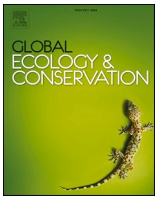
Global Ecology and Conservation 55 (2024) e03218

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Insect conservation in agricultural landscapes needs both high crop heterogeneity and semi-natural habitats

Sara Tassoni [a,*,1], David Becker [a,2], Marit Kinga Kasten [a,3], Jérôme Morinière [b,4], Ingo Grass [a,c,5]

[a] *Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany*
[b] *Advanced Identification Methods (AIM) GmbH, Leipzig, Germany*
[c] *Center for Biodiversity and Integrative Taxonomy (KomBioTa), University of Hohenheim, Stuttgart, Germany*

ARTICLE INFO

Keywords:
Landscape complexity
Crop heterogeneity
Insect richness
Agricultural diversification
Semi-natural habitat

ABSTRACT

Identifying landscapes that are suitable for both biodiversity conservation and agricultural production is a major challenge. Traditionally, much research has focused on biodiversity conservation outside of agricultural production areas, e.g., in semi-natural habitats. In contrast, recent research has mainly focused on the potential of crop heterogeneity. This includes both compositional (crop diversity) and configurational heterogeneity (field border density). However, if and how crop heterogeneity, and semi-natural habitats interact to shape insect diversity in agricultural landscapes remains poorly understood. Here we investigated the combined effects of crop diversity, field border density, and semi-natural habitats (i.e., grassland proportion, hedge density) on insect diversity. We sampled insect communities from 14 – 17 June 2021 with pan traps in 27 study landscapes (500 m x 500 m) covering independent gradients of these landscape variables and identified a total of 587 insect species with DNA metabarcoding. We found that field border density mediated the effects of crop diversity, grassland proportion, and hedge density on insect richness. At low levels of field border density (i.e., landscapes with mostly large fields), effects were either neutral (crop diversity), negative (grassland proportion) or weakly positive (hedge density). By contrast, at high levels of field border density, crop diversity, grassland proportion, and hedge density all exerted positive effects on insect richness. Responses to crop heterogeneity and semi-natural habitat differed among trophic groups of insects (decomposers, herbivores, parasitoids, predators). While variation in richness of herbivorous insects followed the patterns of the overall richness, decomposer richness was not related to any of the investigated variables. Predator richness increased with hedge density in landscapes, whereas parasitoid richness increased when high levels of field border density and grassland proportion coincided. Our study shows that increasing crop heterogeneity is a viable strategy for promoting insect diversity in agricultural landscapes. However, the effects of the amount of remaining semi-natural habitats, such as grassland or hedges, are mediated by configurational heterogeneity, and vary

---

* Corresponding author.
E-mail addresses: sara.tassoni@uni-hohenheim.de (S. Tassoni), d.becker@uni-hohenheim.de (D. Becker), marit.kasten@uni-hohenheim.de (M.K. Kasten), jerome.moriniere@aim.science (J. Morinière), ingo.grass@uni-hohenheim.de (I. Grass).

[1] https://orcid.org/0009-0000-3659-1824
[2] https://orcid.org/0009-0009-3339-3430
[3] https://orcid.org/0009-0006-4412-7283
[4] https://orcid.org/0000-0001-9167-6409
[5] https://orcid.org/0000-0001-7788-1940

https://doi.org/10.1016/j.gecco.2024.e03218
Received 9 August 2024; Received in revised form 20 September 2024; Accepted 25 September 2024

between trophic groups. Efforts to conserve insects in agricultural landscapes must therefore focus on both increasing the heterogeneity of the crop matrix by promoting crop diversity and increasing the density of field borders, while also maintaining or restoring semi-natural habitats as important source habitats for insect species.

1. Introduction

Faced with dramatic insect declines (Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019) and increasing food demand of a growing population (Van Dijk et al., 2021), more sustainable management of agricultural landscapes is urgently needed. Past research emphasizes the benefits of preserving semi-natural habitats to mitigate negative impacts of intensive agriculture on biodiversity (Batáry et al., 2011; Duflot et al., 2015; Holland et al., 2017; Shi et al., 2021; Tscharntke et al., 2005, 2021). Maintaining such non-arable sites, however, may come at the cost of reductions in cropping area. In addition, in intensively managed agricultural landscapes, semi-natural habitats may cover only negligible land shares (< 5 %) or have been completely lost. Furthermore, there has been an increasing awareness that biodiversity conservation in agricultural landscapes also necessitates high permeability of the agricultural matrix to promote colonization and dispersal dynamics of species (Grass et al., 2019, 2021). This has led to an increasing interest in the potential of a heterogenous crop matrix for biodiversity conservation (Batáry et al., 2017; Fahrig et al., 2011; Hass et al., 2018; Sirami et al., 2019). Recent studies emphasize that both enhanced crop compositional heterogeneity (e.g., crop diversity) and configurational heterogeneity (e.g., field border density) can benefit farmland biodiversity (Beillouin et al., 2021; Lichtenberg et al., 2017; Priyadarshana et al., 2021, 2024; Sirami et al., 2019; Tamburini et al., 2020).

A remaining key question is to what extent the benefits of a more heterogeneous crop matrix for farmland biodiversity depend on the availability and extent of semi-natural habitats (Tscharntke et al., 2024). Semi-natural habitat, such as permanent grassland or hedgerows, can provide important resources for species (e.g., nesting sites, flower resources) and refuge areas in crop-dominated landscapes (Grass et al., 2021; Tscharntke et al., 2021). Without semi-natural habitat, measures to increase crop heterogeneity, such as reducing field size, may not be as effective as when some semi-natural habitat is retained (Tscharntke et al., 2012, 2024). For example, a large-scale study found that the effect of increasing crop diversity on multi-trophic diversity depended on the amount of semi-natural habitat cover (Sirami et al., 2019). In the same study, decreasing field size benefited multitrophic diversity even in the absence of semi-natural habitats (Sirami et al., 2019). In general, the potential interactions between crop diversity, field border density, and semi-natural habitat, however, are still poorly understood (Tscharntke et al., 2024).

A major part of farmland biodiversity is made up by insects. Insects exhibit different responses to land-use depending on their trophic position in food webs (Scherber, 2015). The vulnerability of species to environmental perturbations typically increases towards higher trophic levels. This may be the case as top consumers (e.g., predators, parasitoids) depend not only on the landscape heterogeneity, but also on prey availability (Jonsson et al., 2012; Klaus et al., 2023; Trebilco et al., 2013; Voigt et al., 2003). So far, it is little

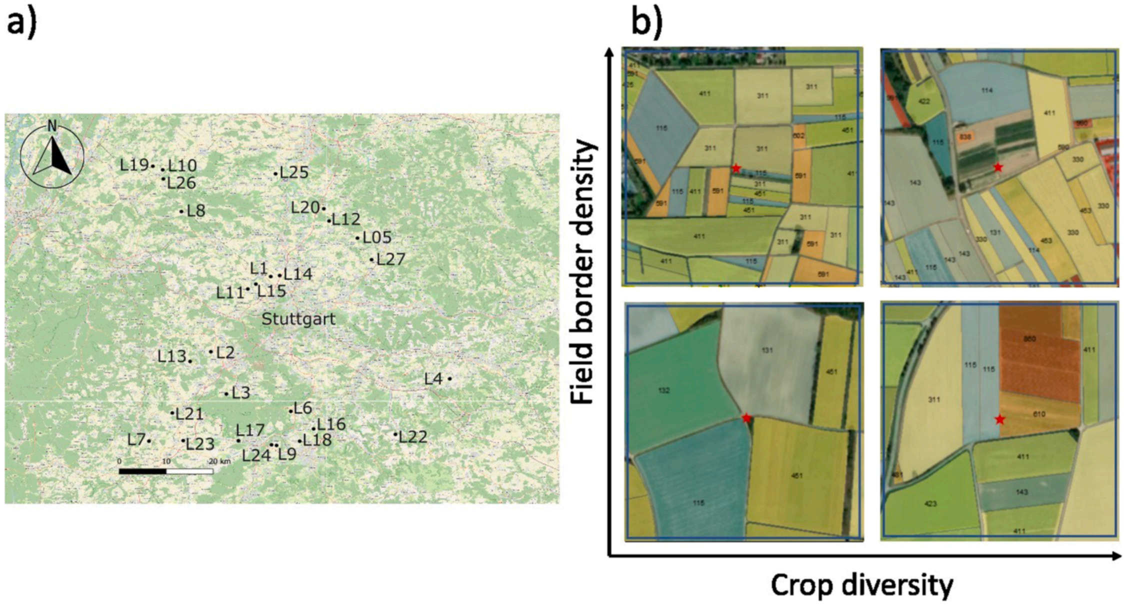


Fig. 1. a) Overview of the study landscapes located around Stuttgart (in the centre of the map). b) Four exemplary study landscapes representing different combinations of the independent gradients of configurational heterogeneity, i.e. field border density, and compositional heterogeneity, i.e. crop diversity (from top left to lower right: L9, L1, L10, L3). See Table 1 for the descriptive statistics of field border density and crop diversity across all 27 landscapes.

studied, whether and how the effects of landscape-level crop heterogeneity on insects are moderated by their trophic group. Here we studied the combined effects of crop heterogeneity, both compositional (e.g., crop diversity) and configurational (e.g., field border density), and semi-natural habitats (grassland and hedgerows) on flying insect diversity. We focused on overall insect diversity and different trophic groups in landscapes of 500 m x 500 m. We hypothesized that:

H1: Crop heterogeneity (crop diversity and field border density) interacts with the amount of semi-natural habitat (grassland proportion and hedge density) in shaping insect richness in agricultural landscapes. This shall result in the highest insect richness in landscapes with high crop heterogeneity and large amounts of semi-natural habitats.

H2: Insect species' response to crop heterogeneity and semi-natural habitat is mediated by their trophic position in food webs. While we anticipate that greater crop heterogeneity and semi-natural habitat will generally enhance insect richness, the specific drivers may vary across different trophic groups.

2. Materials and methods

2.1. Landscape selection and mapping

We conducted our study in the agricultural landscapes surrounding the city of Stuttgart, southwestern Germany (48°46′39″N 09°10′48″E). The study region covered 60 km x 65 km. In the region, we identified 27 study landscapes, measuring 500 m x 500 m each. We chose this landscape extent because of the low mobility of many target taxa, e.g., wild bees with home ranges of a few hundred metres (Gathmann and Tscharntke, 2002), and to be able to comprehensively ground-truth landscape composition and configuration during field surveys. Landscapes were chosen along independent gradients of compositional (i.e., crop diversity) and configurational (i.e., field border density) heterogeneity (Fig. 1). All landscapes had at least 45 % agricultural field cover (range: 45–97 %; mean ± SD = 75 % ± 14 %). The minimum pairwise distance between study landscapes was 1081 m (37,598 m ± 18,683 m). Study landscapes were selected using land use information from the State Ministry for Agriculture Baden-Württemberg, based on farmers cropping in the year 2020. For final classification of crop types, we ground-truthed crops in all landscapes in the study year 2021. Agricultural areas were classified into crop species, permanent grassland, or other, following the classification scheme of the State Ministry for Agriculture of Baden-Württemberg (Table A.1 in Supplementary Material; Table B.1 in Supplementary Data).

To assess the compositional heterogeneity of the agricultural crop matrix we assessed the crop diversity per study landscape. To do so, we calculated the Shannon-Diversity of the crop types with their proportional covers as weights (Table 1; Table B.2 in Supplementary Data). To assess the configurational heterogeneity of the crop matrix, we calculated the field border density in metres per hectare within the study landscapes (Table 1; Table B.2 in Supplementary Data). In addition, we assessed the proportional cover of grassland and the hedge density in metres per hectare in each study landscape as important elements of semi-natural habitat (Table 1). None of the landscape variables (crop diversity, field border density, grassland proportion, and hedge density) were correlated (pairwise Pearson's $r \leq 0.52$ in all cases) (Table A.2 in Supplementary Material).

2.2. Insect collection

We used UV-bright yellow pan traps to collect flying insects (Waldstein, neon-yellow; Fig. A.1 in Supplementary Material). UV-bright yellow pan traps are known to be a highly effective and standardized method to collect flying arthropods with high sample coverage (Buffington et al., 2021; Saunders and Luck, 2013; Vrdoljak and Samways, 2012; Wang et al., 2017; Westphal et al., 2008). Between June 14th and June 17th 2021, we set-up three yellow pan traps in each study landscape. Traps were always placed next to cereal fields, with one trap placed at the centre of the study landscape and the two other traps spaced ca. 50 m apart from the central trap. Pan traps were placed on poles, standardized to ca. 80 cm above ground level and filled with water and dish washing liquid. The traps were exposed for 48 h, after which all captured insects were collected and preserved in a 70 % ethanol solution.

2.3. Insect identification with DNA metabarcoding

We counted all trapped insect individuals, and afterwards identified them using DNA metabarcoding. The data obtained from metabarcoding and bioinformatic analysis underwent the following processing steps: we excluded non-arthropod entries, entries with identification accuracy below 95 %, and those shorter than 300 base pairs. Afterwards, we aggregated entries sharing the same Barcode Index Numbers (BINs). In this study, we use the term 'species' to refer to unique BINs identified through the metabarcoding

Table 1
Overview of the landscape variables representing crop heterogeneity (crop diversity, measured as crop shannon diversity index, and field border density) and semi-natural habitat (grassland proportion and hedge density). For each variable, the minimum, the average, the maximum and standard deviation are given.

	Variable	Min.	Mean	Max.	Std. Dev.
Crop composition	Crop Shannon diversity Index	0.74	1.38	1.95	0.25
Crop configuration	Field border density (m ha^{-1})	137.8	389.6	576.5	97.6
Semi-natural habitat	Grassland proportion	0	0.11	0.38	0.12
	Hedge density (m ha^{-1})	0	9.9	23.2	6.7

method. An overview of the resulting 587 species and their corresponding information on class, order, family, genus and species (if applicable) is available in Table B.3 in the Supplementary Data). More details on the methods of DNA metabarcoding and bioinformatics are provided in the Supplementary Material.

2.4. Assignment of insects to trophic groups

Each species was assigned to one of the following four trophic groups: decomposer, herbivore, predator, parasitoid, based on their larval feeding behaviour as provided by the insect trait tool 1.0 (Hörren et al., 2022) that covers 586 insect families (> 34,000 species) of Central Europe. Herbivores included both insects feeding on vegetative plant parts (e.g., leaves) as well as insects feeding on pollen or nectar. Parasitic larvae were classified as predators, since they feed on living animals, reducing their fitness. For species identified at family level, if one trait was present in more than 50 % of the species within that family, we assigned that trait to the species. In cases where two trophic groups had an equal probability of 50 %, or when a species could not be identified at the family level, we marked the trophic group as "NA" (not available). Where insect families were not included in the database, additional literature sources were consulted to determine their trophic groups (listed in the Supplementary Material). When an insect family covered two or more trophic groups and the entry was identified to the species level, we searched the literature to determine its larval feeding behaviour.

2.5. Statistical analysis

For each landscape, we calculated insect richness as the sum of all species across its three pan traps. In addition to the overall insect richness, we calculated the insect richness of each trophic group: parasitoids, predators, herbivores and decomposers (see Table B.3 in the Supplementary Data). For each of our measures of insect richness (overall and richness per group) we set up a generalized linear model with Poisson distribution. We included insect richness as response variable, and crop diversity, field border density, grassland proportion, and hedge density as predictors. In addition to the main effects, we included all possible two-way interactions of the predictor variables. In cases where a two-way interaction was not statistically significant ($p > 0.05$), we omitted the interaction. Thus, the final model for each measure of insect richness only included significant interactions, as well as the main effects of all predictors. All models met assumptions of normality of residuals and homogeneity of variance. All statistical analyses were done in *R* 4.2.0 (R Core Team, 2022), using the *R*-packages MASS (Ripley et al., 2013) and vegan (Dixon, 2003).

3. Results

We sampled a total of 4501 individuals. From these, we identified 587 unique insect species. We differentiated these 587 insect species into 109 decomposers, 262 herbivores, 152 predators, and 55 parasitoid species; 9 species could not be assigned to a trophic group.

The effects of crop diversity on overall insect richness depended on field border density. At low levels of field border density (e.g., 100 m ha^{-1}), crop diversity and species richness were not related. At high levels of field border density (e.g., 500 m ha^{-1}), higher crop diversity led to increasing species richness (Estimate = 0.170, SE = 0.049, $P < 0.001$; Table 2; Fig. 2a). A similar interaction was found for field border density and grassland proportion in the study landscapes. Increasing grassland proportion led to a reduced insect richness in landscapes with low field border density, but led to increasing richness in landscapes with high field border density (Estimate = 0.173, SE = 0.045, $P = < 0.001$; Table 2; Fig. 2b). Lastly, field border density and hedge density exerted interactive effects, with more positive effects of hedge density on insect richness in landscapes with high field border density (Estimate = 0.087, SE = 0.031, P = 0.006; Table 2; Fig. 2c).

The different functional groups varied in their response to landscape heterogeneity and semi-natural habitat elements. Herbivore richness followed the patterns found for the overall insect richness (Fig. 3). Thus, herbivore richness increased in landscapes where high crop diversity coincided with high field border density (Estimate = 0.157; SE = 0.077; P = 0.039; Table 3b, Fig. 3a). Likewise, increasing field border density led to positive effects of grassland proportion (Estimate = 0.188, SE = 0.069, P = 0.007) and hedge

Table 2
Results from a generalized linear model investigating the effects of crop diversity, field border density, grassland proportion and hedge density on overall species richness of all insects sampled with pan traps across 27 study landscapes. Statistically significant two-way interactions of predictors were also fitted. Predictors were scaled to zero mean and unit variance; effect strengths are thus directly comparable. Statistically significant ($p < 0.05$) effects are highlighted in boldface type.

	Insect richness			
	Estimate	SE	Z	P
(Intercept)	**4.078**	**0.029**	**142.728**	**< 0.001**
Crop diversity	0.011	0.034	0.315	0.753
Field border density	0.045	0.039	1.151	0.249
Grassland proportion	**−0.097**	**0.031**	**−3.126**	**0.002**
Hedge density	**0.114**	**0.029**	**3.896**	**< 0.001**
Crop diversity: Field border density	**0.170**	**0.049**	**3.479**	**< 0.001**
Field border density: Grassland proportion	**0.173**	**0.045**	**3.836**	**< 0.001**
Field border density: Hedge density	**0.087**	**0.031**	**2.769**	**0.006**

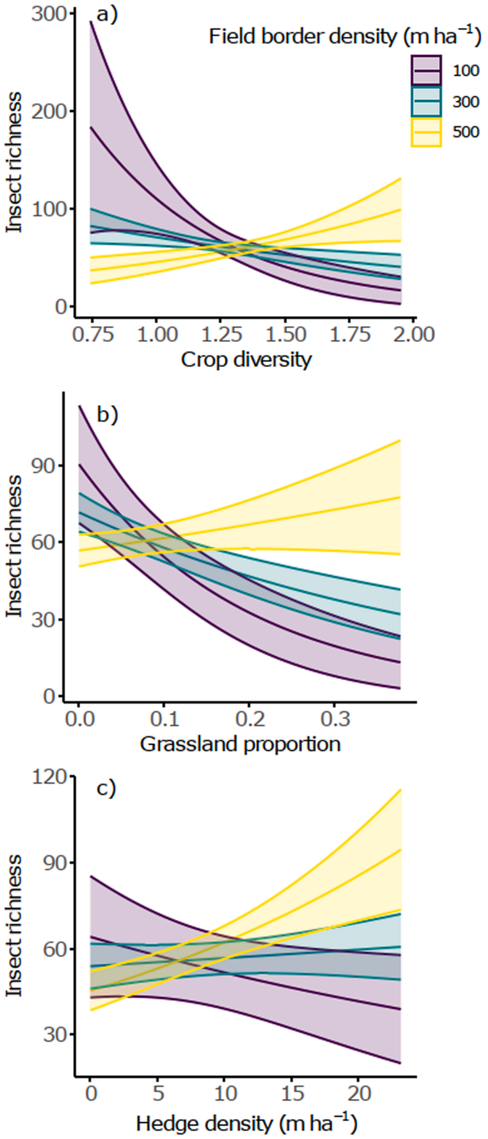


Fig. 2. Field border density mediates the effects of (a) crop diversity, (b) grassland proportion, and (c) hedge density on insect richness in agricultural landscapes. Shown are model predictions (solid lines) from a generalized linear model with 95 % confidence intervals (shaded areas). See Table 2 for model estimates.

density on herbivore richness (Estimate = 0.126, SE = 0.050, P = 0.012; Table 3b, Fig. 3b-c). By contrast, decomposers did not respond significantly to any of the tested predictors (crop diversity, field border density, grassland proportion, hedge density) or their two-way interactions (Table 3a; Fig. 4). Predator richness increased with greater hedge density in the study landscapes (Estimate = 0.160, SE = 0.053, P = 0.003; Table 3c; Fig. 4d) but was not additionally affected by any other of the tested variables (Table 3c; Fig. 4a-c). Lastly, the interaction of field border density and grassland proportion affected parasitoid richness, (Estimate = 0.379, SE = 0.150; P = 0.012; Table 3d), with more positive effects of increasing grassland proportion at higher levels of field border density (Fig. A.2 in Supplementary Material).

4. Discussion

Here we studied the potential of increasing crop heterogeneity and semi-natural habitats for insect conservation in agricultural landscapes. We found that increasing crop diversity and the amount of grassland as well as hedge density promoted insect richness, but only when field border density was high. While in landscapes with high field border density (e.g., 500 m ha^{-1}) crop diversity, grassland proportion, and hedge density were all positively related to overall insect richness, these positive effects were less pronounced or missing from landscapes with low field border density (e.g., 100 m ha^{-1}). Similar patterns were found for the richness of

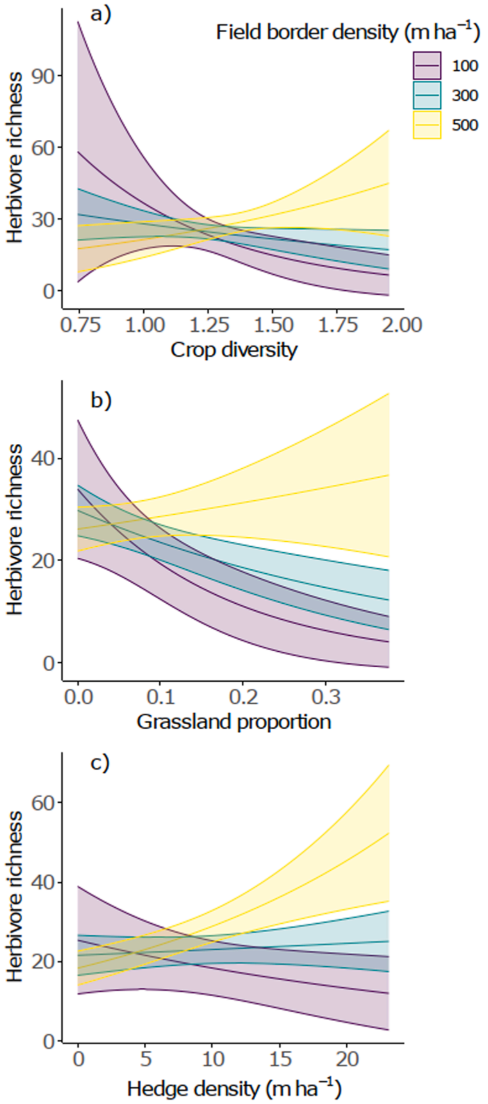


Fig. 3. Herbivore richness in agricultural landscapes is driven by interactions between field border density and (a) crop diversity, (b) grassland proportion, and (c) hedge density. Shown are model predictions (solid lines) from a generalized linear model with 95 % confidence intervals (shaded areas). See Table 3 for model estimates.

herbivores, while parasitoid richness was only influenced by the interaction of field border density and grassland proportion. Predator richness only responded positively to increasing hedge density. Decomposer richness was not influenced by any of the tested variables.

4.1. Field border density mediates the effect of crop diversity and of semi-natural habitats on insect richness

Our data did not reveal simple additive effects of crop diversity and field border density, as suggested by a large body of literature (e.g., Batáry et al., 2017; Fahrig et al., 2011; Priyadarshana et al., 2021, 2024; Reynolds et al., 2018; Tscharntke et al., 2021). Instead, as hypothesized, we found that field border density mediated the effects of crop diversity on insect richness: increasing crop diversity had a positive effect on insect richness in landscapes with high field border density (i.e., fields were smaller on average), but not in landscapes with low field border density. This could be due to higher spatial and temporal resource complementarity and enhanced connectivity in landscapes with high crop heterogeneity (Grass et al., 2019; Tscharntke et al., 2024). The presence of different crop species in close spatial proximity, due to smaller field sizes, increases the diversity of insects' foraging resources and nesting sites. This arrangement also makes these resources more accessible, as insects do not have to cover long distances to fulfil their life cycle requirements (e.g., Dunning et al., 1992; Priyadarshana et al., 2021; Reynolds et al., 2018). A second benefit of increased resource heterogeneity for insects is that the varying phenological stages of crops provide a wider range of resources over an extended period (Schellhorn et al., 2015). Functional traits of crop plants (i.e. plant size, leaf shape, stoichiometry, palatability, flower shape, nectar

Table 3

Model results from generalized linear models showing the effects of crop diversity, field border density, grassland proportion and hedge density on species richness of (a) decomposers, (b) herbivores, (c) predators, and (d) parasitoids. Models include only statistically significant two-way interactions of predictors. Predictors were scaled to zero mean and unit variance; effect strengths are thus directly comparable. Statistically significant (p <0.05) effects are highlighted in boldface type.

	(a) Decomposer richness				**(b) Herbivore richness**				**(c) Predator richness**				**(d) Parasitoid richness**			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
(Intercept)	**2.312**	**0.061**	**38.088**	**< 0.001**	**3.238**	**0.044**	**73.956**	**< 0.001**	**2.877**	**0.046**	**62.603**	**< 0.001**	**1.420**	**0.099**	**14.421**	**< 0.001**
Crop diversity	−0.005	0.073	−0.073	0.942	0.017	0.051	0.325	0.745	−0.023	0.056	−0.409	0.682	−0.015	0.125	−0.117	0.907
Field border density	−0.104	0.079	−1.302	0.193	0.109	0.059	1.855	0.064	−0.047	0.059	−0.781	0.435	−0.184	0.134	−1.372	0.170
Grassland proportion	−0.015	0.071	−0.207	0.836	**−0.106**	**0.047**	**−2.245**	**0.025**	−0.066	0.052	−1.257	0.209	−0.223	0.121	−1.844	0.065
Hedge density	−0.015	0.072	−0.214	0.830	**0.159**	**0.045**	**3.558**	**< 0.001**	**0.160**	**0.053**	**3.001**	**0.003**	0.019	0.113	0.174	0.862
Crop diversity: Field border density					**0.157**	**0.077**	**2.057**	**0.039**								
Field border density: Grassland proportion					**0.188**	**0.069**	**2.693**	**0.007**					**0.379**	**0.150**	**2.528**	**0.012**
Field border density: Hedge density					**0.126**	**0.050**	**2.517**	**0.012**								

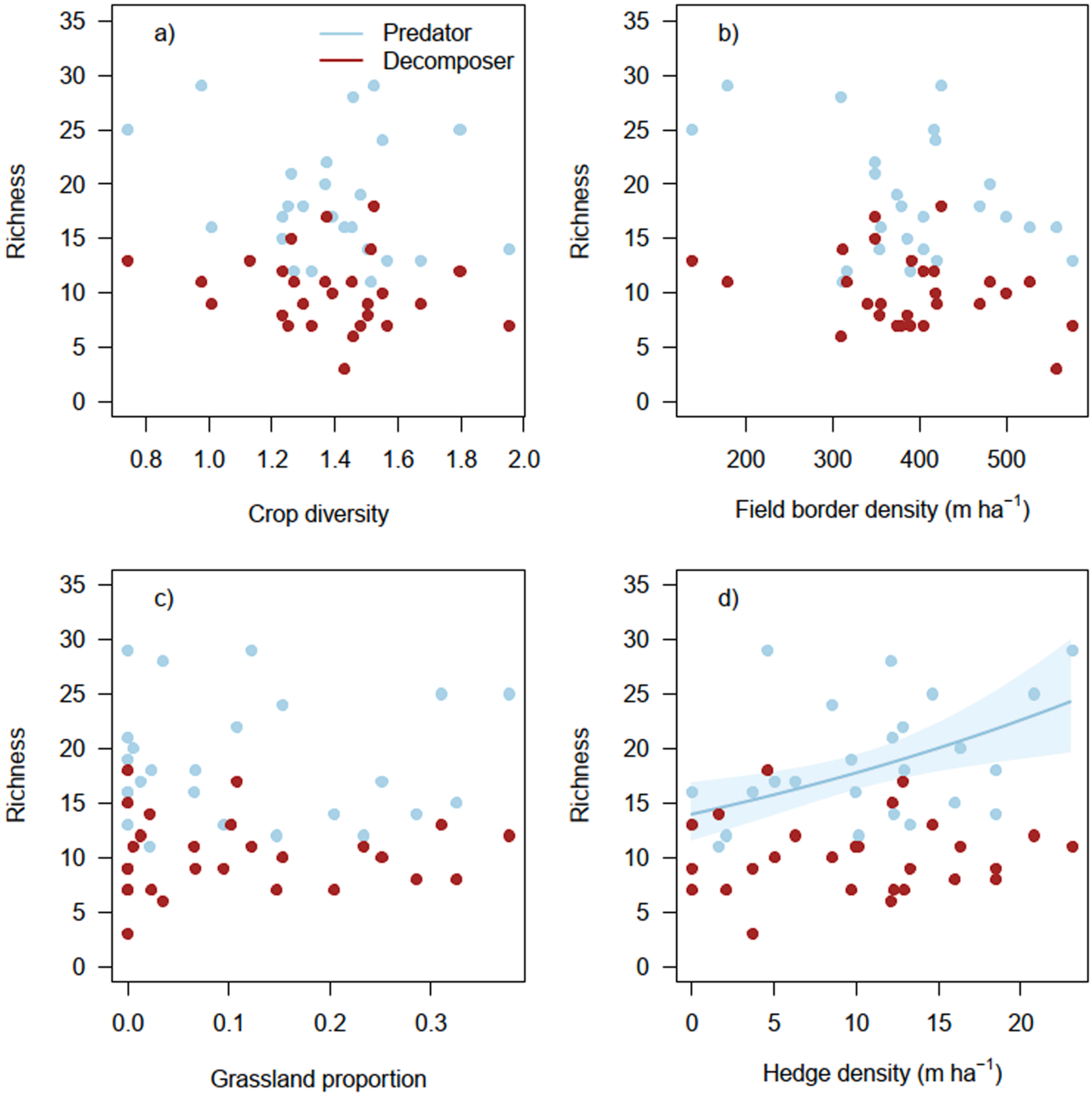


Fig. 4. Species richness of predators (blue dots) and decomposers (brown dots) with variation in a) crop diversity, b) field border density, c) grassland proportion, and d) hedge density in the 27 study landscapes. Dots indicate raw data. The statistically significant effect of hedge density on predator richness (solid blue line) is shown with its 95 % confidence interval (shaded blue area). See Table 3 for model estimates.

amount) play a major role for insect perception and their use of the agricultural matrix (Dafni and Kevan, 1996). Placing functionally complementary crops next to each other can create more foraging and reproductive opportunities for insects (Fahrig et al., 2011; Hass et al., 2018; Martin et al., 2019; Priyadarshana et al., 2021; Schlinkert et al., 2016).

Similar to the effect of crop diversity on insect richness, the effects of increasing the amount of semi-natural habitats depended on field border density, i.e., landscapes with smaller fields and higher grassland proportion or hedge density had greater insect richness. Generally, smaller fields may result in grasslands being closer together, which increases connectivity across the agricultural matrix and thus promotes immigration of species into habitat patches (Etienne, 2004; Ricketts et al., 2008). Thereby, especially extensively managed grasslands can contribute to insect spillover, e.g., of wild bees, into the adjacent crop matrix (Klaus et al., 2021). In addition to grassland, hedge density had a positive effect on the overall insect richness. The benefits of hedgerows for insect conservation in agricultural landscapes are widely acknowledged (Blitzer et al., 2012; Dover et al., 2000; Fahrig et al., 2011; Martin et al., 2019; Van Geert et al., 2010). Hedgerows act as shelters and reservoirs for insects, providing important food resources and nesting sites, even if hedges can sometimes become an obstacle to their movement (Coulthard et al., 2016; Klaus et al., 2015). The interaction between hedge density and field border density can be attributed to the fact that larger fields may result in hedges being further apart, reducing connectivity within the landscape (Grass et al., 2019). By contrast, their positive impact is amplified when high hedge density coincides with high field border density, facilitating insect movement and spillover across the landscape matrix and thus the survival of insect species in meta-populations (Dover et al., 2000; Fahrig et al., 2011; Joyce et al., 1999; Martin et al., 2019).

4.2. Effects of crop heterogeneity and semi-natural habitats differ between trophic groups

As hypothesized, insect trophic groups responded differently to crop heterogeneity and semi-natural habitat. Herbivores were very similar in their response to the overall richness of all insects. Accordingly, herbivores benefited from increasing crop diversity, grassland proportion and hedge density in landscapes with high field border density. This can be explained by the fact that herbivores accounted for 45 % of the overall species richness. Among insects with herbivorous larvae, the most species-rich families were Cecidomyiidae (38 species), Chloropidae (24) and Aphididae (20). Cecidomyiid midges are mostly monophagous (Hall et al., 2012), so it is likely that different species benefited from increased crop diversity in the landscape. Grass flies (Diptera: Chrolopidae) are more likely to feed on monocots of the Cyperales and Poales groups, which include several cereal crops and grass species (Nartshuk, 2014). So, it is plausible that they benefited from heterogeneous landscapes with higher crop diversity and proportion of semi-natural habitats. Among the aphids (Hemiptera: Aphididae), we have found several specialist species that may benefit from host plants present in grasslands, e.g., *Hydaphias molluginis* feeding on *Gallium* sp., *Hyalopteroides humilis* feeding on *Dactylis* sp. and *Uroleucon taraxaci* feeding on *Taraxacum* sp. (Blackman and Eastop, 2008). Other species may benefit from a high crop diversity, because they are specialized on certain crops or grasses, e.g., *Syphia maydis* feeding on *Poa* sp. and *Hordeum* sp., *Megoura viciae* feeding on leguminous plants or *Sitobion avenae* feeding on Poaceae (Blackman and Eastop, 2008). A few other species have adopted a host-alternation strategy (woody and non-woody host plants), e.g. *Aphis spiraecola* or *Dysaphis plantaginea*, benefitting both from hedgerows and grasslands (Blackman and Eastop, 2008). In general, our findings support the idea of bottom-up effects: higher plant diversity, due to a more heterogeneous landscape, supports a greater diversity of primary consumers (Moreira et al., 2016; Scherber et al., 2010).

Compared to herbivores, richness of predatory insects was mainly driven by hedge density, in line with previous studies (e.g., Bartual et al., 2019; Ferrante et al., 2024; Garratt et al., 2017; Haenke et al., 2014; Morandin et al., 2014; Pfister et al., 2017). Among the predatory insects, the most species-rich families were Hybotidae (17 species), Dolichopodidae (15) and Syrphidae (13). Our findings are supported by Delettre et al. (1998), Pfister et al. (2017) and Schirmel et al. (2018), who found that hedgerows and water bodies generally had a positive effect on these three families of predatory flies. It is likely that the first two families prefer moist conditions and use woody structures as hunting grounds (Pfister et al., 2017).

Parasitoids, of which 24 species out of a total of 55 belonged to the family Ichneumonidae, benefited from the interaction between grassland proportion and field border density. It is important to note that the landscape with the highest richness had only 9 species (mean ± SD = 4.1 ± 2.2) and landscape effects on parasitoids are usually influenced by host availability (Corcos et al., 2017; Holzschuh et al., 2010; Klaus et al., 2023). Increased connectivity likely made it easier for parasitoids to find suitable hosts that benefit from grassland areas, as well as acquiring additional grassland resources such as flower resources used by parasitoid imagoes (Corcos et al., 2017; Holzschuh et al., 2010; Kruess, 2003; Kruess and Tscharntke, 2000).

Finally, decomposer richness was not related to any of the tested landscape variables, neither related to crop heterogeneity nor semi-natural habitats. Within this group, the most species-rich families were Phoridae (13 species), Sciaridae (12) and Calliphoridae (10). The lack of landscape effects on their richness distribution may be because they experience the landscape at a smaller scale: larvae feed on decaying matter in the soil or within plants (Sánchez et al., 2022), while adults tend to fly low above the soil surface (Frouz and Paoletti, 2000). Thus, they may be more affected by local farmland management (i.e. high fertilisation input) rather than by large-scale landscape heterogeneity. However, as we were not able to collect management data on crops and grasslands at landscape level in our study, the role of agricultural management intensity for insect diversity needs further study. In addition, future studies should consider differences in trophic behaviour of insects between larval and adult life stages, as well as temporal dynamics in general. In this study we collected data during a single time point in midsummer. Therefore, our results should be interpreted with caution with regard to possible seasonal variations and population dynamics of plants and insects.

5. Conclusion

Our findings provide evidence that heterogeneous landscapes that combine high crop heterogeneity with sufficient semi-natural habitats can contribute to conserving insect richness in agricultural landscapes. Promoting connectivity by decreasing field size appears to play a major role, as the largest benefits of enhanced crop diversity, grassland proportion, and hedge density for insect richness were achieved in landscapes with high field border density. At the same time, variation in the responses of different insect trophic groups necessitate the combination of measures to foster crop heterogeneity and to preserve or to restore semi-natural habitat to benefit a wide diversity of insects. Policies that promote crop heterogeneity and the preservation or restoration of semi-natural habitats at the landscape level are encouraged.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

Funding sources

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRediT authorship contribution statement

Sara Tassoni: Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Validation. **David Becker:** Investigation, Writing - review & editing. **Marit Kinga Kasten:** Visualization, Writing - review & editing, Validation. **Jerome Moriniere:** Resources, Writing - review & editing. **Ingo Grass:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Supervision, Visualization, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Research data have already been submitted as supplementary data

Acknowledgements

We thank the local nature conservation authorities for granting us the necessary collection permits. We would also like to thank Yasha Auer and Philipp Merx for their help in the field.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03218.

References

Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., et al., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. Agric., Ecosyst. Environ. 279, 43–52.

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B: Biol. Sci. 278, 1894–1902.

Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.-K., et al., 2017. The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. Nat. Ecol. Evol. 1, 1279–1284.

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., Makowski, D., 2021. Positive but variable effects of crop diversification on biodiversity and ecosystem services. Glob. Change Biol. 27, 4697–4710.

Blackman, R.L., Eastop, V.F., 2008. Aphids on the world's herbaceous plants and shrubs, 2 vol set. John Wiley & Sons.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agric., Ecosyst. Environ. 146, 34–43.

Buffington, M.L., Garretson, A., Kula, R.R., Gates, M.W., Carpenter, R., Smith, D.R., Kula, A.A., 2021. Pan trap color preference across Hymenoptera in a forest clearing. Èntomol. Exp. Et. Appl. 169, 298–311.

Corcos, D., Inclán, D.J., Cerretti, P., Mei, M., Di Giovanni, F., Birtele, D., Rosa, P., De Biase, A., Audisio, P., Marini, L., 2017. Environmental heterogeneity effects on predator and parasitoid insects vary across spatial scales and seasons: a multi-taxon approach. Insect Conserv. Divers. 10, 462–471.

R. Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Coulthard, E., McCollin, D., Littlemore, J., 2016. The use of hedgerows as flight paths by moths in intensive farmland landscapes. J. Insect Conserv. 20, 345–350.

Dafni, A., Kevan, P.G., 1996. Floral symmetry and nectar guides: ontogenetic constraints from floral development, colour pattern rules and functional significance. Bot. J. Linn. Soc. 120, 371–377.

Delettre, Y.R., Morvan, N., Tre\' Hen, P., Grootaert, P., 1998. Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). Biodivers. Conserv. 7, 9–25.

Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930.

Dover, J., Sparks, T., Clarke, S., Gobbett, K., Glossop, S., 2000. Linear features and butterflies: the importance of green lanes. Agric., Ecosyst. Environ. 80, 227–242.

Duflot, R., Aviron, S., Ernoult, A., Fahrig, L., Burel, F., 2015. Reconsidering the role of 'semi-natural habitat'in agricultural landscape biodiversity: a case study. Ecol. Res. 30, 75–83.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 169–175.

Etienne, R.S., 2004. On optimal choices in increase of patch area and reduction of interpatch distance for metapopulation persistence. Ecol. Model. 179, 77–90.

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.

Ferrante, M., Schulze, M., Westphal, C., 2024. Hedgerows can increase predation rates in wheat fields in homogeneous agricultural landscapes. J. Environ. Manag. 349, 119498.

Frouz, J., Paoletti, M.G., 2000. Spatial distribution of different life stages of one Dipteran community along hedgerow and field margin. Landsc. Urban Plan. 48, 19–29.

Garratt, M.P., Senapathi, D., Coston, D.J., Mortimer, S.R., Potts, S.G., 2017. The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. Agric., Ecosyst. Environ. 247, 363–370.

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71, 757–764.

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., et al., 2019. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. People Nat. 1, 262–272.

Grass, I., Batáry, P., Tscharntke, T., 2021. Combining land-sparing and land-sharing in European landscapes. in: Advances in Ecological Research. Elsevier, pp. 251–303.

Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharntke, T., Holzschuh, A., 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. J. Appl. Ecol. 51, 505–513.

Hall, D.R., Amarawardana, L., Cross, J.V., Francke, W., Boddum, T., Hillbur, Y., 2012. The chemical ecology of cecidomyiid midges (Diptera: Cecidomyiidae). J. Chem. Ecol. 38, 2–22.

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C., Fahrig, L., Martin, J.-L., Baudry, J., Bertrand, C., et al., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc. R. Soc. B: Biol. Sci. 285, 20172242.

Holland, J., Douma, J., Crowley, L., James, L., Kor, L., Stevenson, D., Smith, B., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. Agron. Sustain Dev. 37, 31.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79, 491–500.

Hörren, T., Sorg, M., Hallmann, C.A., Zizka, V.M., Ssymank, A., Noll, N.W., Schäffler, L., Scherber, C., 2022. A universal insect trait tool (ITT, v1. 0) for statistical analysis and evaluation of biodiversity research data. BioRxiv 2022–01.

Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. J. Appl. Ecol. 49, 706–714.

Joyce, K., Holland, J., Doncaster, C., 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. Bull. Èntomol. Res. 89, 523–531.

Klaus, F., Bass, J., Marholt, L., Müller, B., Klatt, B., Kormann, U., 2015. Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. J. Landsc. Ecol. 8, 22–31.

Klaus, F., Tscharntke, T., Uhler, J., Grass, I., 2021. Calcareous grassland fragments as sources of bee pollinators for the surrounding agricultural landscape. Glob. Ecol. Conserv. 26, e01474.

Klaus, F., Tscharntke, T., Grass, I., 2023. Trophic level and specialization moderate effects of habitat loss and landscape diversity on cavity-nesting bees, wasps and their parasitoids. Insect Conserv. Divers.

Kruess, A., 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. Ecography 26, 283–290.

Kruess, A., Tscharntke, T., 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on Vicia sepium. Oecologia 122, 129–137.

Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batary, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., et al., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob. Change Biol. 23, 4946–4957.

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., et al., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22, 1083–1094.

Morandin, L.A., Long, R.F., Kremen, C., 2014. Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agric., Ecosyst. Environ. 189, 164–170.

Moreira, X., Abdala-Roberts, L., Rasmann, S., Castagneyrol, B., Mooney, K.A., 2016. Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent findings, and future directions. Curr. Opin. Insect Sci. 14, 1–7.

Nartshuk, E., 2014. Grass-fly larvae (Diptera, Chloropidae): diversity, habitats, and feeding specializations. Èntomol. Rev. 94, 514–525.

Pfister, S.C., Sutter, L., Albrecht, M., Marini, S., Schirmel, J., Entling, M., 2017. Positive effects of local and landscape features on predatory flies in European agricultural landscapes. Agric., Ecosyst. Environ. 239, 283–292.

Priyadarshana, T.S., Lee, M., Ascher, J.S., Qiu, L., Goodale, E., 2021. Crop heterogeneity is positively associated with beneficial insect diversity in subtropical farmlands. J. Appl. Ecol. 58, 2747–2759. https://doi.org/10.1111/1365-2664.14005.

Priyadarshana, T.S., Martin, E.A., Sirami, C., Woodcock, B.A., Goodale, E., Martínez-Núñez, C., Lee, M.-B., Pagani-Núñez, E., Raderschall, C.A., Brotons, L., et al., 2024. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. Ecol. Lett. 27, e14412.

Reynolds, C., Fletcher, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C., Lukhele, M.B., Mamba, M.L., Sibiya, M.D., Austin, J.D., et al., 2018. Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon investigation. Landsc. Ecol. 33, 241–255.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., et al., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11, 499–515.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package ‘mass.’. Cran R. 538, 113–120.

Sánchez, A.C., Jones, S.K., Purvis, A., Estrada-Carmona, N., De Palma, A., 2022. Landscape complexity and functional groups moderate the effect of diversified farming on biodiversity: A global meta-analysis. Agric., Ecosyst. Environ. 332, 107933.

Sánchez-Bayo, F., Wyckhuys, K.A., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232, 8–27.

Saunders, M.E., Luck, G.W., 2013. Pan trap catches of pollinator insects vary with habitat. Aust. J. Entomol. 52, 106–113.

Schellhorn, N.A., Gagic, V., Bommarco, R., 2015. Time will tell: resource continuity bolsters ecosystem services. Trends Ecol. Evol. 30, 524–530.

Scherber, C., 2015. Insect responses to interacting global change drivers in managed ecosystems. Curr. Opin. Insect Sci. 11, 56–62.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., et al., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.

Schirmel, J., Albrecht, M., Bauer, P.-M., Sutter, L., Pfister, S.C., Entling, M.H., 2018. Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. J. Appl. Ecol. 55, 1747–1758.

Schlinkert, H., Westphal, C., Clough, Y., Grass, I., Helmerichs, J., Tscharntke, T., 2016. Plant size affects mutualistic and antagonistic interactions and reproductive success across 21 Brassicaceae species. Ecosphere 7, e01529.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., et al., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674.

Shi, X., Xiao, H., Luo, S., Hodgson, J.A., Bianchi, F.J., He, H., van der Werf, W., Zou, Y., 2021. Can landscape level semi-natural habitat compensate for pollinator biodiversity loss due to farmland consolidation? Agriculture. Ecosyst. Environ. 319, 107519.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., et al., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc. Natl. Acad. Sci. 116, 16442–16447.

Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., Van Der Heijden, M.G., Liebman, M., Hallin, S., 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci. Adv. 6, eaba1715.

Trebilco, R., Baum, J.K., Salomon, A.K., Dulvy, N.K., 2013. Ecosystem ecology: size-based constraints on the pyramids of life. Trends Ecol. Evol. 28, 423–431.

Tscharntke, 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.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., et al., 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. Biol. Rev. 87, 661–685.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming–harnessing biodiversity-friendly landscapes. Trends Ecol. Evol. 36, 919–930.

Tscharntke, T., Batáry, P., Grass, I., 2024. Mixing on-and off-field measures for biodiversity conservation. Trends Ecol. Evol.

Van Dijk, M., Morley, T., Rau, M.L., Saghai, Y., 2021. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. Nat. Food 2, 494–501.

Van Geert, A., Van Rossum, F., Triest, L., 2010. Do linear landscape elements in farmland act as biological corridors for pollen dispersal? J. Ecol. 98, 178–187.

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bährmann, R., Fabian, B., Heinrich, W., Köhler, G., Lichter, D., et al., 2003. Trophic levels are differentially sensitive to climate. Ecology 84, 2444–2453.

Vrdoljak, S.M., Samways, M.J., 2012. Optimising coloured pan traps to survey flower visiting insects. J. Insect Conserv. 16, 345–354.

Wang, M., Lu, X., Ding, S., Ren, J., Bian, Z., Xu, Z., 2017. Pollinator diversity in different habitats of the agricultural landscape in the middle and lower reaches of the Yellow River based on the three-color pan trap method. Acta Ecol. Sin. 37, 148–155.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P., Szentgyörgyi, H., Tscheulin, T., et al., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78, 653–671.