

Trophic level and specialization moderate effects of habitat loss and landscape diversity on cavity-nesting bees, wasps and their parasitoids

Felix Klaus^{1,2}  | Teja Tscharntke¹ | Ingo Grass³

¹Department of Agroecology, University of Göttingen, Göttingen, Germany

²Institute for Bee Protection, Julius Kühn-Institute (JKI) – Federal Research Centre for Cultivated Plants, Braunschweig, Germany

³Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany

Correspondence

Felix Klaus, Department of Crop Sciences, Agroecology Group, Georg August University Göttingen, Göttingen, Germany.
Email: felix.klaus.sc@gmail.com

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 152112243

Editor/associate editor: Raphael K. Didham

Abstract

1. Habitat loss is a primary driver of biodiversity decline, but differences in species responses to habitat loss from local to landscape scales are poorly understood.
2. Trophic level, food and habitat specialization have been suggested to be important predictors of species responses to habitat loss, landscape diversity and landscape scale.
3. Using cavity-nesting communities of bees, wasps and their parasitoids on calcareous grasslands as a model system allowed us to compare responses of species differing regarding their trophic level, and degree of specialization on habitat and food.
4. We found that species from higher trophic levels experienced semi-natural habitat at larger spatial scales than those of lower trophic levels, but only, when they were generalists (abundance of bees, 150 m radius, vs. wasps feeding on herbivores, 450 m radius), not specialists (bees, 150 m, vs. bee parasitoids, 150 m).
5. Parasitoids, which are typically more specialized regarding their food resources (hosts), compared to predators such as predatory wasps, responded to habitat loss at the same spatial scales as their hosts, suggesting strong bottom-up effects of resource availability, that is, host availability driving parasitoid abundance.
6. Bees were mostly habitat specialists of calcareous grasslands and mainly driven by local habitat loss, whereas wasps as habitat generalists were mostly affected by landscape diversity.
7. Our study highlights the need to consider the different spatial scales contingent on trophic level and specialization of target species groups, maintaining or restoring both local habitat and landscape diversity, as this is needed for their successful conservation.

KEYWORDS

bee, calcareous grassland, parasitoid, spatial scale, trap nest, wasp

INTRODUCTION

Habitat loss is a primary driver of local and global biodiversity decline (Brondizio et al., 2019; Dobson et al., 2006). However, differences in species responses to habitat loss, such as the strength of their population decline, are difficult to predict. One reason species respond

differently to habitat loss is their trophic position in food webs and the spatial scale at which they experience the surrounding landscape, which drives their response to habitat loss at local and landscape scales (Cagnolo et al., 2009; Mayr et al., 2020; Steckel et al., 2014; van Nouhuys, 2005). A reduction in local spatial extent of habitat (within a few hundred metres) should mostly affect species at lower

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

trophic levels, such as bees as primary consumers, which often have lower dispersal abilities and thus are dependent on plants as locally available resources (Holt, 2009; Raffaelli, 2004). By contrast, species at higher trophic levels, such as predators or parasitoids, ought to be more mobile to follow their prey and to switch between prey populations (Holt, 1996). Consequently, species at higher trophic levels should often perceive the landscape at larger spatial scales. Their occurrence is therefore not only dependent on local habitat quantity but also on the availability of habitat patches and habitat diversity at the landscape scale (Grass et al., 2018; Tschamtkke et al., 2005).

However, the notion that the spatial scale at which species respond to habitat loss increases with their trophic position is not always true and does not appear to apply to all food webs (Thies et al., 2003). A potential reason is that the scale at which the landscape is perceived by predators also depends on their level of food and habitat specialization. Regarding food, parasitoids, for example, which are often specialized on one or few host species, are strongly affected by host availability, and hence may experience the landscape at similar scales as their hosts (Thies et al., 2003). By contrast, more generalist predators may be more mobile to switch between prey populations (Fornoff et al., 2021; Grass et al., 2018; Green, 2009; Holt, 1996; Rand & Tschamtkke, 2007). Regarding habitat specialization, habitat area has been shown to be the most important for habitat specialist species, while generalists are mainly driven by habitat diversity and connectivity (Holzschuh et al., 2010; Steffan-Dewenter, 2003).

Trap nests for bees, wasps and their parasitoids, which are of high ecological importance providing ecosystem services such as pollination and pest control (Klein et al., 2007; Staab et al., 2018; Tschamtkke et al., 1998), provide the opportunity to study and compare a small and well-defined community of species from different trophic levels, from primary to quaternary consumers and with different grades of specialization in a standardized manner (Fornoff et al., 2021; Staab et al., 2018; Steckel et al., 2014; Tschamtkke et al., 1998) (Figure 1a). These artificial nesting resources for cavity-nesting insects are often made from common reed and placed at study sites to attract females to build nests, which can then be studied (Maclvor, 2017). Trap nests enable us to compare responses of both specialized (parasitoids), as well as generalist (hosts) species (Krombein, 1967). In addition, the community of trap-nesting insects can be related to the spatial scale at which species from different trophic levels experience local- and landscape-level habitat amount (Holzschuh et al., 2010).

Calcareous grasslands are hotspots of plant and insect diversity in central Europe (Steffan-Dewenter & Tschamtkke, 2002; WallisDeVries et al., 2002). Most of the calcareous grasslands have greatly decreased in area and distribution as a result of agricultural intensification in the 20th century, because of which today mostly small and isolated fragments can be found in the agricultural landscape (Grass et al., 2018; Krauss et al., 2010; Poschlod & WallisDeVries, 2002). In this study, we use trap nests on calcareous grasslands to study the effects of habitat loss and habitat diversity at local and landscape scales on species responses at different trophic levels.

Differences between trophic levels regarding their responses to habitat loss, diversity and spatial scales may be expected because

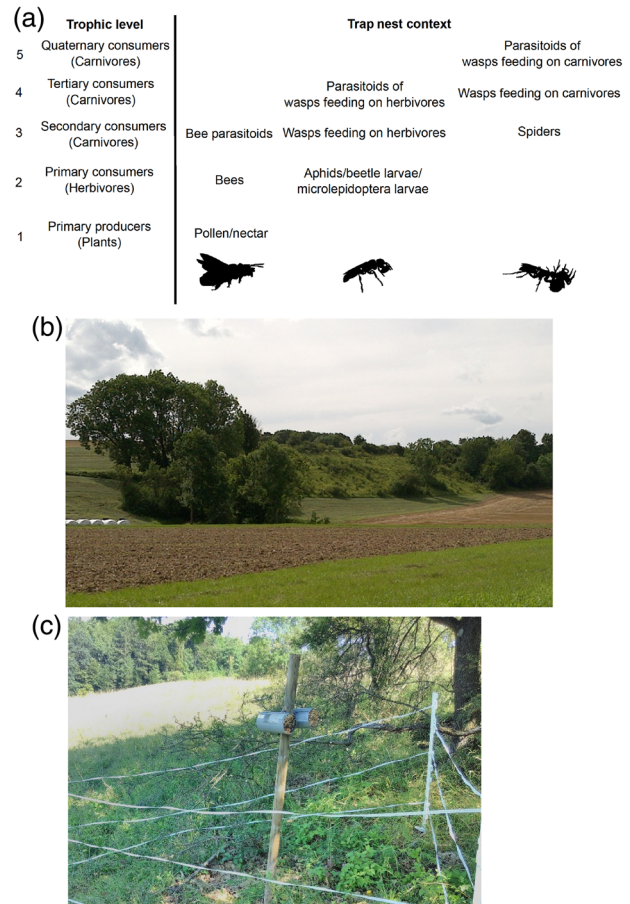


FIGURE 1 (a) Overview of the trophic levels in the food chain and their representatives in the trap nest system. (b) A calcareous grassland fragment (centre) embedded in the agricultural landscape. (c) A trap nest consisting of two plastic tubes filled with reeds attached to a wooden post, and protected from grazing animals by a fence.

their food resources are either directly (bees as herbivores) or more indirectly (wasps as carnivores) driven by the habitat types (Kruess & Tschamtkke, 2000; Raffaelli, 2004). More specialized consumers with a more narrow diet breadth such as parasitoids can be expected to be more closely linked to the availability and distribution of their food resources (hosts), and to be more affected by landscape change (Kruess & Tschamtkke, 2000), compared to more generalist predators.

Regarding responses to habitat loss and habitat diversity, primary consumers such as bees have been shown to be affected mainly by habitat availability, while secondary and tertiary consumers (wasps) respond positively to higher landscape heterogeneity (Holzschuh et al., 2010). The responses of species from the same trophic level with different grades of specialization (e.g., bee parasitoids and wasps feeding on herbivorous prey, both being secondary consumers) to habitat loss and diversity can also be expected to differ. Compared to the responses of primary consumers (here, bees), bee parasitoids can be expected to respond at similar scales due to the strong tie to their hosts, while the generalist wasps may respond at larger scales.

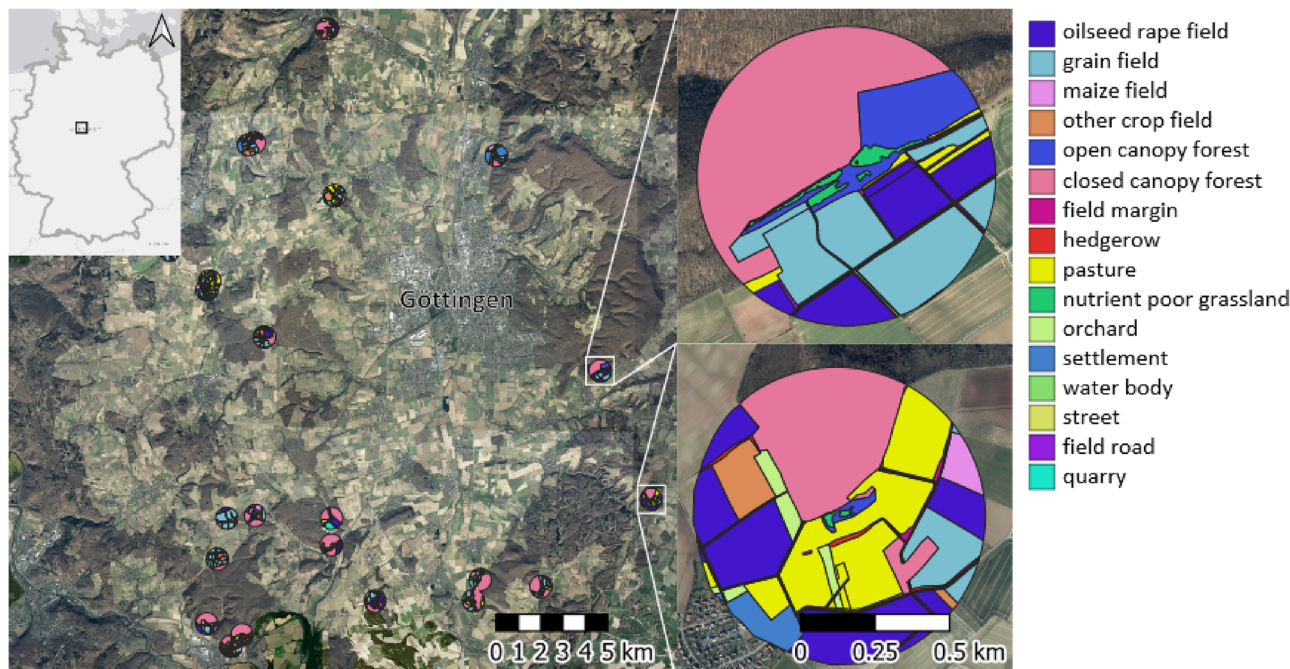


FIGURE 2 Map of the location of the study region within Germany (top left); locations of the calcareous grasslands studied in the surroundings of the city of Göttingen, with 500 m buffers showing the landscape types (centre), and detailed maps of contrasting landscapes around two sample sites (right). Basemap© ESRI.

The following hypotheses were addressed:

1. Generalist species of higher trophic levels, that is, wasps, perceive the landscape at larger scales compared to species at lower trophic levels (bees), while specialist species at higher trophic levels, that is, parasitoids, are affected at similar scales as their hosts.
2. Bee abundance in trap nests is more strongly driven by calcareous grassland area than additional semi-natural habitats in the surrounding landscape, making bees habitat specialists.
3. Bees, which are mainly habitat specialists on calcareous grasslands, are mainly driven by local habitat loss, while habitat generalists (predatory wasps) are mostly affected by habitat diversity at the landscape scale.

MATERIALS AND METHODS

The study took place in the agricultural landscapes of the surroundings of the city of Göttingen, central Germany (lat: 51.532717, long: 9.935154, 20 km radius around the city). The region is dominated by intensive agricultural land use. There are 285 extensively managed calcareous grasslands in the study region making up 0.26% of the total area (Krauss et al., 2003). Twenty-three of these grassland fragments were used as study sites (see Figure 1b for an example; see Figure 2 for a map of the study area and distribution of study sites in the landscape). The sites were selected along independent gradients ($\hat{=}$ treatments) of grassland area (minimum: 82 m², maximum: 50673 m², mean 6902 m² and median 3465 m²), amount of other semi-natural habitat in the

surroundings and landscape diversity (based on Shannon Index of habitat types) (Table A1). The intensity of the management of the sites (grazing or mowing) was required to not differ substantially to avoid differences in habitat quality. All sites were more than 300 m apart from each other (2406 ± 444 m; mean \pm 1 standard error), and spatial independence was ensured by calculating spatial autocorrelation for all relevant variables and for residuals of all models (Moran's I with $p > 0.05$ in all cases). Adjacent forest fragments or hedgerows offered nesting habitat for cavity-nesting bees and wasps at all sites.

Six trap nests were set up at each site in mid-April 2017. They were evenly spread across each site, and placed in spots that were not shaded most of the day and close to vegetation to resemble preferred natural nesting sites. Each trap nest consisted of two plastic tubes with a diameter of 10.5 cm, which were filled with common reed (*Phragmites australis* (Cav.) Trin. ex Steud.; approximately 200 reeds per tube) with diameters between 2 and 10 mm, cut to the length of the tube (20 cm) and attached to a wooden post 1.3 m above the ground (Figure 1c) (Staab et al., 2018; Tschamtket et al., 1998). Sites were sampled every 3 weeks, starting from end of May 2017 (when we noted the first nests had been plugged, meaning closed by a bee or wasp using natural materials such as mud or resin, indicating a nest was built and completed) until mid-October 2017 (when nesting had stopped; total of seven sampling rounds). Plugged nests were collected and replaced with reeds of a similar diameter, to ensure the constant availability of nesting sites, and to not miss the nests of the first generation of those species that have two generations per year. Plugged nests were brought to the lab and dissected, to determine the identity of host species, number of brood cells,

parasitoid species and number of parasitized brood cells. Nest inhabitants (hosts and parasitoids) were identified to species level, if possible, using a stereomicroscope (for literature used for identification, see Table A2). For later analyses, nests were categorized into species groups based on the type of food provided to the larvae. The six groups were *bees* (providing larvae with pollen and nectar), *wasps*

hunting herbivorous prey (such as aphids), *wasps hunting carnivorous prey* (spiders) and their respective parasitoids (parasitoids of bees, of wasps hunting herbivorous prey and of wasps hunting carnivorous prey). For the analyses, all nests from a site were pooled across sampling rounds and trap nests to obtain total abundance (number of brood cells \triangleq sampling unit) for each of the species groups.

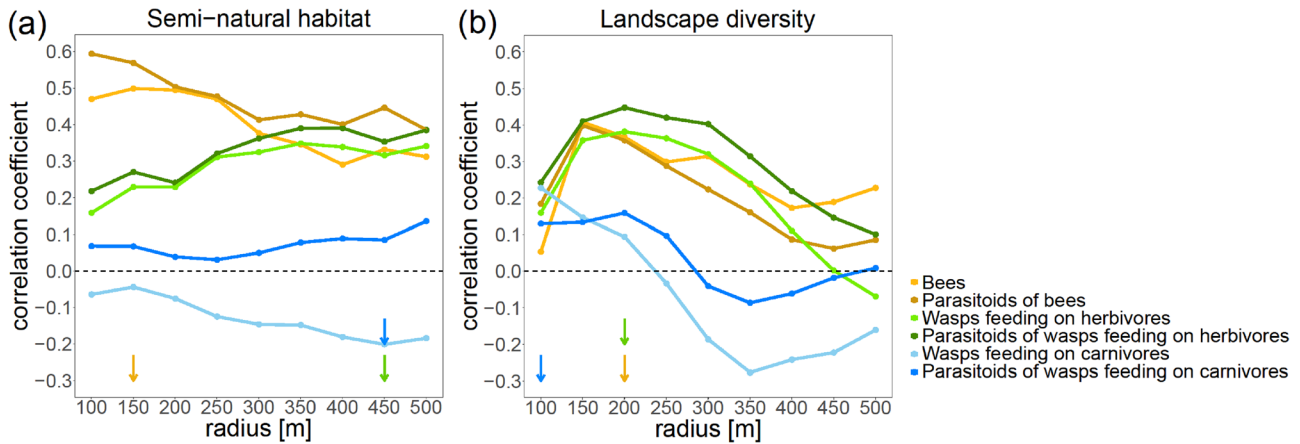


FIGURE 3 Correlation coefficient of abundance of the different groups (brood cell numbers in trap nests per site; $n = 23$ sites) and (a) semi-natural habitat (including focal grasslands) and (b) landscape diversity respectively, at different scales (radii around centre of focal grasslands). Scales most correlated (using the same scale for each pair of host and parasitoid) and used for further analyses for the different trophic levels are pointed out by arrows.

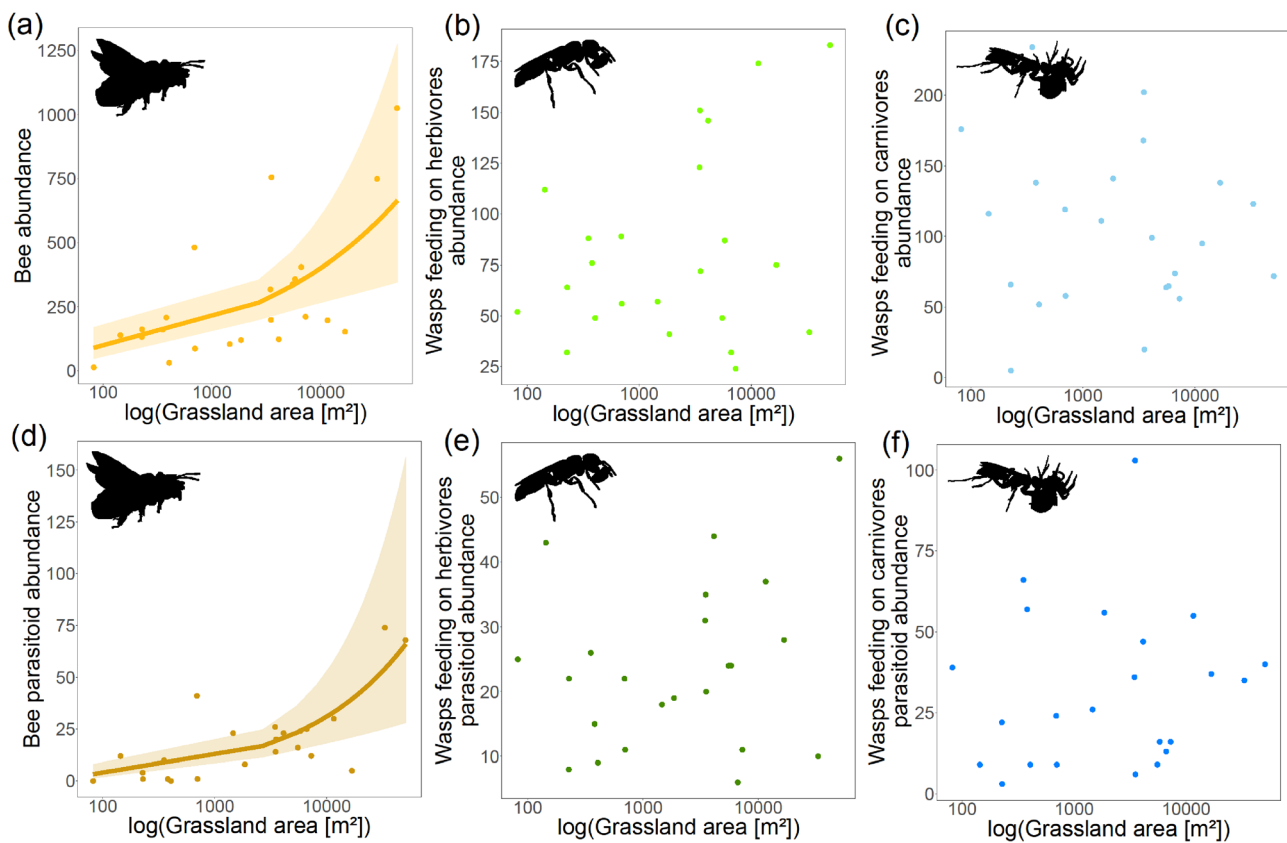


FIGURE 4 Abundance (number of brood cells per site) of different trophic levels in relation to grassland area (log-transformed). Solid lines represent significant relationships ($p < 0.05$). Envelopes show 95% confidence intervals.

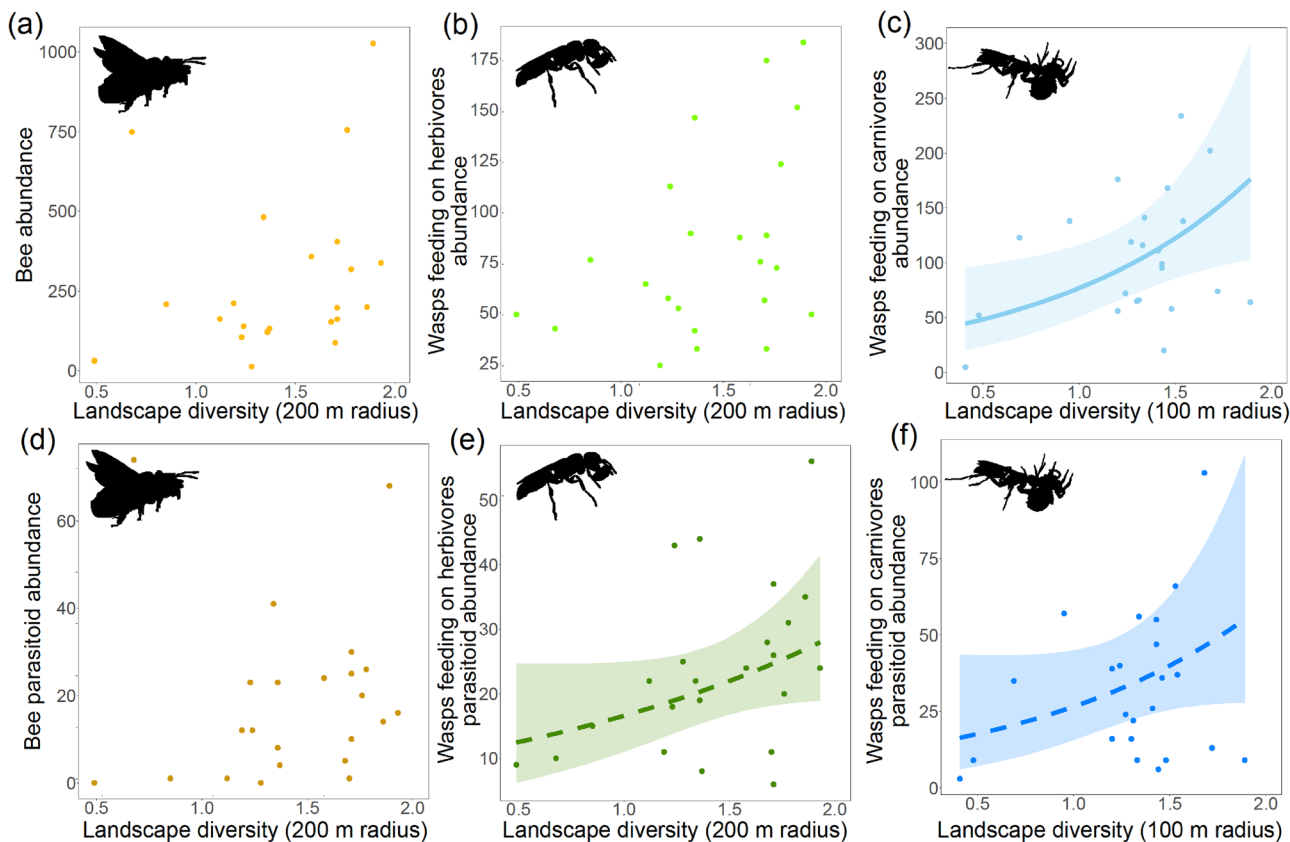


FIGURE 5 Abundance (number of brood cells per site) of different trophic levels in relation to the diversity of the surrounding landscape (different radii). Solid lines represent significant relationships ($p < 0.05$). Dashed lines represent marginally significant relationships ($p \geq 0.05$ and < 0.10). Envelopes show 95% confidence intervals.

The landscape within a 500 m radius around each study site was mapped by ground-truthing. Habitats were categorized in 16 categories: *oilseed rape field, grain field, maize field, other crop field, open canopy forest, closed canopy forest, field margin, hedgerow, pasture, nutrient poor grassland, orchard, settlement, water body, street, field road and quarry*. The landscape data was digitized and analysed using the software QGIS, version 2.14.3 (QGIS Development Team, 2016) and R (R Core Team, 2020). The variables *open canopy forest, field margin, hedgerow, nutrient poor grassland, orchard, field road and quarry* were combined to *semi-natural habitats*. The proportion of semi-natural habitat (excluding the focal grassland), and the diversity of landscape types were calculated for different scales (from 100 to 500 m, 50 m steps) using the R package ‘landscapemetrics’ (Hesselbarth et al., 2019). The maximum scale of 500 m was chosen to avoid spatial autocorrelation between sites, and has been shown to be suitable resembling the maximum foraging distance for most bee species of trap nests (Gathmann & Tscharrtkte, 2002; Zurbuchen et al., 2010).

Statistical analysis

First, to determine the spatial scales at which the species groups at the different trophic levels were affected by the landscape composition, the correlation coefficients (using the Spearman method) of

abundance (using brood cell numbers in trap nests) and the proportion of semi-natural habitat (including extensively managed grasslands) and the landscape diversity within different radii around the centre of each grassland were calculated (Figure 3a,b). The most appropriate scales (highest correlation coefficients, but choosing the same scale for parasitoids and hosts of one trophic level) were used as variables for further analyses. The correlation coefficients of the hosts and respective parasitoids for the chosen scale were for semi-natural habitats: 0.50 and 0.57 for bees (150 m scale), 0.32 and 0.35 for wasps feeding their larvae with herbivorous prey (450 m scale) and -0.20 and 0.08 for wasps feeding their larvae with carnivorous prey (450 m scale); and for landscape diversity: 0.37 and 0.36 for bees (200 m scale), 0.38 and 0.45 for wasps feeding their larvae with herbivorous prey (200 m scale) and 0.23 and 0.13 for wasps feeding their larvae with carnivorous prey (100 m scale) (see Figure 3).

Trap nest inhabitants were split into three groups based on their trophic levels: bees, wasps feeding their larvae with herbivorous prey and wasps feeding their larvae with carnivorous prey. All three groups were attacked by parasitoids. Effects of *grassland area*, proportion of *semi-natural habitat* (excluding extensively managed grasslands) in the surrounding landscape and *landscape diversity* on species abundance were analysed separately for each group. Generalized linear models (GLMs) with negative binomial distribution were used. All models included the three explanatory variables: *grassland area, semi-natural habitat* and

TABLE 1 Model results of generalized linear models for abundance across species groups.

	Bees				Wasps feeding on herbivores				Wasps feeding on carnivores			
	Estimate	Std. error	Z	p	Estimate	Std. error	Z	p	Estimate	Std. error	Z	p
Response: Abundance (number of brood cells) per site												
(Intercept)	5.481	0.135	40.500	<0.001	4.363	0.097	45.075	<0.001	4.610	0.119	38.684	<0.001
Scale(log(Grassland area))	0.555	0.153	3.615	<0.001	-0.015	0.118	-0.124	0.902	0.006	0.145	0.044	0.965
Scale(Semi-natural habitat)	-0.066	0.205	-0.322	0.748	0.150	0.129	1.165	0.244	-0.204	0.147	-1.394	0.163
Scale(Landscape diversity)	0.139	0.198	0.701	0.484	0.167	0.118	1.417	0.157	0.337	0.130	2.604	0.009
Response: Abundance (number of brood cells) per site												
	Parasitoids of bees				Parasitoids of wasps feeding on herbivores				Parasitoids of wasps feeding on carnivores			
	Estimate	Std. error	Z	p	Estimate	Std. error	Z	p	Estimate	Std. error	Z	p
(Intercept)	2.668	0.184	14.539	<0.001	3.119	0.095	32.812	<0.001	3.431	0.152	22.557	<0.001
Scale(log(Grassland area))	0.830	0.208	3.995	<0.001	-0.098	0.119	-0.822	0.411	0.123	0.185	0.664	0.507
Scale(Semi-natural habitat)	-0.293	0.275	-1.066	0.286	0.188	0.126	1.488	0.137	-0.098	0.187	-0.525	0.600
Scale(Landscape diversity)	0.301	0.269	1.117	0.264	0.219	0.118	1.854	0.064	0.298	0.166	1.789	0.074

Note: The effects of *grassland area*, *semi-natural habitat* excluding extensive grasslands in the surrounding landscape and *landscape diversity* on the abundances (brood cell numbers) are shown. All three predictor variables were scaled to zero mean and unit variance and additionally, *grassland area* was log-transformed. Estimates, standard errors, Z values and p-values rounded to three digits after the comma are reported. Significant and marginally significant predictors ($p < 0.10$) are shown in bold.

landscape diversity. All predictors were scaled to zero mean and unit variance to be able to compare effect sizes, and *grassland area* was additionally log-transformed. Model assumptions of GLMs were met and we tested for potential collinearity of predictor variables for all models. We refer to results as statistically significant when $p < 0.05$ and marginally statistically significant when $0.05 \leq p < 0.10$.

All statistical analyses were done in R version 4.0.3 (R Core Team, 2020) using dedicated packages lme4 (for the implementation of mixed effect models) (version 1.1.26; Bates et al., 2015), DHARMA (for residual model diagnostics) (version 0.3.3.0; Hartig, 2020), multcomp (for univariate testing via z-tests of estimated model coefficients) (version 1.4.15; Hothorn et al., 2008), effects (for extracting model outputs) (version 4.2.0; Fox, 2003, Fox & Sanford, 2019), ggplot2 (for plotting) (version 3.3.6; Wickham, 2016), raster (for reading shapefiles) (version 3.4.5; Hijmans, 2020), sf (for calculating distances between points) (version 1.0.7; Pebesma, 2018) and corplot (for extracting correlation coefficients) (version 0.84; Wei & Simko, 2017).

RESULTS

From the 138 trap nests (23 sites \times 6 trap nests each), 3124 nests were collected throughout the study period, containing 10,736 brood

cells. Of these, 6470 brood cells belonged to bees, 438 of which to their parasitoids, 1874 to wasps hunting herbivorous prey, 544 of which to their parasitoids and 2392 to wasp hunting carnivorous prey, 733 of which to their parasitoids.

Sixteen species of bees were collected. *Osmia bicornis* (Linnaeus, 1758) (Megachilidae) was by far the most abundant bee species (73% of all bee brood cells), followed by *Osmia trunctorum* (Linnaeus, 1758) (Megachilidae) and *Hylaeus communis* (Nylander, 1852) (Colletidae). There were 26 species of wasps hunting herbivorous prey, with *Ancistrocerus nigricornis* (Curtis, 1826) (Vespidae) being the most abundant (43% of all brood cells belonging to this species), followed by *Ancistrocerus gazella* (Panzer, 1798) (Vespidae) and *Ancistrocerus antilope* (Panzer, 1789) (Vespidae). The wasps hunting carnivorous prey (six species) were dominated by *Trypoxylon clavicerum* (Lepeletier de Saint Fargeau & Audinet-Serville, 1828) (Crabronidae; 72%) followed by *Deuteragenia subintermedia* (Magretti, 1886) (Pompilidae). The most abundant of the 27 parasitoid species were *Melittobia acasta* (Walker, 1839) (Eulophidae; in 6.4% of all brood cells), *Chrysis terminata* (Dahlbom, 1854) (Chrysididae; 2.2%) and *Cacoxenus indagator* (Loew, 1858) (Drosophilidae; 1.5%). As a side note, to our knowledge, this is the first record of the wasp species *Microdynerus timidus* (Saussure, 1856) (three brood cells) and *Passaloecus vandeli* (Ribaut, 1952) (20 brood cells) in the German state of Lower Saxony. They have previously been recorded in the state of Hessen, to the south of Lower

Saxony (Jacobs, 2007; Tischendorf et al., 2015), and seem to be moving north, presumably due to climate change. See Table A3 for a full list of species and their abundances. Because of trap nests being a system relatively poor in species numbers, especially, when the community is split into sub-groups, we focused on abundances, and did not consider species richness here.

Abundances of bees (primary consumers) and their parasitoids were most strongly positively correlated with semi-natural habitat (including extensively managed grasslands) at small scales (150 m; Figure 3a). Wasps feeding on herbivores (secondary consumers) and their parasitoids were similarly positively affected by semi-natural habitats, but at larger scales (450 m; Figure 3a) and landscape diversity at small to medium scales (200 m; Figure 3b). When splitting up this group into sub-groups based on prey type, it became apparent that this pattern was driven by the most numerous group of wasps feeding on Microlepidoptera larvae, and not by those feeding on aphids or Chrysomelidae larvae (Figure A1). Abundances of wasps feeding on carnivores (tertiary consumers) and their parasitoids were not well predicted by semi-natural habitat and landscape diversity (correlation coefficient <0.3) (Figure 3a,b).

Regarding local and landscape effects, bee and bee parasitoid abundances were significantly positively correlated with the local area of the focal grassland fragments ($p < 0.001$; Figure 4a,d; Table 1). The host species from higher trophic levels and their parasitoids were not significantly correlated with local grassland area (Figure 4b,c,e,f; Table 1). Regarding landscape diversity, no significant correlations were found for bees and their parasitoids (Figure 5a,d; Table 1). The parasitoids of wasps feeding on herbivores were marginally significantly correlated with landscape diversity ($p = 0.06$; Figure 5e; Table 1), while their hosts were not (Figure 5b; Table 1). Wasps feeding on carnivores and their parasitoids were positively affected by landscape diversity (marginally significant for parasitoids; $p = 0.01$; $p = 0.07$; Figure 5c,f; Table 1). None of the groups were significantly correlated with semi-natural habitat other than the focal grassland (Table 1).

In general, the patterns of hosts and their parasitoids were similar, while the host species from different trophic levels showed different patterns regarding responses to scale, grassland area and landscape diversity (Figures 3–5; Table 1).

DISCUSSION

We found in this study that species from different trophic levels and with different food and habitat specializations are differently affected by habitat area and landscape diversity. Using cavity-nesting bees, wasps and their parasitoids on calcareous grasslands as model systems, we found that species at different trophic levels perceive habitat loss and landscape diversity of the agricultural landscape at different spatial scales. Depending on the target species/community, maintaining and restoring local habitat islands may not be sufficient for conservation, but the landscape must be considered as well, especially for species of higher trophic levels and habitat generalists.

Bee and wasp abundance was influenced by the availability of semi-natural habitats, with species of higher trophic levels (wasps) perceiving the landscape at larger spatial scales than those of lower trophic levels (bees). This is in line with the concept by Holt (1996), stating that higher trophic levels perceive the landscape at larger spatial scales, which is assumed to be caused by the higher mobility of the predators' prey and the predators' need to switch between prey populations, compared to herbivores that feed on non-mobile food, that is, sessile plants. Comparing trophic levels of parasitoids and their hosts, no differences regarding the landscape scale best suited to explain their abundances were found. This has been shown before and is likely due to the typically high food specialization of parasitoids on their hosts, causing them to be tied more closely to the spatial scale at which their hosts respond to local- and landscape-level habitat availability than generalists (Grass et al., 2018; Holt, 2009; Rand & Tschardtke, 2007; Steffan-Dewenter & Tschardtke, 2000; Thies et al., 2003). These results suggest that in addition to the trophic level of consumers, the degree of food specialization mediates how species experience the landscape.

We found that the scales at which abundances of the same trophic level relate to different landscape variables can be quite different. This could be shown by their responses to the *amount of semi-natural habitat* and *landscape diversity*. This contrast was most distinct for wasps feeding on herbivores, representing the trophic level of secondary consumers, being affected at large scales by *semi-natural habitat*, and at smaller scales by *landscape diversity*. This may be caused by flexible foraging strategies. The availability of large amounts of semi-natural habitat at larger scales seem to be sufficient for providing herbivorous prey to the wasps. When large amounts of semi-natural habitat are not available, a high diversity of habitats at smaller scales may be needed, with edge habitats providing both food sources and ensuring connectivity and permeability of the landscape (Krewenka et al., 2011; Mallinger et al., 2016). When further dividing the group of wasps feeding on herbivores by prey type, different responses are revealed, with wasps feeding on Microlepidoptera larvae responding strongly to semi-natural habitat, which may be because of the association of their prey with (fruit) trees and shrubs, which are abundant at semi-natural habitats (Hoffmann et al., 2018; MacKay, 1962). Wasps feeding on aphids and Chrysomelidae larvae on the other hand are not associated with semi-natural habitat, which can be explained by their prey not being associated with semi-natural habitats, but with annual crop plants (e.g., aphids as pest species in wheat fields) (Dedryver et al., 2010; Jolivet et al., 2012).

Bee abundance was strongly correlated to grassland area, but not to the amount of additional semi-natural habitats in the surrounding landscape, suggesting that the studied cavity-nesting bees are habitat specialists of the calcareous grasslands. As we provided artificial nesting sites at all sites, food requirements can be expected as the limiting factor for bee occurrence. Bees rely on flowering plants offering nectar and pollen, which were widely available at the focal grasslands (Steffan-Dewenter & Tschardtke, 2002; WallisDeVries et al., 2002). Solitary bees, depending on their body size, can have maximum foraging ranges of up to 1100 m, however, realized foraging distances may

be much lower, when resources are available in close proximity to the nest, as was the case at the calcareous grasslands (Gathmann & Tscharntke, 2002; Zurbuchen et al., 2010).

By contrast, abundances of wasp species were not positively correlated to grassland area, which may be due to their higher trophic level and hence higher mobility weakening species-area relationships, as suggested by Holt (2009). It has also been shown and is supported by our results that habitat specialists (in our case bees) are mainly driven by local habitat loss, while habitat generalists (wasps) are mostly affected by landscape diversity and connectivity (Holzschuh et al., 2010; Steffan-Dewenter, 2003). Furthermore, the prey of most cavity-nesting wasps, such as aphids, Chrysomelidae larvae and spiders, is mostly not associated with extensively managed grasslands, but annual crop fields, suggesting the wasps to use the grasslands for nesting and feeding, but not as much for hunting (Dedryver et al., 2010; Hoffmann et al., 2018; Jolivet et al., 2012).

CONCLUSIONS

In conclusion, we showed that trophic level and specialization moderate species' responses to local habitat loss and landscape diversity and that they perceive the landscape at different scales. These findings highlight the need for conservation or restoration projects to foster habitat heterogeneity, providing resources essential either in close proximity for less mobile species from lower trophic levels and their specialist antagonists or within the wider landscape, while also ensuring high landscape diversity and permeability, for more mobile species from higher trophic levels.

AUTHOR CONTRIBUTIONS

Felix Klaus: Writing – original draft; conceptualization; investigation.

Teja Tscharntke: Writing – review and editing; conceptualization.

Ingo Grass: Writing – review and editing; conceptualization.

ACKNOWLEDGEMENTS

This research was supported by the German Research Association (DFG) Research Training Group 1644 'Scaling Problems in Statistics', grant no. 152112243. We thank Anna Binczik, Denise Castle, Manon Thale-Döring, Erik Reichelt, Nadine Schauder and Leonie Schweer for their great help with field and lab work; Felipe Librán Embid for providing GIS-data and analyses; and Villu Soon from University of Tartu, Estonia, for help with the identification of specimens from the *Chrysis ignita* group. Furthermore, we thank the local nature conservation agency for granting permission to carry out this study. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Felix Klaus  <https://orcid.org/0000-0001-7587-0412>

REFERENCES

- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Brondizio, E.S., Settele, J., Díaz, S. & Ngo, H.T. (2019) Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services.
- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M. & Zak, M. (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation Biology*, 23, 1167–1175.
- Dedryver, C.-A., Le Ralec, A. & Fabre, F. (2010) The conflicting relationships between aphids and men: a review of aphid damage and control strategies. *Comptes Rendus Biologies*, 333, 539–553.
- Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J. et al. (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87, 1915–1924.
- Fornoff, F., Staab, M., Zhu, C.-D. & Klein, A.-M. (2021) Multi-trophic communities re-establish with canopy cover and microclimate in a subtropical forest biodiversity experiment. *Oecologia*, 196, 289–301.
- Fox, J. & Sanford, W. (2019) *An R companion to applied regression*, 3rd edition. Thousand Oaks, CA: Sage.
- Fox, J. (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8, 1–27.
- Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *The Journal of Animal Ecology*, 71, 757–764.
- Grass, I., Jauker, B., Steffan-Dewenter, I., Tscharntke, T. & Jauker, F. (2018) Past and potential future effects of habitat fragmentation on structure and stability of plant-pollinator and host-parasitoid networks. *Nature Ecology & Evolution*, 2, 1408–1417.
- Green, D.M. (2009) Coevolution of dispersal in a parasitoid–host system. *Population Ecology*, 51, 253–260.
- Hartig, F. (2020) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models.
- Hesselbarth, M.H., Scaini, M., Nowosad, J. & Hanss, S. (2019) landscapemetrics: Landscape metrics for categorical map patterns. R package version 1.0.
- Hijmans, R.J. (2020) raster: Geographic Data Analysis and Modeling.
- Hoffmann, U.S., Jauker, F., Lanzen, J., Warzecha, D., Wolters, V. & Diekötter, T. (2018) Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. *Insect Conservation and Diversity*, 11, 42–49.
- Holt, R.D. (1996) Food webs in space: an Island biogeographic perspective. In: Polis, G.A., Winemiller, K.O. (eds) *Food Webs*. Springer, pp. 313–323.
- Holt, R.D. (2009) Toward a trophic Island biogeography. In: J. Losos & R. Ricklefs (Ed.), *The Theory of Island Biogeography Revisited*, pp. 143–185.
- 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? *The Journal of Animal Ecology*, 79, 491–500.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.
- Jacobs, H.-J. (2007) *Die Grabwespen Deutschlands Ampulicidae, Sphecidae*. Goecke & Evers, Keltern: Crabronidae Bestimmungsschlüssel.
- Jolivet, P., Petitpierre, E. & Hsiao, T.H. (2012) *Biology of chrysomelidae*. In: Series Entomologica (SENT, volume 42). Springer Science & Business Media.
- Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313.

- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M. et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, 13, 597–605.
- Krauss, J., Steffan-Dewenter, I., & Tschardtke, T. (2003) Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia*, 137, 591–602.
- Krewenka, K.M., Holzschuh, A., Tschardtke, T. & Dormann, C.F. (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation*, 144, 1816–1825.
- Krombein, K.V. (1967) *Trap-nesting wasps and bees: Life histories, nests, and associates*. Washington, DC: Smithsonian Institution. 570p.
- Kruess, A. & Tschardtke, T. (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, 122, 129–137.
- MacIvor, J.S. (2017) Cavity-nest boxes for solitary bees: a century of design and research. *Apidologie*, 48, 311–327.
- MacKay, M.R. (1962) Larvae of the North American Tortricinae (Lepidoptera: Tortricidae). *Memoirs of the Entomological Society of Canada*, 94, 5–182.
- Mallinger, R.E., Gibbs, J. & Gratton, C. (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, 31, 1523–1535.
- Mayr, A.V., Peters, M.K., Eardley, C.D., Renner, M.E., Röder, J. & Steffan-Dewenter, I. (2020) Climate and food resources shape species richness and trophic interactions of cavity-nesting hymenoptera. *Journal of Biogeography*, 47, 854–865.
- Pebesma, E. (2018) Simple features for R: standardized support for spatial vector data. *R Journal*, 10, 439–446.
- Poschlod, P. & WallisDeVries, M.F. (2002) The historical and socio-economic perspective of calcareous grasslands—lessons from the distant and recent past. *Biological Conservation*, 104, 361–376.
- QGIS Development Team, A.E. (2016) QGIS geographic information system. Open Source Geospatial Foundation Project.
- R Core Team. (2020) R Foundation for Statistical Computing; Vienna, Austria: 2020. R: A Language and Environment for Statistical Computing.
- Raffaelli, D. (2004) How extinction patterns affect ecosystems. *Science*, 306, 1141–1142.
- Rand, T.A. & Tschardtke, T. (2007) Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos*, 116, 1353–1362.
- Staab, M., Pufal, G., Tschardtke, T. & Klein, A.-M. (2018) Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods in Ecology and Evolution*, 9, 2226–2239.
- Steckel, J., Westphal, C., Peters, M.K., Bellach, M., Rothenwoehrer, C., Erasmí, S. et al. (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation*, 172, 56–64.
- Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, 17, 1036–1044.
- Steffan-Dewenter, I. & Tschardtke, T. (2000) Butterfly community structure in fragmented habitats. *Ecology Letters*, 3, 449–456.
- Steffan-Dewenter, I. & Tschardtke, T. (2002) Insect communities and biotic interactions on fragmented calcareous grasslands—A mini review. *Biological Conservation*, 104, 275–284.
- Thies, C., Steffan-Dewenter, I. & Tschardtke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, 101, 18–25.
- Tischendorf, S., Engel, M., Flügel, H.-J., Frommer, U., Geske, C. & Schmalz, K.-H. (2015) *Atlas der Faltenwespen Hessens*. Gießen: FENA Wissen.
- Tschardtke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, 35, 708–719.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, 8, 857–874.
- van Nouhuys, S. (2005) Effects of habitat fragmentation at different trophic levels in insect communities. In: *Annales Zoologici Fennici*, 42(4), JSTOR, pp. 433–447.
- WallisDeVries, M.F., Poschlod, P. & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104(3), 265–273.
- Wei, T. & Simko, V. (2017) R package “corrplot”: visualization of a correlation matrix.
- Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143, 669–676.

How to cite this article: Klaus, F., Tschardtke, 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 Conservation and Diversity*, 1–12. Available from: <https://doi.org/10.1111/icad.12688>

APPENDIX A

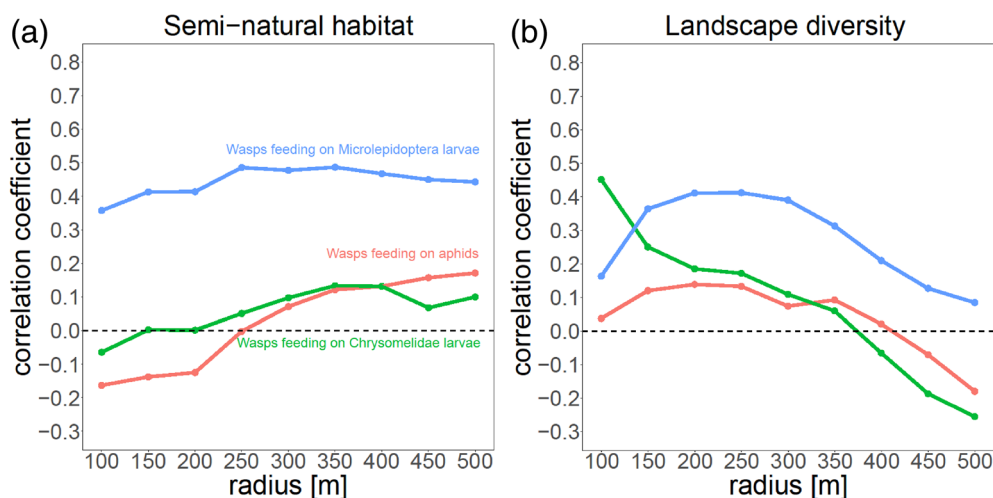


FIGURE A1 Correlation coefficient of abundance of different sub-groups of wasps feeding on herbivorous prey (brood cell numbers in trap nests per site; $n = 23$ sites) and (a) semi-natural habitat (including focal grasslands) and (b) landscape diversity respectively, at different scales (radii around centre of focal grasslands). The sub-groups are based on the type of prey: wasps feeding on Microlepidoptera larvae (eight out of 25 species, 1330 out of 1874 brood cells), wasps feeding on aphids (seven spp., 264 brood cells) and wasps feeding on Chrysomelidae larvae (six spp., 240 brood cells). Additional prey types (Curculionidae—two spp., Thysanoptera—one sp., Diptera—one sp., 40 brood cells in total) are not shown.

TABLE A1 Correlation matrices showing Pearson correlation coefficients comparing explanatory variables used in the same models for (a) bees, (b) wasps feeding on herbivores and (c) wasps feeding on carnivores.

(a) Bee models			
	Grassland area	Semi-natural habitat (150 m scale)	Landscape diversity (200 m scale)
Grassland area			
Semi-natural habitat (150 m scale)	0.257		
Landscape diversity (200 m scale)	0.123	0.712	
(b) Wasps feeding on herbivore models			
	Grassland area	Semi-natural habitat (450 m scale)	Landscape diversity (200 m scale)
Grassland area			
Semi-natural habitat (450 m scale)	0.339		
Landscape diversity (200 m scale)	0.123	0.530	
(c) Wasps feeding on carnivore models			
	Grassland area	Semi-natural habitat (450 m scale)	Landscape diversity (100 m scale)
Grassland area			
Semi-natural habitat (450 m scale)	0.339		
Landscape diversity (100 m scale)	-0.089	0.305	

TABLE A2 Literature used for the identification of nest inhabitants.

Reference
Gathmann, Achim, & Tschardt, Teja (1999). <i>Landschafts-Bewertung mit Bienen und Wespen in Nisthilfen: Artenspektrum, Interaktionen und Bestimmungsschlüssel</i> . Naturschutz und Landschaftspflege Baden-Württemberg, 73, 277–305.
Amiet, F., Müller, A., & Neumeyer, R. (1999). <i>Apidae 2: Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha</i> (Vol. 4). Schweizerische Entomologische Gesellschaft.
Scheuchl, E. (2006). <i>Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs</i> . Apollo books.
Kunz, P. X. (1994). <i>Die Goldwespen (Chrysididae) Baden-Württembergs: Taxonomie, Bestimmung, Verbreitung, Kartierung und Ökologie: mit einem Bestimmungsschlüssel für die deutschen Arten</i> (Vol. 77). Landesanstalt für Umweltschutz Baden-Württemberg.
Dollfuss, H. (1991). Bestimmungsschlüssel der Grabwespen Nord- und Zentraleuropas. <i>Stapfia</i> , 24, 1–247.
Oehlke, J., & Wolf, H. (1987). Beiträge zur Insekten-Fauna der DDR: Hymenoptera-Pompilidae. <i>Beiträge zur Entomologie = Contributions to Entomology</i> , 37(2), 279–390.
Oehlke, J. (1974). Beiträge zur Insektenfauna der DDR: Hymenoptera-Scolioidea. <i>Beiträge zur Entomologie = Contributions to Entomology</i> , 24(5–8), 279–300.
Schmid-Egger, C. H. (1994). Bestimmungsschlüssel für die deutschen Arten der solitären Faltenwespen (Hymenoptera: Eumeninae). <i>Deutscher Jugendbund für Naturbeobachtung</i> , 5, 106.

TABLE A3 List of species recorded at different trophic levels in trap nests and their total brood cell numbers.

Species	# Brood cells
Bees	6470
<i>Hylaeus communis</i>	283
<i>Hylaeus confusus</i>	26
<i>Hylaeus difformis</i>	135
<i>Hylaeus leptcephalus</i>	9
<i>Hylaeus</i> sp.	22
<i>Megachile alpicola</i>	18
<i>Megachile centuncularis</i>	58
<i>Megachile ligniseca</i>	41
<i>Megachile</i> sp.	11
<i>Megachile versicolor</i>	175
<i>Osmia bicornis</i>	4711
<i>Osmia brevicornis</i>	77
<i>Osmia caerulea</i>	54
<i>Osmia campanularum/cantabrica/florisomnis/rapunculi</i>	2
<i>Osmia florisomnis</i>	248
<i>Osmia florisomnis/rapunculi</i>	4
<i>Osmia leiana</i>	59
<i>Osmia rapunculi</i>	79
<i>Osmia truncorum</i>	328
<i>Osmia truncorum/crenulatus</i>	109
<i>Osmia uncinata</i>	21
Bee parasitoids	438
Acari	20
<i>Cacoxenus indagator</i>	165
<i>Chrysis cyanea</i>	3
<i>Chrysis fulgida</i>	3
<i>Chrysis terminata</i>	6
<i>Chrysura hirsuta</i>	5
<i>Coelioxys inermis</i>	4
<i>Coelioxys mandibularis</i>	6
<i>Ephialtes manifestator</i>	3
<i>Gasteruption assectator</i>	12
<i>Gasteruption erythrostomum</i>	1
<i>Gasteruption jaculator</i>	2
<i>Megatoma undata</i>	18
<i>Melittobia acasta</i>	140
<i>Sapyga clavicornis</i>	24
<i>Sapygina decemguttata</i>	15
<i>Stelis breviscula</i>	9
<i>Stelis minuta</i>	2
Wasps hunting herbivorous prey	1874
<i>Ancistrocerus antilope</i>	121
<i>Ancistrocerus claripennis</i>	42

(Continues)

TABLE A3 (Continued)

Wasps hunting herbivorous prey	1874
<i>Ancistrocerus gazella</i>	201
<i>Ancistrocerus nigricornis</i>	813
<i>Ancistrocerus parietinus</i>	74
<i>Ancistrocerus parietum</i>	3
<i>Ancistrocerus trifasciatus</i>	24
<i>Crossocerus cetratus</i>	28
<i>Discoelius zonalis</i>	52
<i>Gymnomerus laevipes</i>	5
<i>Microdynerus timidus</i>	3
<i>Nitela/Pemphredon/Psenulus</i> sp.	38
<i>Passaloecus brevilabris</i>	13
<i>Passaloecus corniger</i>	103
<i>Passaloecus eremita</i>	29
<i>Passaloecus insignis</i>	39
<i>Passaloecus singularis</i>	8
<i>Passaloecus</i> sp.	14
<i>Passaloecus vandeli</i>	20
<i>Spilomena beata/troglydytes</i>	4
<i>Symmorphus bifasciatus</i>	45
<i>Symmorphus connexus</i>	16
<i>Symmorphus crassicornis</i>	13
<i>Symmorphus debilitatus</i>	7
<i>Symmorphus gracilis</i>	93
<i>Symmorphus murarius</i>	35
<i>Symmorphus</i> sp.	31
Parasitoids of wasps hunting herbivorous prey	544
Acari	6
<i>Chrysis angustula</i>	2
<i>Chrysis corusca</i>	39
<i>Chrysis cyanea</i>	18
<i>Chrysis fulgida</i>	2
<i>Chrysis solida</i>	44
<i>Chrysis terminata</i>	228
<i>Ephialtes manifestator</i>	6
<i>Ephialtes</i> sp.	9
<i>Megatoma undata</i>	13
<i>Melittobia acasta</i>	136
<i>Nematopodius debilis</i>	12
<i>Omalus aeneus</i>	1
<i>Poemenia collaris</i>	7
<i>Poemenia hectica</i>	8
<i>Poemenia notata</i>	3
<i>Poemenia</i> sp.	1
<i>Pseudomalus auratus</i>	9
Wasps hunting carnivorous prey	2392

(Continues)

TABLE A3 (Continued)

Wasps hunting carnivorous prey	2392
<i>Agonioideus cinctellus</i>	8
<i>Auplopus carbonarius</i>	2
<i>Deuteragenia subintermedia</i>	306
<i>Trypoxylon clavicerum</i>	1727
<i>Trypoxylon figulus</i>	137
<i>Trypoxylon figulus/minus</i>	16
<i>Trypoxylon minus</i>	195
<i>Trypoxylon</i> sp.	1
Parasitoids of wasps hunting carnivorous prey	733
<i>Chrysis corusca</i>	17
<i>Chrysis cyanea</i>	138
<i>Chrysis terminata</i>	3
<i>Ephialtes manifestator</i>	5
<i>Gasteruption assectator</i>	1
<i>Ichneumonidae</i> sp.	4
<i>Megatoma undata</i>	15
<i>Melittobia acasta</i>	414
<i>Nematopodius debilis</i>	136