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Organic fields sustain weed metacommunity dynamics in farmland landscapes

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Abstract

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

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

INTRODUCTION

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

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

In this context, studying ecological processes at the scale of the meta-community (Leibold et al., 2004) can be relevant to assess potential regional (i.e. landscape) effects on local community richness. Indeed in highly heterogeneous and dynamic landscapes such as agro-ecosystems, dispersal is expected to be an essential driver that allows communities to persist in spite of landscape instability. Here we hypothesise that local and regional processes interact in shaping biodiversity, such that landscape scale processes may outcompete local processes. In other words, the presence of OF at the landscape scale could balance the field-level negative effects of conventional agricultural management through mass effect (species dispersing from favorable habitats in organic fields into surrounding conventional fields). To test this hypothesis, we used weed communities of winter wheat, the major crop in Europe and in France (c.10% of the total country area is cropped with wheat). Weeds represent the basic trophic component in agricultural food webs (Marshall et al. 2003), but may induce crop yield loss (Oerke 2006). Many weed species occur both in crop and non-crop areas (Alignier et al. 2012, Fried et al. 2009), especially field edges where management practices are less intensive (Wilson and Aebischer 1995). At the field scale, weeds strongly respond to OF: species richness may be about 70% higher and abundance doubled compared to CONV (Hyvönen et al. 2003; Tück et al. 2014). Furthermore, weed communities respond also to landscape scale processes (Gabriel et al. 2006, 2010, Gaba et al. 2010, Perronne et al. 2015). While almost all previous studies compared pairs of organic and conventional farming along a gradient of landscape complexity (e.g. Winqvist et al. 2011) or regions (e.g. Gabriel et al. 2010), here we used an unusually large dataset collected within a single landscape of 450km² in which proportion of OF varies from 0 to >50% in 1km² buffers. Using a spatially stratified design on 465 fields we quantify the relative contribution of landscape (proportion of OF in a 1km buffer around a focal field) *versus* field scale processes (organic or conventional management; field core *versus* field margin) on weed diversity at several spatial scales: within-field, field scale, between-fields and landscape. Since OF systems are characterized by more diversified crop successions (Lechenet et al. 2014) which favours weed richness (Romero et al. 2008) as well as a clumped distribution of farms (Gabriel et al. 2009), we controlled for crop successions, field size, soil type and land use and semi-natural elements in our models to account for these confounding spatio-temporal effects.

MATERIALS AND METHODS

Study area

The study site (c. 430 km^2) is the LTER “Zone Atelier Plaine & Val de Sèvre”, located in central western France, Poitou-Charentes Region, France (46.23°N, 0.41 W; Fig. 1a, b). It is an agricultural landscape dominated by intensive cereal production, with an average field size of 3.7 ha. Since 1994, the land use for each of the about 14000 fields has been recorded twice per year. Using eight crop categories, land use in 2010 consisted in 38.4 % cereals (mainly winter wheat, 33.5 %), 10.8 % meadows and alfalfa,12.1% sunflower, 8.6% corn, 8.7% oilseed rape, 2.8% pea, 2.3% ryegrass, 3.8 % other crops; and 9.5 % urban and 3.0 % woodland (see ESM 3 for details). For this study we selected fields situated in landscapes with at least 55 % crop cover (grasslands included). In 2011 eighteen out of about 450 farms used organic farming methods (410 arable fields, excluding grassland), corresponding to a surface of 15.7 km^2 (3.7% of the study area; Fig 1c), with farms having converted since 1 to 14 years (mean=5.7 years).

Weed sampling

Between 2009 and 2012, weed species were sampled in 465 wheat fields (see ESM 1 for details and ESM 11 for species list), both in the field core and in the field margin. The latter is defined as the tilled zone between the field boundary and the first crop row (Fig. 1d). Over the years, field surveys varied slightly (either 32 quadrats of $4m^2$ in a star arrangement in the field core or 10 quadrats of $4m^2$ in a linear arrangement orthogonal to the tractor tracks and spaced by 10m (Fig 1d)). In both protocols, the first quadrat was located at least 20m from a field corner to avoid border effects. In field margin, transect started 30m from the field margin. To homogenize sampling effort between the two protocols, species richness per field in field core was estimated over 10 quadrats using a bootstrap procedure in fields where the star arrangement protocol was applied.

Landscape analyses

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

Multi-model selection in multiple regression analysis

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

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

Additive partitioning analysis

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

RESULTS

Field size varied greatly across the 465 sampled fields (range 0.37–50.7 ha), and was to some extent related to management type (Welch Two Sample test, mean OF=6.7ha, mean CONV=5.4ha, t=1.34, p=0.18). As expected, crop successions were more diverse in OF fields than in CONV ones, with a higher number of crops in ten-year successions (OF=6.53, CONV=5.06, t=7.64, p<0.001). There was a higher percentage of spring cereal, corn and other crops and a reduced frequency of winter cereal, rape and sunflower in OF than in CONV, while the percentage of grasslands and alfalfa were similar (ESM 2). Similarly, landscape composition at 1km around the fields differed between OF and CONV fields, with more alfalfa, corn or pea around OF fields and less hedgerows, winter wheat, rape or sunflower (ESM3). Furthermore, as OF fields are spatially aggregated, there were more OF around the OF sampled field than the CONV ones (ESM 3).

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

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

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

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

Diversity partitioning: effect of organic farming on beta-diversity

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

DISCUSSION

Weed diversity in organic and conventional wheat fields

Weed community composition is strongly affected by application of herbicides, fertilisation and mechanical weed control, the latter being mostly used in organic farms (José-Maria & Sans 2011, Doucet et al. 1999, Hyvönen and Salonen 2002, Hawes et al. 2010). OF fields in general harbour more insect-pollinated plants (Hald, 1999), forbs (Moreby *et al*., 1994), rare or threatened weeds (Rydberg and Milberg, 2000; Van Elsen, 2000), and less nitrophilous species (Hyvönen *et al*., 2003; Rydberg and Milberg, 2000), while conventional fields have less broad-leaved species due to the use of auxin herbicides to control them (Kudsk and Streibig 2003), and more herbicide resistant weeds, in particular grasses (Heap, 1997). Though in some cases OF may not increase weed species richness (Kleijn et al. 2001, Weibull et al. 2003), our results agree with most previous studies (Hole et al. 2005, Gabriel et al. 2010, Tuck et al. 2014), indicating a positive effect on weed species richness (+c.30% in the latter studies compared to +48.9% in the field core and +30% in the field margin in the present study). We also found that magnitude of the difference between field core and margin was higher in CONV than in OF, in accordance with Gabriel et al. (2010) and other studies that demonstrated that field boundaries can act as refugia for many weeds species including species threatened by agricultural intensification (Fried et al., 2009, Smart et al., 2002). Our results support that the release of herbicides and the combination of less intense agricultural practices (e.g. weed harrow, reduced use of fertilizers) in OF fields may favour weed species which are not adapted to conventional systems either because of their sensitivity to chemical control or high level of nitrogen (Romero et al., 2008, Hald 1999, José-Maria & Sans 2011). A greater proportion of grassland in the succession may also explain this pattern, since the presence of grassland (and alfafa) tends to increase weed diversity while decreasing the relative abundance of annual weed species (Meiss et al. 2010). Therefore, at the local scale, both the agricultural practices associated with OF and the field history (crop succession), seem to act on weed richness.

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

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

The role of organic fields in sustaining metacommunity dynamics

We showed that differences in weed richness between OF and CONV systems were mostly explained by the higher diversity of less frequent species in OF fields, suggesting that the main effect of OF at the landscape scale on species richness acts through the effect on less frequent species in field margins. Higher values of diversity and higher density of weeds in the seed bank of organic fields have already been reported, both in field cores and margins (José-Maria & Sans 2011). However the main proposed factor determining seed bank size was crop seed origin from organic farms, which would favour the entry of weed seeds, but this argument cannot explain the increased weed diversity in CONV fields found in our study. We alternatively suggest that spatio-temporal flows of seeds influence weeds in local communities (i.e. semi-natural or crop fields) by generating mass effect (Shmida & Wilson 1985) and source–sink dynamics (Holt 1985; Pulliam 1988). Such dynamics involve interactions among local communities at large scales, i.e. the agricultural landscape, as in a metacommunity (Leibold et al. 2004). Among the metacommunity paradigms, the 'species-sorting' and 'mass effects' require that different patches have different conditions and be sufficiently connected to allow local coexistence of species with different performances and competitive abilities (Leibold et al. 2004). Therefore mass effect through dispersal from field margins could act at the field scale, as previously proposed by Poggio *et al*. (2010), while heterogeneous habitats provided by variation in farming systems across the agricultural landscape may ensure weed regional coexistence through species sorting, as suggested by Perronne *et al*. (2015). Spatial dispersal is not recognised as the main process involved in weed landscape dynamics, with temporal dispersion through the seed bank typically suggested as the main process as a buffer memory of past infestations (Bàrberi et al. 1998). However, weed species spatial dispersal by farming practices has long been present in the agroecosystem (Benvenuti 2007). Based on our results, we propose that the persistence of species (especially the less frequent ones) in agricultural landscapes relies on two different strategies, both belonging to the storage effect (Chesson 2000), in response to the high disturbance regime typical of crop successions in intensively farmed landscapes. Species with high dispersal rates will benefit from variation in the occurrence of habitat disturbances across the agricultural landscape (i.e. a spatial storage effect), while other less frequent species will have a high persistence rate in the seed bank allowing to respond to temporal variation in habitat disturbances. The role of organic farming within the metacommunity dynamic would thus be twofold. First, as less intensively disturbed habitat, OF enhances the diversity of less frequent species through a temporal storage effect. Second, species loss in more intensively disturbed habitats (i.e. conventional fields) would be compensated by a spatial storage effect allowing for dispersal. Interestingly, some evidence for the storage effect hypothesis has recently been provided for weed coexistence. García De León *et al*. (2014), in a long-term experiment, showed that the variation of climatic conditions can modify inter-specific competition, for species sharing similar resource requirement (fertilisation type and level) but differing by the adaptation to climate, allowing to maintain coexistence between these species, and suggesting the importance of storage effects to maintain diversity. Moreover, using simulations Bianchi *et al*. (2013) showed that the response of organisms to the landscape proportion of OF may depend on the movement ability of the organisms (see also Schellhorn et al. 2014), as well as on the degree of spatial aggregation of OF fields, especially at intermediate levels of proportion of OF.

CONCLUSION

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

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Author's contribution

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

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Caption

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

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

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

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

D. Sampling design of weeds (location of the quadrats and transects in a field). In each field, 10 quadrats of $4m^2$ were sampled in the field core, and 10 transect of 5 meters in the field margin.

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

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

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

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

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

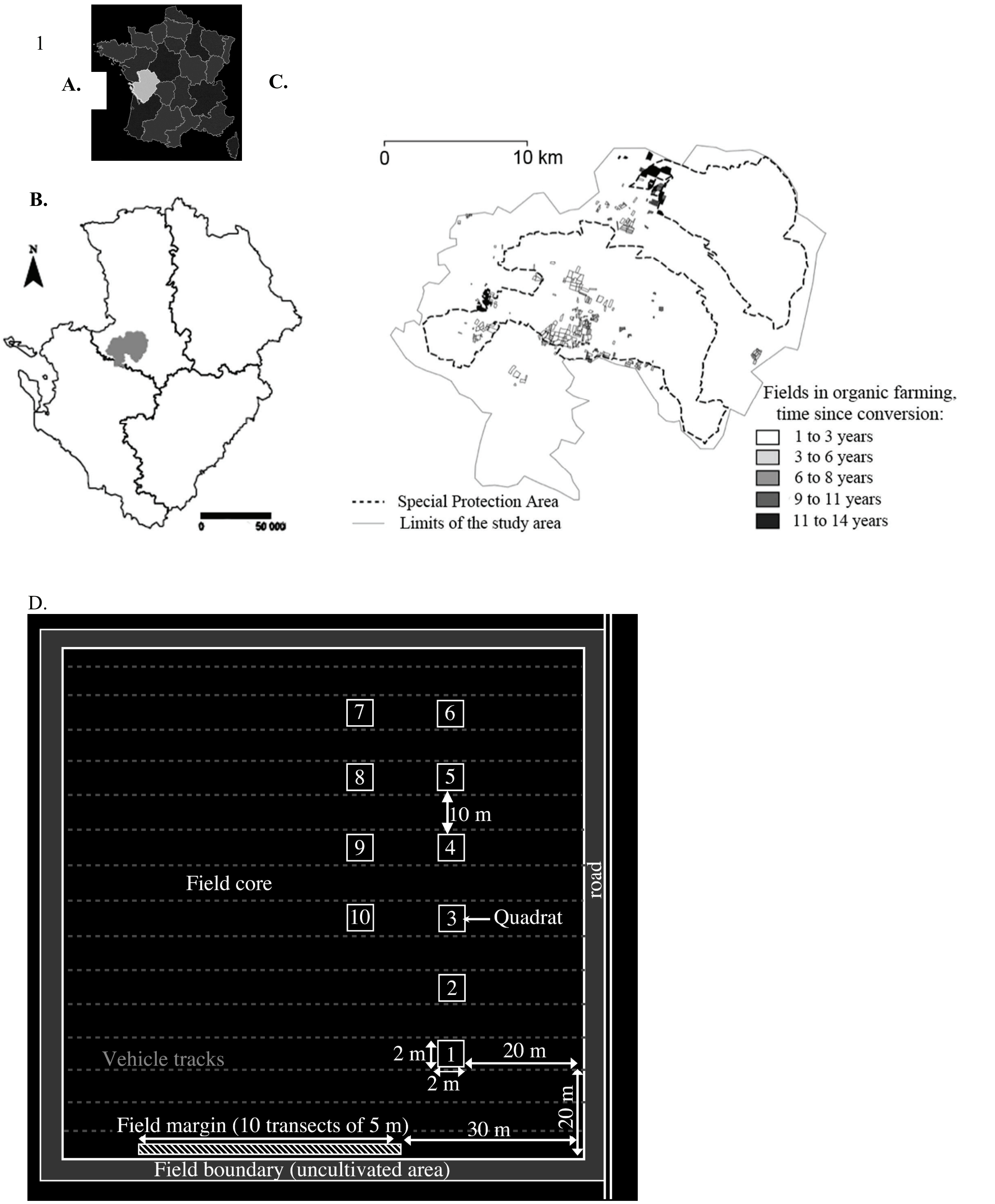
- **C.** Additive partitioning approach of biodiversity (less frequent species)

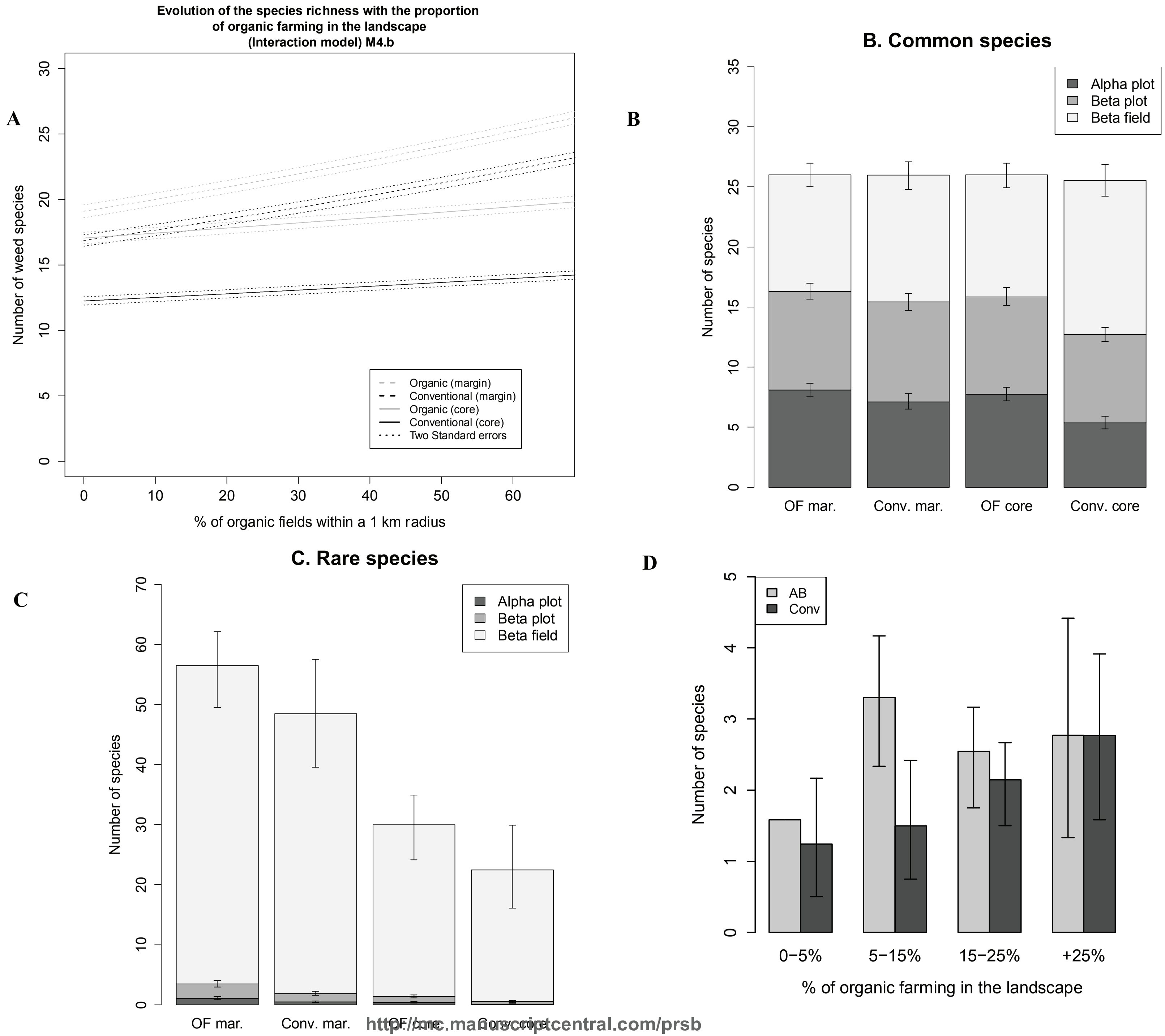
1000 repetitions were done by bootstrapping and we calculated the mean and the 95% confidence interval for species richness by class on these repetitions (74 fields).

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

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

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


A.
C.
B.
N
0
50 000
0
10 km
Fields in organic farming, time since conversion:
1 to 3 years
3 to 6 years
6 to 8 years
9 to 11 years
11 to 14 years
Special Protection Area
Limits of the study area
D.
7
6
8
5
10 m
9
4
Field core
road
10
3
Quadrat
2
Vehicle tracks
2 m
1
20 m
2 m
Field margin (10 transects of 5 m)
30 m
20 m
Field boundary (uncultivated area)


A
Evolution of the species richness with the proportion
of organic farming in the landscape
(Interaction model) M4.b
Number of weed species
% of organic fields within a 1 km radius
Organic (margin)
Conventional (margin)
Organic (core)
Conventional (core)
Two Standard errors
B
B. Common species
Number of species
Alpha plot
Beta plot
Beta field
OF mar.
Conv. mar.
OF core
Conv. core
C
C. Rare species
Number of species
Alpha plot
Beta plot
Beta field
OF mar.
Conv. mar.
D
Number of species
AB
Conv
0−5%
5−15%
15−25%
+25%
% of organic farming in the landscape