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

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53 al., 2020).

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54 **Abstract**

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

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

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

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

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

77

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

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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

128 effects of compositional and configurational crop heterogeneity on species diversity are rarely
129 disentangled because they are typically highly correlated (Kareiva et al., 2007).

130 The few attempts to tease apart the effects of crop heterogeneity components on species diversity
131 have found positive effects of compositional crop heterogeneity, i.e. Shannon crop diversity and/or
132 configurational crop heterogeneity, i.e. edge density or mean field size, on predatory arthropods
133 (Palmu et al., 2014; Fahrig et al., 2015; Bertrand et al., 2016; Boserup Baillod et al., 2017; Martin et al.,
134 2019), butterflies (Perović et al., 2015) and wild bees (Hass et al., 2018). Studies addressing this issue
135 for the diversity of plants within agricultural fields are rarer (but see Fahrig et al., 2015).

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

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

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

170 **Materials and methods**

171 *Region and landscape selection*

172 The study was conducted in eight agricultural regions comprising seven regions in Europe and one
173 region in eastern Canada (near *Ottawa*; Fig. 1). The European regions followed a south-to-north
174 gradient, with four regions in France (near *Arles*, *Niort*, *Rennes*, *Toulouse*), one in England (centred on
175 *Ely*, Cambridgeshire), one in Germany (near *Goettingen*) and one in Spain (near *Lleida*; Fig. 1). Within
176 these agricultural regions, we selected a total of 432 1 km × 1 km landscapes, with 60 to 90 % of crop
177 cover in each. These landscapes represented, by design, uncorrelated gradients of compositional
178 crop heterogeneity, assessed by the Shannon diversity index of the crop cover types, and of

179 configurational crop heterogeneity, assessed by the total length of crop field borders (see Pasher et
180 al., 2003 and Sirami et al., 2019 for details). The landscape selection process used the most recent
181 remotely sensed data or land cover map available for each agricultural region (see Table S1 in
182 Supporting Information).

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

192 Based on these more accurate and recent maps, several landscape variables were calculated.

193 Compositional crop heterogeneity was assessed using the Shannon diversity index of agricultural
194 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
195 grasslands) in the agricultural mosaic. Configurational crop heterogeneity was measured as the total
196 field border length (TBL). TBL was the sum of perimeters of all fields within the 1 x 1 km landscape
197 minus the length of perimeters artificially created by intersection with the limits of the 1 km x 1 km
198 landscape. The percentage of semi-natural cover types ($SemiNatCover$) was calculated as the sum of
199 the proportions of woodland, open land and wetland in the landscape. The length of semi-natural
200 boundaries ($SemiNatBound$) was calculated as half of the sum of the perimeter of woody, grassy and
201 watery boundaries in the landscape. We checked for correlations among landscape variables to avoid
202 distortion in models caused by multi-collinearity. There was no collinearity between $SHDI$ and TBL
203 (Pearson correlation test, $r = 0.01$, $P = 0.62$; Fig. S1). Due to strong correlation between

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

208 *Sampling site selection*

209 Within each landscape, we selected three to four sampling sites. Sampling sites were fields managed
210 for agricultural production including crops, temporary and permanent grasslands. Fields were
211 selected such that at least one contained the dominant crop type in the region, the other fields being
212 representative of crops present within the focal landscape (Table S3). Fields were at least 200 m
213 apart, at least 50 m away from the border of the 1 km × 1 km landscape and at least 50 m away from
214 large non-crop cover type patches such as woodland. We selected fields bordered by a similar
215 boundary types within each region, i.e. only grassy strips or hedgerows, wherever possible. In total,
216 1451 agricultural fields were sampled.

217 *Vegetation sampling*

218 Within each sampling site, we surveyed within-field plant species along two parallel, 1 m wide and 50
219 m long transects, one located on the field border, the other within the field interior resulting in 2788
220 transects surveyed. Transects were about 25 m distant from each other. We sampled five plots (4 m
221 × 1 m) along each transect, i.e. 20 m² per transect (Fig. 2). Note that in *Ottawa*, transects were 2 m
222 wide and the field border transect encompassed part of the boundary vegetation. We verified that
223 this slight difference in sampling protocol did not affect our conclusions (Appendix S2). Percentage
224 cover of all vascular plant species was recorded. We conducted these plant surveys over two years
225 between 2011 and 2014, each sampling site being sampled only within a single year. Surveys were
226 conducted once before crop harvesting, except in *Ely*, *Goettingen* and *Ottawa* where surveys were
227 conducted twice (Table S4). In those regions, we pooled within-field plant data from the two visits

228 per year and retained the total number of plant species for each sampled plot. Plant nomenclature
229 followed TaxRef (Gargominy et al., 2014).

230 *Data analysis*

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

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

247 *Model 1: $y \sim SHDI + TBL + POS + SemiNatCover + SHDI:TBL + SHDI:POS + TBL:POS +$*
248 *$SemiNatCover:SHDI + SemiNatCover:TBL + SemiNatCover:POS +$*
249 *$(1|Region/Landscape) + (1|Region/Crop\ type)) + (1|IDfield)$*

250 Visual inspection of residual plots reveal no large deviations from homoscedasticity or normality. We
251 then performed a multi-model inference procedure based upon the bias-corrected Akaike

252 information criterion (AICc). We built all possible alternative candidate models based on the linear
253 additive functions of explanatory variables. We averaged the parameters of all models for which the
254 respective variables were present. We considered variables as significant when confidence intervals
255 did not include zero (Burnham and Anderson 2002). Finally, we estimated variance explained by
256 models using the marginal and conditional pseudo- R^2 statistic (Nakagawa and Schielzeth, 2013).
257 Statistical analyses were carried out using the “lme4” package for mixed models (Bates et al., 2015)
258 and “MuMIn” for multimodel inference (Barton, 2017) in R 3.2.3 (R Core Team, 2015).

259 **Results**

260 We recorded a total of 899 plant species across the eight agricultural regions. Each region contained
261 16 – 33 % of the total species richness.

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

270 Beta diversity ranged from 1 to 5 and averaged 1.95 (SE 0.44) in field border transects and 2.13 (SE
271 0.85) in field interior transects. Within-field position (*POS*) had a strong independent effect on beta
272 diversity (Table 2). The only landscape variable to have a significant effect on beta diversity was
273 configurational crop heterogeneity (*TBL*), through an interaction with within-field position (*POS*).
274 However, when separating field border transects and field interior transects, the effects of *TBL* were
275 no longer significant (Appendix S3). *SHDI* and *SemiNatCover*, alone or in interaction, had no
276 significant effect on beta diversity (Table 2).

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

284 **Discussion**

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

288 Alpha and gamma plant diversity increased with increasing configurational crop heterogeneity in
289 field interior transects. Because of their high disturbance levels compared to natural ecosystems,
290 agricultural fields are usually seen as depauperate features sheltering only a small proportion of the
291 regional plant species pool (Landis and Marino, 1999). Heterogeneous agricultural landscapes
292 contain a diversity of crop types which can enlarge the landscape-level plant species pool from which
293 local communities are drawn (Tscharntke et al., 2005), resulting in higher local species richness. The
294 strong positive effect of increasing configurational crop heterogeneity on alpha and gamma plant
295 diversity in field interior transects is consistent with the findings of Fahrig et al. (2015) and Sirami et
296 al. (2019). In landscapes with higher field border length, the probability of short-distance dispersal
297 events being successful is enhanced. Thus, immigration towards the inner field from the
298 neighbourhood is facilitated through mass effect (Schmida et al., 1985; Henckel et al., 2015).

299 However, this result questions the viability of plant populations in the inner field if viable source
300 populations were not maintained in the neighbourhood. The fact that beta diversity decreased with
301 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 (Tschardt 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

327 results are important for agri-environment schemes. They confirm that conservation of plant
328 biodiversity in agricultural systems requires a landscape perspective (Tscharntke et al., 2005).

329 Besides the influence of configurational crop heterogeneity, we also detected a significant and
330 positive effect of the amount of semi-natural cover types in the landscape on alpha and gamma
331 diversity. This effect was slightly stronger than the effect of crop configurational heterogeneity
332 (Table2). This result provides additional evidence that increasing the amount of semi-natural cover in
333 the landscape enhances local diversity in agroecosystems (Tscharntke et al., 2005; Concepción et al.,
334 2012).

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

342 *Conclusions and management implications*

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

348 The length of field borders benefits plant diversity as much as semi-natural cover. Thus, managing
349 configurational crop heterogeneity opens new effective and complementary approaches to farmland
350 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

377 heterogeneity of the crop mosaic itself appears as a promising alternative way to preserve farmland
378 biodiversity even in landscapes dominated by intensively cultivated lands.

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394 **Authors' contribution**

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

400 **References**

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

422 Bosem Baillod, A., Tschardtke, 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.

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

- 533 Tschardtke, 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 Tschardtke, 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

546 Table 2 : Model-averaged standardized estimates and *P* values from LMMs of alpha, beta and gamma
 547 within-field plant diversity in relation to compositional and configurational crop heterogeneity,
 548 within-field position and the amount of semi-natural cover. Data are from 2788 transects pertaining
 549 to 432 1 km x 1 km landscapes in eight agricultural regions. Six transects were sampled in each
 550 landscape, one at the edge and one in the interior of each of three agricultural fields. Each transect
 551 contained five plots, over which the diversity measures were calculated (see Fig 1). *SHDI* : Shannon
 552 crop diversity index, *TBL*: Total length of crop borders, *SemiNatCover*: Proportion of semi-natural
 553 cover types in the landscape, *POS*: within-field position, ns: not significant, *: *P* < 0.05, **: *P* < 0.01,
 554 ***: *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	

555 **Figure captions**

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

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

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

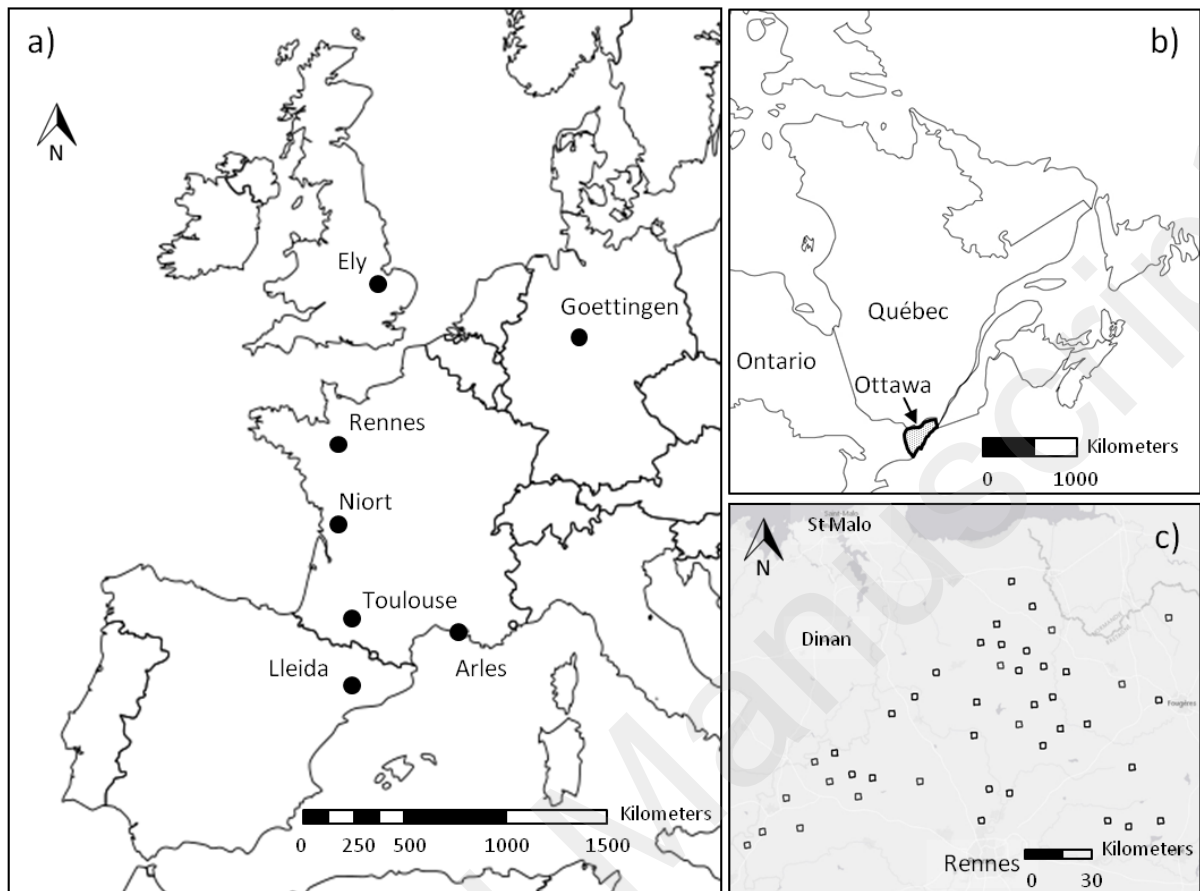
571 Figure 4. Interaction plot of the effect on beta diversity (i.e. ratio between gamma and alpha
572 diversity) of within-field plants with configurational crop heterogeneity measured as the total crop
573 border length (*TBL*), according to within-field position. The dotted line fits field interior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

576 Figure 5. Interaction plot of the effect on gamma diversity (i.e. total number of species across all five
577 plots sampled in a transect) of within-field plants with configurational crop heterogeneity measured
578 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.

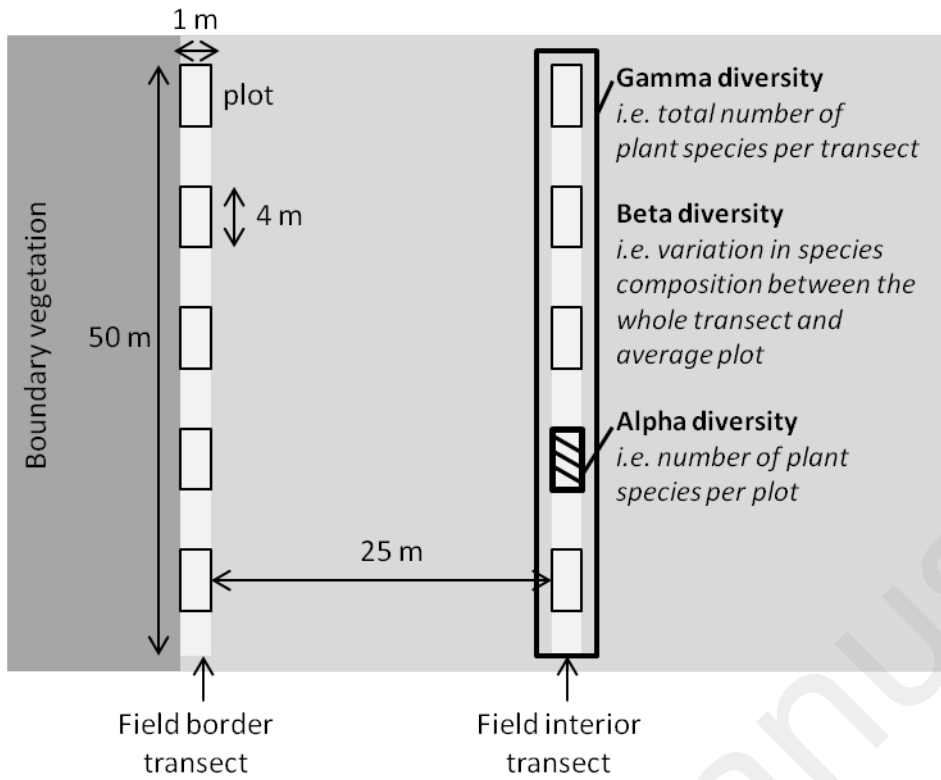
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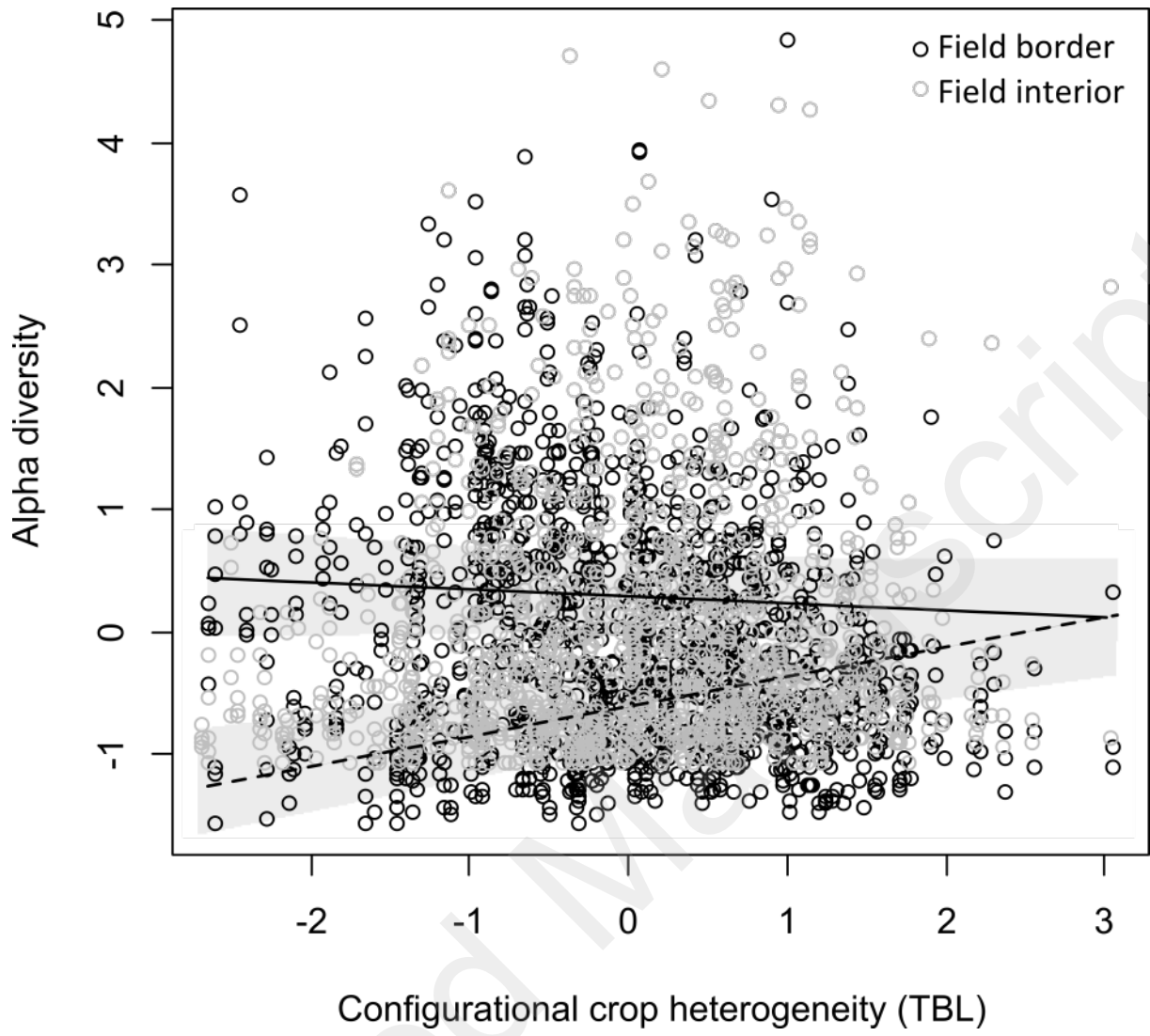
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584 Figure 1.



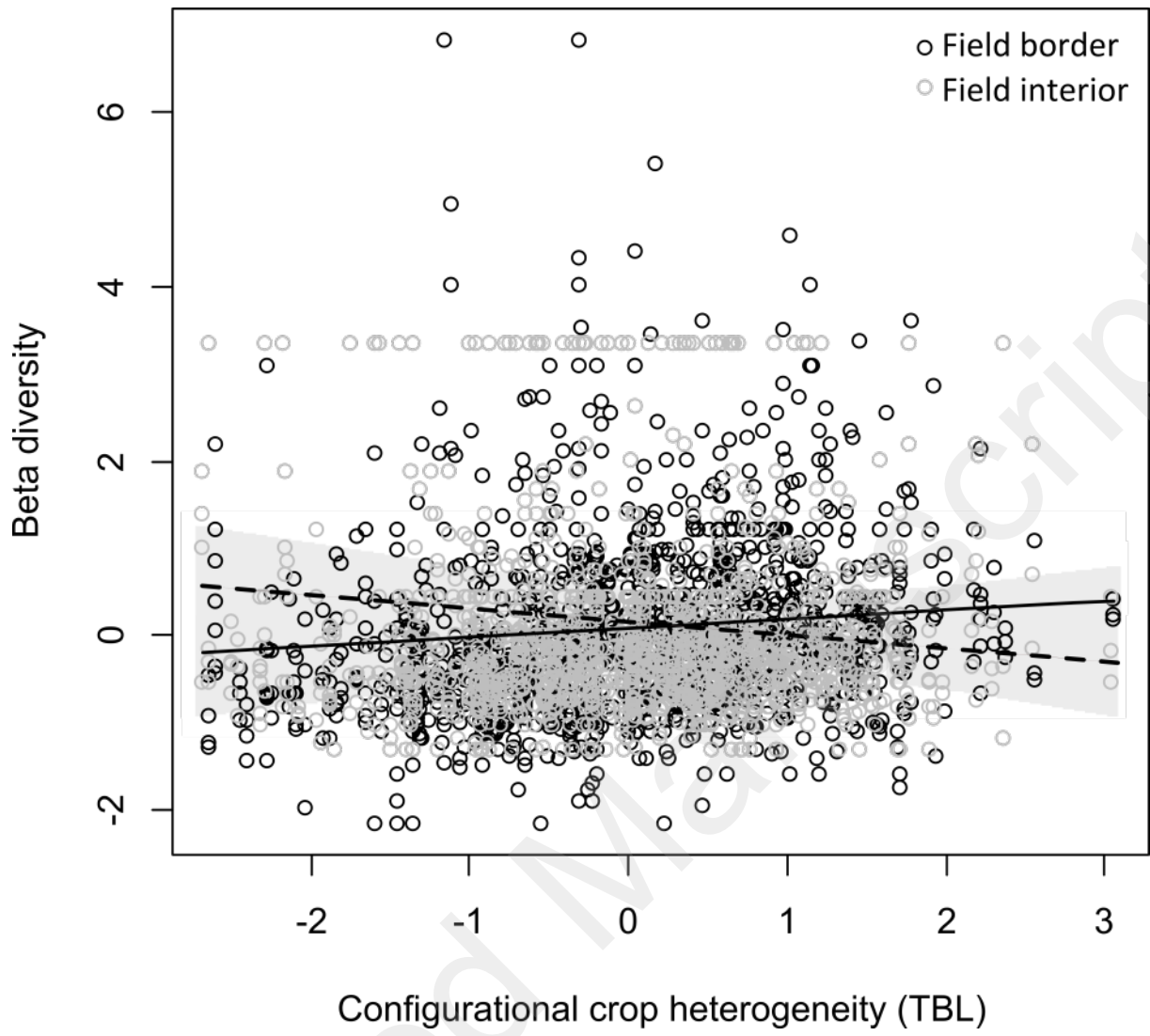
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586 Figure 2.



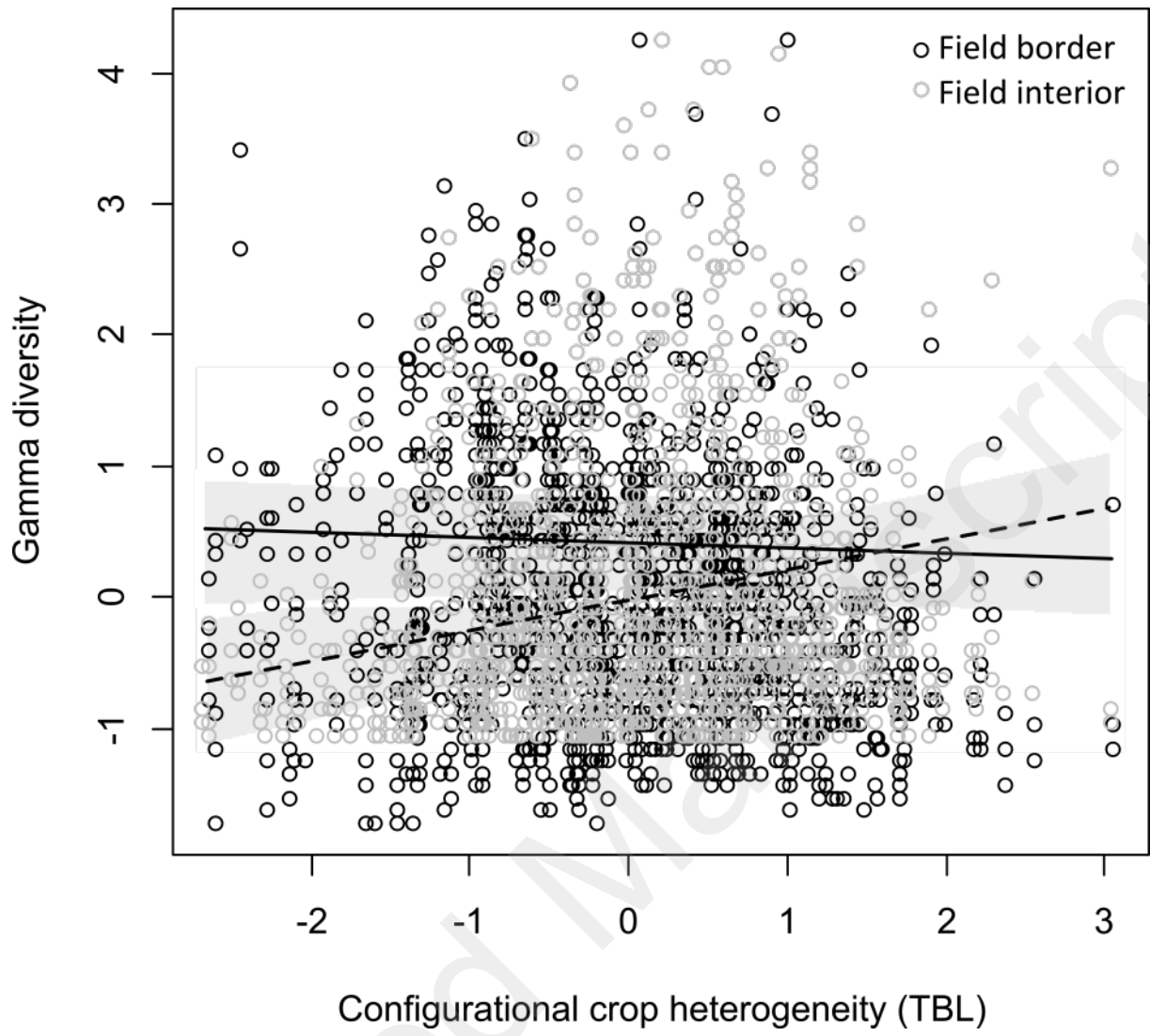
587

588 Figure 3.



589

590 Figure 4.



591

592 Figure 5.