
Importance of Habitat Area and Landscape Context for Species Richness of Bees and Wasps in Fragmented Orchard Meadows

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Abstract: *I investigated how habitat area, habitat connectivity, and landscape context affect the species richness and abundance of trap-nesting bees, wasps, and their natural enemies. The research was done on 45 orchard meadows ranging in size from 0.08 to 5.8 ha and differing in habitat connectivity and the surrounding landscape matrix. Effects of the surrounding landscape matrix were restricted to circles with a radius of 250 m. Only the species richness of natural enemies increased with landscape diversity in the surrounding matrix. Population densities of bees increased with habitat connectivity. Total species richness and species richness of bees, eumenid wasps, and natural enemies significantly increased with habitat area. Significant species-area relationships existed for insect groups but not for plants, thereby confirming the hypothesis that higher trophic levels are more affected by habitat fragmentation than lower trophic levels. The slope of species-area relationships was steeper for mutualistic bees than for predatory wasps and natural enemies. In contrast to expectations, the rate of parasitism did not depend on habitat area but only on the local and regional abundance of hosts. My results suggest that the area and connectivity of habitat fragments is most important for the conservation of habitat specialists, whereas generalists may profit from a diverse surrounding landscape matrix.*

Key Words: connectivity, conservation, habitat fragmentation, landscape ecology, parasitism, spatial scale, species-area and abundance-area relationships, trophic rank

La Importancia del Área del Hábitat y del Contexto del Paisaje para la Riqueza de Especies de Abejas y Avispas en Praderas de Huertos Fragmentadas

Resumen: *Se investigó como el área de hábitat, la conectividad del hábitat y el contexto del paisaje afectan la riqueza de especies y la abundancia de abejas, avispas y sus enemigos naturales. La investigación se realizó en praderas con frutales cuya superficie varía entre 0.08 y 5.8 Ha y que difieren en cuanto a conectividad y la matriz que las rodea. Los efectos de la matriz circundante se restringieron a círculos de 250 m de radio. Solo incrementó la riqueza de enemigos naturales con la diversidad del paisaje en la matriz circundante. Las densidades poblacionales de abejas incrementaron con la conectividad del hábitat. La riqueza total de especies y la riqueza de especies de abejas, avispas euménidas y de enemigos naturales incrementó significativamente con el área del hábitat. Se identificaron relaciones especie-área significativas para grupos de insectos pero no para plantas, lo que confirma la hipótesis de que los niveles tróficos superiores son más afectados por la fragmentación del hábitat que los niveles tróficos inferiores. La pendiente de la relación especie-área fue más pronunciada para abejas mutualistas que para avispas depredadoras y enemigos naturales. Contrario a lo esperado, la tasa de parasitismo no dependió del área del hábitat sino de la abundancia local y regional de hospedadores. Los resultados sugieren que el área y la conectividad de fragmentos de hábitat son muy importantes para la conservación de especialistas en hábitat, mientras que los generalistas pueden aprovechar una matriz paisajística circundante diversa.*

Palabras Clave: conectividad, conservación, ecología del paisaje, escala espacial, fragmentación del hábitat, parasitismo, relaciones especie-área y abundancia-área

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Introduction

The importance of spatial context for understanding ecological systems is increasingly recognized by ecologists of different disciplines such as community, population, and theoretical ecology (Kareiva 1990; Tilman & Kareiva 1997; Turner et al. 2001). Similarly, conservationists are increasingly aware that the landscape context within which habitat fragments exist may be as important as the local habitat fragments themselves (Perfecto & Vandermeer 2002; Tschardt et al. 2002). Worldwide, the spatial patterns of habitat arrangement and the structure of whole landscapes have been greatly changed by the destruction and fragmentation of both natural and seminatural habitats and intensified agricultural land use. This process is assumed to be one of the main reasons for loss of biodiversity (Saunders et al. 1991; Harrison & Bruna 1999; Dale et al. 2000).

For habitat fragments, the positive relationship between the number of species found at a site and its area, the species-area relationship, is one of the most robust and general patterns in ecology (Connor & McCoy 1979; Rosenzweig 1995; Gaston & Blackburn 2000). The population density of animals may also increase with fragment size, the so-called abundance-area relationship, but for insects only few and ambiguous studies exist (Connor et al. 2000). Habitat fragmentation does not affect all species equally (Davies et al. 2000). Species of higher trophic levels (Holt et al. 1999), mutualists (Rathcke & Jules 1993), and habitat and food plant specialists (Steffan-Dewenter & Tschardt 2000) are expected to go extinct first when habitat size declines or habitat isolation increases. As a result, community structure is altered and species interactions such as parasitism or pollination may become disrupted (Steffan-Dewenter & Tschardt 2002). Although species-area relationships have been studied many times, it is still unclear how functional species groups such as pollinators, predators, or parasitoids respond to habitat area and how ecosystem functions are affected (Didham et al. 1996; Harrison & Bruna 1999; Debinski & Holt 2000).

In contrast to oceanic islands, terrestrial habitat fragments are embedded in a landscape matrix that may not be totally inhospitable (Andr n 1994; Kareiva & Wennergren 1995; Gustafson 1998; Moilanen & Hanski 1998; Norton et al. 2000; Perfecto & Vandermeer 2002). The surrounding matrix of a habitat fragment may increase the amount of available resources or provide additional resources that do not occur within the local habitat fragment. Some bee species, for example, need different habitat types within their foraging range to fulfil their specific requirements with respect to food resources, nest sites, and building material (Westrich 1996; Steffan-Dewenter et al. 2002). The surrounding matrix can significantly influence the "structural connectivity" of habitat patches, thereby possibly increasing or decreasing lo-

cal population density and extinction risk (Gonzales et al. 1998; Ricketts 2001). The spatial scale at which dispersing or foraging individuals perceive and interact with landscape structure depends on the species' life-history traits (Keitt et al. 1997; With et al. 1999; Steffan-Dewenter et al. 2002). The most relevant scale is difficult to assess a priori and has to be identified by testing for a correlation between the population-dynamic features of interest and landscape characteristics at different spatial scales (Kareiva 1990; Wiegand et al. 1999). The quantification of landscape context is possible in many ways, but the proportion of suitable habitat and the diversity of habitat types have been useful and ecologically relevant parameters (Gustafson 1998; Tischendorf 2001).

I studied the effects of habitat size, habitat connectivity, and landscape context on bees, wasps, and their natural enemies in 45 fragmented orchard meadows. These insect groups include important functional groups such as pollinators, predators, and parasitoids (LaSalle & Gauld 1993). A recent review by Cane (2001) demonstrates that few studies have directly addressed the consequences of habitat fragmentation for communities of pollinating insects, particularly bees, and none have addressed their nesting needs or interactions with natural enemies. To measure the species richness and abundance of bees and wasps simultaneously and on a large spatial scale with sufficient replication, I used nesting traps that provide a standardized nesting resource and allow for the analyses of parasitism by natural enemies (Tschardt et al. 1998). I predicted that (1) species richness and abundance of plants, bees, wasps, and natural enemies increase with habitat area, (2) species at higher trophic levels are more affected by habitat fragmentation than those at lower trophic levels, and (3) habitat connectivity and the surrounding landscape matrix influence species richness, abundance, and species interactions in the habitat fragments.

Methods

Study Region and Study Sites

My study was conducted in 1998 and 1999 in southern Lower Saxony, Germany. The study region is a typical central European agricultural landscape. The main land-use types are annual crops, grasslands, and forest. As in many human-dominated landscapes, natural habitats have been destroyed and seminatural habitats are most important for nature conservation (Tschardt et al. 2002). A complete mapping of orchard meadows exists for the study region, covering a total of 743 habitat fragments in an area of about 875 km² (Untere Naturschutzbeh rde G ttingen, unpublished data). These orchard meadows are characterized by old, tall fruit trees

and are of particular importance for providing habitats for native plant and insect species. Many conservation efforts are focused on this seminatural habitat type in Germany (Bünger & Köhlbach 1995). Intensification of agricultural land use leads to the destruction and fragmentation of these seminatural habitats. During recent decades, the area of orchard meadows has been reduced by 80% in Germany (Bünger & Köhlbach 1995).

Altogether 45 orchard meadows with a size range of 0.08–5.8 ha were selected as study sites. The mean distance to the nearest neighboring study site was 2056 ± 246 m (range 208–8430 m), and only 4 out of 45 study sites were closer than 500 m from the nearest neighboring study site. The distances between the study sites were significantly larger than the expected foraging distances of solitary bees and wasps (e.g., Gathmann & Tscharrntke 2002). Therefore, the spatial correlation of the study sites should have played a minor role, and each study site was considered an independent replicate. The study sites comprised three different management regimes—mowing, grazing, or lying fallow—but these had no significant effect on insect communities (I.S.-D., unpublished data). No pesticides were used on the study sites. Dominant fruit tree species on orchard meadows were apples (*Malus domestica*), sweet cherries (*Prunus avium*), and plums (*Prunus domestica*).

Vegetation and Landscape Context

Floristic composition of herbs and grasses was recorded from June to July 1998 in a centrally located plot of 25 m² at each study site. Percent cover of each plant species, total cover of vegetation, and mean plant height were recorded.

I quantified landscape context by using digital thematic maps (ATKIS-DLM 25/1 Landesvermessung and Geobasisinformationen Niedersachsen 1991–1996), which allow for the separation of arable land, grassland, hedgerow, garden land, forest, and settled area. Additionally, all orchard meadows and calcareous grasslands in the study region were digitized with a geographical information system (TopoL 4.506) because they are the two most important seminatural habitat types for conservation in the study region. I quantified landscape context for each fragment inside a nested set of circles of 250, 500, 750, 1000, and 1500 m radius. I used two different parameters to quantify landscape context at different spatial scales: (1) the percent cover of seminatural habitats (orchard meadows, calcareous grasslands, hedgerows, and gardenlands) and (2) the diversity (H_s) of all habitat types (or landscape diversity) with

$$H_s = -\sum p_i \ln p_i,$$

where p_i is the proportion of each land use type (Krebs 1989). All habitat types were included because each can

be expected to contribute certain habitat requirements such as nesting sites or food plants for bees or wasps. Additionally, for each study site an index was calculated to quantify connectivity to other orchard meadows with

$$C = \sum e^{-d_{ij}} A_j,$$

where A_j is the area of neighboring orchard meadows and d_{ij} is the distance (km) to the study site i , including all orchard meadows in the surrounding landscape up to 3 km distance from the central study site (derived from Hanski & Thomas 1994). Increasing C corresponds to less isolated or better connected study sites, respectively.

Nesting Traps

I used nesting traps to monitor the species richness and abundance of bees, wasps, and their natural enemies (Tscharrntke et al. 1998). At each of the 45 study sites, three wooden posts (1.5 m in height, 5–7 cm in diameter), each with four traps attached, were set up at regular distances (minimum 25 m) between 23 and 30 March 1998. The effects of different sampling efforts were prevented because I measured species richness most conservatively by using the same number of traps in each fragment (Connor & McCoy 1979; Rosenzweig 1995). Each nesting trap consisted of 150–180 20-cm-long internodes from the common reed *Phragmites australis* (Cav.) placed inside plastic tubes 10.5 cm in diameter. The reed internodes ranged in diameter from 2 to 10 mm.

Between 14 and 16 September 1998, at the end of the growing season, all nesting traps were collected and placed in a cold store at 4° C. In the laboratory, all reed internodes with nests from bees or wasps were taken out of the traps and opened. For each nest, the genus (and species if possible; see Gathmann & Tscharrntke 1999), the number of intact brood cells, and the number of brood cells attacked by natural enemies were recorded. I selected 10% of the intact brood cells of each species group per study site and reared them separately in the laboratory to get the adults of hosts and enemies for species identification. I left other brood cells in the reed internodes, which were closed and placed in the cold store until spring to mimic hibernation.

In 1999 I repeated the experiment at the same study sites. Again, nesting traps were exposed in April and collected at the end of September. Additionally, all bee and wasp nests from 1998 were placed in separate emergence boxes and returned to the same post from which they were removed.

Statistical Analyses

I performed statistical analyses of the data with Statgraphics Plus for Windows 3.0 (Statgraphics 1995).

Where necessary, logarithmic or square-root transformation of variables was used to achieve normality. I used the arcsine transformation ($\arcsin\sqrt{p}$) for proportional data (Sokal & Rohlf 1995). To separate possible effects of habitat area, habitat connectivity, and landscape context, I used step-wise multiple-regression analyses. This was done for all species and separately for bees, natural enemies, eumenid wasps (Eumeninae), and sphecid wasps (Sphecidae). Separate analysis for spider wasps (Pompilidae) was not performed because of the low abundance and species richness of this species group. I calculated the z values of log-log models for a scale-independent comparison with other species-area studies (Rosenzweig 1995). Arithmetical means and standard errors are given in the text.

Results

Community Structure

Altogether, I analyzed 13,422 brood cells in 1998 and 18,301 in 1999. These comprised 17,278 brood cells of 13 solitary bee species (Hymenoptera: Apidae), 8701 brood cells of 12 eumenid wasp species (Hymenoptera: Eumeninae), 5491 brood cells of 13 sphecid wasp species (Hymenoptera: Sphecidae), and 253 brood cells of 2 spider wasp species (Hymenoptera: Pompilidae). The local abundance of species was positively correlated with their regional distribution (i.e., the mean number of brood cells per species for occupied sites increased with the number of occupied orchard meadows) ($r = 0.606$, $n = 40$ species, $p < 0.001$).

A total of 5401 brood cells of the trap-nesting bees and wasps were attacked by 26 species of natural enemies from nine different families. Most species belonged to parasitic Hymenoptera of the families Chrysididae, Ichneumonidae, Gasteruptionidae, Eulophidae, Encyrtidae, and Sapygidae, but some Diptera and Coleoptera were also found. The mean rate of parasitism was 16.9% and was similar in both years (17.3% in 1998 and 16.6% in 1999). The proportion of parasitised brood cells of the 40 trap-nesting species increased with local host abundance (number of brood cells; $r = 0.433$, $n = 40$, $p = 0.005$) and regional distribution (number of occupied sites; $r = 0.373$, $n = 40$, $p = 0.018$).

Species-Area and Species-Abundance Relationships

In step-wise multiple-regression analyses with habitat area, habitat connectivity, and landscape diversity as predictor variables, habitat area was the most significant factor (Table 1). The total species richness of bees, wasps, and their natural enemies significantly increased

with the fragment size of orchard meadows (Fig. 1). When I analyzed each species group separately, bees, eumenid wasps, and natural enemies showed a significant species-area relationship, whereas no correlation existed for sphecid wasps (Table 1). For a comparison of slopes of the species-area relationship, I also calculated z values for log-log models. The z values were similar for hosts (bees and wasps, $z = 0.15$) and natural enemies ($z = 0.16$). Analyzing each species group separately, the highest z values were found for solitary bees ($z = 0.23$), followed by eumenid wasps ($z = 0.17$) and natural enemies. No significant species-area relationship existed for plants ($z = 0.03$).

I used the total number of brood cells to estimate abundance-area relationships. For the total abundance of trap-nesting species there was a marginally significant increase with habitat area (Table 1; Fig. 1). However, this pattern was based on the significant abundance-area relationship of eumenid wasps, whereas bee and sphecid wasp abundance did not correspond to area (Table 1). I also asked whether the strength of trophic interactions increased with fragment size. Although the species number of natural enemies increased with fragment area, neither the absolute number nor the proportion of parasitised brood cells correlated with fragment area (Table 1).

Habitat Connectivity

The fragment size of orchard meadows was positively correlated with the connectivity index C ($r = 0.395$, $p = 0.008$), indicating that the spatial arrangement of orchard meadows in the landscape resulted in a significantly higher connectivity of large meadows than of small meadows. In addition to the correlation with habitat area, the total number of species and the species number of eumenid wasps was negatively correlated with habitat connectivity in step-wise multiple-regression analyses (Table 1). The abundance of bees significantly increased with habitat connectivity (Table 1; Fig. 2). Neither abundance of wasps or natural enemies nor rate of parasitism correlated with habitat connectivity (Table 1).

Landscape Context at Different Spatial Scales

To analyze the impact of landscape context, I used the proportion of seminatural habitats and the diversity of habitat types (i.e., landscape diversity) at different spatial scales. First, I asked at which spatial scale the parameters of landscape context had the greatest impact on the studied insect communities. Species richness of bees and wasps and of natural enemies correlated significantly to landscape diversity only in a radius of 250 m (Fig. 3). No significant correlation existed for the proportion of seminatural habitats (data not shown).

Table 1. Multiple-regression analysis of the relationship of species richness, abundance, and percent parasitism of bees, wasps, and natural enemies to habitat area, connectivity, and landscape diversity.*

<i>Dependent variable</i>	<i>Variable in model</i>	<i>Effect</i>	F	p	r ²
Species richness					
total species richness	habitat area	positive	16.43	<0.0001	0.338
	connectivity	negative	4.55	0.0390	
	final model		10.49	0.0002	
species richness of natural enemies	habitat area	positive	13.97	0.0006	0.305
	landscape diversity	positive	4.05	0.0508	
	final model		9.01	0.0006	
species richness of bees	habitat area	positive	13.25	0.0007	0.240
species richness of sphecic wasps	—	—	—	ns	—
species richness of eumenid wasps	habitat area	positive	11.78	0.0014	0.4087
	landscape diversity	negative	8.19	0.0067	
	connectivity	negative	7.68	0.0084	
	final model		9.22	0.0001	
Abundance					
total number of brood cells	habitat area	positive	5.05	0.0290	0.107
brood cell number of natural enemies	—	—	—	ns	—
brood cell number of bees	connectivity	positive	9.19	0.0041	0.180
brood cell number of sphecic wasps	—	—	—	ns	—
brood cell number of eumenid wasps	habitat area	positive	5.15	0.0285	0.109
Parasitism (%)					
bees and wasps	—	—	—	ns	—
bees	—	—	—	ns	—
sphecic wasps	—	—	—	ns	—
eumenid wasps	—	—	—	ns	—

*Only significant explanatory variables are given in the table (ns, not significant). Backward selection of variables was used ($F > 4.0$). Habitat area and connectivity were \log_{10} -transformed, brood cell number was square-root-transformed, and percent parasitism was angular-transformed.

Second, I asked how much variability of insect communities could be explained by landscape context in addition to habitat area and habitat connectivity. The multiple-regression analysis was restricted to the most significant spatial scale (i.e., 250 m). The species richness of natural enemies was positively correlated with both habitat area and the surrounding landscape diversity, which together explained more variation than each factor alone (Table 1; Fig. 4). The species richness of bees and sphecic wasps did not respond to landscape diversity (Table 1). In contrast, the species richness of eumenid wasps significantly increased with habitat area but was negatively correlated with landscape diversity at a radius of 250 m (Table 1). No additional variation of total abundance of all species or of separate species groups was explained by landscape diversity (Table 1). The rate of parasitism of all brood cells and of brood cells of bees and sphecic and eumenid wasps was not correlated with landscape diversity (Table 1).

Discussion

My main objective was to analyze the combined effects of landscape context, habitat area, and habitat connectivity on insects in a fragmented landscape. The results indicate that landscape context and habitat connectivity

affected some species groups, but habitat area was the most important factor.

The inclusion of the surrounding landscape matrix is an approach that rarely has been realized in empirical studies on habitat fragmentation. A few other researchers have analyzed species occurrence in habitat fragments and asked about additional matrix effects (e.g., Aberg et al. 1995; Stouffer & Bierregaard 1995; Burke & Goulet 1998; Gascon et al. 1999; Norton et al. 2000). In my study, matrix effects on the local insect communities were found only for the diversity of habitat types in the surrounding landscape but not for the proportion of seminatural habitats. The species richness of natural enemies tended to increase with surrounding landscape diversity, whereas eumenid wasps showed an unexpected negative response.

The landscape matrix surrounding a habitat fragment may consist partly of other suitable habitat types. Depending on the degree of habitat specialization of the studied species group, these habitats may increase the amount of available resources in addition to the target habitat, or, even more important, certain resources may be restricted to other habitat types in the surrounding landscape. In the latter case, only the spatial neighborhood of different habitat types would enable species survival, and this may have been the case for natural enemies in my system.

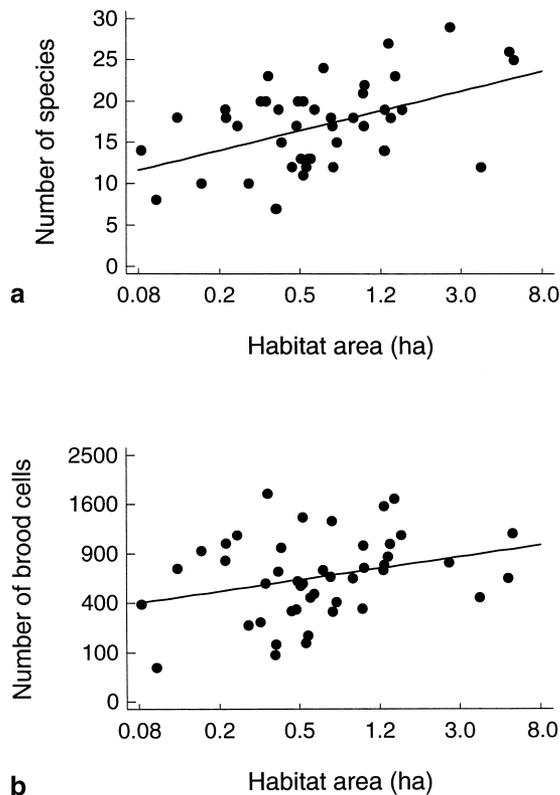


Figure 1. Relationship between (a) species richness and (b) abundance of bees, wasps, and natural enemies and the habitat area of orchard meadows. Statistics are given in Table 1.

Furthermore, landscape context can alter the functional connectivity of habitat fragments by increasing or decreasing the dispersal success of migratory species (Ricketts 2001). The results of other landscape studies suggest that the spatial scale at which species interact with landscape patterns depends on foraging or dis-

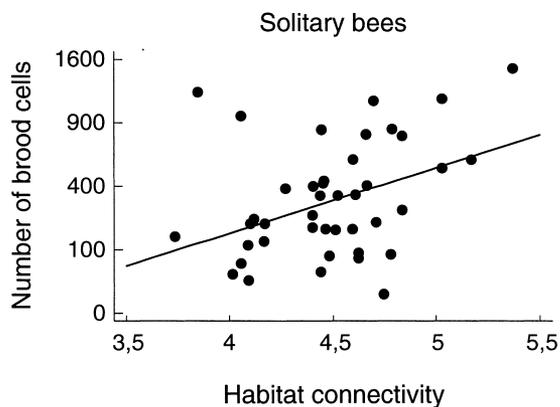


Figure 2. Relationship between the number of brood cells of bees and habitat connectivity (log-transformed). Statistics are given in Table 1.

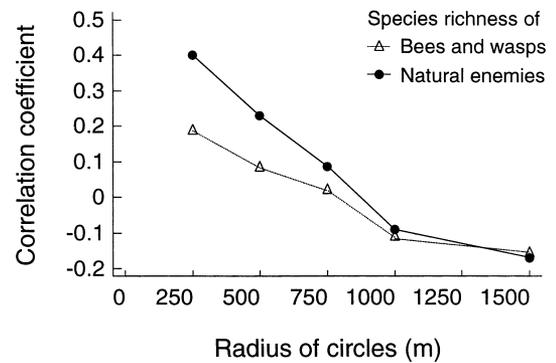


Figure 3. Correlation between species richness of bees and wasps and natural enemies and the diversity of habitat types (H_s) at five spatial scales (circle radii). Correlation coefficients of >0.3 are significant at $p < 0.05$.

persal distances (Keitt et al. 1997). For example, the species richness of moths in a tropical agricultural landscape was most strongly affected by the proportion of forest at radii between 1000 and 1400 m (Ricketts et al. 2001). The species richness of solitary bees with foraging distances of a few hundred meters depended on landscape context at a 250-m radius, whereas the abundance of honeybees with large foraging distances most significantly responded to a 3000-m radius (Steffan-Dewenter et al. 2002). In contrast to bees, little is known about foraging distances of aboveground nesting wasps. In my research, significant effects of landscape structure existed only at a small spatial scale (250-m radius), indicating that the foraging distances of the studied species groups are restricted to several hundred meters.

I found significant species-area relationships for total species richness and for bees, eumenid wasps, and natural enemies, but not for sphecid wasps. The strength of

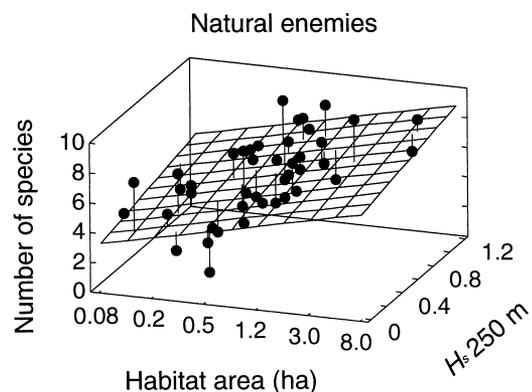


Figure 4. Dependence of species richness of natural enemies on habitat area and diversity of habitat types (H_s) in a 250-m radius around the study sites ($n = 45$). Statistics are given in Table 1.

species-area relationships is expected to be higher for habitat specialists and for higher trophic levels (Harrison & Bruna 1999; Holt et al. 1999). In my study, plants at the lowest trophic level did not show a species-area relationship, whereas the higher trophic levels of bees, wasps, and natural enemies did, thereby partly confirming the trophic-level hypothesis. In contrast to this hypothesis, however, predatory eumenid wasps and natural enemies of bees and wasps had lower z values than pollen-feeding bees. This was an unexpected result because most natural enemies are relatively specialized on certain bee or wasp groups as hosts. However, the occurrence of some prevalent unspecialized antagonists may have prevented close dependencies among trophic levels.

Alternatively, the different z values may reflect the different degrees of habitat specialization of the studied species groups. Trap-nesting bees have specialized resource requirements, which include preexisting tunnels in dead wood and flowering plants as pollen resources. Orchard meadows with old fruit trees can be expected to adequately fulfill these habitat requirements. The other wasp species depend similarly on nesting cavities. Eumenid wasps often use larvae of apple tortricids for nest provisioning, whereas sphecid wasps use a variety of prey, mostly aphids, spiders, and flies (Gathmann & Tscharrntke 1999), which are also abundant in arable fields. Thus, the food resources of sphecid wasps were presumably less restricted to orchard meadows, and this may have been the reason for their independence from fragment area.

The z values varied between 0.16 for natural enemies and 0.23 for bees and were high for terrestrial habitat fragments (Rosenzweig 1995). The z values of butterflies on fragmented calcareous grasslands, which were studied in the same region, varied between 0.06 for equal sample size and 0.12 for sample size adjusted to fragment area. Only the most specialized species group of monophagous butterflies had comparable z values (0.22) (Steffan-Dewenter & Tscharrntke 2000).

Bolger et al. (2000) did not find significant species-area relationships for bees and wasps sampled by pitfall traps and vacuums in urban habitat fragments. However, their sampling methods may have been unsuitable for these species groups (Cane 2001). Alfert et al. (2001) found significantly steeper species-area relationships for floral specialist bees and cuckoo bees than for unspecialized bees in abandoned limestone quarries.

In conclusion, the aboveground-nesting bees and eumenid wasps, recorded by trap nests in this study, and floral specialists appear to be more sensitive to habitat fragmentation than unspecialized bees and other insect groups. Other ecological traits such as body size, foraging distance, and migratory ability may further influence species-area relationships (Davies et al. 2000), but data were not available for all of the studied species groups. In contrast to other studies (Kruess & Tscharrntke 2000),

I found no area-dependent effects on parasitism by natural enemies. It is possible that interactions between hosts and natural enemies varied between different species, and their strength may have been influenced more by host densities and temporal dynamics than by spatial parameters.

The abundance of eumenid wasps significantly increased with habitat area, supporting the area dependence and habitat specialization of this species group. Increases of population densities with fragment size were also found for beetles (Burke & Goulet 1998; Didham et al. 1998) and specialized butterflies, whereas densities of polyphagous butterflies decreased with area (Steffan-Dewenter & Tscharrntke 2000). Results for other insect taxa are ambiguous (Connor et al. 2000).

Orchard meadows are relatively homogenous, well-defined habitat fragments. Therefore, it seems more plausible that area per se, and not increasing habitat diversity, was responsible for species-area effects. Similar conclusions were drawn by Kruess and Tscharrntke (2000) for herbivorous insects on *Vicia sepium*, whereas most other studies favor increasing habitat diversity as the biological explanation for species-area relationships (Rosenzweig 1995; Ricklefs & Lovette 1999).

The spatial arrangement of habitat fragments in the landscape (i.e., habitat connectivity of orchard meadows) did not have significant effects on the species richness of bees, sphecid wasps, and natural enemies. In contrast to expectations, the species richness of eumenid wasps was negatively correlated with habitat connectivity. Perhaps the increasing abundance of bees in well-connected habitats resulted in stronger competition for nesting places and thereby indirectly caused this negative relationship. It is interesting to note that the abundance of bees, which already showed the strongest species-area effect, and that of no other species group, was positively correlated with habitat connectivity. This supports the hypotheses that habitat connectivity increases local population density and thereby possibly reduces extinction risk, as has been shown for arthropods in experimental microecosystems (Gonzales et al. 1998). The effects of habitat connectivity may have been partly concealed by the intercorrelation between habitat area and connectivity. Therefore, the spatial arrangement in the landscape may also favor large habitats because they have better connectivity than small fragments.

My results have some important implications for conservation. First, bees seem to be more strongly affected by the fragmentation of seminatural habitats than other insect groups. Because bees are the most important group of pollinators, at least in temperate climates, this may change or disrupt plant-pollinator interactions (Rathcke & Jules 1993; Steffan-Dewenter et al. 2001). Second, the abundance of bees, and thus their effective population size, increased with connectivity to other orchard meadows, thereby presumably reducing the ex-

inction risk of well-connected local populations. Third, for natural enemies, species richness in local habitat fragments also increased with landscape diversity. Thus the conservation of habitat specialists depends mainly on the area and connectivity of local habitats. On the other hand, the conservation of habitat generalists or species that depend on resources from different habitat types within a limited spatial scale could possibly be supported by a structurally complex landscape matrix. My study underlines the importance of large-scale studies that account not only for the size of target habitats but also for the structure of the surrounding landscape matrix.

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