



Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies



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ABSTRACT

The spatiotemporal stability of wild organisms, such as flower-visiting insects, is critical to guarantee high levels of biodiversity in agroecosystems. Whereas the proportion of semi-natural habitats in the landscapes has been shown to stabilize the species richness of flower visitors, the effect of farming intensity has not yet been studied. In this study, we compared the temporal and spatial stability (continuity of species richness in space and time) of two groups of flower-visiting insects (butterflies and bumblebees) between nine conventional and ten organic farms, distributed along a gradient of semi-natural grassland proportion. We surveyed bumblebees, butterflies and local flower cover during the growing season, covering multiple years and several habitat types per farm (cereal fields, temporary grasslands and semi-natural grasslands). At the field scale we found that within-year stability of bumblebee species richness was higher in organic than in conventional temporary grasslands (leys), because of a higher continuity of in-field flower resources. Further analyses showed that late-season flower resources in organic ley fields were critical to maintain a high within-year stability of bumblebee species richness by reducing resource bottlenecks during that period, when most bumblebee colonies produce new queens. The among-year stability of bumblebee species richness was higher in organic than in conventional cereal fields, whereas the within and among-year stability of butterfly species richness was not influenced by farming system. On the farm scale, we found that the spatial stability of butterfly and bumblebee species richness was higher in organic than in conventional farms, but this was not explained by a greater spatial continuity of flower resources. Our study shows that organic farming reduces the spatiotemporal fluctuations in bumblebee and butterfly species richness. In addition, increasing floral resources as such benefits bumblebees and butterflies irrespective of farming system. Organic farming and increasing availability in floral resources therefore contribute to maintaining the within and between-year stability of bumblebees and butterflies in agricultural landscapes.

1. Introduction

Biodiversity in agroecosystems has declined significantly during the last four decades, mainly caused by the intensification of agricultural practices and loss of semi-natural habitats (Biesmeijer et al., 2006; Bommarco et al., 2011; Robinson and Sutherland, 2002; Tilman, 1999). The loss of undisturbed, non-cropped habitats in agricultural landscapes has reduced the availability of shelters, nesting sites and food resources for farmland species (Hendrickx et al., 2007; Tschamtkke et al., 2012). The in-field intensification of agriculture can disturb the establishment and persistence of diverse communities by creating large resource-poor areas, disrupting crucial ecological processes such as dispersion or landscape complementation (Henckel et al., 2015; Tschamtkke et al., 2012; Vasseur et al., 2013).

These two drivers of biodiversity loss are particularly important for flower-visiting insects such as butterflies and bumblebees, as these two taxa depend to a large extent on flower resources provided by multiple habitats in mosaic landscapes (Ekroos et al., 2016; Gathmann and Tschamtkke, 2002; Öckinger and Smith, 2007). In particular, they rely on semi-natural habitats such as permanent grasslands (Hopfenmüller et al., 2014; Öckinger and Smith, 2007; Svensson et al., 2000). Bumblebees and butterflies are interesting to consider because they can utilize spatially scattered resources in agricultural landscapes, altered by landscape structure and agricultural management (Halder et al., 2017; Holzschuh et al., 2016; Jönsson et al., 2015) and they are relatively easy to monitor. However, little is known about how farming intensity and landscape structure independently and jointly affect resource availability and spatiotemporal stability in species richness of

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flower-visiting insects.

Agricultural landscapes are highly dynamic, because of rapid changes in resource availability (crop rotation, seasonal peak of mass flowering crops or weeds) and frequent disturbances due to farm management (pesticide spraying, harvest) (Schellhorn et al., 2015; Vasseur et al., 2013). Therefore, local or periodical shortage of resources can prevent species from completing their life cycle (Schellhorn et al., 2015), endangering the maintenance of diverse flower visitor communities. Hence, the spatiotemporal discontinuity of floral resources is expected to lead to declines or local extinctions of bumblebee and butterfly species and consequently to high temporal fluctuations in their diversity (Garibaldi et al., 2011). As the spatiotemporal stability of insect communities (continuity in their community structure in space and time; Lehman and Tilman, 2000) can be an essential component of the stability of ecosystem functioning (Garibaldi et al., 2011; Klein, 2009; Kremen et al., 2004), there is a need to understand the factors affecting their landscape-scale and long-term persistence.

Increasing the proportion of semi-natural habitats in agricultural landscapes has been shown to enhance spatiotemporal stability of flower visitor species richness at the field scale and along the growing season (Garibaldi et al., 2011). However, it still unknown whether the stability of bumblebee and butterfly species richness, measured at the landscape-scale and among several years, also benefit from a reduction in farming intensity. In general, organic farming benefits biodiversity due to the exclusion of pesticides and inorganic fertilizers (Batáry et al., 2011; Lichtenberg et al., 2017; Tuck et al., 2014) and to lower livestock density (Power et al., 2012). As species-rich communities are predicted to display higher stability over time and space (Loreau et al., 2002; Tilman et al., 2006; Weigelt et al., 2008), organic farming can in turn be expected to increase spatiotemporal stability of flower-visiting insect communities in agricultural landscapes. In particular, organic farming has the potential to reduce resource deprivation that flower-visiting insects face in agricultural landscapes by providing more in-field flowering resources (Holzschuh et al., 2008, 2010). As bumblebees commonly experience a lack of floral resources early and late in the growing season (Rundlöf et al., 2014; Westphal et al., 2009), an outstanding question is to determine whether organic farming could contribute to maintaining the persistence of flower visitors by reducing such resource bottlenecks. Hence, by reducing in-field management intensity, organic farming could enhance the long-term persistence of flower visitor communities in agricultural landscapes.

The aim of this study was to explore the influence of farming intensity (organic vs. conventional farming) on the spatial (landscape-scale) and temporal (among-year and within-year) stability of bumblebee and butterfly species richness, while controlling for effects caused by landscape context. In particular, we explored if increased spatiotemporal stability of bumblebee and butterfly species richness could be explained by increased spatiotemporal continuity of flower resources. We tested the following hypotheses: (1) organic farms increase the spatiotemporal stability of flower resources, bumblebee and butterfly species richness compared with conventional farms; (2) the higher spatiotemporal stability in bumblebee and butterfly species richness in organic farms can be explained by higher spatiotemporal continuity of flower resources; and (3) early and late-season flower resources are more abundant in organic farms, which contributes to maintaining high flower-visitor species richness during those critical periods.

2. Materials and methods

2.1. Site selection and biodiversity sampling

The study was conducted during 2015–2017 in Scania, in southern Sweden (Fig. 1). This region is dominated by agricultural landscapes, but with large variations in terms of structural complexity (semi-natural grasslands, forests) and farming intensity within a relatively small

region (Persson et al., 2010). The majority of the land is covered by arable crops (mean = 45%) and by grasslands (mean = 20%) with relatively large fields (mean = 12 ha), with low tree cover (forests, hedgerows), 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, Blockdatabasen), 19 farms (10 organic, 9 conventional) were selected along a gradient of percentage of semi-natural grasslands within a radius of 1 km around the farm center (Fig. 1).

Surveys were conducted during 2015–2017 for butterflies and flower resources, and during 2016–2017 for bumblebees. Sampling periods were between 20th May to 7th August in 2015, 13th May to 14th August in 2016 and 18th May to 24th August in 2017. On each farm, three habitat types were sampled, consisting of a cereal field, a ley field (rotational, sown and improved temporary grassland, usually mown but sometimes grazed) and a semi-natural grassland (c.f. Hodgson et al., 2010). These three habitat types represent the major land use in farms as well as a major land-use intensity gradient in the region (Persson et al., 2010). The three habitat types were sampled five times within each growing season. Due to crop rotation, some cereal and ley fields changed location among years within the sampled farms. Each survey round was separated by approximately two weeks. In each site (i.e. habitat type) per farm, flower and insect surveys were conducted on two transects of 100 m (one along the border of the habitat and one within the habitat). The transects were placed as far away from neighboring mass-flowering crops as possible, since they might influence local abundance of flower visitors (Holzschuh et al., 2016). Transects were placed in the most flower-rich parts of the site to maximize sample size in each site. Each transect was surveyed only under sufficiently good weather conditions during warm ($\geq +15^\circ\text{C}$) and sunny days, when wind speed did not exceed 4 on the Beaufort Scale. Transects were surveyed by slowly walking along them during 10 min. Bumblebee and butterfly individuals were recorded in a 2-m-sector along the transect (1 m on both sides of the observer, 200 m² transect) and were identified to species levels on the field. We treated *Bombus lucorum* (s.l.) and *Bombus terrestris* as one species because they are often impossible to identify in the field. Flowering plants were surveyed along the same transects, but within a 1 m-sector (0.5 m on both sides of the observer, 100 m² transect) and were identified to species level. Total flower cover was recorded using a cover scale accounting for the percentage cover of flower corollas per ground surface area (1: < 2%; 2: < 6%; 3: < 10%; 4: < 20%; 5: < 25%; 6: > 25%). In the border and inside of each sites, an additional free transect walk was conducted for an extra 5 min to record extra individuals of bumblebees and butterflies. For this study we only considered the transects situated within the three habitat types.

2.2. Landscape variables

Around each sampling site, the proportion of semi-natural grasslands was calculated using the IACS database, within a buffer of 1 km radius centered on the centroid of the sampling site. To analyze the effect of landscape context on the spatial stability of floral resources and flower-visitor species richness, landscape context in each farm was quantified by averaging the proportion of semi-natural grasslands over the three sites. Similarly, to analyze the effect of landscape context on the long-term temporal stability of flower and flower-visitor species richness, landscape context around each habitat type (cereal, ley and semi-natural grassland) was quantified by averaging the proportion of semi-natural grasslands over the three years. The proportion of semi-natural grasslands around the sampling sites ranged from 1% to 18% and was not associated with farming system (Kruskal-Wallis $\chi = 0.69$, $P = 0.40$).

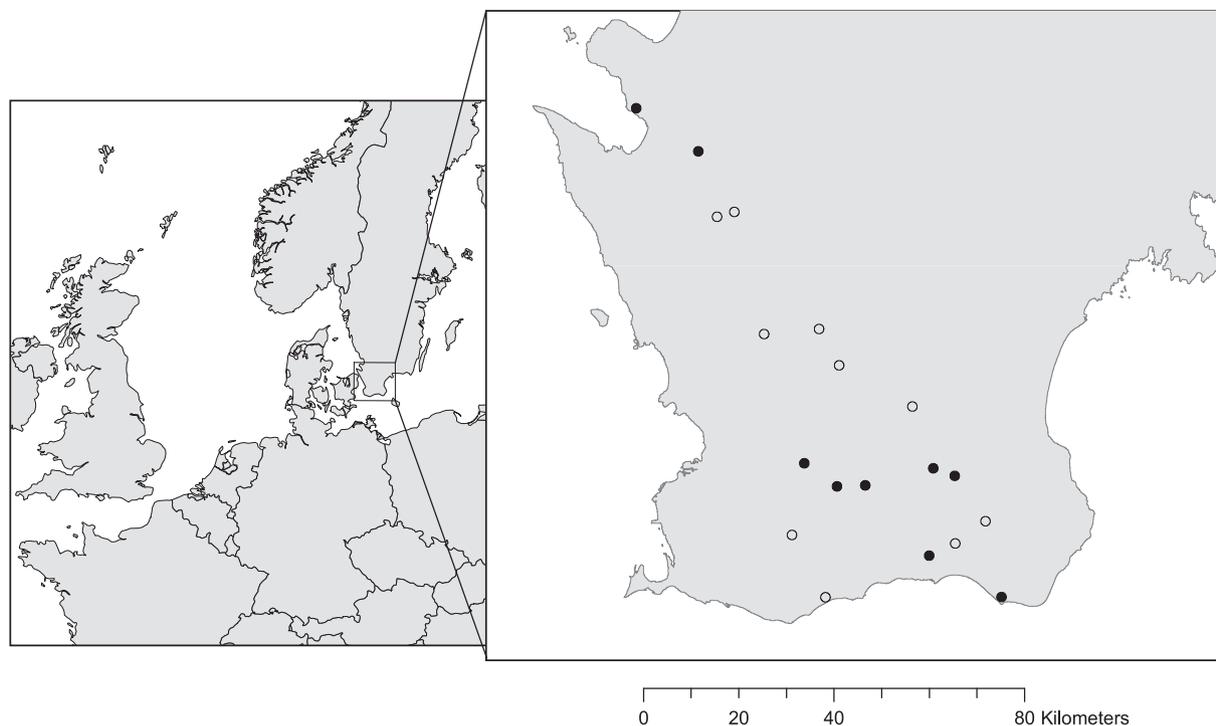


Fig. 1. Location of the study region in the southernmost part of Sweden and the selected farms. White circles: organic farms, black circles: conventional farms.

2.3. Statistical analysis

The coefficient of variation of butterfly and bumblebee species richness or flower cover was used as an inverse measure of their spatiotemporal stability (Ebeling et al., 2008; Garibaldi et al., 2011; Klein, 2009), with $CV = \text{standard deviation}/\text{mean}$. Therefore, a high temporal or spatial CV of these variables corresponded to a low temporal or spatial stability. We chose to use CV instead of CV^{-1} to avoid excluding sites that displayed a standard deviation of zero (Garibaldi et al., 2011). Bumblebee and butterfly species richness and flower cover were calculated for each habitat type, year and survey round and were used to calculate the following spatiotemporal stability indices: (i) the *within-year* CV per habitat type, defined as the ratio of their SD and mean over the five survey rounds, per each farm and year; (ii) the *among-year* CV per habitat type, defined as the ratio of their SD and mean over the three sampled years, per each farm; and (iii) *spatial* CV per landscape, defined as the ratio of their SD and mean over the three sampling sites in the landscapes, per each farm and year.

Mixed-effect linear models (LMER) were used to test the direct association of *within-year* and *spatial* CV of butterfly species richness and flower cover with farming system (organic versus conventional) and the proportion of semi-natural grasslands. Sampling year was included as a random factor to account for the repeated surveys in the farms over the three years. Because bumblebees were only surveyed during two years, we used linear models (LM) to test the direct association of *within-year* and *spatial* CV of bumblebees with farming system and landscape context, adding year as a fixed effect. We used linear models (LM) to test the direct association of *among-year* CV of flower cover, butterfly and bumblebee species richness with farming system and landscape context.

To test whether the relationship between spatiotemporal CV of flower-visitor species richness and farming system was mediated through variations in spatiotemporal CV of flower cover, we used Structural Equation Modelling (SEM), using the R package *piecewiseSEM* (Lefcheck, 2016). SEM allows testing for indirect effect of variables in the form of causal pathway network, including variables that can be a response and explanatory variable at the same time. For each flower-visitor group, we built a hypothetical model testing the combined effect

of farming system and landscape context, controlling for year-to-year variations:

$$CV_{\text{flower-visitor richness}} \sim CV_{\text{flower cover}} + \text{Farm_type} + \% \text{semi} \\ - \text{natural grassland} + \text{Year}$$

$$CV_{\text{flower cover}} \sim \text{Farm_type} + \% \text{semi} - \text{natural grassland} + \text{Year}$$

Linear models (LM) were used to estimate those indirect relationships. In the models on the *among-year* CV as a response variable, the year fixed factor was removed from the models. SEM were used only in cases when parallel trends in the relationship between farming system and stability of flower cover, and between farming system and stability of flower-visitor species richness were detected.

Generalized linear mixed-effect models (GLMER) assuming a Poisson error distribution (log-link function) were used to test the relationship between farming system and flower cover, and between farming system and flower-visitor species richness depending on the sampling visit. This analysis was conducted only on flower-visitor groups (bumblebees and/or butterflies) for which within-year CV was affected by farming system. We fitted a model for each sampling visit. We included a year random factor to account for repeated surveys in the farms over the two or three years. An observation level effect, i.e. a landscape random factor, nested into the year factor, was added to the model to account for a possible overdispersion of the data (Lee and Nelder, 2000). In each sampling visit in which butterfly or bumblebee species richness varied significantly between farming systems, we fitted a SEM to find out if the difference in butterfly or bumblebee species richness could be attributed to differences in flower cover. We used LM with a year as a fixed factor and nested the equations as following:

$$\text{Flower} - \text{visitor_richness} \sim \text{Flower_cover} + \text{Farm_type} + \% \text{semi} \\ - \text{natural grassland} + \text{Year}$$

$$\text{Flower_cover} \sim \text{Farm_type} + \% \text{semi} - \text{natural grassland} + \text{Year}$$

In each model, continuous explanatory variables were standardized (mean = 0, SD = 1). Normality and homoscedasticity of model residuals were verified graphically for LM. Spatial autocorrelation of

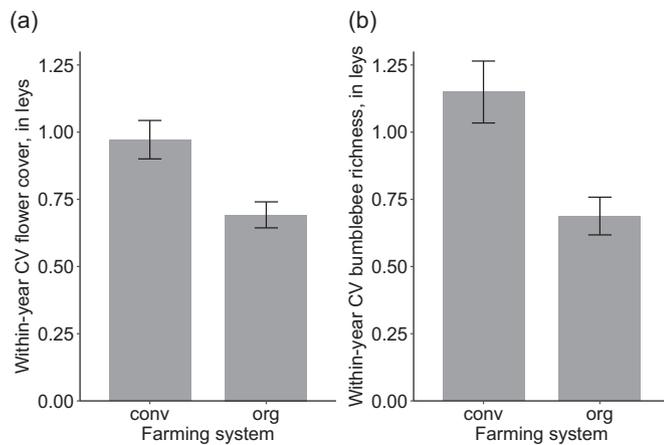


Fig. 2. Parallel trends in the effect of farming system on the $CV_{within-year}$ of (a) flower cover and (b) bumblebee species richness in ley fields. Means and standard errors are shown. Note that a lower CV indicates a higher stability.

model residuals was checked, and site coordinates were added to the two models displaying autocorrelated residuals (Table S1), without changing the outputs of the models (Table S2). The R package *lme4* was used to fit the LMER and GLMER (Bates et al., 2014). All analyses were performed using R 3.4.0 (R Development Core Team, 2011).

3. Results

In this study, we observed 13,879 butterfly individuals from 34 species and 5415 bumblebee individuals from 21 species (Tables S3 & S4). The spatiotemporal CV of flower cover, butterfly and bumblebee species richness was either negatively correlated or not correlated to the overall flower cover, butterfly and bumblebee species richness, respectively (Figs. S1–S3).

3.1. Direct effect of farming system on temporal stability

In leys, organic farms had significantly lower within-year CV, i.e. a higher within-year stability, of both flower cover and bumblebee species richness (Fig. 2, Table 1). While organic cereal fields had higher within-year stability in flower cover, we did not find similar trends in within-year stability of butterfly or bumblebee species richness in cereal fields. In semi-natural grasslands, neither the within-year stability of flower resources nor of flower-visitor species richness responded to farming system (Table 1).

The among-year CV of flower cover and bumblebee species richness were significantly lower in organic cereal fields than in conventional ones (Table 1, Fig. 3), whereas for the among-year CV of butterfly species richness this difference was marginally non-significant. In ley fields and semi-natural grasslands, farming system did not have any effect on the among-year stability of either flower-visitor species richness or flower resources (Table 2). The surrounding proportion of semi-natural grasslands did not affect the long-term stability of either flower-visitor species richness or flower cover.

3.2. Direct effect of farming system on spatial stability

The landscape-scale spatial CV of flower cover, butterfly and bumblebee species richness were significantly lower in organic than in conventional farms. In contrast, the surrounding proportion of semi-natural grasslands did not affect the spatial CV of any taxa investigated (Table 3).

Table 1

Results of the linear mixed (flower cover and butterfly) and non-mixed models (bumblebee) testing the effect of farming system (org/conv) on $CV_{within-year}$ controlling for the effect of the proportion of semi-natural grasslands, for each habitat type. Significant coefficients are shown in bold.

Response variable	Habitat type	Variable	Estimate	SE	P value	
$CV_{within-year}$ flower cover	Cereal	Farming system (org)	-0.48	0.10	0.000	
		% grassland	0.11	0.05	0.038	
	Ley	Farming system (org)	-0.28	0.08	0.001	
		% grassland	0.07	0.04	0.084	
	Grassland	Farming system (org)	-0.03	0.05	0.614	
		% grassland	0.01	0.03	0.715	
$CV_{within-year}$ butterfly species richness	Cereal	Farming system (org)	-0.27	0.14	0.057	
		% grassland	0.05	0.07	0.444	
	Ley	Farming system (org)	-0.16	0.13	0.228	
		% grassland	0.04	0.06	0.564	
	Grassland	Farming system (org)	-0.03	0.07	0.621	
		% grassland	-0.07	0.03	0.055	
	$CV_{within-year}$ bumblebee species richness	Cereal	Farming system (org)	0.02	0.14	0.899
			% grassland	0.18	0.07	0.021
		Ley	Year	-0.14	0.14	0.331
			Farming system (org)	-0.46	0.12	0.001
		Grassland	% grassland	0.09	0.06	0.173
			Year	-0.26	0.12	0.044
	Grassland	Farming system (org)	-0.25	0.15	0.100	
		% grassland	0.03	0.07	0.708	
		Year	-0.16	0.14	0.272	

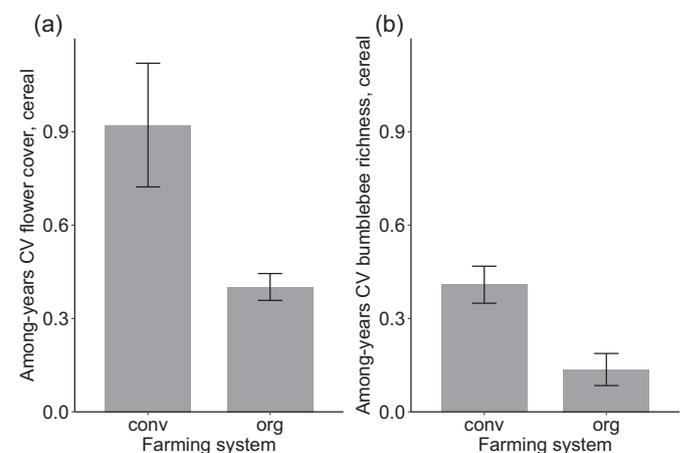


Fig. 3. Parallel trends in the effect of farming system on the $CV_{among-year}$ of (a) flower cover and (b) bumblebee species richness in cereal fields. Means and standard errors are shown. Note that a lower CV indicates a higher stability.

3.3. Indirect effect of farming system on the stability of flower-visitor species richness

The parallel trend detected in the effect of farming system on the within-year CV of flower cover and bumblebee species richness was explained by a causal relationship between a lower within-year CV of bumblebee species richness and a lower within-year CV of flower cover in organic ley fields (Fig. 5a). In addition, farming system also had a direct effect on the within-year CV of bumblebee species richness in ley fields, independently of the effects of within-year CV of flower cover (Fig. 5a).

In contrast to the within-year CV of bumblebee richness in ley fields,

Table 2

Results of the linear models testing the effect of farming system (org/conv) on CV_{among-year} of flower cover, butterfly and bumblebee species richness, controlling for the effect of the proportion of semi-natural grasslands, for each habitat type. Significant coefficients are shown in bold.

Response variable	Habitat type	Variable	Estimate	SE	P value	
CV _{among-year} flower cover	Cereal	Farming system (org)	-0.52	0.20	0.019	
		% grassland	0.03	0.10	0.797	
	Ley	Farming system (org)	-0.18	0.13	0.196	
		% grassland	-0.13	0.07	0.086	
	Grassland	Farming system (org)	-0.04	0.05	0.517	
		% grassland	0.02	0.03	0.436	
CV _{among-year} butterfly species richness	Cereal	Farming system (org)	0.07	0.14	0.640	
		% grassland	-0.01	0.07	0.899	
	Ley	Farming system (org)	0.06	0.09	0.513	
		% grassland	0.00	0.05	0.989	
	Grassland	Farming system (org)	-0.06	0.04	0.135	
		% grassland	0.01	0.02	0.534	
	CV _{among-year} bumblebee species richness	Cereal	Farming system (org)	-0.27	0.08	0.004
			% grassland	-0.03	0.04	0.461
		Ley	Farming system (org)	-0.07	0.11	0.509
% grassland			-0.01	0.06	0.898	
Grassland		Farming system (org)	-0.08	0.14	0.570	
		% grassland	0.01	0.07	0.930	

Table 3

Results of the linear mixed models testing the effect of farming system (org/conv) on CV_{spatial} of flower cover, butterfly and bumblebee species richness controlling for the effect of the proportion of semi-natural grasslands. Significant coefficients are in bold.

Response variable	Variable	Estimate	SE	P value
CV _{spatial} flower cover	Farming system (org)	-0.28	0.07	< 0.001
	% grassland	-0.04	0.03	0.257
CV _{spatial} butterfly species richness	Farming system (org)	-0.16	0.06	0.012
	% grassland	-0.03	0.03	0.353
CV _{spatial} bumblebee species richness	Farming system (org)	-0.17	0.06	0.011
	% grassland	-0.01	0.03	0.763
	Year	-0.05	0.06	0.399

none of the other parallel trends between CV in flower-visitor richness and flower cover (Figs. 2–4) were causally related (Fig. 5b–d). Instead, organic farming had direct negative effects on the among-year and spatial CV of bumblebee richness, and on the spatial CV of butterfly richness. These were not mediated by changes in the spatial or temporal stability of flower resources.

3.4. Seasonal changes in flower cover and flower-visitor species richness

Finally, we analyzed within-year changes in bumblebee species richness in ley fields separately, as these were the only flower-visitor group and habitat type in which within-year CV of species richness was affected by farming system. Flower cover in organic ley fields was consistently higher compared to conventional farms, irrespective of survey round (Fig. 6a). However, bumblebee species richness was significantly higher in organic than in conventional ley fields only during the 4th and 5th survey rounds (mid-July to mid-August, Fig. 6b). The SEM performed for these two survey rounds showed that the effect of farming system on bumblebee species richness was strongly influenced by variation in flower cover, explaining up to 69% of the variation in species richness (Fig. S4). Thus, the higher late-season bumblebee species richness in organic ley fields was explained by higher flower cover in those fields.

4. Discussion

In this study, we investigated the effect of organic farming on the spatiotemporal stability of butterfly and bumblebee species richness and whether this effect could be explained by the spatiotemporal stability of in-field flower resources. We investigated multiple habitat types at two temporal scales, using data on bumblebees, butterflies and floral resources throughout the growing season over two to three years.

Our hypothesis stating that organic farming supports higher spatiotemporal stability of flower resources and flower-visitor species richness was partly validated. We found three parallel trends between plants and flower-visiting insects: (i) a positive effect of organic farming on the within-year stability of flower resources and species richness of bumblebee in ley fields, (ii) a positive effect of organic farming on the among-year stability of flower resources and bumblebee richness in cereal fields, and (iii) a positive effect of organic farming on the landscape-scale stability of flower resources, butterfly and bumblebee species richness. We also found that an increasing stability of flower resources and flower-visiting insect species richness did not involve a decrease in overall flower resources or species richness of flower-visiting insects. Our study therefore demonstrated that organic farming can enhance the spatiotemporal stability of flower-visitor species richness.

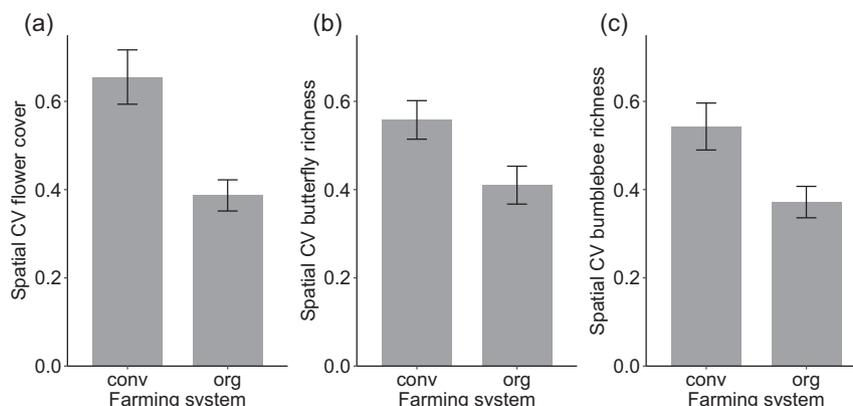


Fig. 4. Parallel trends in the effect of farming system on the CV_{spatial} of (a) flower cover, (b) butterfly species richness and (c) bumblebee species richness. Means and standard errors are shown. Note that a lower CV indicates a higher stability.

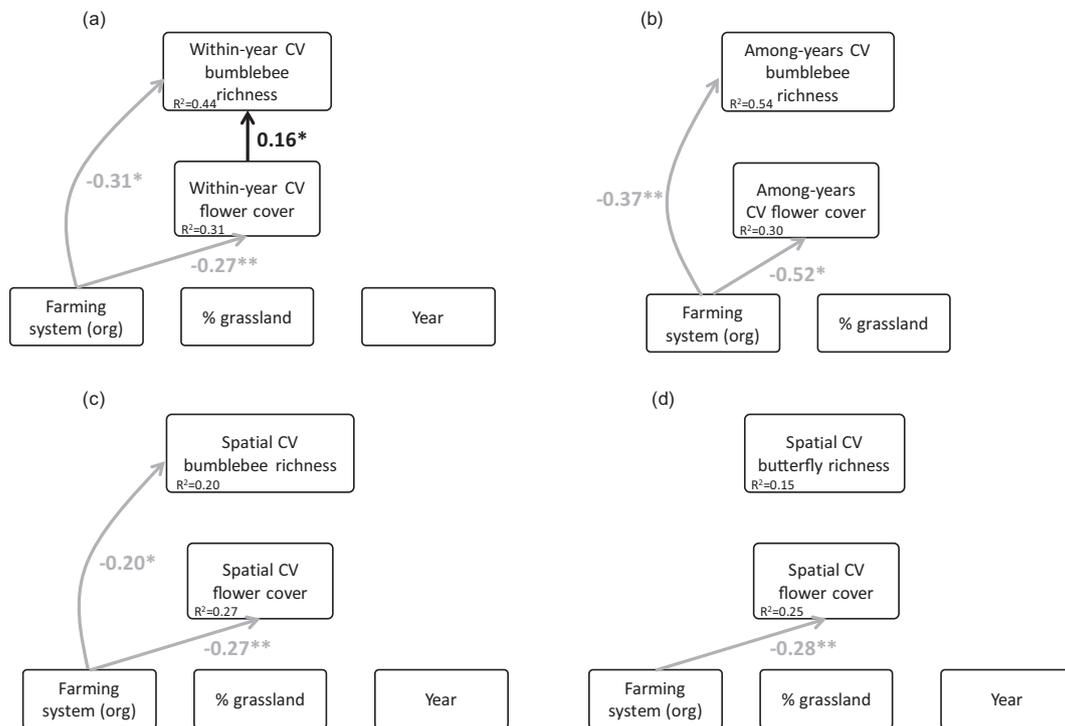


Fig. 5. Path models of the effects of farming system, via changes in the stability of flower resources, on $CV_{\text{within-year}}$ of bumblebee species richness in ley fields (a), on $CV_{\text{among-year}}$ of bumblebee species richness in cereal fields (b), on CV_{spatial} of bumblebee species richness (c) and on CV_{spatial} of butterfly species richness (d). We controlled for the effects of the proportion of semi-natural grasslands and year of measurement. Only significant relationships are displayed. Grey arrow: negative effect, black arrow: positive effect ($P < 0.05$ *; $P < 0.01$ **; $P < 0.001$ ***). Note that a lower CV indicates a higher stability.

However, contrary to our expectations, the effect of organic farming on the within-year stability of bumblebee species richness could only be attributed to a higher stability of flower resources in ley fields. Ley fields have the potential to provide important pollen and nectar sources for bumblebees in the studied region, especially when sown with clover (Persson and Smith, 2013; Rundlöf et al., 2014). Mass-flowering legumes, like clover, have relatively deep corollas which benefit long-tongued bumblebees (Carvell et al., 2011). However, we did not find any difference in the within-year stability of clover cover between organic and conventional farms that had clover fields (Fig. S5), suggesting that the positive effect of organic farming on bumblebees rather involved the flowering plant communities more broadly in ley fields. Differences in ley management might explain the contrasting continuity of flowering weed cover between organic and conventional leys. Indeed, the use of mineral fertilizers in conventional farming is known to decrease plant diversity, which can lead to reduced cover of flowering forb species in pastures (Blüthgen et al., 2012; Hudewenz et al., 2012; Kleijn et al., 2009). Moreover, organic farms might have lower mowing frequency due to reduced hay yields, which in turn could favor the maintenance of diverse flowering plant community (Blüthgen et al., 2012; Socher et al., 2013).

Our third hypothesis, stating that organic farming reduces resource bottlenecks by providing higher early and late flowering resources, was partly validated. In particular, we found that organic farming increased bumblebee species richness by providing higher flower cover at the end of the growing season. Although ley fields on organic farms had consistently higher amounts of flowering resources compared with conventionally managed leys, these differences in resources seemed to influence bumblebee species only during the two last survey rounds. The presence of late-flowering resources in the form of mass flowering crops is known to sustain bumblebee abundances (Rundlöf et al., 2014) by providing resources during the critical period of queen production (Williams et al., 2012). Our results suggest that higher flower resources in organic ley fields reduced the late-season resource bottleneck that

bumblebee communities may experience in conventional farmland. Therefore, organic farming could effectively contribute to increasing temporal stability of bumblebee species richness along the entire growing season.

In the other cases of parallel trends between the stability of flower resources and flower-visitor species richness, our results suggest that organic farming had an effect not related to the stability of flower resources. However, organic farming could affect stability or variation in plant communities by benefitting plant species preferred by flower-visiting insects, such as legumes. Such shifts in the presence of preferred flower species could also benefit only a subset of butterfly or bumblebee species with specific ecological requirements, and not the whole communities (Ekroos et al., 2013; Halder et al., 2017; Rundlöf et al., 2008b). Future studies based on trait-based approaches might shed more light on the mechanisms that increase stability in species richness of flower-visiting insects in organic and conventional farming systems. Moreover, farming system can also have a direct effect on flower-visiting insects. The use of insecticides in conventional farms can cause losses of butterfly and bumblebee species richness by affecting the reproduction and foraging behavior of some species, but also by causing direct lethal damages (butterflies: Davis et al., 1991; Longley and Sotherton, 1997; bumblebees: Arena and Sgolastra, 2014; Baron et al., 2017; Brittain et al., 2010). The higher spatiotemporal fluctuations in bumblebee and butterfly species richness that we observed in conventional farms might therefore be linked to the different use of insecticides between years or crop types (Vasseur et al., 2013), causing local or periodic declines in the species richness of bumblebees and butterflies.

Despite the fact that of organic farming did not enhance stability of flower-visitor species richness by increased stability of flower resources in the majority of habitat types, our results nevertheless suggest that resource continuity can benefit bumblebees and butterflies irrespective of farming system. In fact, we found that within-year stability of butterfly and bumblebee richness was correlated with within-year

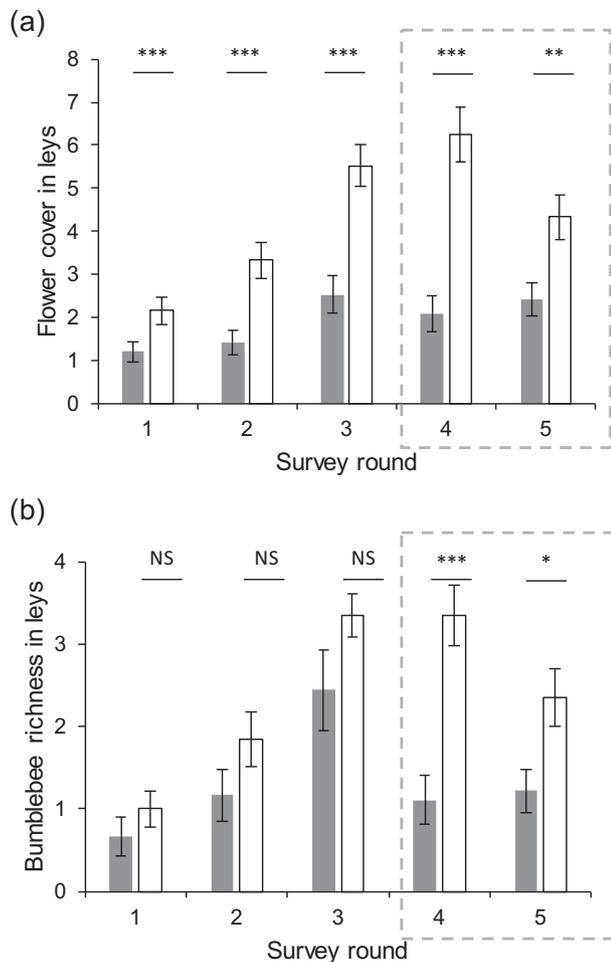


Fig. 6. Effect of farming system on the flower cover (a) and bumblebee species richness (b) in ley fields depending on the survey round. Means and standard errors are shown. Dashed rectangles show the parallel trend in the effect farming system on flower cover and bumblebee richness, only during the visit number 4 and 5 ($P > 0.05$ NS; $P < 0.05$ *; $P < 0.01$ **; $P < 0.001$ ***).

continuity of flower cover in cereal and ley fields (Table S5), irrespective of the farming system. Our study therefore highlights that the management of resource stability in arable crops is critical to sustain bumblebee and butterfly communities during the growing season, independently of farming system.

In contrast to cereal fields and leys, we did not find any effect of farming system on the spatiotemporal stability of flower-visitor species richness in semi-natural grasslands. This result might be expected given that the management of organic and conventional grazed grasslands did not differ substantially. Semi-natural grasslands are only used for grazing and are not treated with mineral fertilizers or herbicides in the studied region (Persson et al., 2010), which might lead to similar floral qualities for conventional and organic grasslands.

Contrary to bumblebees, the temporal stability of butterfly species richness was either marginally or not affected by organic farming. This absence of significant temporal trends might stem from the differential use of resources between grassland-specialist and generalist butterfly species, since cereal and ley fields further away from grasslands are more likely to be dominated by generalist and mobile species (Ekroos et al., 2013) that might be less affected by farming practices than grassland-specialist butterfly species. However, the positive effect of organic farming on the spatial stability of butterfly species richness suggest that butterflies benefit from less intensive practices at large spatial scales.

Although we found a strong effect of farming system on the stability

of the species richness of flower-visiting insects, we surprisingly found no effect of increasing proportions of semi-natural habitats in the surrounding landscapes (c.f. Garibaldi et al., 2011). It is possible that the gradient in proportions of grasslands (1–18%) in the surrounding landscapes was not large enough to affect the stability of bumblebee and butterfly species richness in our study. In addition, the proximity of a sampling site to a semi-natural habitat can have stronger effects on local flower-visitor diversity compared with landscape-wide proportions of semi-natural habitat (Ekroos et al., 2013). Semi-natural grasslands might therefore have influenced spatiotemporal stability of flower-visitors via a local effect (proximity) rather than a landscape-scale effect (total proportion). Given our gradient in proportions of semi-natural grassland, an alternative explanation could be that only a subset of bumblebee or butterfly species responded to the proportion of grasslands in the landscapes (Ekroos et al., 2013). The flower-visitor communities we sampled could be dominated by generalist, common species that are usually visiting arable crops on a larger extent than species characterized by a higher habitat specificity (Kleijn et al., 2015). Further studies are needed to shed light on whether organic farming benefits the persistence of both common and rare species (but see Lichtenberg et al., 2017).

We conclude that the conversion to organic farming has the potential to generate beneficial large-scale and multi-year effect on the diversity of flower-visiting insects. Landscapes with more organic fields has earlier been shown to increase local biodiversity in crop fields and at the landscape scale (Holzschuh et al., 2008; Rundlöf et al., 2008a), and our study suggests that these benefits could lead to higher species richness stability in agricultural landscapes. Moreover, there is evidence showing that the conversion to organic farming leads to rapid increase in plant and butterfly diversity (Jonason et al., 2011), meaning that the stabilizing effect of organic practices on species diversity might occur with no or small time-lags after the conversion. Although organic farming carries costs in terms of yield loss (Seufert and Ramankutty, 2017), stabilizing effects of organic farming on species diversity could be a promising way to enhance the sustainability of agricultural landscapes by increasing the predictability and provision of key ecosystem services important for crop production such as pollination.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.08.022>.

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