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Paper:

Henckel, L., Borger, L., Meiss, H., Gaba, S. & Bretagnolle, V. (2015). Organic fields sustain weed metacommunity dynamics in farmland landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 282(1808), 20150002-20150002.

<http://dx.doi.org/10.1098/rspb.2015.0002>

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PROCEEDINGS B

Organic fields sustain weed metacommunity dynamics in farmland landscapes

| | |
|-------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Journal: | <i>Proceedings B</i> |
| Manuscript ID: | RSPB-2015-0002.R1 |
| Article Type: | Research |
| Date Submitted by the Author: | 15-Apr-2015 |
| Complete List of Authors: | Bretagnolle, Vincent; CNRS, Borger, Luca; Swansea University, Biosciences Gaba, Sabrina; UMR1347 Agroécologie, INRA Meiss, Helmut; ENSAIA, UMR, INRA Henckel, Laura; CNRS, CEBC |
| Subject: | Ecology < BIOLOGY, Environmental Science < BIOLOGY, Plant science < BIOLOGY |
| Keywords: | organic farming, agricultural intensification, plants , landscape heterogeneity, spatial scale, Agro ecology |
| Proceedings B category: | Population and community Ecology |
| | |

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**Organic fields sustain weed metacommunity dynamics
in farmland landscapes**

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1 **Abstract**

2 Agro-ecosystems constitute essential habitat for many organisms. Agricultural intensification,
3 however, has caused a strong decline of farmland biodiversity. Organic farming is often
4 presented as a more biodiversity friendly practice, but the generality of the beneficial effects
5 of organic farming is debated as the effects appear often species and context dependent and
6 current research has highlighted the need to quantify the relative effects of local and
7 landscape scale management on farm-land biodiversity. Yet, very few studies have
8 investigated the landscape level effects of organic farming; that is to say, how the biodiversity
9 of a field is affected by the presence or density of organically farmed fields in the surrounding
10 landscape. We addressed this issue using the metacommunity framework, with weed
11 species richness in winter wheat within an intensively farmed landscape in France as model
12 system. Controlling for the effects of local and landscape structure we showed that organic
13 farming leads to higher local weed diversity and that the presence of organic farming in the
14 landscape is associated with higher local weed biodiversity also for conventionally farmed
15 fields, and may reach a similar biodiversity level to organic fields in field margins. Based on
16 these results we derive indications for improving the sustainable management of farming
17 systems.

18

19

20 **Key-words:** organic farming, agricultural intensification, landscape heterogeneity, spatial
21 scale, weeds, agroecology

22 INTRODUCTION

23 Agricultural landscapes occupy about 40% of all terrestrial ecosystems (Fahrig et al. 2011),
24 providing habitat for many animal and plant species worldwide (Pimentel et al. 1992). The
25 intensification of agricultural practices has however resulted in a general decline of farmland
26 species adapted to more extensive farming (Benton et al. 2003; Batary et al. 2011; Storkey
27 et al. 2012), in response to a mixture of local (field or farm levels) and regional (landscape)
28 processes, such as increased use of pesticides (Hyvönen 2007) and fertilizers (Bischoff and
29 Mahn 2000), shortened crop-succession (Benton et al. 2003), landscape simplification
30 (Farhig et al. 2011) and territory specialisation (Stoate et al. 2001). To mitigate this
31 biodiversity decline, agri-environmental schemes (AES, Henle *et al.* 2008) and other policy
32 initiatives were set up, often targeting reduced agrochemical applications (Barzman and
33 Dachbrodt-Saaydeh 2011). Organic farming (OF), an AES under European regulation, is
34 presented as a potential compromise between assuring food security and conserving
35 biodiversity, thanks to the banishment of chemical and inorganic fertilizer and higher crop
36 diversity (Hole et al. 2005).

37 Many studies have assessed the potential biodiversity benefits of OF in comparison
38 to conventional farming (CONV) but a general consensus is still lacking (Hole 2005, Tuck et
39 al. 2014). At the field level, an overall positive effect of OF was detected on plant species
40 richness (Fuller et al., 2005; Gibson et al., 2007) though the response is highly taxon
41 dependent (Tuck et al. 2014). However, due to lower yields, larger surfaces are needed to
42 maintain food production under OF, hence the net balance between positive and negative
43 impacts is still debated (De Ponti et al. 2012; Gabriel et al. 2013; Tuck et al. 2014). OF
44 effects at the field level may further depend on surrounding landscapes (Conception et al.
45 2012, Batary et al. 2011, Bianchi et al. 2013). Bengtsson et al. (2005) proposed that OF
46 benefits on biodiversity should increase linearly with agriculture intensification at the
47 landscape scale. However, contrasted effects of landscape complexity have been reported
48 (Rundlöf and Smith 2006, Batary *et al.* 2011, Winqvist *et al.* 2011, Batary et al. 2013).
49 Alternatively, Conception *et al.* (2008) proposed that landscape complexity may non-linearly
50 modify the biodiversity effects of field management, whereby below a minimal landscape
51 complexity threshold, as well as above a saturation point, biodiversity will not increase with
52 landscape complexity. Thus scale-dependent processes and the interplay between local and
53 regional factors determining biodiversity loss under agricultural intensification must be further
54 investigated (Winqvist et al. 2011, Luscher et al. 2014).

55 In this context, studying ecological processes at the scale of the meta-community
56 (Leibold et al., 2004) can be relevant to assess potential regional (i.e. landscape) effects on
57 local community richness. Indeed in highly heterogeneous and dynamic landscapes such as
58 agro-ecosystems, dispersal is expected to be an essential driver that allows communities to

59 persist in spite of landscape instability. Here we hypothesise that local and regional
60 processes interact in shaping biodiversity, such that landscape scale processes may
61 outcompete local processes. In other words, the presence of OF at the landscape scale
62 could balance the field-level negative effects of conventional agricultural management
63 through mass effect (species dispersing from favorable habitats in organic fields into
64 surrounding conventional fields). To test this hypothesis, we used weed communities of
65 winter wheat, the major crop in Europe and in France (c.10% of the total country area is
66 cropped with wheat). Weeds represent the basic trophic component in agricultural food webs
67 (Marshall et al. 2003), but may induce crop yield loss (Oerke 2006). Many weed species
68 occur both in crop and non-crop areas (Alignier et al. 2012, Fried et al. 2009), especially field
69 edges where management practices are less intensive (Wilson and Aebischer 1995). At the
70 field scale, weeds strongly respond to OF: species richness may be about 70% higher and
71 abundance doubled compared to CONV (Hyvönen et al. 2003; Tück et al. 2014).
72 Furthermore, weed communities respond also to landscape scale processes (Gabriel et al.
73 2006, 2010, Gaba et al. 2010, Perronne et al. 2015). While almost all previous studies
74 compared pairs of organic and conventional farming along a gradient of landscape
75 complexity (e.g. Winqvist et al. 2011) or regions (e.g. Gabriel et al. 2010), here we used an
76 unusually large dataset collected within a single landscape of 450km² in which proportion of
77 OF varies from 0 to >50% in 1km² buffers. Using a spatially stratified design on 465 fields we
78 quantify the relative contribution of landscape (proportion of OF in a 1km buffer around a
79 focal field) *versus* field scale processes (organic or conventional management; field core
80 *versus* field margin) on weed diversity at several spatial scales: within-field, field scale,
81 between-fields and landscape. Since OF systems are characterized by more diversified crop
82 successions (Lechenet et al. 2014) which favours weed richness (Romero et al. 2008) as
83 well as a clumped distribution of farms (Gabriel et al. 2009), we controlled for crop
84 successions, field size, soil type and land use and semi-natural elements in our models to
85 account for these confounding spatio-temporal effects.

86

87 **MATERIALS AND METHODS**

88 *Study area*

89 The study site (c. 430 km²) is the LTER “Zone Atelier Plaine & Val de Sèvre”, located in
90 central western France, Poitou-Charentes Region, France (46.23°N, 0.41 W; Fig. 1a, b). It
91 is an agricultural landscape dominated by intensive cereal production, with an average field
92 size of 3.7 ha. Since 1994, the land use for each of the about 14000 fields has been
93 recorded twice per year. Using eight crop categories, land use in 2010 consisted in 38.4 %
94 cereals (mainly winter wheat, 33.5 %), 10.8 % meadows and alfalfa, 12.1% sunflower, 8.6%
95 corn, 8.7% oilseed rape, 2.8% pea, 2.3% ryegrass, 3.8 % other crops; and 9.5 % urban

96 and 3.0 % woodland (see ESM 3 for details). For this study we selected fields situated in
97 landscapes with at least 55 % crop cover (grasslands included). In 2011 eighteen out of
98 about 450 farms used organic farming methods (410 arable fields, excluding grassland),
99 corresponding to a surface of 15.7 km² (3.7% of the study area; Fig 1c), with farms having
100 converted since 1 to 14 years (mean=5.7 years).

101

102 *Weed sampling*

103 Between 2009 and 2012, weed species were sampled in 465 wheat fields (see ESM 1 for
104 details and ESM 11 for species list), both in the field core and in the field margin. The latter is
105 defined as the tilled zone between the field boundary and the first crop row (Fig. 1d). Over
106 the years, field surveys varied slightly (either 32 quadrats of 4m² in a star arrangement in the
107 field core or 10 quadrats of 4m² in a linear arrangement orthogonal to the tractor tracks and
108 spaced by 10m (Fig 1d)). In both protocols, the first quadrat was located at least 20m from a
109 field corner to avoid border effects. In field margin, transect started 30m from the field
110 margin. To homogenize sampling effort between the two protocols, species richness per field
111 in field core was estimated over 10 quadrats using a bootstrap procedure in fields where the
112 star arrangement protocol was applied.

113

114 *Landscape analyses*

115 Spatial data were treated using QGis version 1.7.3 (Development Team 2002-2010). The
116 landscape was characterized by the proportion of each landscape component (forest,
117 grassland, built area) and crop types (eight categories), and the linear length of hedgerows,
118 road/paths and rivers in buffer areas around each sampled field. The most relevant scale
119 (buffer areas of six radii; 500, 1000, 1250, 1500, 2000 and 2500m) at which landscape
120 variables better explained weed diversity, was selected using a model selection procedure
121 based on the Akaike Criterion (AIC Burnham and Andersson 2004). The model most
122 supported by the data (lowest AIC value; M3 in the following section) was the one at 1000m.
123 In this 1km radius, the landscape around the focal fields was composed of 0-33% of
124 grassland, 0-38% of forest, 0-42% of built area and 0-55% of OF with annual crops (see
125 ESM 3). A Principal Component Analysis (PCA) was then conducted using the set of
126 selected landscape variables (at the 1km radius; see ESM 9) to obtain a synthetic indicator
127 of landscape complexity. The first PCA component (PC1, 25% of variance explained)
128 summarised a gradient from simple landscapes (annual crops only and without any semi-
129 natural elements) to more complex landscapes (mosaic of annual crops and semi-natural
130 components, with a large proportion of grasslands, hedgerows and built areas). The second
131 axis (PC2, 15.3% of variance explained), opposed woodland and roads/paths.

132

133 *Multi-model selection in multiple regression analysis*

134 We first investigated the effects of local (field) *versus* regional (landscape) parameters on
135 weed diversity per field (considering the ten quadrats, equivalent to the γ -plot used in the
136 Additive partitioning analysis, see below), using generalized additive mixed models (GAMMs,
137 R Development Core team 2012, package “*gamm4*”: Scheipl, 2009; Wood, 2004) to allow for
138 nonlinear relationships. In all cases, these could be approximated to quadratic functions in
139 GLMM (*lme4* version 1.1-6 (Bates et al. 2014) in R 3.1.0 (2014)). We then used an
140 information-theoretic multi-model selection framework to evaluate the support from the data
141 for five competing models of increasing complexity. A first model (M0, the “Baseline model”)
142 investigated independent variables that were considered *a priori* as confounding factors
143 acting on species richness, i.e. year (4-level factor) and date of sampling (in Julian day as
144 quadratic polynomial), soil type (3-level factor), and field area (log-transformed). Since the
145 effect of date varied spatially (in field margin, species richness increased linearly throughout
146 the season), we included an interaction term between date and position in the field (field core
147 or margin). To account for the survey design (repeated measures within each field and
148 several fields per farmer), we used a nested random intercept structure (Bolker et al. 2009;
149 Pinheiro & Bates 2000), the “field ID” (442 levels) nested within the “farmer ID” (131 levels).
150 This basic model structure was included in all the four other competing models. A second
151 model (M1, the “Local management model”), hypothesized that weed species richness varied
152 consistently with the management type in the field (OF vs. CONV, fitted as a 2-level fixed
153 effect factor), the position of sampling within the field (margin vs. core), and their interaction.
154 The third model (M2, the “Crop Successions model”) aimed at disentangling direct (i.e. ban
155 of herbicides) *versus* indirect effects (i.e. crop succession diversity) of organic farming on
156 weed species richness. In preliminary analysis, we tested five-year and ten-year
157 successions, using the percentage of the eight crop categories in the succession (see ESM2
158 for details), and kept the ten-year successions in the analysis as we obtained the lowest AIC
159 value for this duration. Then we tested the effect of the number of crops in the succession,
160 and the effect of the preceding crop. Since the presence of grassland and corn in the ten-
161 year succession and preceding crop were the only variables supported by the data (lowest
162 AIC values), we kept these as proxies of OF effect. The fourth model (M3, the “Landscape
163 complexity model”) aimed at investigating the effect of landscape complexity, modelled as
164 PC1 and PC2. Finally, in the fifth model (M4, the “Organic farming in the landscape model”)
165 we added the proportion of OF in the landscape (% of the total area in the 1km buffer around
166 the sampled plot) including annual crops and grasslands (M4.a and M4.b) or annual crops
167 only (M4.c and M4.d). We also tested the interaction between the % OF in the landscape and
168 the position in the field (field core or margin).

169 The model selection procedure started with all 2-way interactions and main effects, and was
170 based on minimizing the AIC criterion using the MuMIn library in R (version 1.6.5., Barton
171 2011) and the *dredge* function to test all covariate combinations. All retained covariates of
172 the lower-level models had to be included in the more complex competing models, thus the
173 model selection procedure started with the baseline model M0). For each model, we
174 checked for spatial autocorrelation in the model residuals (using variograms in the geoR
175 library version 1.6-29, Ribeiro Jr and Diggle 2001); since none was found, we did not
176 include a random effect for each point count (Betts *et al.* 2009). To aid model convergence
177 and facilitate the interpretation, we mean-centred all numerical covariates and standardized
178 variables by dividing by two standard deviations (Scielzeth 2010).

179

180 *Additive partitioning analysis*

181 We also analysed the effect of OF and the position in the field (field core or margin) on the α ,
182 β and γ components of diversity (Crist *et al.*, 2003). To avoid sample bias we selected the
183 same number of fields between organic and conventional fields, i.e. 77 fields in both cases
184 by randomly selecting the same number of conventional fields. The α -plot diversity
185 corresponds to the mean number of species in the sampled unit (i.e., quadrat). The β -plot
186 diversity corresponds to the difference between quadrats within a field and is calculated by
187 the γ -plot minus the average of the α -plots, where γ -plot is the total species richness per field
188 (sum of the ten quadrats). The γ -field diversity is the total number of species found by class
189 (e.g. in all the centres of organic fields). β -field diversity corresponds to the difference
190 between fields (β -field = γ -field minus α -field), where α -field corresponds to species richness
191 per field (so α -field = γ -plot). All analyses were undertaken first using all weed species, then
192 repeated separately for the more common species and the less frequent species of the study
193 area.

194

195 **RESULTS**

196 Field size varied greatly across the 465 sampled fields (range 0.37–50.7 ha), and was to
197 some extent related to management type (Welch Two Sample test, mean OF=6.7ha, mean
198 CONV=5.4ha, $t=1.34$, $p=0.18$). As expected, crop successions were more diverse in OF
199 fields than in CONV ones, with a higher number of crops in ten-year successions (OF=6.53,
200 CONV=5.06, $t=7.64$, $p<0.001$). There was a higher percentage of spring cereal, corn and
201 other crops and a reduced frequency of winter cereal, rape and sunflower in OF than in
202 CONV, while the percentage of grasslands and alfalfa were similar (ESM 2). Similarly,
203 landscape composition at 1km around the fields differed between OF and CONV fields, with
204 more alfalfa, corn or pea around OF fields and less hedgerows, winter wheat, rape or

205 sunflower (ESM3). Furthermore, as OF fields are spatially aggregated, there were more OF
206 around the OF sampled field than the CONV ones (ESM 3).

207 In total, 175 weed species were detected (see ESM 13), including 28 common
208 species (present in more than 25% of the fields) and 104 less frequent species (present in
209 less than 5% of the fields; no red-listed species were recorded). As expected weed richness
210 was significantly higher in OF fields than in CONV ones (by c.50%) and in field margin than
211 in field core. Differences in weed richness between field core and margin were higher in
212 CONV systems (ESM 4).

213

214 **Relative effects of local farming practices versus landscape complexity on weed α** 215 **diversity**

216 Overall, we found an increase in the goodness of fit of the competing models (ESM 12,),
217 suggesting contributing effects of local (management type and position in the field, Model 1,
218 and crop succession diversity, Model 2) and landscape (Model 3) on weed species richness.
219 Adding the percentage of grassland and corn in the ten-year succession and the preceding
220 crop type increased the goodness of fit of the model (ESM 12), having a positive effect on
221 weed richness, but it did not really affect the variation explained by OF (4.28% and 4.09% of
222 the variation is explained by OF without and with crop succession, respectively), suggesting
223 that the main effect of OF was not due to the differences in crop sequences. Landscape
224 complexity (modelled as PC1 and PC2) had no significant effects on weed richness.
225 However, the percentage of alfalfa and the length of road/paths in a 1km buffer around the
226 fields had a positive effect, as did the landscape percentage of OF (ESM 5). Moreover, the
227 variance explained by the farming system (OF versus CONV) at the local scale was nearly
228 halved when the percentage of OF fields in the landscape was included in the models
229 (2.28% in M4.b model vs 4.51% in the landscape model, ESM 12). Overall, the fixed effects
230 in these two final models explained around 35 % of the variation compared to the null model
231 (ESM 12).

232 Importantly, all final models predicted an increase of species richness with the percentage of
233 OF in the landscape (both for OF and CONV fields and both in field margin and field core),
234 but the interaction models (M4.b and M4.c) further indicated that species richness was
235 especially increased in the field margin: a field margin in a CONV field surrounded by OF
236 fields had a higher weed richness (21 species) than a field margin in OF field surrounded by
237 CONV fields (19 species; see ESM 5 & 8). Indeed model M4.b predicted an increase from
238 12.4 to 13.6 species for the core of conventional field whether surrounded by 0% or 50% OF,
239 whereas the increase was from 17.4 to 21.2 in its field margin. For an OF field, the increase
240 was from 17.1 to 18.8 (0 to 50% OF in the landscape) in the field core and 19.5 to 23.7 in
241 field margin.

242

243 Diversity partitioning: effect of organic farming on beta-diversity

244 In the 74 fields of each class, we found a γ -diversity of 118 species in field margins and 90 in
245 field cores for OF, compared to 110 and 82 respectively in CONV fields; of all species, 40
246 were only found in OF fields while 22 were only found in CONV. The additive partitioning
247 approach indicated that the largest part of the diversity was due to the β -field diversity, i.e.
248 diversity between fields (ESM 10), especially for less frequent species (Fig.2c). For the less
249 frequent species, γ -diversity in field margin was higher in OF (56species) than in CONV (48
250 species), with a similar difference in field core, (30 vs 22 sp, see Fig. 2c). The α -field diversity
251 of less frequent species increased with the percentage of OF in the surrounding landscape,
252 especially in field margins (Figure 2d). A similar trend was observed in field cores (ESM 6).
253 For the common species (Fig. 2b), we did not observe any differences in γ -diversity between
254 OF and CONV or between field margin and field core, suggesting similar species pools (ESM
255 7). Diversity components of common species varied between the core field in CONV vs OF
256 fields, with a higher contribution of the β field-diversity and lower α plot and β plot-diversity in
257 CONV (Fig 2b), suggesting that common weeds were less frequent in CONV leading to
258 differences in the between fields diversity. Altogether these results support the positive effect
259 of OF in the landscape on weed diversity, an effect larger in the field margins than in the
260 core, and larger also for less frequent than for common species.

261

262 DISCUSSION**263 Weed diversity in organic and conventional wheat fields**

264 Weed community composition is strongly affected by application of herbicides, fertilisation
265 and mechanical weed control, the latter being mostly used in organic farms (José-Maria &
266 Sans 2011, Doucet et al. 1999, Hyvönen and Salonen 2002, Hawes et al. 2010). OF fields in
267 general harbour more insect-pollinated plants (Hald, 1999), forbs (Moreby *et al.*, 1994), rare
268 or threatened weeds (Rydberg and Milberg, 2000; Van Elsen, 2000), and less nitrophilous
269 species (Hyvönen *et al.*, 2003; Rydberg and Milberg, 2000), while conventional fields have
270 less broad-leaved species due to the use of auxin herbicides to control them (Kudsk and
271 Streibig 2003), and more herbicide resistant weeds, in particular grasses (Heap, 1997).
272 Though in some cases OF may not increase weed species richness (Kleijn et al. 2001,
273 Weibull et al. 2003), our results agree with most previous studies (Hole et al. 2005, Gabriel et
274 al. 2010, Tuck et al. 2014), indicating a positive effect on weed species richness (+c.30% in
275 the latter studies compared to +48.9% in the field core and +30% in the field margin in the
276 present study). We also found that magnitude of the difference between field core and
277 margin was higher in CONV than in OF, in accordance with Gabriel et al. (2010) and other
278 studies that demonstrated that field boundaries can act as refugia for many weeds species

279 including species threatened by agricultural intensification (Fried et al., 2009, Smart et al.,
280 2002). Our results support that the release of herbicides and the combination of less intense
281 agricultural practices (e.g. weed harrow, reduced use of fertilizers) in OF fields may favour
282 weed species which are not adapted to conventional systems either because of their
283 sensitivity to chemical control or high level of nitrogen (Romero et al., 2008, Hald 1999, José-
284 Maria & Sans 2011). A greater proportion of grassland in the succession may also explain
285 this pattern, since the presence of grassland (and alfafa) tends to increase weed diversity
286 while decreasing the relative abundance of annual weed species (Meiss et al. 2010).
287 Therefore, at the local scale, both the agricultural practices associated with OF and the field
288 history (crop succession), seem to act on weed richness.

289

290 **Regional effects are driven by the amount of organic farms in the landscape**

291 Several studies have demonstrated the role of landscape in shaping weed communities
292 (Batary *et al.*, 2011, Duelli & Obrist, 2003, Kleijn & Sutherland 2003, Conception et al. 2008),
293 though in some cases this was only detected in OF and not in CONV fields (Gabriel et al.
294 2010), or even not supported (Armengot et al. 2011). In all these studies, regional effects
295 were accounted for by semi-natural elements. In our study, we did not observe a landscape
296 complexity effect. Instead, we found a strong landscape effect of OF that can even exceed
297 local effects of field management. Gabriel et al. (2010) also found a beneficial effect of OF in
298 the landscape, however in the latter study, the beneficial effect was only found in OF fields,
299 contrary to our results showing positive effects for both OF and CONV fields (especially in
300 field margins). In Gabriel et al.'s (2010) study, conventional farms surrounded by organic
301 farms used more synthetic fertilizers and herbicides than conventional farms surrounded
302 mainly by conventional farms, possibly removing the landscape effect on CONV fields. This
303 difference between the two studies may highlight the filtering effect of conventional
304 management (especially chemical fertilization and herbicides) in field cores, that prevent
305 species richness to equalize that of OF, conversely to field margins where farming practices
306 are less intensive. In addition, despite a large range of landscape complexity around focal
307 fields, local effects (OF vs CONV) did not vary with landscape complexity, as also found in
308 Winqvist et al. (2011), and contrary to Conception et al (2008), weed richness was not higher
309 in intermediate landscape complexity but increased linearly with the percentage of organic
310 farming in the landscape, as predicted by Bengtsson et al. (2005).

311

312 **The role of organic fields in sustaining metacommunity dynamics**

313 We showed that differences in weed richness between OF and CONV systems were mostly
314 explained by the higher diversity of less frequent species in OF fields, suggesting that the
315 main effect of OF at the landscape scale on species richness acts through the effect on less

316 frequent species in field margins. Higher values of diversity and higher density of weeds in
317 the seed bank of organic fields have already been reported, both in field cores and margins
318 (José-Maria & Sans 2011). However the main proposed factor determining seed bank size
319 was crop seed origin from organic farms, which would favour the entry of weed seeds, but
320 this argument cannot explain the increased weed diversity in CONV fields found in our study.
321 We alternatively suggest that spatio-temporal flows of seeds influence weeds in local
322 communities (i.e. semi-natural or crop fields) by generating mass effect (Shmida & Wilson
323 1985) and source–sink dynamics (Holt 1985; Pulliam 1988). Such dynamics involve
324 interactions among local communities at large scales, i.e. the agricultural landscape, as in a
325 metacommunity (Leibold et al. 2004). Among the metacommunity paradigms, the ‘species-
326 sorting’ and ‘mass effects’ require that different patches have different conditions and be
327 sufficiently connected to allow local coexistence of species with different performances and
328 competitive abilities (Leibold et al. 2004). Therefore mass effect through dispersal from field
329 margins could act at the field scale, as previously proposed by Poggio *et al.* (2010), while
330 heterogeneous habitats provided by variation in farming systems across the agricultural
331 landscape may ensure weed regional coexistence through species sorting, as suggested by
332 Perronne *et al.* (2015). Spatial dispersal is not recognised as the main process involved in
333 weed landscape dynamics, with temporal dispersion through the seed bank typically
334 suggested as the main process as a buffer memory of past infestations (Bàrberi et al. 1998).
335 However, weed species spatial dispersal by farming practices has long been present in the
336 agroecosystem (Benvenuti 2007). Based on our results, we propose that the persistence of
337 species (especially the less frequent ones) in agricultural landscapes relies on two different
338 strategies, both belonging to the storage effect (Chesson 2000), in response to the high
339 disturbance regime typical of crop successions in intensively farmed landscapes. Species
340 with high dispersal rates will benefit from variation in the occurrence of habitat disturbances
341 across the agricultural landscape (i.e. a spatial storage effect), while other less frequent
342 species will have a high persistence rate in the seed bank allowing to respond to temporal
343 variation in habitat disturbances. The role of organic farming within the metacommunity
344 dynamic would thus be twofold. First, as less intensively disturbed habitat, OF enhances the
345 diversity of less frequent species through a temporal storage effect. Second, species loss in
346 more intensively disturbed habitats (i.e. conventional fields) would be compensated by a
347 spatial storage effect allowing for dispersal. Interestingly, some evidence for the storage
348 effect hypothesis has recently been provided for weed coexistence. García De León *et al.*
349 (2014), in a long-term experiment, showed that the variation of climatic conditions can modify
350 inter-specific competition, for species sharing similar resource requirement (fertilisation type
351 and level) but differing by the adaptation to climate, allowing to maintain coexistence
352 between these species, and suggesting the importance of storage effects to maintain

353 diversity. Moreover, using simulations Bianchi *et al.* (2013) showed that the response of
354 organisms to the landscape proportion of OF may depend on the movement ability of the
355 organisms (see also Schellhorn *et al.* 2014), as well as on the degree of spatial aggregation
356 of OF fields, especially at intermediate levels of proportion of OF.

357

358 CONCLUSION

359 Our results suggest that a major benefit of OF systems lies in the persistence, at the
360 landscape scale, of less frequent species (see also Aavik & Liira, 2010, Pywell *et al.* 2012,
361 Hyvönen, 2007) through a metacommunity effect: OF fields, and field margins of both
362 management types, provide habitats for less frequent weed species (Rydberg and Milberg,
363 2000; Van Elsen, 2000) and high density of OF fields enhances weed diversity in farmland
364 landscapes. Thus landscape heterogeneity *per se* is not sufficient for maintaining regional
365 weed diversity, but rather the finer grain heterogeneity and availability of ruderal habitats
366 (characteristic of OF), acting as refugia for annual plants, is the key driver. Improving such
367 habitats may have a lower effect on crop production (i.e. less frequent species are in field
368 margins and are rarely abundant in the field core), but may support other ecological services
369 such as pollination (Isaacs *et al.*, 2009, Marshall *et al.*, 2003, Bretagnolle and Gaba, in
370 press). Our results also suggest that biodiversity and crop production may be supported in
371 landscapes with less intensively farmed fields according to a land sharing strategy, although
372 further studies incorporating weed abundance (rather than just richness) need to be
373 conducted.

374

375 Acknowledgments

376 We thank M. Roncorini, E. Cadet, and T. Fanjas for carrying the main part of field work. We
377 acknowledge ANR AGROBIOSE, BIODIAVGRIM and DYNARURABIO for funding the study.
378 For very useful comments we thank Jan Bengtsson and an anonymous reviewer, as well as
379 the Associate Editor Colin Osborne.

380

381 Author's contribution

382 VB conceived and coordinated the study. VB, SG, LB and LH designed the study. LH & HM carried
383 out part of fieldwork. HM managed the data sets. LH & SG drafted the manuscript; LH, LB, SG & VB
384 carried out the statistical analyses. All authors gave final approval for publication and contributed to
385 the writing.

386

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- 592
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- 594

595 Caption

596 **Figure 1.** Location of the study area « Plaine & Val de Sèvre » and weed sampling design.

597 **A.** Geographic location of the Poitou-Charente region in France.

598 **B.** Location of the study area « Plaine & Val de Sèvre » in the Poitou-Charente region, department of
599 Deux-Sèvres.

600 **C.** Distribution of organic farming in the study area; overall it covers 3.7 % of the study area.

601 **D.** Sampling design of weeds (location of the quadrats and transects in a field). In each field, 10
602 quadrats of 4m² were sampled in the field core, and 10 transect of 5 meters in the field margin.

603

604 **Figure 2.** Predictions of the final model for weed species richness (α field diversity) (A), Biodiversity
605 partitioning (α , β , γ) of species richness for the common (B), and less frequent species (C), observed
606 mean species richness of less frequent species in field margins (α field diversity), depending on the %
607 of organic farming (OF) in the landscape

608 **A.** Model predictions for the response of species richness (α field diversity) to the proportion of
609 OF in the landscape (model M4.b) in both organic and conventional fields, and both in field
610 margins and field cores.

611 The model shows an increase of species richness both in OF and conventional fields, and both in field
612 cores and margins with the % of OF in the landscape but this response is stronger for field margins.

613 **B.** Additive partitioning approach of biodiversity (more common species). The figure shows the
614 mean α , β and γ diversity for organic and conventional fields (core and margin) with the same
615 number of fields per category (74 fields). 1000 repetitions were done by bootstrapping and we
616 calculated the mean and the 95% confidence interval for species richness by class on these
617 repetitions.

618 This figure shows that if gamma diversity for abundant species seems equal between field cores and
619 margins and OF and conventional fields, we observe that alpha diversity of conventional field cores
620 appears lower.

621 **C.** Additive partitioning approach of biodiversity (less frequent species)

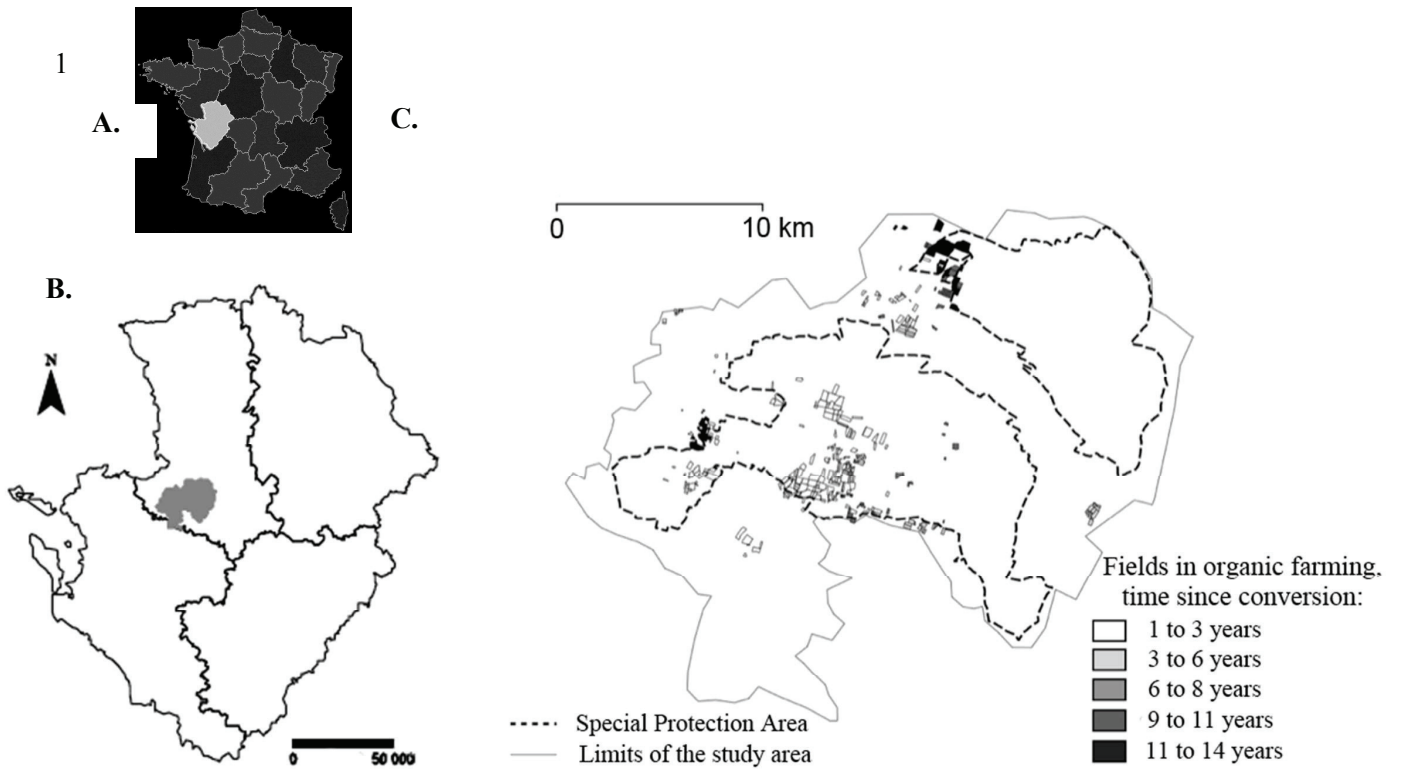
622 1000 repetitions were done by bootstrapping and we calculated the mean and the 95% confidence
623 interval for species richness by class on these repetitions (74 fields).

624 We observe that the diversity of rare species is mostly explained by beta field diversity, and that
625 diversity (both alpha and beta) appears lower in field core than in field margin and in conventional than
626 in OF fields.

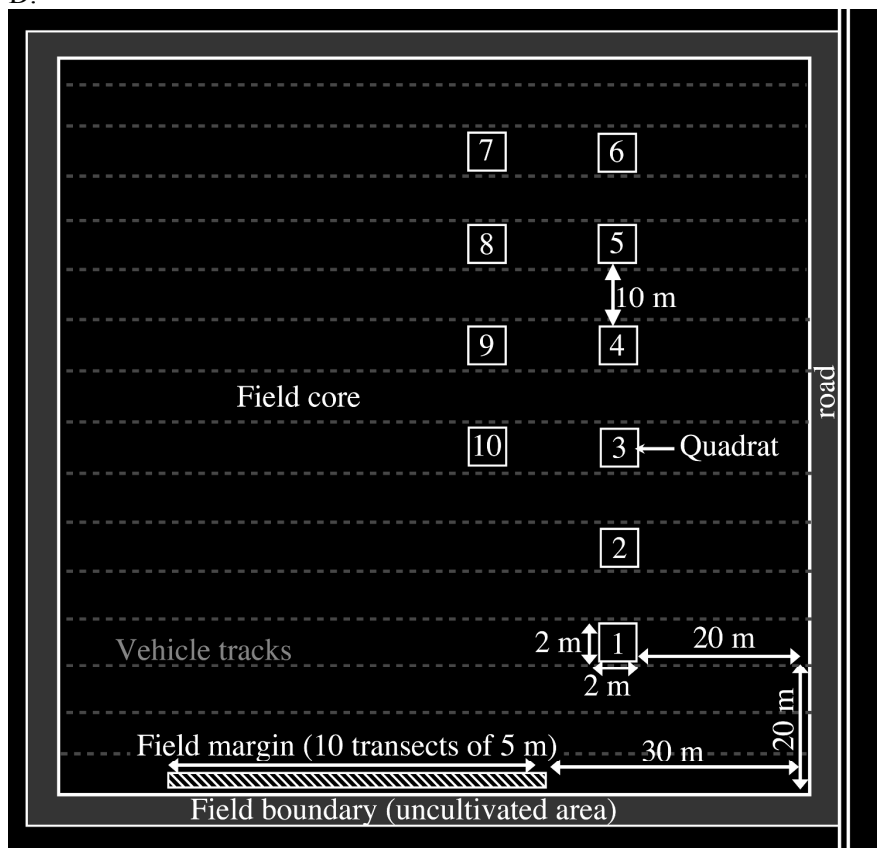
627 **D.** Mean diversity of the field margins for less frequent species depending on the percentage of
628 organic farming in the landscape. The species richness of each class was calculated on the
629 same number of fields (12 fields). 1000 repetitions were done by bootstrapping and we
630 calculated the mean and the 95% confidence interval for species richness by class on these
631 repetitions.

632 We observe that diversity increase with the percentage of OF in the landscape, both for OF and
633 conventional fields.

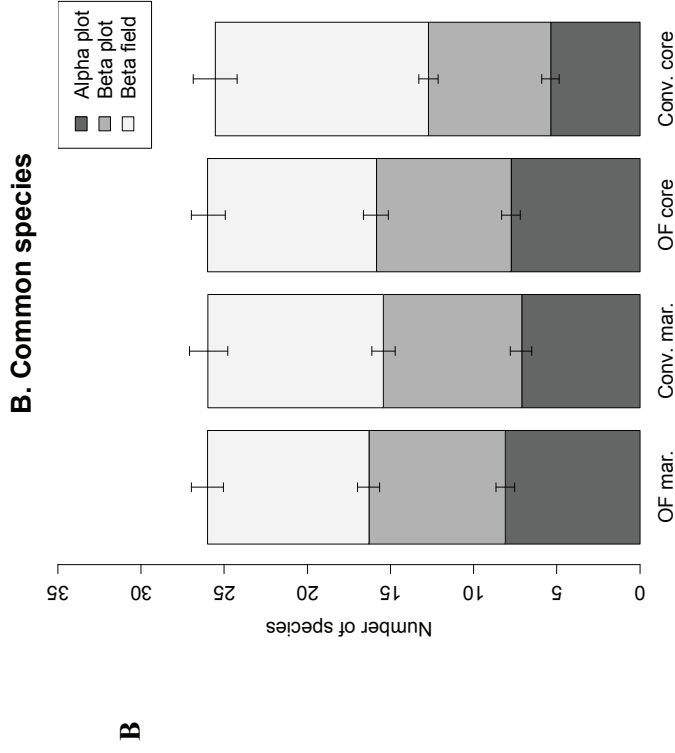
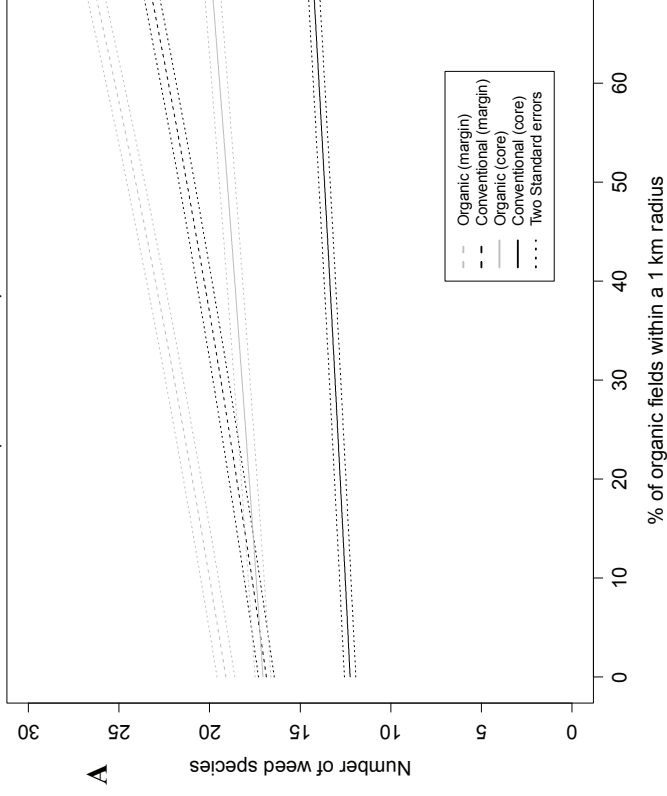
634



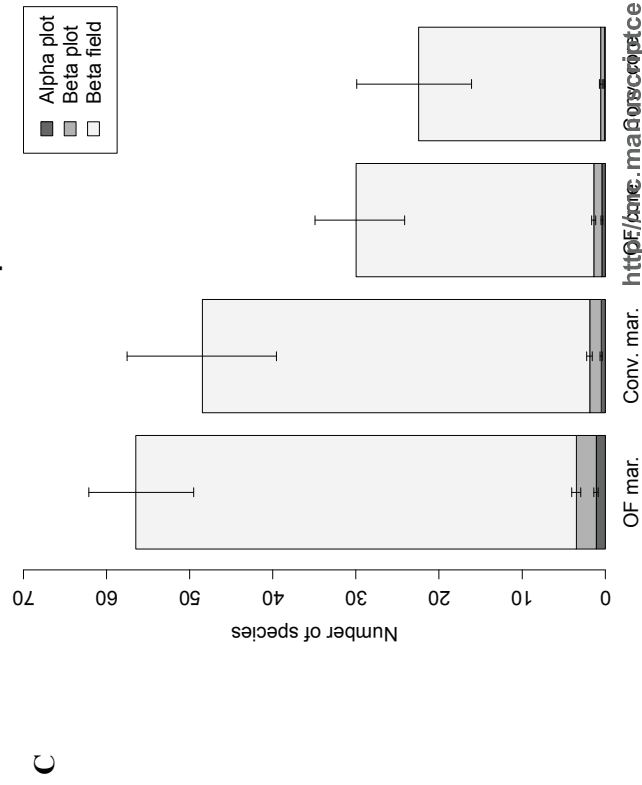
D.



Evolution of the species richness with the proportion of organic farming in the landscape (interaction model) M4.b



C. Rare species



D

