



Spatial community turnover of pollinators is relaxed by semi-natural habitats, but not by mass-flowering crops in agricultural landscapes



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ABSTRACT

Understanding beta-diversity, i.e. species turnover in space and time, is essential for informing conservation actions. Soaring cultivation of mass flowering crops (e.g. oil seed rape OSR) and loss of semi-natural habitats (SNH) can strongly affect populations of native pollinators, yet it remains unclear how OSR and SNH affect spatial and temporal turnover of pollinator communities. Here, we examined how the landscape-scale proportions of OSR and SNH affect spatial and temporal community turnover in solitary bees and hoverflies, two key provider groups of pollination and pest control services in temperate agro-ecosystems. Using a novel grid-based landscape-wide sampling approach, we quantified pollinator communities within ten 1 km × 1 km landscapes representing independent gradients in OSR and SNH availability. We sampled during and after OSR flowering, in two subsequent years, yielding app. 8800 specimens representing 160 species. Spatial community turnover, measured as the slope of the dissimilarity-distance relationship, was not influenced by the proportion of OSR at any time. In contrast, SNH decreased community turnover for bees during OSR flowering and for hoverflies after flowering, likely caused by pollinator movement between land use types. This suggests that a high availability of SNH may help to promote an even distribution of native bees and hoverflies within temperate agricultural landscapes, hereby potentially stabilizing landscape-wide pollination services.

1. Introduction

Agricultural landscapes comprise 40% of the terrestrial surface of the Earth (Foley et al. 2005; Martin et al. 2012); maintaining biological diversity in such landscapes is therefore crucial for worldwide biodiversity conservation (Tscharntke et al. 2005; Fahrig et al. 2011). Semi-natural habitats (SNH) such as low-intensity grasslands are ecological key-elements for many species (e.g. Tscharntke et al. 2005; Kormann et al. 2015). Worldwide, SNH are increasingly lost through intensified agricultural practices, with strongly negative effects on local species richness (e.g. Kormann et al. 2015; Scherber 2015). In parallel, the global production of mass-flowering crops is expanding rapidly: The global harvest of oil seed rape (OSR) for example, Europe's most common biofuel crop, has increased by a factor 22.4 between 1961 and 2013 (FAOSTAT 2016).

Although several recent studies have investigated the effect of SNH and OSR on biotic communities (e.g. Westphal et al. 2003; Gladbach et al. 2011; Diekötter et al. 2014; Holzschuh et al. 2016), it remains largely unknown how these two landcover types affect biotic

communities beyond simple descriptors of species richness and abundance. Importantly, local species richness or abundance may be inappropriate descriptors for changes in community composition, and only weakly, if at all, reflect patterns of species identities in space and time (Tscharntke et al. 2012; Gámez-Virués et al. 2015; Socolar et al. 2016). This is particularly the case for agro-ecosystems, which are characterized by heterogeneous habitat patches and rapid changes in composition in response to harvest and crop rotation (Wissinger 1997; Thies et al. 2005; Thies et al. 2008). Thus, to understand the processes that shape biodiversity in agricultural landscapes, scientists must explicitly investigate the organization of species assemblages in space and time (Socolar et al. 2016). For example, the few studies that assess the relationship between agricultural intensification and community structure at landscape scales often ignore spatial community turnover, focusing only on alpha or gamma diversity and disregarding the spatial distance between communities in their analyses (Liebhold and Gurevitch 2002; Soininen et al. 2007). This may be risky, as high spatial turnover in species identities (high β-diversity) has been associated with high levels of ecosystem functions and services (Van Der Plas et al.

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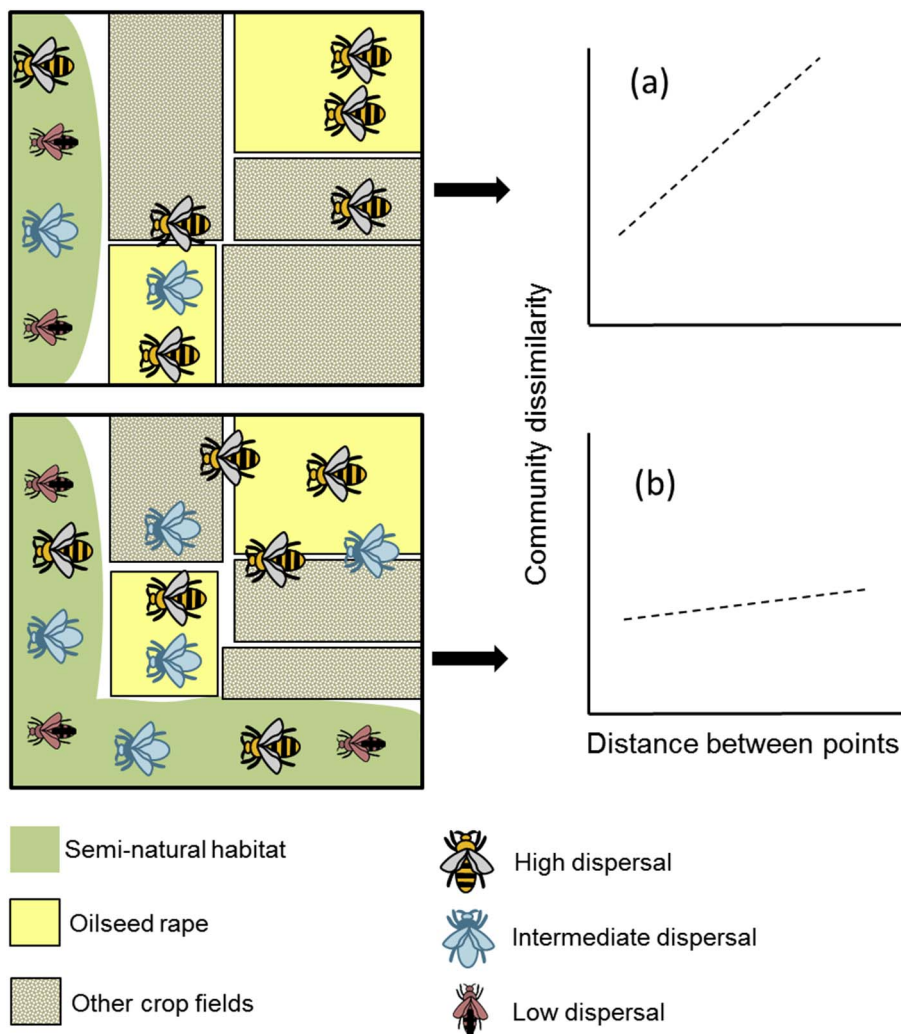


Fig. 1. Hypothesized relationships between geographical distance and community dissimilarity. (a) Example of a landscape with low proportion of semi-natural habitats (meadows, pastures or forest margins). In this scenario, bees with low or intermediate dispersal abilities (as central place foragers) forage in proximity to semi-natural habitats but cannot access distant resources. This generates a steeper slope for the community dissimilarity-distance relationship. (b) Example of a landscape with high proportion of semi-natural habitats. In this case, there are more resources in arable fields within the foraging distance of bees with low or intermediate dispersal abilities, and thus, a higher proportion of the landscape can be used by those bees for foraging. This generates a shallower slope for the community dissimilarity-distance relationship. Because hoverflies generally disperse over longer distances, and their resources are not habitat-restricted, we predict that they will be characterized by shallower slopes than bees, regardless of the proportion of semi-natural habitats.

2016), which are very important for increasing productivity in agricultural land, reducing the need for further arable land. Moreover, examining spatial patterns of species turnover, in contrast to alpha or gamma diversity, can provide valuable information on how biological communities respond to climate and environmental change (Wiersma and Urban 2005). This information is crucial to understand how the edges of species' ranges are delineated and to help in the planning of conservation areas (Wiersma and Urban 2005; Holt et al. 2005).

Pollinators are critically important for crop production (Klein et al. 2007) and the sexual reproduction of most wild plants (Ollerton et al. 2011). Yet, pollinator populations are known to be highly variable across space and time (Williams et al. 2001), and a diverse set of species can guarantee pollination for a broader suite of plants (Kremen et al. 2002). Similarly, the stability of pollination services in space and time is crucial for agriculture, and has been shown to often increase with the number of pollinator species present in a landscape (McCann 2000; Garibaldi et al. 2011). Diverse pollinator communities can further meet the pollination requirements of a greater number of crops, and provide insurance in the event of shortages of individual species (Kremen et al. 2002; Winfree and Kremen 2009; Garibaldi et al. 2013).

Spatial dispersal processes have been shown to considerably affect community composition and turnover (Cottenie 2005). Communities in agricultural landscapes often consist of species adapted to frequent disturbance events, with dispersal-related traits positively selected for (Harrison and Taylor 1997; Leibold et al. 2004). While (semi-) natural habitats provide spatiotemporally stable resources (Duelli and Obrist 2003) in rather low abundance or quality, temporary cropland habitats,

such as oilseed rape, often contain larger amounts of resources (Tschamntke et al. 2012), generating source-sink dynamics in agricultural landscapes and spillover of organisms among crops and other habitats. Cross-habitat spillover is a function of the movement ability of the species and tends to be restricted for organisms with limited dispersal capacity (Tschamntke and Brandl 2004; Tschamntke et al. 2012).

In this study, we use a novel landscape-wide grid-based sampling scheme (Beduschi et al. 2015; Scherber et al. 2012) to sample mobile pollinating insects across ten 1-km² landscapes. We focus on the spatial turnover of solitary bees and hoverflies, two groups that have been shown to respond differentially to landscape structure as a result of distinct resource requirements and dispersal abilities (i.e., foraging ranges) (Gathmann and Tschamntke 2002; Steffan-Dewenter et al. 2002; Holzschuh et al. 2008). For example, solitary bees have a small foraging range of only up to 600 m in agricultural landscapes (Gathmann and Tschamntke 2002). Given that they commute between nesting and feeding sites in order to collect pollen for their offspring, they require small distances between nesting and foraging sites (Gathmann and Tschamntke 2002; Steffan-Dewenter et al. 2002). Hoverflies, on the other hand, have no need to return to their oviposition sites and are able to disperse over greater distances (Jauker et al. 2009; Raymond et al. 2013). Additionally, hoverflies are often more generalist flower-feeders than bees (Biesmeijer et al. 2006), and predatory species often find their prey in arable fields (Meyer et al. 2009). Consequently, hoverflies tend to be less severely affected by agricultural intensification or may even benefit from it (Jauker et al. 2009). Thus, even though bees are considered to be more efficient pollinators (Jauker et al. 2012),

hoverflies have been shown to play a significant role in sustaining and stabilizing pollination services, particularly in highly simplified agricultural areas unsuitable for less mobile bee species (Jauker et al. 2009; Hänke et al. 2014, Rader et al. 2016).

In the present study, we assess how landscape context (i.e., proportion of OSR and SNH in the landscape) affects landscape-wide spatial community turnover. We investigate the drivers of community dissimilarity between local assemblages by sampling pollinators in different habitat types within the same landscape (and thus species pool). In particular, we investigate two habitat types that potentially shape pollinator abundance and diversity: semi-natural habitats and mass flowering crops. Semi-natural habitats, such as grasslands managed with low intensity, provide continuous food and nesting resources over the season (Steffan-Dewenter et al. 2002). On the other hand, local diversity and community composition may differ at different times of the year, depending on the presence or absence of mass-flowering crops (flowering period: during vs. post OSR flowering).

We test the following hypotheses:

- (1) spatial community turnover within landscapes is affected by landscape context, i.e., proportion of semi-natural habitats and/or of oilseed rape fields (Fig. 1);
- (2) hoverfly communities are generally more homogeneously distributed throughout the landscape than solitary bees and are, therefore, less affected by landscape context;
- (3) the effect of landscape composition on spatial turnover of the two pollinator groups will vary with time (before and after oilseed rape flowering);
- (4) local diversity in different habitat types will be affected by flowering period.

2. Methods

2.1. Sampling procedures

The study was conducted in the surroundings of Göttingen (51° 32' N, 9° 56' E) in Central Germany. The region is dominated by intensive agriculture interspersed with semi-natural non-crop areas such as meadows, calcareous grasslands, and woodlands (Steffan-Dewenter et al. 2002). The 10 sampling landscapes measured c. 1 km × 1 km (mean area ± SD = 0.93 ± 0.23 km²) and represented non-correlated gradients of percent area occupied by oilseed rape fields and semi-natural habitats (for more details on the gradients see Supplementary Material Table A1 and Beduschi et al. 2015). In order to avoid settlements, three landscapes were slightly smaller than 1 km². However, there was no correlation between community turnover and landscape size ($r = -0.10$ and $r = 0.22$ for bees and hoverflies, respectively). In each landscape, we sampled insects with pan-traps (0.75 L,

diameter = 150 mm) arranged in a 5 × 5 grid (25 points per landscape), following an approach suggested by Scherber et al. (2012) (Fig. 2). Sampling points were placed at approximately 250 m distance. Each sampling grid contained forest margins and grasslands (semi-natural habitats) as well as crop fields. As a consequence of this design, habitat types were sampled proportionally to the area they occupied in each landscape. At each of the 25 points per landscape, we sampled pollinators with yellow pan traps, filled with water and placed at vegetation height to reduce the visibility of pan traps at larger distances. Traps were exposed for three days in four periods: May 2011 and 2012 (during oilseed rape flowering) and June 2011 and 2012 (after oilseed rape flowering; Fig. 2), and were always placed at exactly the same locations. Out of 1000 samples (10 landscapes × 25 traps × 4 sampling periods), 29 had to be omitted from the analyses because traps had been damaged. All wild bees and hoverflies were determined to species level by specialists. Sampling habitats included oilseed rape fields, semi-natural habitats (grasslands), and other crop fields (mainly cereal, corn and sugar beet fields). Satellite-based image classification was used to measure the proportion covered by oilseed rape fields, semi-natural habitats and other fields for each landscape and year separately. Satellite imagery was provided by RapidEye™ and image classification was performed using ENVI EX® and ESRI® ArcMap™10.

2.2. Data analyses

Statistical analyses were performed at two spatial scales: (i) On a landscape scale, we analyzed the effect of landscape components (proportion of OSR and SNH) on the rate of spatial community turnover for both pollinator groups and sampling rounds separately. For this, we followed the modeling approach suggested by Anderson et al. (2016), (see “T4. Estimate the rate of turnover in community structure along a spatial gradient” therein), where the response variable is the rate of community turnover in space per landscape, and the gradients of OSR and SNH the continuous predictor variables. For this, we first calculated a matrix of pairwise community dissimilarities between sampling points, separately for each landscape, sampling period and pollinator group (bees and hoverflies). We used Bray–Curtis dissimilarity which incorporates both species composition and absolute abundances, and excludes joint absences. There is a great variety of community similarity measures (Anderson et al., 2016), and the measure we used was highly correlated with alternative dissimilarity measures such as Chao ($r = 0.95$) or Raup Crick ($r = 0.92$). Spatial distance was calculated for each pair of sampling points using Euclidean distances. To assess the within-landscape spatial community turnover, we then calculated a linear regression between pair wise dissimilarities and Euclidean distances for each landscape, sampling period and pollinator group (Anderson et al., 2016). Small slope values correspond to landscapes with low rates of spatial community turnover, and large slope values

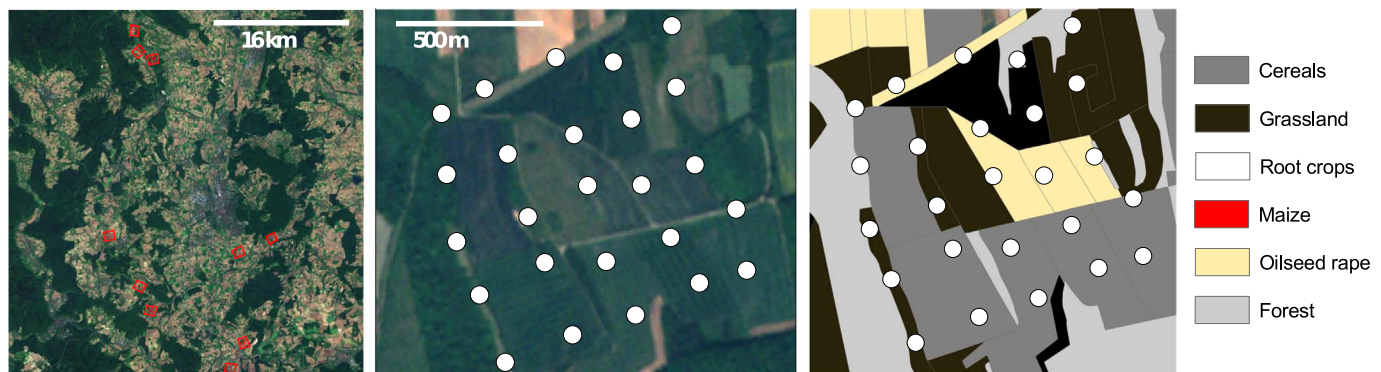


Fig. 2. Grid-based sampling in ten replicated 1-km² landscapes. (a) Overview of the study area showing all ten individual sampling grids; (b) example 1-km² landscape with regularly spaced sampling locations; background image: RapidEye satellite image, channels R = 3, G = 2, B = 1, with Gamma correction and stretched by 1 standard deviation (c) after image classification with ENVI EX. Image source for Fig. 2(a) GeoBasis Germany.

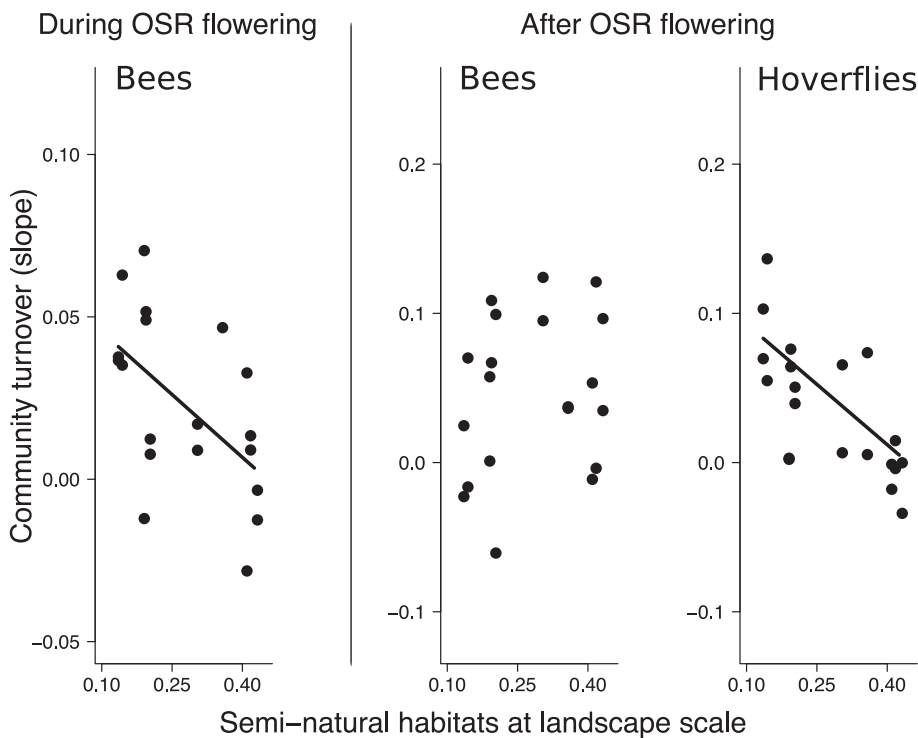


Fig. 3. Landscape scale: Effects of the proportion of semi-natural habitats within landscapes on the rate of spatial community turnover (slope of the regression “dissimilarity – Euclidean distance”) for solitary bees (left and center) and hoverflies (right) obtained in linear mixed-effects models. Lines show model estimates and are only present when proportion of semi-natural habitats was present as an explanatory variable in the final model. Community turnover was expressed as the slope obtained from a linear model relating a Bray-Curtis dissimilarity matrix for the species for each landscape with a dissimilarity matrix based on Euclidean distances between sampling plots (i.e., traps). Greater slopes indicate higher spatial community dissimilarity. Each point represents one landscape ($N = 10$) in one year (2011 or 2012). Results are shown for the period during oilseed rape (OSR) flowering (left) and after oilseed rape flowering (center and right).

correspond to a landscape that exhibit high rates of spatial community turnover (Fig. 1). Although pairwise dissimilarities between samples are not independent (e.g., the dissimilarity between sample 1 and sample 2 is not independent of the dissimilarity between sample 1 and sample 3), the rate of spatial turnover, e.g. the slope of the similarity decay (not its significance) can be assessed with a simple linear function (Anderson et al., 2016). We did not calculate spatial community turnover if we did not catch any specimen. Thus, we had to exclude one OSR bloom landscape for bees, and one post-OSR-bloom landscape for hoverflies from the analysis, respectively.

Using linear mixed-effects models, we related the slopes of the dissimilarity-distance relationship, as a measure of spatial community turnover per landscape, to the landscape-wide availability of oilseed rape fields and semi-natural habitats (Anderson et al., 2016). The slopes were used as response variables, and explanatory variables were year as a categorical variable, proportion of oilseed rape fields, and proportion of semi-natural habitats in each landscape. We also included a random intercept for each sampling landscape. Oil seed rape fields have high abundance of floral resources, but show lower diversity, while semi-natural habitats have higher floral diversity, which are less abundant but more continuously available (Duelli and Obrist 2003). Hence, we expected the communities to respond differently to the landscape variables during and after oilseed rape flowering (high availability versus no availability of mass flowering resources), and used two different models: one for samples collected during oilseed rape flowering (May 2011 and 2012), and another for samples collected after oilseed rape flowering (in June 2011 and 2012). Model selection was done using backward stepwise selection in order to minimize Akaike's Information Criterion (Crawley 2013), corrected for small sample sizes (AICc, Burnham and Anderson 2002). (ii) On a local scale, we compared local species richness between habitats, individually for each trap. We used generalized linear mixed-effects models with Poisson error distribution. The response variable was the number of species in each plot (i.e., trap) and the explanatory variables were year and the habitat type where sampling was performed (semi-natural habitat, oilseed rape field or other crop fields). A random intercept for each sampling landscape was used and different models were performed for during and after

oilseed rape flowering. Maximal models were simplified in a manual stepwise backward selection on the basis of AICc-values. Variables were kept in the model when they provided a decrease in $\Delta AICc$ of more than 3 (Burnham and Anderson 2002). Dispersion parameters of the Poisson models were all within the suitable boundaries [0.7–1.4] suggested by Bates (2005).

All statistical analyses were conducted with R (3.0.2 R Core Team, 2013). Models were fitted using the packages nlme for the large spatial scale (Pinheiro et al. 2013) and lme4 for the small spatial scale (Bates, 2005, count data). For each model, we assessed residuals for variance homogeneity, normality and independence of errors. We accounted for non-independence by introducing random effects and appropriate spatial correlation structures. Residual spatial autocorrelation was assessed for both small and large scale models using Moran's autocorrelation coefficient (Bivand et al. 2008) and the package spdep 0.5–71 (Bivand 2014), but no remaining spatial pattern was found.

3. Results

3.1. Overall insect community structure

We collected a total of 3526 hoverfly individuals, representing 67 species, and 5241 bee individuals from 93 species. Total trapping effort per habitat type, summed over both years and periods was 300 traps in SNH, 193 traps in OSR, and 487 traps in other crop fields. Species lists are available in the Supplementary material (Electronic Supplemental Material, Tables A1 and A2). In both years, overall abundance was highest in the period after oilseed rape flowering (79% of bee and 96% of hoverfly individuals).

3.2. Spatial turnover of local communities (landscape scale)

As hoverflies were not sufficiently abundant during oilseed rape flowering, community similarity could not be calculated for most landscapes. Therefore, we only estimated the effect of landscape composition on the spatial community turnover for hoverflies after flowering.

Table 1

Landscape scale: Results of linear mixed models with spatial community turnover, i.e. slopes of the regressions “dissimilarity – Euclidean distance”, as a response variable, and year (2011 or 2012), proportion of oilseed rape (OSR) and proportion of semi-natural habitats (SNH) within each sampling landscape as explanatory variables. Intercepts, model coefficients and one standard error of the mean (in brackets) are given. Values not shown (–) were not retained in final models (after backwards stepwise removal of terms, based on AICc). Results for hoverflies during flowering were not available (NA) due to abundance at that period.

Period	Taxon	Intercept	OSR	SNH	Year
During flowering	Bees	0.06 (0.01)	–	–0.12 (0.05)	–
	Hoverflies	NA	NA	NA	NA
After flowering	Bees	0.05 (0.01)	–	–	–
	Hoverflies	0.09 (0.02)	–	–0.27 (0.07)	0.03 (0.01)

Spatial community turnover, measured as the slope of the dissimilarity - distance relationship, decreased with increasing proportion of semi-natural habitat (Fig. 3, Table 1). That was the case for bees during oilseed rape flowering (Fig. 3, left) and for hoverflies after flowering (Fig. 3, right). Conversely, proportion of oilseed rape had no substantial effect at any time or for any taxon (Table 1). A year effect was only important for hoverflies after flowering (Table 1).

Our results were robust even when data were re-analyzed with restricted numbers of data points in semi-natural habitats (for more details see Electronic Supplemental Material, Section “Effect of number of samples in semi-natural habitats”, Figs. A1 and A2).

3.3. Species richness (local scale)

While total hoverfly species richness on a local scale was always higher on non-oilseed rape arable fields such as cereals, corn and sugar beet (Table 2, Fig. 4, right), bee species richness was higher in semi-natural habitats during oilseed rape flowering and in non-oilseed rape crop fields afterwards (Table 2, Fig. 4, left). When both sampling periods were pooled, more bee and hoverfly species were found in semi-natural habitats than in crop fields (Table 3). Generally, more individuals were collected in the first year than in the second, except for bees during flowering, where year was not retained in the final model.

4. Discussion

Our results show that increased landscape-wide proportion of semi-natural habitats dampens spatial community turnover between local assemblages in two key pollinator groups: solitary bees and hoverflies. The proportion of oilseed rape fields did not influence community turnover. However, semi-natural habitats affected bees only during, and hoverflies only after oilseed rape flowering, indicating that mass-flowering crops can indirectly affect the importance of semi-natural habitats for pollinator communities.

Table 2

Local scale: Results of generalized linear mixed models relating species richness at local level to habitat type. The effect of year is shown only when it decreased model AICc by at least 3. Model coefficients and one standard error of the mean (in brackets) are given. Intercepts were removed from the models to obtain the mean value of species richness per habitat type. Values were back-transformed using the exponential function. Habitat types are: semi-natural habitats (SNH), oilseed rape fields (OSR) and other crop fields (Other).

Period	Taxon	SNH	OSR	Other	Year
During flowering	Bees	1.75 (1.09)	0.86 (1.12)	1.34 (1.09)	–
	Hoverflies	0.44 (1.24)	0.06 (1.61)	0.17 (1.28)	–1.03 (0.15)
After flowering	Bees	2.29 (1.09)	1.73 (1.11)	2.53 (1.10)	–0.16 (0.04)
	Hoverflies	2.69 (1.06)	3.56 (1.08)	3.97 (1.07)	–2.04 (0.17)

4.1. Spatial turnover of local communities

Semi-natural habitats dampened community turnover for bees during OSR flowering, as SNH-rich landscapes showed shallower slopes for the dissimilarity with distance relationship. However, this was only the case during oilseed rape flowering. This pattern may be explained by increased movement of bee individuals throughout the landscape during oilseed rape flowering or by temporal variations in bee community composition.

The movement of individuals in agricultural landscapes may increase because oilseed rape has been shown to be very attractive to pollinators (Holzschuh et al. 2011). Bumblebees may move large distances to exploit the great supply of pollen and nectar present in these fields (Westphal et al. 2003). Small solitary bees, on the other hand, are generally much more constrained by their nesting requirements (Westrich 1996) and fly only short distances for foraging (Gathmann and Tscharrntke 2002; Steffan-Dewenter et al. 2002). Nonetheless, solitary bees have been shown to spillover to flowering oilseed rape fields once the distance was small enough (Holzschuh et al. 2011; Kovács-Hostyánszki et al. 2013). Higher proportions of semi-natural habitat may therefore increase the probability that oilseed rape fields are within a bee's foraging distance, increasing resource availability for solitary bees. The lack of a relevant effect of semi-natural areas after oilseed rape flowering supports this idea, since bees would no longer have a stimulus to spillover to crops and community turnover would depend mainly on distance between sampling points and habitat type. However, the transience of the effect could be a result of temporal variations in the species composition of bees. Evidence shows that not only spatial, but also temporal dynamics can be an important component of regional species diversity (Tylianakis et al. 2005). Bee communities are also known to show substantial variation, not only between years, but also within shorter time spans (Williams et al. 2001). Temporal variation was certainly important as “year” effects were always retained in final models.

The extremely low abundance of hoverflies during oilseed rape flowering did not allow us to investigate the effect of landscape context on the spatial community dissimilarity in this period, but a similar response was observed after flowering. However, semi-natural habitats strongly affected hoverfly spatial community turnover after oilseed rape flowering. Species richness was higher in crop fields, which is in line with the literature. Hoverflies have been reported to profit from abundant larval prey in arable fields (Meyer et al. 2009), and their richness can even increase with distance to semi-natural habitats (Jauker et al. 2009). In this sense, increasing proportions of arable land may homogenize communities more strongly than semi-natural habitats. Nonetheless, even though hoverfly communities are often dominated by aphidophagous species (Frank 1999; Hänke et al. 2009; Meyer et al. 2009), semi-natural habitats may offer more stable resources and may be essential to other guilds, such as xylophagous, phytophagous or coprophagous species (Meyer et al. 2009). Additionally, adult hoverflies of all feeding guilds generally depend on nectar for high-energy flight and pollen for egg maturation (Haslett 1989). Large amounts of semi-natural habitats may therefore decrease spatial community turnover in two ways: First, they increase habitat availability and, consequently, the spatial distribution of hoverfly species that depend on these areas for feeding and reproduction. Second, they may also offer flower resources to generalists that spillover from arable fields. The proximity between foraging and oviposition sites could increase the spillover between habitats and decrease spatial turnover of local communities. In fact, although local diversity was lower at individual sampling points placed in semi-natural areas, once all sampling points located within this habitat type were pooled, a higher species richness was sampled in comparison to crop fields. This suggests both a higher number of unique species (i.e., sampling points in semi-natural habitats are more varied than those in crop fields) and a considerable overlap with the other habitats. Therefore, while semi-natural habitats as a

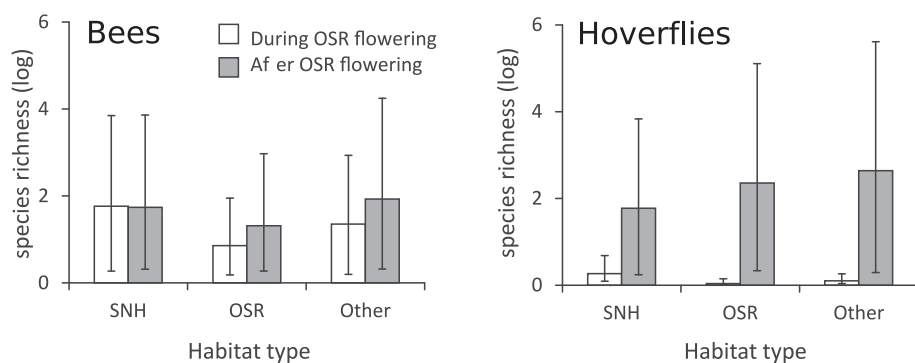


Fig. 4. Local scale: Mean bee (left) and hoverfly (right) species richness (log scale) observed on each plot (i.e., trap) within a landscape ($N = 25$ plots \times 10 landscapes) during and after oilseed rape flowering in semi-natural habitats (SNH, $n = 300$ traps in total), oilseed rape fields (OSR, $n = 193$ traps in total) and other crop fields (Other, $n = 487$ traps in total). Values were obtained from data pooled across the two years and analyzed using a generalized linear mixed model with landscape ($N = 10$) as a random intercept. Error bars represent 95% confidence intervals.

Table 3

Total number of species sampled in each habitat type during and after flowering per year. Habitat types are: semi-natural habitats (SNH), oilseed rape fields (OSR) and other crop fields (Other).

Year	Habitat	Bees		Hoverflies	
		During flowering	After flowering	During flowering	After flowering
2011	Other	32	34	11	23
	OSR	17	16	4	21
	SNH	33	36	16	24
2012	Other	28	36	7	27
	OSR	15	15	1	11
	SNH	37	27	10	20

whole present more diversity, the species are less homogeneously distributed throughout this habitat type.

In contrast to our expectations, bee and hoverfly communities responded similarly to landscape composition. This result indicates that the differences in resource requirements and dispersal abilities between the two groups are less important than the diversity within each taxonomic group. While hoverflies are generally able to move larger distances than bees, their movement can be hindered by certain landscape features (Wratten et al. 2003). Moreover, the dispersal capacity of bees varies with body size and, along with degree of specialization, has been shown to affect how and at what scale they respond to landscape factors (Benjamin et al. 2014; Bommarco et al. 2010).

Isolation from semi-natural habitats has been shown to reduce both stability and mean levels of flower-visitor richness, visitation rates and fruit-set in crop areas (Garibaldi et al. 2011). Likewise, decreases in evenness and dependence on few species for pollination can be especially detrimental to stability in seed yield (Bommarco et al. 2012). This capacity to recover functions after disturbance is especially important in agricultural areas, which are characterized by regular changes due to harvest and crop rotation (Wissinger 1997).

4.2. Species richness

The higher species richness of bees and hoverflies observed in arable fields other than oilseed rape may be counter intuitive, but concurs with other studies that found higher local diversity of butterflies (DeVries et al. 1997; DeVries, Walla, and Greeney, 1999) and bees and wasps (Klein et al. 2007; Tylianakis et al. 2005) in more disturbed areas when compared to semi-natural habitats. In accordance to Tylianakis et al. (2005), this pattern did not always translate into an overall (i.e., all sampling rounds pooled) higher landscape-wide diversity in such habitat types. This could be a consequence of the diversity of crop types or of different management approaches among fields. These results reinforce the idea that managed land cannot be seen as a barren matrix, deprived of biodiversity. Extensively managed crop fields (Kovács-Hostyánszki et al. 2011) and field margins (Meek et al. 2002) may

enable high species richness at local and landscape scale. Yet, it should be noted that temporary ‘habitats’ such as arable fields usually don’t allow the completion of an insect’s life cycle and stable semi-natural habitats are often required for the provision of nesting sites.

5. Conclusions

Our study expands beyond previous research, showing that semi-natural habitats can not only (i) act as a refuge for red-listed pollinators (e.g. Kormann et al. 2015) and (ii) stabilize pollination services in pollinator dependant crops (Garibaldi et al. 2011), but also that semi-natural habitats can relax the spatial community turnover of two important pollinator groups, solitary bees and hoverflies. Several studies have shown that agricultural intensification can promote homogenization of local communities through loss of disturbance-intolerant species (e.g., Flohre et al. 2011; Dormann et al. 2007; Hendrickx et al. 2007; Ekroos et al. 2010). However, these studies usually only account for species composition per habitat type and do not consider differences in the distribution of species throughout the landscape, characterized by many habitat types. Our spatially explicit approach allowed us to demonstrate that semi-natural habitats can dampen spatial turnover in community structure, at least temporarily. This was true for both bees and hoverflies, indicating that, in this case, the diversity of resource requirements and dispersal abilities within the taxonomic groups was more important than between groups. Larger proportions of semi-natural habitats could foster movements throughout the landscape, thereby generating the observed community homogenization, but further studies are necessary to define the mechanisms driving this effect. Given its homogenizing effect, increasing percentages of semi-natural habitats should promote community resilience after disturbances in response to agricultural disturbance of the landscape, disturbance of the landscape, soliciting a recolonisation and of the landscape by pollinators. Additionally, the temporal scale was also shown to be an important factor influencing the effect of semi-natural habitats and local diversity. Using a novel grid-based approach to study biodiversity turnover in replicated landscapes, our study may serve as a basis to unravel community turnover in space and time. From a conservation point of view, our study shows that semi-natural habitats can act as stepping stones for individuals between habitats, allowing movement across larger distance in an agricultural matrix.

Author contributions

TB, TT and CS conceived and designed the study. TB conducted fieldwork. TB and UK performed statistical analyses. TB, UK, TT and CS wrote the manuscript.

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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.2018.01.016>.

References

- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113, 146–151.
- Bates, D., 2005. Fitting linear mixed models in R - using the lme4 package. In: *R News - The Newsletter of the R Project*. vol. 5. pp. 27–30.
- Beduschi, T., Tschamtké, T., Scherber, C., 2015. Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes. *Landsc. Ecol.* 1–12.
- Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., ... Settele, J., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313 (5785), 351–354.
- Benjamin, F.E., Reilly, J.R., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J. Appl. Ecol.* 51 (2), 440–449.
- Bivand, R., 2014. *spdep: Spatial Dependence: Weighting Schemes, Statistics and Models*. R Package Version 0.5-71.
- Bivand, R.S., Pebesma, E.J., Gómez-Rubio, V., 2008. *Applied Spatial Data Analysis with R*. Springer, New York.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B* 277, 2075–2082 (rsbp20092221).
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.
- Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8, 1175–1182.
- Crawley, M.J., 2013. *The R Book*. John Wiley & Sons, West Sussex.
- DeVries, P.J., Murray, D., Lande, R., 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.* 62, 343–364.
- DeVries, P.J., Walla, T.R., Greeney, H.F., 1999. Species diversity in spatial and temporal dimensions of fruit feeding butterflies from two Ecuadorian rainforests. *Biol. J. Linn. Soc.* 68, 333–353.
- Diekötter, T., Peter, F., Jauker, B., Wolters, V., Jauker, F., 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy* 6 (3), 219–226.
- Dormann, C.F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., De Blust, G., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J.P., Schmidt, T., Speelmann, M., Van Wingerden, W.K.R.E., Zobel, M., 2007. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Glob. Ecol. Biogeogr.* 16, 774–787.
- Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic Appl. Ecol.* 4, 129–138.
- Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *J. Appl. Ecol.* 47, 459–467.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14, 101–112.
- FAOSTAT, 2016. *The global harvest of oil seed rape*. <http://faostat3.fao.org/download/Q/QD/E> (Accessed on Tue Aug 09 09:02:29 CEST 2016).
- Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M.B., Oñate, J.J., Pärt, T., Weisser, W.W., Winqvist, C., Thies, C., Tschamtké, T., 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecol. Appl.* 21, 1772–1781.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Frank, T., 1999. Density of adult hoverflies, Dipt., Syrphidae. In sown weed strips and adjacent fields. *J. Appl. Entomol.* 123, 351–355.
- Gámez-Virués, S., Perovic, D.J., Gossner, M.M., Borschig, C., Bluthgen, N., de Jong, H., Simons, N.K., Klein, A.M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothewohrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tschamtké, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* 6, 8568.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschamtké, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
- Gathmann, A., Tschamtké, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71, 757–764.
- Gladbach, D.J., Holzschuh, A., Scherber, C., Thies, C., Dormann, C.F., Tschamtké, T., 2011. Crop–noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats. *Oecologia* 166, 433–441.
- Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tschamtké, T., Holzschuh, A., 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. *J. Appl. Ecol.* 51, 505–513.
- Hänke, S., Scheid, B., Schaefer, M., Tschamtké, T., Thies, C., 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *J. Appl. Ecol.* 46, 1106–1114.
- Harrison, S., Taylor, A.D., 1997. *Empirical Evidence for Metapopulation Dynamics*. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA, pp. 27–42.
- Haslett, J.R., 1989. Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris*, Diptera: Syrphidae. *Oecologia* 81, 361–363.
- Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speelmann, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacsek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R., 2007. How landscape structure, landuse intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* 44, 340–351.
- Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A., Taper, M.L., 2005. Theoretical models of species' borders: single species approaches. *Oikos* 108, 18–27.
- Holzschuh, A., Steffan-Dewenter, I., Tschamtké, T., 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117, 354–361.
- Holzschuh, A., Dormann, C.F., Tschamtké, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B* 278, 3444–3451.
- Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vila, M., Vujic, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* 19 (10), 1228–1236.
- Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landsc. Ecol.* 24, 547–555.
- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81–87.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtké, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313.
- Kormann, U., Rösch, V., Batáry, P., Tschamtké, T., Orsi, K.M., Samu, F., Scherber, C., 2015. Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. *Divers. Distrib.* 21 (10), 1204–1217.
- Kovács-Hostyánszki, A., Batáry, P., Báldi, A., 2011. Local and landscape effects on bee communities of Hungarian winter cereal fields. *Agric. For. Entomol.* 13, 59–66.
- Kovács-Hostyánszki, A., Haenke, S., Batáry, P., Jauker, B., Báldi, A., Tschamtké, T., Holzschuh, A., 2013. Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecol. Appl.* 23, 1938–1946.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–16816.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Liebold, A.M., Gurevitch, J., 2002. Integrating the statistical analysis of spatial data in ecology. *Ecography* 25, 553–557.
- Martin, L.J., Blossy, B., Ellis, E., 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.* 10, 195–201.
- McCann, K.S., 2000. The diversity-stability debate. *Nature* 405, 228–233.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H., Nowakowski, M., 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biol. Conserv.* 106, 259–271.

- Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10, 178–186.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Core Team, R., 2013. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-113.
- R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P., Howlett, B.G., Winfree, R., ... Bommarco, R., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* 113 (1), 146–151.
- Raymond, L., Plantegenest, M., Vialatte, A., 2013. Migration and dispersal may drive to high genetic variation and significant genetic mixing: the case of two agriculturally important, continental hoverflies, *Episyrphus balteatus* and *Sphaerophoria scripta*. *Mol. Ecol.* 22, 5329–5339.
- Scherber, C., 2015. Insect responses to interacting global change drivers in managed ecosystems. *Curr. Opin. Insect Sci.* 11, 56–62.
- Scherber, C., Lavandero, B., Meyer, K.M., Perovic, D., Visser, U., Wiegand, K., Tschardtke, T., 2012. Scale effects in biodiversity and biological control: methods and statistical analysis. In: Gurr, G.M., Wratten, S.D., Snyder, W.E. (Eds.), *Biodiversity and Insect Pests: Key Issues for Sustainable Management*. John Wiley & Sons, pp. 137–153.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? *Trends Ecol. Evol.* 31 (1), 67–80.
- Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. *Ecography* 30, 3–12.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tschardtke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Thies, C., Roschewitz, I., Tschardtke, T., 2005. The landscape context of cereal aphid–parasitoid interactions. *Proc. R. Soc. B* 272, 203–210.
- Thies, C., Steffan-Dewenter, I., Tschardtke, T., 2008. Interannual landscape changes influence plant–herbivore–parasitoid interactions. *Agric. Ecosyst. Environ.* 125, 266–268.
- Tschardtke, T., Brandl, R., 2004. Plant–insect interactions in fragmented landscapes. *Annu. Rev. Entomol.* 49, 405–430.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8, 857–874.
- Tschardtke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, H.M., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol. Rev.* 87, 661–685.
- Tylianakis, J.M., Klein, A.M., Tschardtke, T., 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology* 86, 3296–3302.
- Van Der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., ... Barbaro, L., 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proc. Natl. Acad. Sci.* 113 (13), 3557–3562.
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965.
- Westrich, P., 1996. *Habitat Requirements of Central European Bees and the Problems of Partial Habitats*. Linnean Society Symposium Series. Vol. 18. Academic Press Limited, pp. 1–16.
- Wiersma, Y.F., Urban, D.L., 2005. Beta-diversity and nature reserve system design: a case study from the Yukon. *Conserv. Biol.* 19, 1262–1272.
- Williams, N.M., Minckley, R.L., Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. *Conserv. Ecol.* 5, 7.
- Winfree, R., Kremen, C., 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. B* 276, 229–237.
- Wissinger, S.A., 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biol. Control* 10, 4–15.
- Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R., Tylianakis, J.M., 2003. Field boundaries as barriers to movement of hoverflies, Diptera: Syrphidae, in cultivated land. *Oecologia* 134 (4), 605–611.