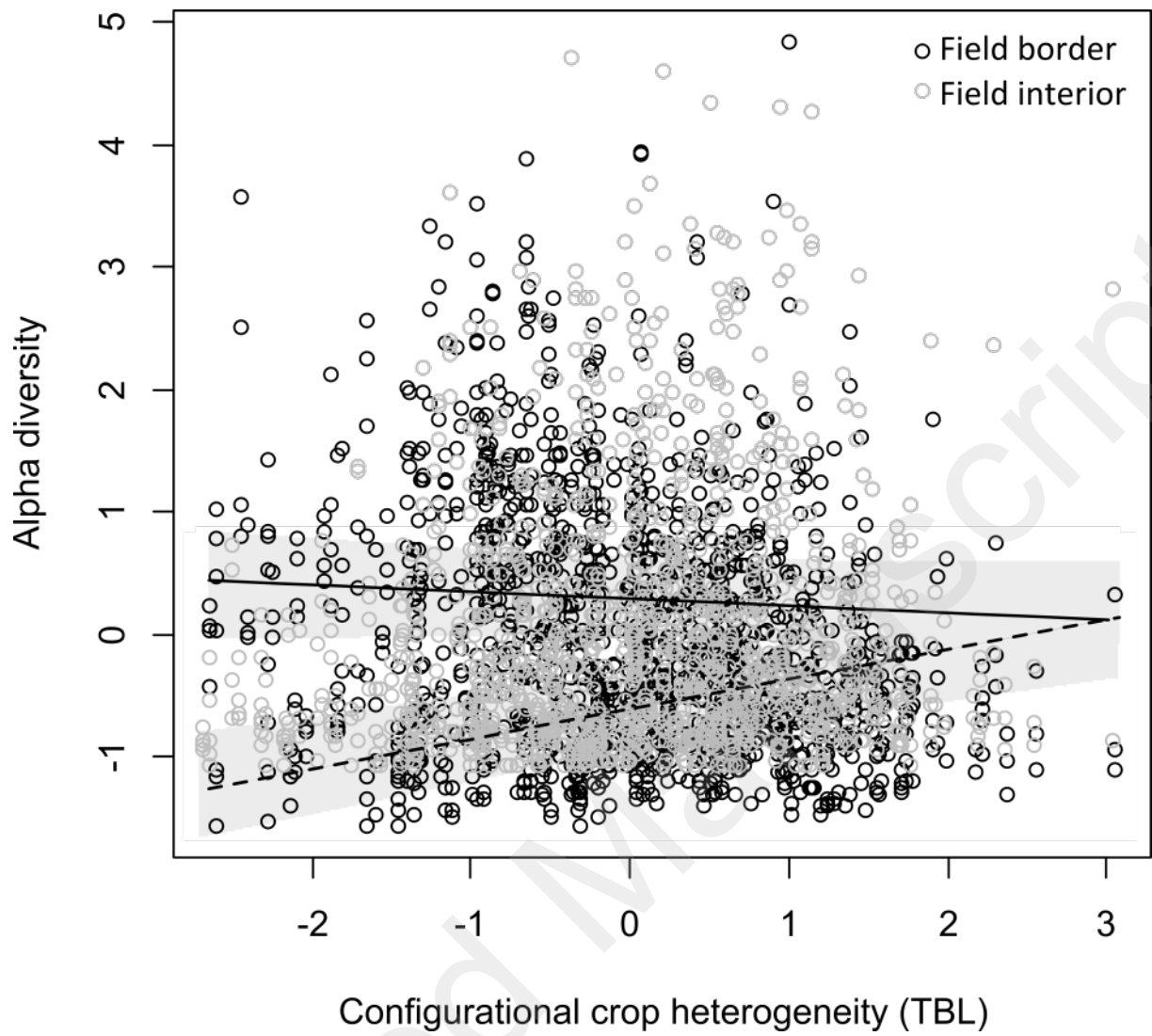
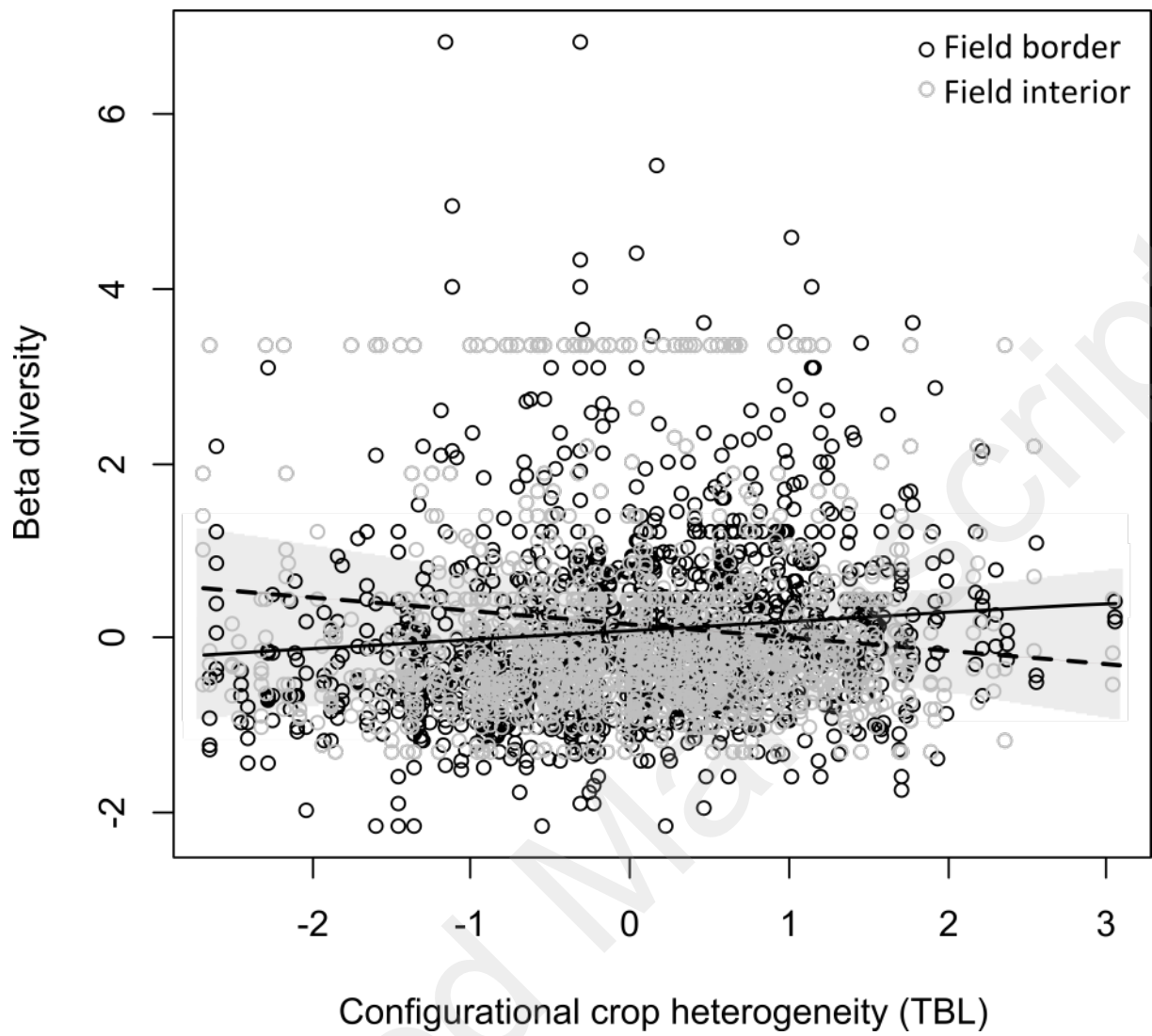


Figure 2.



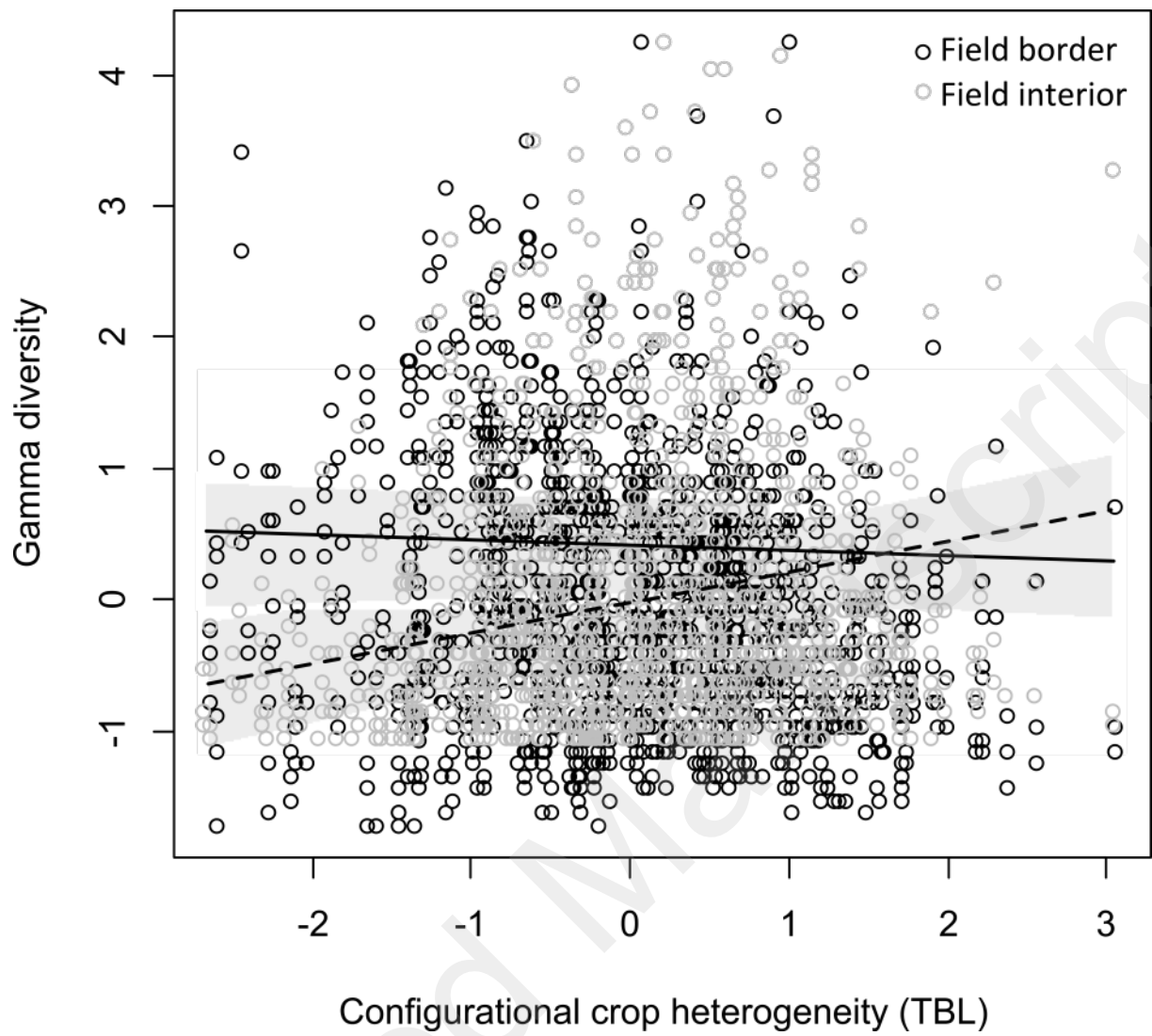
587

588 Figure 3.



589

590 Figure 4.



591

592 Figure 5.