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ARTICLE

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Turnover and nestedness drive plant diversity benefits of organic farming from local to landscape scales

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Abstract

Biodiversity-benefits of organic farming have mostly been documented at the field scale. However, these benefits from organic farming to species diversity may not propagate to larger scales because variation in the management of different crop types and seminatural habitats in conventional farms might allow species to cope with intensive crop management. We studied flowering plant communities using a spatially replicated design in different habitats (cereal, ley and seminatural grasslands) in organic and conventional farms, distributed along a gradient in proportion of seminatural grasslands. We developed a novel method to compare the rates of species turnover within and between habitats, and between the total species pools in the two farming systems. We found that the intrahabitat species turnover did not differ between organic and conventional farms, but that organic farms had a significantly higher inter-habitat turnover of flowering plant species compared with conventional ones. This was mainly driven by herbicide-sensitive species in cereal fields in organic farms, as these contained 2.5 times more species exclusive to cereal fields compared with conventional farms. The farm-scale species richness of flowering plants was higher in organic compared with conventional farms, but only in simple landscapes. At the interfarm level, we found that 36% of species were shared between the two farming systems, 37% were specific to organic farms whereas 27% were specific to conventional ones. Therefore, our results suggest that that both community nestedness and species turnover drive changes in species composition between the two farming systems. These large-scale shifts in species composition were driven by both species-specific herbicide and nitrogen sensitivity of plants. Our study demonstrates that organic farming should foster a diversity of flowering plant species from local to landscape scales, by promoting unique sets of arable-adapted species that are scarce in conventional systems. In terms of biodiversity conservation, our results call for promoting organic farming over large spatial extents, especially in simple landscapes, where such transitions would benefit plant diversity most.

KEYWORDS
beta-diversity, flowering plants, landscape, organic farming, species turnover

INTRODUCTION

Agricultural intensification has been identified as a major driver of biotic homogenization in temperate agricultural systems (Newbold et al., 2015). In the past 70 years, farmlands have become more intensively used in terms of both landscape simplification and increased in-field farming intensity (Donald et al., 2001; Firbank et al., 2008; Robinson & Sutherland, 2002). The consequences of large-scale structural landscape change on biodiversity have been widely studied: both the loss of permanent seminatural habitats and the decrease in the heterogeneity of the crop mosaic has contributed to the decline of a wide range of organisms (Carvalheiro et al., 2013; Donald et al., 2006; Robinson & Sutherland, 2002; Tyler et al., 2020). Although the intensification of farming practices also takes place at large spatial extents, it is often characterized locally in ecological studies (Herzog et al., 2006; Hole et al., 2005). However, as most of the farmland-inhabiting organisms operate at larger spatial scales compared with individual crop fields, both within and between generations (Smith et al., 2014; Tscharntke et al., 2012), it is crucial to understand how they are affected by large-scale changes in farming intensity.

The partitioning of diversity is a powerful tool to predict biodiversity patterns at large spatial scales from locally sampled species assemblages (Socolar et al., 2016). Such partitioning can help to reveal processes operating at multiple spatial scales on biodiversity, from local to regional ones, given appropriate levels of replications (Anderson et al., 2011; Socolar et al., 2016). In this methodological approach, total diversity across plots (gamma diversity) is the addition of the average plot-scale diversity (alpha) and the between-plot differences in the species assemblages (beta diversity; Veech et al., 2002). When biodiversity is measured at different spatial scales, beta diversity can be further decomposed into within-site, between-site, and regional components (Gabriel et al., 2006). Other partitioning approaches define gamma diversity as the product of alpha and beta diversity, so that gamma diversity can be expressed as a rate of species change along an environmental gradient (Veech et al., 2002). However, in contrast with multiplicative methods, additive approaches allow for partitioning regional diversity into beta diversity components at multiple spatial scales (Veech et al., 2002), and therefore help explore ecological patterns at multiple nested scales (Ekroos et al., 2016).

This partitioning methodology has been used to explore the multiscale response of biodiversity to organic farming, which is known to benefit biodiversity over entire landscapes (Carrié et al., 2018; Lichtenberg et al., 2017). Studies have found a greater contribution of beta diversity compared with alpha diversity to the regional gamma diversity, and higher between-site beta diversity in organic than in conventional wheat fields for plants (Gabriel et al., 2006; Henckel et al., 2015; Roschewitz et al., 2005) and wild bees (Clough et al., 2007; Holzschuh et al., 2007). Therefore, organic farming has the potential to contribute to a greater biodiversity over entire landscapes compared with conventional management, if promoted over large spatial extents, mainly because of an increased between-site turnover of species (Clough et al., 2007; Holzschuh et al., 2007).

However, more careful spatial replication is necessary to demonstrate that organic farming really contributes to large-scale biodiversity increase. First, previous studies on beta diversity and organic farming have all been done in wheat fields, with only one sampled field per farm (but please refer to Ekroos et al., 2010), which complicates a generalization of how organic farming contributes to farmland biodiversity over entire farms, landscapes, or regions. Because organic and conventional farms may include a variety of crops and permanent habitats, organic and conventional farms could reach similar farm-scale biodiversity levels (Schneider et al., 2014). Therefore, the locally more intensive management in conventional wheat fields could be compensated by farm-scale heterogeneity (Batáry et al., 2011; Tscharntke et al., 2012). Alternatively, organic management could simultaneously increase biodiversity in different farmed habitats (Carrié et al., 2018), which could in turn benefit farm-scale biodiversity via increased interhabitat turnover, given that many species prefer distinct habitat types (Fahrig et al., 2011; Sirami et al., 2019).

Second, previous studies have not explored the changes in community composition when shifting from conventional to organic management, that is beta diversity has hitherto only been partitioned separately for each farming system. Therefore, little information is known about the relative contribution of each farming system to overall biodiversity at larger spatial scales. As an example, some species assemblages could be adapted to highly intensively managed fields (herbicide and fertilizer-tolerant species; José-María et al., 2011), and could be replaced by less disturbance-tolerant species when shifting to organic farming (species turnover). In contrast, species sensitive to intensive practices could be systematically lost and not replaced by other species when

switching to conventional management (Batáry et al., 2013; Rundlöf et al., 2010), leading to nestedness of species assemblages (Baselga, 2010; Socolar et al., 2016). Understanding such turnover and nestedness patterns across larger spatial scales could help to prioritize the management of farm conversion over entire regions, such that either mixed organic and conventional landscapes, or pure organic ones, could potentially maximize biodiversity conservation over large spatial extents.

In this study, we explored the multiscale response of beta diversity in species communities of flowering herbaceous plants to organic farming, from the plot to the regional scale. In particular, we decomposed beta diversity into its turnover and nestedness patterns, to find out the spatial scales at which farming practices contribute most to shifts in plant species composition. We addressed the following hypotheses: (i) intrahabitat beta diversity is higher in organic than in conventional farms due to higher species turnover (intrahabitat heterogeneity hypothesis, Figure 1); (ii) interhabitat beta diversity is higher in organic compared with conventional farms due to higher species turnover (hypothesis of habitat specificity of plant species assemblages); (iii) plant species assemblages in conventional farms are a subset of the ones in organic farms (hypothesis of nestedness of plant communities among differing farming systems); (iv) turnover and nestedness patterns of plant communities in response to farming system are linked to species-specific sensitivity to inputs of synthetic chemicals.

METHODS

Site selection and flowering plant survey

We conducted the study during the spring and summer of 2017 in Scania, in southern Sweden. This region is dominated by arable crops (mean cover = 45%) and leys (mean cover = 11%), with relatively large fields (mean size = 12 ha) and low tree cover, especially in the southwest part of the region (Persson et al., 2010).

Based on land use data obtained from the Integrated Administrative and Control System database (IACS), maintained by the Swedish Board of Agriculture, we selected 19 farms (10 organic, nine conventional) along an independent gradient of percentage of seminatural grasslands within a radius of 1 km around the farm center (please refer to Carrié et al., 2018 for a map). We selected cereal farms with grazed seminatural pastures and rotational grasslands, with matching crop compositions (Appendix S1: Figure S1), so that cropping systems did not strongly differ between conventional and organic farms.

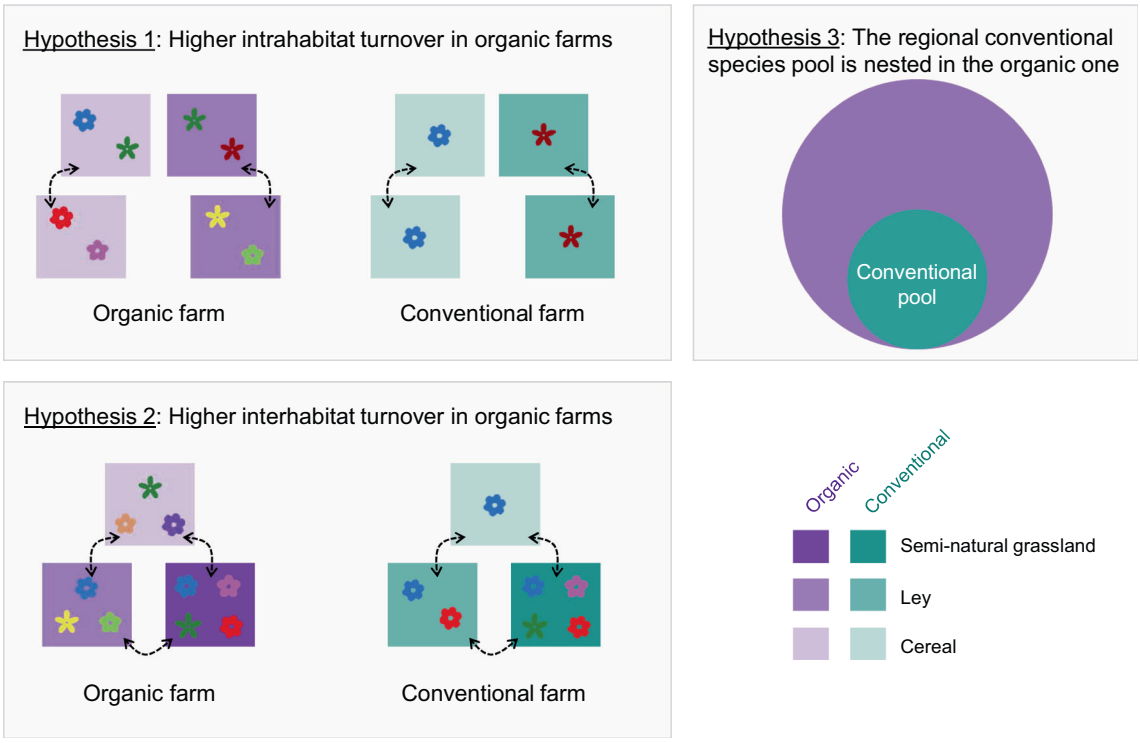

FIGURE 1 Three hypothetical responses of plant beta diversity to organic farming at different spatial scales. In the first hypothesis, organic farms have higher intrahabitat species turnover than conventional ones due to more heterogeneity within habitat types (Gabriel et al., 2006). In the second one, organic farms have a higher interhabitat species turnover than conventional ones due to the specialization of some flower assemblages on certain habitat types. In the last hypothesis, the total plant species pool in conventional farms is a subset of the larger species pool of organic farms

Surveys took place between 18th May and 24th August in 2017. On each farm, we sampled two replicates of three habitat types, consisting of cereal fields, ley fields (rotational, sown, and improved temporary grassland, usually mown but sometimes grazed) and seminatural grasslands (cf. Hodgson et al., 2010). These three habitat types represent the major land use in farms in the region (Persson et al., 2010). Each sampling plot was located on average at 679 m ± 489 from other plots within the same farms. We sampled the three habitat types five times within the growing season. Each survey round was separated by ~2 weeks. In each plot per farm, we surveyed herbaceous dicotyledonous plants in flower (from this point forwards referred to as flowering plants) in one transect of 100 m placed inside the habitat. We placed transects so that the transect walk would intersect flower-rich parts of the plot to maximize sample size in each plot. We recorded flowering plants in a 1 m-sector along the transects (0.5 m on both sides of the observer, 100 m^2 transect) and we identified them to the species level.

Landscape variables

Around each sampling plot, we calculated the proportion of seminatural grasslands using the IACS database, within a buffer of 1-km radius centered on the centroid of the sampling plot. Landscape context in each farm was quantified by averaging the proportion of seminatural grasslands over the six sampling plots. The proportion of seminatural grasslands around the sampling plots ranged from 1% to 19% and was not associated with farming system (Kruskal-Wallis $\chi^2 = 0.33$, $p = 0.57$).

Diversity of flowering plants

We pooled the five survey rounds within habitats and the two replicates per habitat type on each farm to calculate the species richness of flowering plants at the habitat scale (i.e., habitat-level gamma diversity). We calculated the farm-scale flowering plant species richness as the total number of flowering plant species surveyed in the three habitat types.

Multiscale beta diversity indices

Existing methods to estimate species turnover and community nestedness, based on pairwise or multisite dissimilarity metrics (Baselga, 2010), do not allow the determination of which species contribute to observed dissimilarity patterns. We therefore developed a novel method based on species identity to tease apart the turnover component of beta diversity at the intrahabitat, interhabitat, and regional scales to determine which species contribute to community turnover at different spatial scales. Our method can then be used to identify which species characteristics make them more prone to be lost or replaced along environmental gradients. At the plot scale (intrahabitat turnover), we calculated in each farm the lists of species that occurred in only one plot of a given habitat type (i.e., plot-exclusive species). We thereafter calculated the proportion of plot-exclusive species as the ratio of the number of plot-exclusive species on the total number of species found in each of the two plots of the same habitat type. At the habitat scale in each farm (interhabitat turnover), we calculated corresponding lists of species that exclusively occurred in one of the habitat types. The proportion of habitat-exclusive species in each habitat type was calculated as the ratio of the number of habitat-exclusive species on the total number of species found in each farm. At the regional scale (interfarm turnover), to calculate species turnover when shifting farming system, we first listed all the possible pairs of conventional and organic farms, as conventional and organic farms were not spatially paired. For the resulting unique 90 pairs of farms, we calculated species occurrences at the farm level by pooling all the sampling plots of all the habitat types. We then calculated the lists of species that exclusively occurred in each farming system for each pair of conventional–organic farms. We calculated the proportion of farming system-exclusive species in each farm pair as the ratio of the number of farming system-exclusive species on the total number of species found in each unique organic–conventional farm pair. To compute the lists of exclusive species at each spatial scale, we used the function *setdiff()* from the base R software that allows to isolate the elements that differ between two vectors (two lists of species names). At the habitat scale, we used a combination of the functions *intersect()* and *setdiff()* as each habitat type needed to be compared with two others.

To measure the nestedness of flowering plant community in shifting farming system, we used the same farm pairwise comparison as described above for community turnover. In each pair of conventional–organic farms, we calculated the change in species richness when shifting from organic to conventional farms and we calculated the proportion of shared species between the two systems using the R function *intersect()*.

Characterization of flowering plant species

We classified flowering plant species according to different life-history traits or agronomic characteristics that could determine their response to farming intensity. We

based this classification on species-specific sensitivity to nitrogen and herbicide inputs (Appendix S1: Table S1). We assessed species sensitivity to nitrogen inputs by classifying flowering plants into either legumes or forbs excluding legumes, as legume species are particularly sensitive to high levels of nitrogen fertilization (Honsová et al., 2007; José-María et al., 2011). We thereafter assessed species sensitivity to herbicide use based on species-specific sensitivity to MCPA (2-methyl-4-chlorophenoxyacetic acid), which is an active ingredient of the most sold herbicides in Sweden (KemI, 2018), targeting broad-leaved species and responsible for long-term changes in farmland weed flora (Fogelfors, 1979). We obtained data on resistance to MCPA from the field guide of a common commercial formulation containing MCPA as the main active ingredient (Agritox® product label, accessed February 2020). We considered species as sensitive when they showed a level of susceptibility to MCPA ranging from "susceptible" to "moderately resistant."

Statistical analysis

We first tested the effects of habitat type and farming system on habitat-scale flowering plant species richness, while controlling for the effect of the proportion of seminatural grasslands (covariate), using a generalized linear mixed-effects model (GLMM) with a generalized Poisson error distribution to correct for overdispersion in the data (function *glmmTMB()* of the *glmmTMB* R package; Brooks et al., 2017). We included a farm-level random factor to account for repeated surveys in several habitat types per farm. We added an interaction effect between habitat type and farming system. We investigated differences between habitat types using a post-hoc Tukey test. We used a generalized linear model (GLM) to test for the effect of farming system, proportion of seminatural grasslands, and their interaction on the farm-scale species richness of flowering plants. We used a quasi-Poisson error distribution to correct for overdispersion in the data.

We thereafter analyzed the relationship between the proportion of exclusive species (our measure of species turnover, at the within- and interhabitat scales, hypotheses 1 and 2 in Figure 1) and farming system, habitat type and proportion of seminatural grasslands using linear mixed-effects models (LMM), including an interaction between habitat type and the other explanatory variables. We also included a farm-level random factor to account for repeated surveys in several habitat types per farm. We used the function *lmer()* from the *lme4* R package (Bates et al., 2014).

Regarding the regional analysis, we first tested whether the proportion of exclusive species differed between the two farming systems (i.e., between-farm-scale measure of species turnover, hypothesis 3 in Figure 1) within all the possible unique conventional–organic pairs, by using LMM. We included the identifier of the conventional–organic pairs as a random factor (from 1 to 90), nested within an identifier of organic farms (arbitrary choice between organic or conventional identifier to control for the fact that the same farms were included in different unique pairs, and therefore violating the independence assumption) (Zuur et al., 2010). To explore the contribution of the different habitat types to between-farm species turnover, we thereafter ran the exact same test after subsetting the data for each habitat type. The proportion of farming system-exclusive species was then compared for each possible conventional–organic pair and for each habitat type.

Finally, to determine which species groups contributed to community turnover at multiple spatial scales in conventional and organic farms, we used the lists of exclusive species previously computed at several scales and extracted the trait data for each species. We then recalculated the proportion of exclusive species for each categorical trait value (herbicide sensitive/nonsensitive; nitrogen sensitive/nonsensitive). Then, using an LMM (intrahabitat, interhabitat, and regional scales), we tested for an interaction between trait values and the explanatory variables (habitat type and/or farming system) on the proportion on exclusive species, while controlling for the proportion of seminatural grasslands. We created a model for each type of trait (herbicide and nitrogen sensitivity) and scale (intrahabitat, interhabitat scales, and regional scales). Regarding the LMM for the regional scale, we added the identifier of the conventional–organic pairs as a random factor, nested within an identifier of organic farms, to account for nonindependencies of data points. In this test, one organic farm was identified as an outlier when examining the leverage plot, due to an extremely high proportion of unique species ($67 \pm 5\%$) compared with other organic farms ($37 \pm 9\%$) and all the farm pairs containing this particular farm were therefore excluded from the analyses. The two LMM models (herbicide and nitrogen sensitivity) were fitted using the function *lme()* from the *nlme* R package (Pinheiro et al., 2007) that allowed to correct for heterogeneity of variance coming from both the effects of farming system and traits related to chemical sensitivity (*VarIdent()* weight function; Zuur et al., 2010).

To improve model parsimony, nonsignificant interactions were removed from each model. Normality and homoscedasticity of model residuals were verified graphically for LMM. For all LMM, we used the Satterthwaite's method from the *lmerTest* R package (Kuznetsova et al., 2017) to calculate *F*-values, degrees of freedom

(numerator and denominator) and corresponding *p*-values. All analyses were performed using R 3.5.2 (R Development Core Team, 2011).

RESULTS

In this study, we surveyed 112 species of flowering plants over the 114 sampling plots. The four most common ones (found in more than 50% of the plots) were *Trifolium repens* (72% of the plots), *Stellaria holostea* (68%), *Taraxacum* spp. (56%), and *Ranunculus acris* (54%) (Appendix S1: Table S1). Using accumulation curves fitted with six functions that allowed for asymptotes (please refer to Tjørve, 2003), we estimated that with the 114 sampling plots, we surveyed on average 64% (±7.6%), 72% (±6.3%), and 72% (±7%) of the flowering plant species in cereal fields, leys, and seminatural grasslands, respectively (Appendix S1: Figure S2).

Drivers of gamma and beta diversity at the habitat scale

Habitat type and farming system had an interactive effect on habitat-scale species richness of flowering plant species (i.e., habitat-scale gamma diversity; Appendix S1: Table S2). Habitat type had a larger effect on plant species richness in conventional farms, with cereal fields being the most species-poor habitat and seminatural grasslands the richest one, while ley fields had an intermediate plant species richness (Figure 2). Cereal fields in organic farms had a significantly higher species richness than those in conventional ones ($F_{1,18} = 19.8$, $p < 0.001$),

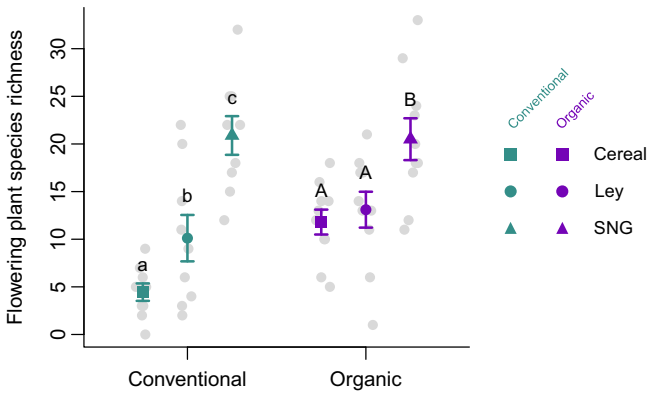

FIGURE 2 Effect of habitat type (cereal, ley and seminatural grasslands) in conventional and organic farms on habitat-scale flowering plant species richness (i.e., habitat-scale gamma diversity). Letters represent the results of the post-hoc Tukey tests, performed in each farming system

approaching the species richness in organic ley fields, which in turn did not differ significantly from conventional ley fields (Figure 2). Species richness in seminatural grasslands did not differ between organic and conventional fields (Figure 2).

At the intrahabitat scale, there was no interaction between farming system and habitat type on the proportion of exclusive species (i.e., intrahabitat species turnover; Table 1). Neither farming system, habitat type nor the surrounding proportion of seminatural habitats influenced the proportion of exclusive species at this scale (Table 1). Within plots, the average proportion of exclusive species was high in all habitat types and in the two farming systems (mean = 60%–75%).

In contrast, a significant interaction between farming system and habitat type on the proportion of habitat-exclusive species showed that the interhabitat community turnover depended on farming system (Table 2). Although seminatural grasslands contained a higher proportion of exclusive species compared with arable fields (cereal and leys) in both farming systems (Figure 3a), habitat-exclusive species were more evenly distributed between habitats in organic farms, with 56% less exclusive species in organic seminatural grasslands and 2.5 times more exclusive species in organic cereals compared with their conventional counterparts (Figure 3b).

TABLE 1 Results of the linear mixed-effects model testing the effects of habitat type, farming system, proportion of surrounding seminatural grasslands (%SNG) on the proportion of plot-exclusive flowering plant species (intrahabitat turnover)

Effect	*df*	*F*	*p*
Habitat type	2, 50	1.86	0.17
Farming system	1, 50	0.03	0.86
% SNG	1, 50	0.45	0.51

Note: The interaction between habitat type and farming system was dropped from the model because it was nonsignificant ($p > 0.05$).

TABLE 2 Results of the linear mixed-effects model testing the effects of habitat type, farming system, proportion of surrounding seminatural grasslands (%SNG) and interaction between habitat type and farming system on the proportion of habitat-exclusive flowering plant species (interhabitat turnover)

Effect	*df*	*F*	*p*
Habitat type	2, 50	**44.93**	**<0.0001**
Farming system	1, 50	0.13	0.82
% SNG	1, 50	0.24	0.62
Habitat × Farming system	2, 50	**8.98**	**0.0005**

Note: Significant coefficients are shown in bold.

Regarding herbicide and nitrogen sensitivity, we found a significant interaction between habitat type and farming system, and habitat type and the trait values (Table 3). The distribution of habitat-exclusive species differed significantly in organic and conventional farms for herbicide-sensitive plants, such that they occurred in significantly lower proportions in arable fields than in seminatural grasslands in conventional farms, but not in organic farms (Figure 4a). Habitat-exclusive, herbicide-sensitive species were instead more evenly distributed among habitats in organic farms, with three times more herbicide-sensitive species specific to cereals in organic cereals compared with conventional ones ($F_{1,16} = 19.06$, $p < 0.001$; Figure 4a). Regarding herbicide-tolerant species, the proportion of habitat-exclusive species had the same distribution between habitats in organic and conventional farms (Figure 4b). The distribution of habitat-exclusive legume species did not differ between organic and conventional farms (Figure 4c), with nearly no legume species exclusive to cereal fields, and equal

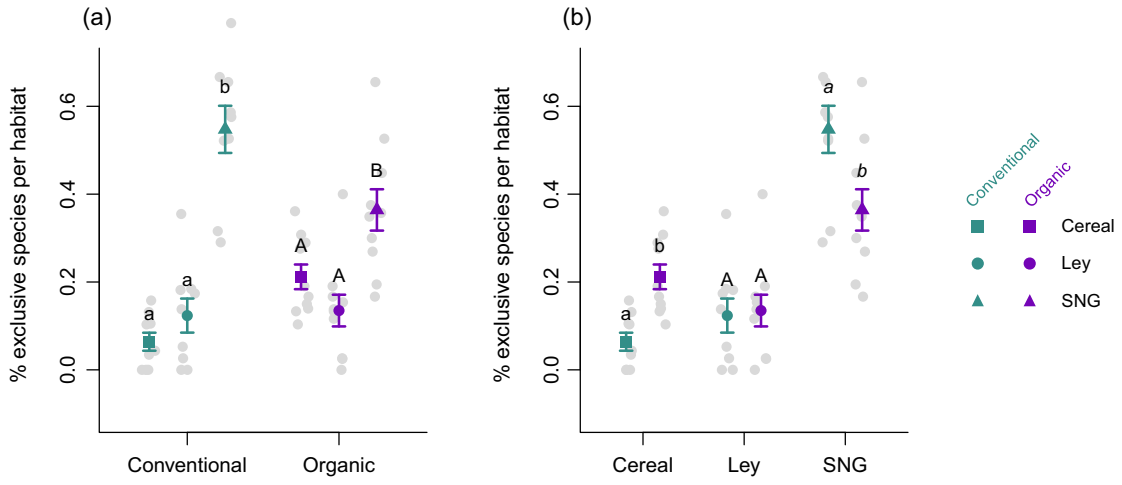

FIGURE 3 Response of the proportion of habitat-exclusive flowering species to habitat type (cereal, ley and seminatural grasslands) in conventional and organic farms (a) and to farming system in each habitat type (b). Means and standard errors are shown. Letters represent the results of the post-hoc Tukey tests, performed in each farming system (a) or habitat type (b) on the same data

TABLE 3 Results of the linear mixed-effects model testing the effects of habitat type, farming system, proportion of surrounding seminatural grasslands (%SNG) and species-specific sensitivity to chemical inputs on the proportion of habitat-exclusive flowering plant species

Response variable	Explanatory variable	*df*	*F*	*p*
Herbicide sensitivity				
	Habitat type	2, 104	**61.88**	**<0.0001**
	Herbicide sensitivity	1, 104	0.64	0.43
	Farming system	1, 104	0.11	0.83
	% SNG	1, 104	0.32	0.57
	Habitat × Herbicide sensitivity	2, 104	**5.72**	**0.004**
	Habitat × Farming system	2, 104	**13.00**	**<0.0001**
Nitrogen sensitivity				
	Habitat type	2, 104	**45.01**	**<0.0001**
	Nitrogen sensitivity	1, 104	1.51	0.22
	Farming system	1, 104	0.62	0.49
	% SNG	1, 104	0.27	0.60
	Habitat × Nitrogen sensitivity	2, 104	**4.32**	**0.016**
	Habitat × Farming system	2, 104	**6.21**	**0.003**

Note: Significant coefficients are shown in bold.

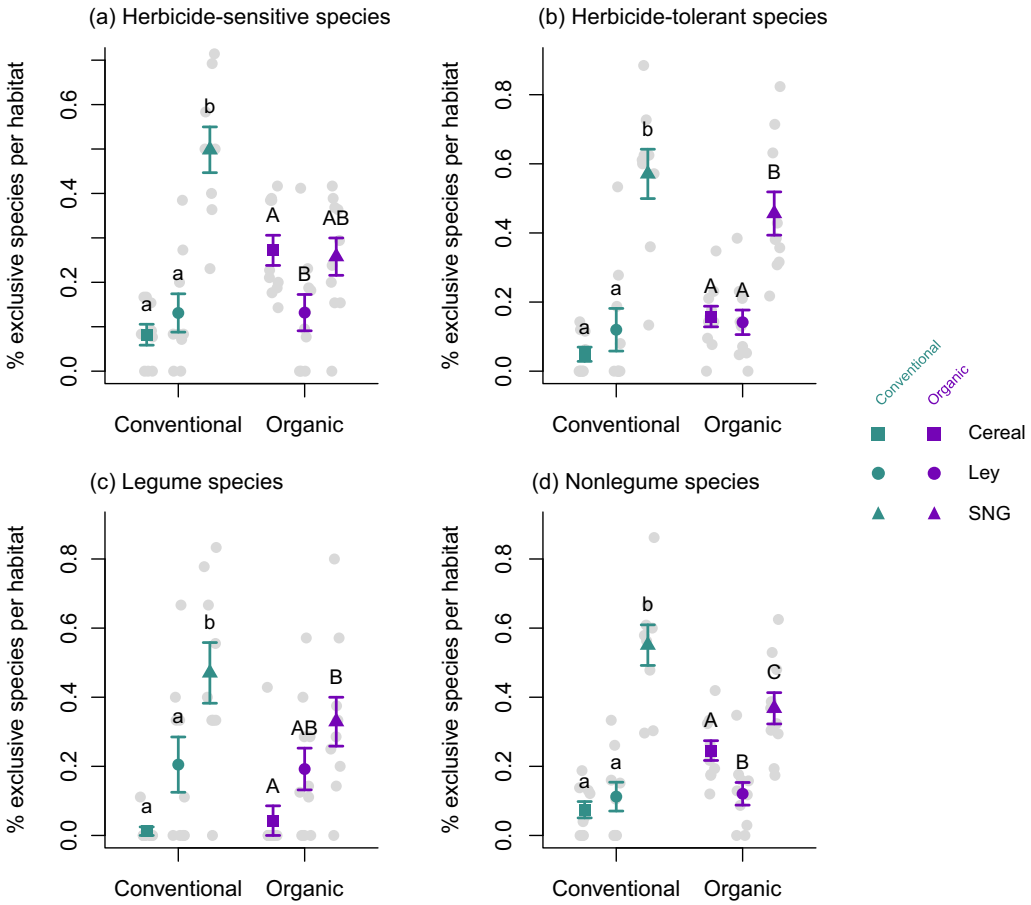

FIGURE 4 Response of the proportion of habitat-exclusive flowering species to habitat type (cereal, ley and seminatural grasslands) in conventional and organic farms, for herbicide-sensitive species (a), herbicide-tolerant species (b), legume species (c, nitrogen sensitive) and nonlegume species (d, nitrogen tolerant). Means and standard errors are shown. Letters represent the results of the post-hoc Tukey tests, performed in each farming system

proportions of legume species exclusive to leys and seminatural grasslands. However, the proportion of habitat-exclusive nonlegume species differed between conventional and organic farm (Figure 4d). They had a more even distribution among habitats in organic farms, with 3.6 times more nonlegume species specific to cereals in organic cereals compared with conventional ones ($F_{1,16} = 19.62$, $p < 0.001$; Figure 4d).

Drivers of gamma and beta diversity at the regional scale

Farming system and the proportion of seminatural grasslands had an interactive effect on the farm-scale number of flowering plant species (i.e., farm-scale gamma diversity; Appendix S1: Table S3). The number of flowering plant species was significantly lower in conventional than in organic farms, but only in landscapes with a low proportion of seminatural grasslands (between 0% and 7%, Figure 5). The species richness of flowering plants in conventional farms increased significantly with increasing proportion of seminatural grasslands ($\beta = 0.036$, SE $= 0.013$, $p = 0.03$), and reached the same level of flower diversity as in organic farms in complex landscapes. Increasing proportion of seminatural grasslands had no effect on species richness of flowering plants in organic farms (Figure 5; $\beta = -0.009$, SE $= 0.015$, $p = 0.59$).

Comparing all the possible pairs of conventional and organic farms revealed that a shift to organic farming significantly increased the number of flowering plant species, with an average gain of 4.3 species (Figure 6a). The number of shared species between the farming systems and unique species in organic farms were similar, whereas organic farms retained significantly more numbers of unique plant species compared with conventional ones ($F_{1,178} = 67.5$, $p < 0.001$, Figure 6b), with on average 40% more exclusive species. There were also less exclusive species in conventional farms than shared ones between the two systems (Figure 6b). Comparing the

organic–conventional pairs for each habitat type showed higher proportions of exclusive species in organic cereal and ley fields (4 and 1.5 times higher than conventional cereal and ley fields, respectively), but similar proportions of exclusive species in seminatural grasslands between the two farming systems (Appendix S1: Figure S3).

Finally, we found a significant interaction between farming system and herbicide sensitivity on the proportion of farm-exclusive species, but not between farming system and nitrogen sensitivity (Appendix S1: Table S4, Figure 7). The difference in the proportion of farm-exclusive species between organic and conventional farms was greater for herbicide sensitive than for non-sensitive species (Figure 7a), while there was no difference between farming systems for nitrogen sensitive or nonsensitive species (Figure 7b). Species exclusive to conventional farms had a 94% higher chance of being herbicide-tolerant than herbicide sensitive, while species exclusive to organic farms had similar probabilities of being sensitive or tolerant to herbicides (Figure 7a).

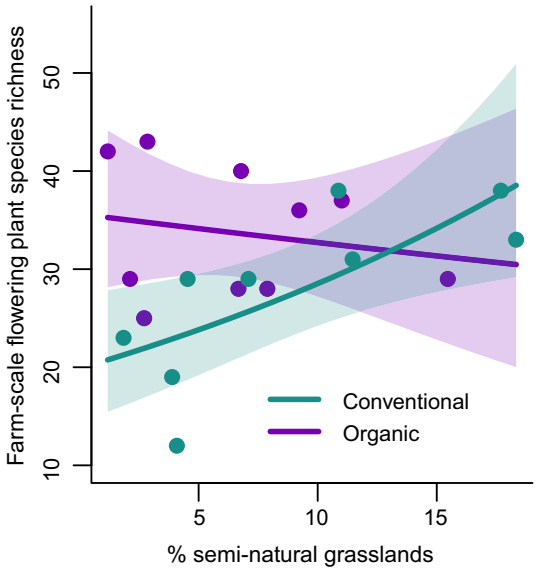

FIGURE 5 Effect of the proportion of seminatural grasslands on farm-scale species richness of flowering plants (i.e., farm-scale gamma diversity), in organic and conventional farms. Shaded area indicates 95% confidence interval

DISCUSSION

Using spatially replicated surveys of flowering plant communities in conventional and organic farms, we demonstrate contrasting responses in plant species turnover to farming intensity depending on the spatial scale. Whereas the intrahabitat species turnover (plot scale) did not differ between organic and conventional farms, organic farms had a significantly higher interhabitat turnover of flowering plants compared with conventional ones. We also found that this in-farm plant species turnover was partly determined by species sensitivity to chemical inputs (both herbicides and mineral fertilizers). Cereal fields differed most strongly between organic and conventional farms in that regard, as they contributed with significantly more cereal-exclusive species in organic than in conventional farms. Furthermore, when comparing species pools between conventional and organic farms, we found that the number of species

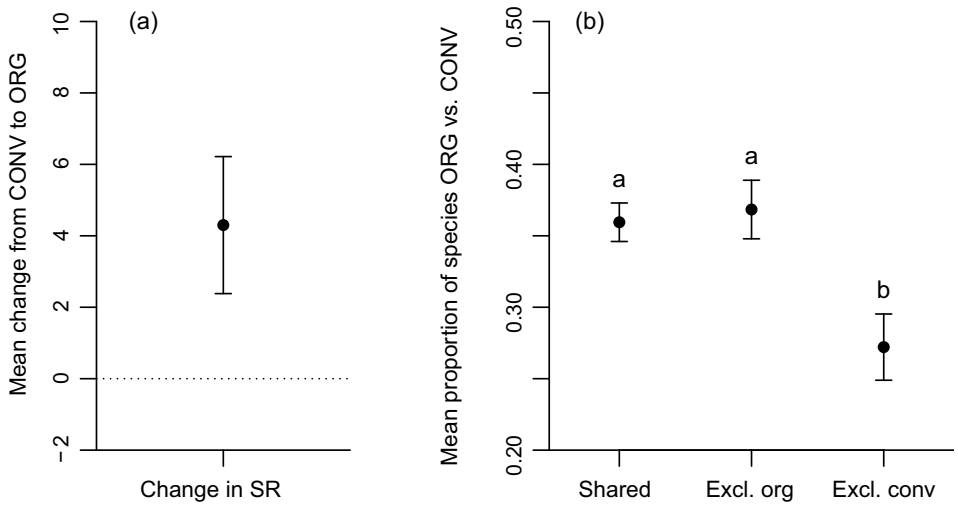

FIGURE 6 Mean change in the species richness of flowering plants when shifting from conventional to organic farms (a), and mean proportions of shared and exclusive species between the two farming systems (b). Letters represent the results of the post-hoc Tukey tests. Means and 95% confidence intervals are shown among all the possible 80 possible pairs of conventional–organic farms (there was originally 90 pairs but one outlier organic farm was excluded due to a particularly high number of unique species compared with all other farms)

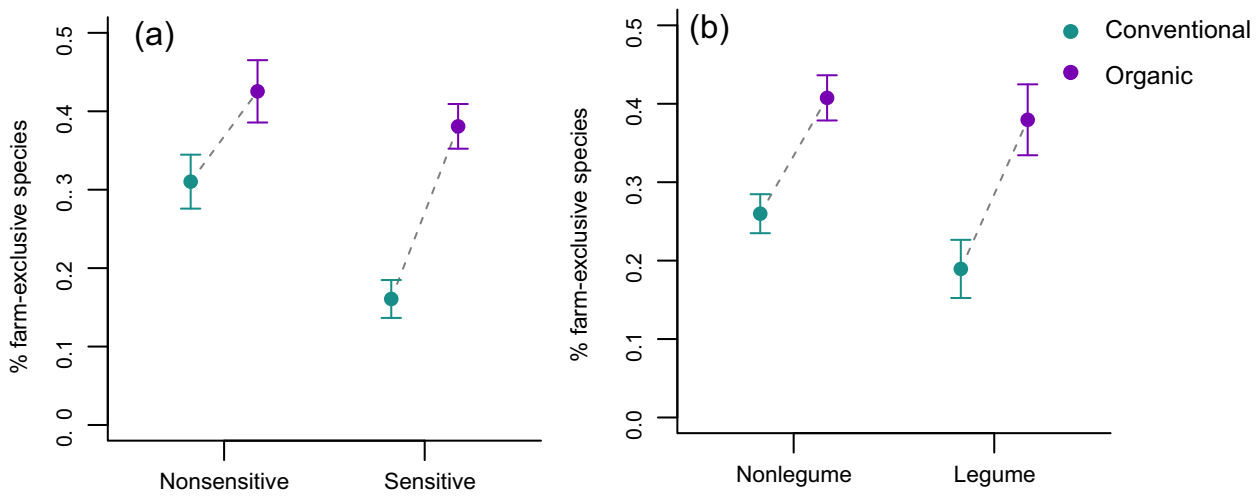

FIGURE 7 Model prediction showing a significant interaction effect between herbicide sensitivity and farming system (a), and a nonsignificant interaction between nitrogen sensitivity and farming system (legume species: nitrogen sensitive, nonlegume species: Nitrogen tolerant) (b) on the proportion of farming system-exclusive flowering species (please refer to Appendix S1: Table S4 for test statistics). Means and 95% confidence intervals are shown

exclusively found in organic farms exceeded by far those exclusively found in conventional ones. Whereas earlier studies have shown similar results regarding one crop type (Clough et al., 2007; Hyvönen & Salonen, 2002), we show for the first time that organic farms significantly increase large-scale plant diversity by supporting higher multihabitat species pools compared with conventional farms. Furthermore, previous work explored the multiscale benefit of organic farming on biodiversity (Azaele et al., 2015; Clough et al., 2007; Gabriel et al., 2006) by assessing multiscale shifts in beta diversity within each farming system separately. Our results show that assessing spatial turnover of communities independently in each systems underestimates the contribution of shared and system-specific species on large-scale beta diversity, which in turn has important implications for farmland biodiversity conservation.

Effects of organic farming on intra and interhabitat beta diversity

Contrary to our expectations, the intrahabitat turnover was not higher in organic than in conventional farms, irrespective of habitat type. Organic arable fields had a richer flora, especially in cereal fields, but had similar spatial rates of species turnover as conventional fields. This absence of difference in intrahabitat turnover could be explained by a relatively low farming intensity in conventional fields compared with other studies in central Europe, leading to reduced richness in flower communities but with the same rate of spatial turnover as organic fields (Ekroos et al., 2010). Alternatively, conventional farms could maintain comparable intrahabitat species turnover to organic ones due to interfield variation in the use of chemical inputs. Farmers can adopt different farming practices for different fields of the same crop, because of differences in pedoclimatic conditions and in-farm location for example (Dury et al., 2012; Vasseur et al., 2013). These in-farm variations in practices could explain the high interfield variation in plant community composition in conventional farms (68%–75% of plot-specific species in conventional fields).

In contrast, and according to our expectations, we found that organic farms had higher interhabitat turnover of species in flowering plant communities than conventional ones. This effect was driven by organic cereal fields, as they contained 2.5 more exclusive species than conventional fields and leys had similar proportions of exclusive species in both farming systems. The lower proportion of exclusive species we found in seminatural grasslands in organic farms compared with conventional ones was most probably linked to the higher proportion of exclusive species in organic cereals. Indeed, organic and conventional seminatural grasslands had the same number of flower plant species on average (Figure 2) and similar low proportions of organic or conventional-exclusive species (Appendix S1: Figure S3c), and therefore similar communities. Then, for similar absolute numbers of grassland-exclusive species, a higher share of cereal-exclusive species made the distribution of exclusive species more even between cereals and seminatural grasslands in organic farms, while most of exclusive species were found in seminatural grasslands in conventional farms.

The trait analysis revealed that flowering species found exclusively in organic cereal fields were mostly herbicide-sensitive, nonlegume species. Low herbicide application is usually associated with richer in-field weed communities (Hyvönen et al., 2003; Petit et al., 2015), and can lead to higher abundance of flower resources (Rundlöf et al., 2010). In addition to confirming the beneficial effect of organic farming on local plant diversity (Clough et al., 2007; Holzschuh et al., 2007; Roschewitz et al., 2005), our results showed that organic practices in cereal fields favored the occurrence of flowering plant species that are most likely to be not found in other farmed habitats, leading to higher farm-scale flowering plant diversity. The use of herbicides in conventional farms seems to act on weed communities through a filtering effect (Fried et al., 2012) in contrast with organically managed fields, which can host richer arable-adapted flower assemblages. Nitrogen sensitivity interacted with farming system to explain interhabitat turnover patterns, but these patterns were mainly driven by nonlegume species, classified as non-nitrogen sensitive in our study. Nearly no legume species were recorded in arable fields, conventional or organic, suggesting that farming interventions in annual arable fields were detrimental to them irrespective of the farming system. High nitrogen fertilization can indeed negatively affect legume species through direct effects (inhibition of the rhizobia-legume symbiosis; Streeter & Wong, 1988; Streeter, 1985) or through increased competition due to nonlegume plant overgrowth (Honsová et al., 2007; Socher et al., 2013). Our results are consistent with earlier studies, using the Ellenberg N index as a measure of nitrogen sensitivity, suggesting that herbicide sensitivity rather than nitrogen sensitivity drives shifts in plant communities between organic and organic farms (Hyvönen et al., 2003; Hyvönen & Salonen, 2002).

Effects of organic farming on farm-scale gamma and interfarm beta diversity

We found that farming intensity greatly structures flowering plant communities at the farm scale, and that this influence is stronger for simple landscapes. While this relationship has previously been established at the field scale for plant communities (Batáry et al., 2011; Holzschuh et al., 2007; Roschewitz et al., 2005), our results showed that it may also hold across larger spatial scales. This is however contrasting with a previous study that found the local beneficial effect of organic fields did not propagate at the landscape scale, due to compensation by plant diversity hosted by nonfarmed habitats in conventional farms (Schneider et al., 2014). In our study, we sampled mainly grazed seminatural habitats that are typically the most species-rich farmland habitats (Hodgson et al., 2010; Lindborg et al., 2014) and probably richer than the sampled set asides in Schneider et al. (2014), most of which were temporary grassy habitats (grass and herbaceous strip). Most likely, we were able to detect a significant farm-scale organic farming effect due to the systematic selection of similar habitat types along the landscape gradient, and to the matching of farming intensity with landscape complexity, that allowed us to explore interactive effects.

Our last hypothesis, stating that species assemblages in conventional farms are a subset of those in organic farms, was validated. We found non-null proportions of shared and farming system-exclusive species, with higher proportions of shared and organic-exclusive species compared with proportions of conventional-exclusive species. This result strongly supports the hypothesis that the species pool in conventional farms represents a nested subset of the plant species pool organic farms, as the latter had the highest proportions of exclusive plant species. Although we also found species turnover between organic and conventional farms due to plant species being exclusive to conventional management, the higher proportions of shared and organic-exclusive species suggest that nestedness was the dominant process driving large-scale beta-diversity patterns. Nestedness implies that conservation efforts should be allocated to high-diversity areas, while high species turnover implies that conservation should focus on multiple areas and identify unique sites (Socolar et al., 2016). Here we found both processes to be important, suggesting that a mix of both farming systems in agricultural landscapes would be an optimal situation for plant communities, but with a higher proportion of organic farms due to community nestedness. We additionally found these large-scale processes to be driven by sensitivity to herbicide and not to nitrogen, similarly to the patterns we detected within habitat types. However, when breaking down these large-scale processes to specific habitats, we found that all herbicide-sensitive species exclusive to organic management were found in cereal fields, while the nitrogen-sensitive ones were found in ley fields (Appendix S1: Figure S4). We therefore believe that nitrogen sensitivity was not an important driver of interfarm beta diversity, compared with herbicide sensitivity. Indeed, the contrast between organic and conventional farms was stronger for cereals (herbicide-related contrast) than for leys (nitrogen-related contrast). Moreover, as leys had the same capacity to retain unique species assemblages compared with other habitats in conventional or organic farms (Figure 3b), contrary to organic cereals or seminatural grasslands (Figure 3), it would be unlikely to detect a

contribution of leys to large-scale biodiversity patterns. Such a contrast between organic and conventional leys could nevertheless make a difference in ley-dominated systems, which needs to be addressed by further studies. The higher probability of organic leys to contain nitrogen-sensitive species compared with conventional ones could be explained by fertilization regimes in conventional farms (detrimental effect on legumes; Socher et al., 2013; Streeter, 1985), or by the higher likelihood of organic farmers to so sow legume-rich leys (such as clover leys) to maintain soil fertility (Röös et al., 2018; Watson et al., 2002).

Whereas earlier studies have shown that organic farming affects community composition in several taxonomic groups (plants: Batáry et al., 2013; Hyvönen et al., 2003; Hyvönen & Salonen, 2002; ground beetles: Clark, 1999; pollinators: Andersson et al., 2013), this study is the first, to our knowledge, to quantify farm-scale beta-diversity components while shifting between the two farming systems. However, we focused on plant communities, which typically display higher rates of spatial turnover due to dispersal limitation compared with more mobile organisms groups, such as arthropods or birds (Clough et al., 2007; Hendrickx et al., 2009; Steinitz et al., 2006). Our results might therefore not apply to more mobile organisms, although some previous work showed that flower-dependent groups such as wild bees could display similar rates of spatial species turnover as plant communities (Clough et al., 2007).

We conclude that conversion to organic farming has the potential to increase the diversity of flowering plants at multiple spatial scales, including large scales that ultimately matter for biodiversity conservation. The diversity of crop types has been identified as a major driver of farmland biodiversity (Sirami et al., 2019), and here we showed that a reduced farming intensity has the potential to enhance this crop type effect. In particular, we show that organic practices have the potential to increase farm-scale biodiversity by increased spatial turnover among habitats, and benefit biodiversity conservation at larger scales via nestedness. Given that farms are not operating under large-scale monoculture regimes (Batáry et al., 2017; Tscharntke et al., 2021), the management implications of our study are therefore two-fold. First, organic farming may, because of increased interhabitat plant species turnover, benefit functionally important species relying on complementary or supplementary resources, such as flower-visiting insects. Second, management plans aiming at the conservation of plant communities in agricultural landscapes more broadly should foster possibilities for farmers to transition toward low-input farming systems, especially in simple landscapes, where such transitions would benefit plant diversity most, from the local to the landscape scale. In our study, we used a carefully designed study to control for confounding factors, but a space-for-time substitution approach cannot control for all potential biases. In particular, future studies should focus on the consequences of the transition to organic farming as such, to understand how time-lags and regional availability of colonizing species affect patterns of beta diversity after conversion to organic farming.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Carrié, 2022) are available in Dryad at https://doi.org/10.5061/dryad.n8pk0p2x1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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