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SCALE-DEPENDENT EFFECTS OF LANDSCAPE CONTEXT ON THREE POLLINATOR GUILDS

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Abstract. Most ecological processes and interactions depend on scales much larger than a single habitat, and therefore it is important to link spatial patterns and ecological processes at a landscape scale. Here, we analyzed the effects of landscape context on the distribution of bees (Hymenoptera: Apoidea) at multiple spatial scales with respect to the following hypotheses: (1) Local abundance and diversity of bees increase with increasing proportion of the surrounding seminatural habitats. (2) Solitary wild bees, bumble bees, and honey bees respond to landscape context at different spatial scales. We selected 15 landscape sectors and determined the percentage of seminatural habitats and the diversity of habitat types at eight spatial scales (radius 250–3000 m) by field inspections and analyses of vegetation maps using two Geographic Information Systems. The percentage of seminatural habitats varied between 1.4% and 28%. In the center of each landscape sector a patch of potted flowering plants (four perennial and two annual species) was placed in the same habitat type, a grassy field margin adjacent to cereal fields. In all, 865 wild bee individuals and 467 honey bees were observed and an additional 475 individuals were caught for species identification. Species richness and abundance of solitary wild bees showed a close positive correlation with the percentage of seminatural habitats at small scales up to 750 m, whereas bumble bees and honey bees did not respond to landscape context at these scales. In contrast, honey bees were correlated with landscape context at large scales. The densities of flower-visiting honey bees even increased with decreasing proportion of seminatural habitats at a radius of 3000 m. We are not aware of any empirical studies showing contrasting foraging patterns related to landscape context at different spatial scales. We conclude (1) that local landscape destruction affects solitary wild bees more than social bees, possibly changing mutualistic plant–pollinator and competitive wild bees–honey bees interactions and (2) that only analyses of multiple spatial scales may detect the importance of the landscape context for local pollinator communities.

Key words: bees; biotic interactions; community structure; connectivity; habitat fragmentation; landscape ecology; pollination; spatial scales; species diversity.

INTRODUCTION

Habitat fragmentation and destruction have been recognized as major threats to biodiversity (e.g., Saunders et al. 1991, Harrison and Bruna 1999). Decreasing size and increasing isolation of habitat patches lead to a decline in species richness and abundance as well as to changes in community structure (Holt et al. 1999, Connor et al. 2000, Debinski and Holt 2000, Steffan-Dewenter and Tscharntke 2000*a*). This process of habitat fragmentation and destruction may greatly change the landscape structure and local ecosystem functions (Kareiva and Wennergren 1995). Most ecological processes and interactions depend on spatial scales much larger than a single habitat patch, and therefore, ecologists have become increasingly aware of the importance of linking spatial patterns and ecological processes at a landscape scale (Turner and Gardner 1991, Kareiva and Wennergren 1995, Gustafson 1998, Wiegand et al. 1999). Changes in landscape structure can be characterized by the proportion of suitable habitat (Andrén 1994), the diversity of habitats, and the size and spatial arrangement of habitats in a landscape (Gustafson 1998).

The analysis of ecological processes on large spatial scales is the subject of three more or less separated disciplines, metapopulation ecology, theoretical ecology, and landscape ecology (Hanski 1998). Metapopulation ecology provides a good framework to understand population dynamics as a consequence of migration, colonization, and extinction in spatially structured habitats. Theoretical ecologists have developed neutral landscape models and individual-based spatially explicit landscape models that emphasize the importance of analyzing different spatial scales (e.g., Keitt et al. 1997, Wiegand et al. 1999). Landscape ecologists are concerned with the description and analyses of real landscapes, using a variety of methods and parameters to quantify landscape structure (e.g., Turner and Gardner 1991, Cain et al. 1997, Gustafson 1998). Although there is an overlap between these disciplines,

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the needed synthesis has yet to emerge (Turner et al. 2001). Furthermore, community studies are mostly focused on habitat fragments and more or less ignore the importance of the surrounding matrix (Ricketts 2001, Tscharntke et al. 2002). Few empirical data provide an insight into how landscape structure determines the diversity and interactions of local communities and which spatial scale matters. Forest fragmentation affects four parasitoids of the forest tent caterpillar at different spatial scales depending on body size (Roland and Taylor 1997). Landscape structure affects biological control of oilseed rape pollen beetles (Thies and Tscharntke 1999) but not parasitism of the armyworm (Menalled et al. 1999). Bird diversity is determined by habitat diversity at intermediate spatial scales, while at large biogeographical scales abiotic factors are more important (Böhning-Gaese 1997). Functional groups of trees are related to landscape structure at different spatial scales (Metzger 2000). These studies indicate that particular patterns and processes occur at particular spatial scales and that the spatial scale at which organisms interact may depend on both the landscape type and the species' traits.

An important element of landscape structure is the degree to which a landscape facilitates or impedes movement of organisms among resource patches, i.e., connectivity (Tischendorf and Fahrig 2000). Structural connectivity by corridors maintains species richness and increases local population abundance in the fragmented landscapes of a microecosystem (Gilbert et al. 1998, Gonzales et al. 1998). Functional connectivity is a scale-dependent feature that depends on the spatial scale at which individuals perceive and interact with landscape structure by dispersal (Keitt et al. 1997, With et al. 1999). This 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).

In this study we analyzed the effects of landscape context on the diversity and abundance of bees (Hymenoptera: Apoidea) at different spatial scales. Bees are an important functional group due to their mutualistic interactions with plants (Allen-Wardell et al. 1998). The possible negative effects of habitat fragmentation and isolation on plant–pollinator interactions have attracted much attention in the last years (e.g., Rathcke and Jules 1993, Kearns et al. 1998), and some evidence exists that small or isolated plant populations receive fewer flower visits and may suffer from pollinator limitation (Jennersten 1988, Aizen and Feinsinger 1994, Steffan-Dewenter and Tscharntke 1999, Cunningham 2000). Almost nothing is known about the relation between landscape composition and pollinator diversity.

Bees can be subdivided into three pollinator guilds: solitary wild bees, social wild bumble bees, and managed honey bees. These groups greatly differ with respect to foraging distances and life history traits (Eickwort and Ginsberg 1980, Dramstad 1996, Osborne et al. 1999). The landscape in central Europe has been greatly changed by humans for several thousand years and almost no natural, primary bee habitats such as moors, inland dunes, or floodplains of rivers exist (Klemm 1996, Küster 1999). Today, native bees mainly depend on man-made seminatural habitats such as calcareous grasslands, meadows, and fallows, which developed by extensive land use (Osborne et al. 1991). Many bee species have specific requirements with respect to flowers providing pollen and nectar, nest sites, and building material, and these resources may occur spatially separated in different habitats within their foraging range (Westrich 1996). Therefore, not only the proportion of suitable habitat but also the diversity of habitat types may be important for the occurrence of a bee species in a landscape sector.

To standardize recording of pollinators, an experimental approach was used that is analogous to the ''hybrid patch-landscape scale'' approach suggested recently by theoretical ecologists (Tischendorf and Fahrig 2000). They recommend the use of nonoverlapping landscapes as study units and the sampling of a single patch in the center of each landscape. Each single data point is obtained from a separate landscape and therefore replicated at the landscape scale thus maintaining independence (Tischendorf and Fahrig 2000). Here, we selected 15 landscape sectors using a gradient from structurally simple to structurally rich landscapes. In the center of each landscape a patch of flowering plants was placed in the same local habitat (grassy field margins adjacent to cereal fields) to measure the diversity and abundance of bees associated with landscape context at multiple spatial scales. We expected (1) that abundance and diversity of bees increase with increasing percentage of seminatural habitats in a landscape and (2) that solitary bees, bumble bees, and honey bees respond to landscape context to a different extent and at different spatial scales.

MATERIAL AND METHODS

Study region and study sites

The study was conducted in 1997 in southern Lower Saxony, Germany, around Göttingen. The study region is characterized by intensively managed agricultural areas and patchily distributed fragments of forests and several other seminatural habitat types (Fig. 1a; Plate 1). The average temperature during the study period from June to August was 19.7°C (2.4°C above the long-term mean), the rainfall was 223.8 mm (17.6 mm above the long-term mean), and the duration of sunshine was 699.9 h (96.5 h above the long-term mean; data from the meteorological station in Hanover).

We selected 15 study sites that covered all levels of landscape context in the study area from structurally simple to structurally rich landscapes. Study sites with

FIG. 1. Study region and study sites in southern Lower Saxony, Germany. (a) Location of the 15 landscape sectors and the distribution of the main habitat types. (b) Four study sites (marked A, B, C, and D in Fig. 1a) with the eight nested spatial scales used in the analyses.

PLATE 1. (Left) A structurally rich landscape sector 5 km northeast of Göttingen, Germany (C in fig. 1a). Photograph by Carsten Thies. (Right) Flower-visiting bumble bee (*Bombus pascuorum*) on *Centaurea jacea*. Photograph by Ute Münzenberg.

different types of landscape structure were randomly distributed to prevent possible autocorrelation and correlations between landscape structure and abiotic factors (Fig. 1a). The effects of landscape context on bee visitation to the experimental plots were analyzed at eight radii of 250, 500, 750, 1000, 1500, 2000, 2500, and 3000 m, which represented a nested set of spatial scales (Fig. 1b). These scales were chosen due to known flight and forage distances of several hundred meters for solitary bees and up to 3 km for honey bees (Eickwort and Ginsberg 1980, Visscher and Seeley 1982, Dramstad 1996, Osborne et al. 1999, Steffan-Dewenter and Tscharntke 2000*b*).

Quantifying landscape context

Landscape context was quantified using two different methods. First, for the three smallest scales (radius 250–750 m), intensive field inspections were made to quantify the total area of each habitat type in the landscape sector. Field inspections were supported by infrared aerial photographs (1 : 10 000). The results of field inspections were incorporated into topographical maps with a scale of 1 : 5000. Habitat types were classified according to von Drachenfels (1996) into: arable land; fallow fields and ruderal areas (including field margins); intensively used grasslands; extensively used grasslands (including orchard meadows); calcareous grasslands; hedgerows, forest; water area and settlement area; rock habitats and vegetation along inshore waters (Table 1). Forests were further divided into a core area and forest margins (10 m deep boundary) adjacent to nonforest habitats. To characterize landscape context we calculated for each spatial scale the percentage (p_i) of seminatural habitats that were ex-

TABLE 1. Habitat composition in the landscape sectors in Southern Lower Saxony, Germany.

Habitat type	Area (%)	Minimum (%)	Maximum (%)
a) Quantification based on own field inspections (radius 750 m)			
Arable land	77.98 ± 17.17	49.9	96.76
Calcareous grasslands†	3.17 ± 5.36	0	20.43
Extensive grasslands†	2.88 ± 3.68	0	10.66
Intensive grasslands	2.35 ± 1.97	0	6.44
Fallows and ruderal areas†	2.54 ± 2.10	0	6.16
Hedgerows†	1.15 ± 1.58	0	5.82
Forests	8.46 ± 9.95	0	28.01
Forest margins†	0.54 ± 0.67	0	2.20
Vegetation along inshore waters†	0.53 ± 0.46	0	1.35
Rock habitats†	0.04 ± 0.11	0	0.36
Settlement	0.33 ± 0.11	0.09	0.49
b) Quantification based on digital thematic maps (radius 750 m)			
Arable land	74.63 ± 17.08	50.86	98.33
Grasslands†	12.0 ± 9.75	0	36.58
Hedgerows†	0.18 ± 0.42	0	1.37
Forests	9.61 ± 11.23	0	29.28
Garden land†	0.05 ± 0.13	0	0.48
Settlement	2.15 ± 3.34	0	12.67

Note: Means ± 1 SD, minimum, and maximum are given for 15 study sites.
† Habitat types classified as seminatural habitat.

pected to represent potential bee habitats (see Table 1) and total habitat diversity using the Shannon-Wiener index ($H's = -\Sigma p_i \times \log(p_i)$; Krebs 1989).

Second, for all spatial scales (radius 250–3000 m), a less-detailed method was used to quantify landscape structure using existing commercially available, digital maps (ATKIS-DLM 25/1, 1991–1996; Landesvermessungsamt + Geobasisinformationen Niedersachsen, Hannover, Germany) covering the habitat types arable land, grassland, hedgerows, garden land, forest, and settlement area (Table 1). For each of the eight nested spatial scales the total area of each habitat type was quantified separately using the Geographic Information Systems ARC/View 3.1 (ESRI Geoinformatik, Hannover, Germany) and TopoL 4.506 (Gesellschaft für digitale Erdbeobachtung und Geoinformationen, Göttingen, Germany). Again, the proportion of seminatural habitats (grasslands including intensively and extensively used grasslands, calcareous grasslands and orchard meadows, hedgerows, and garden land; see Table 1) and total habitat diversity (Shannon-Wiener index) were calculated for each of the eight spatial scales separately.

Field experiments

To measure the effect of landscape context on pollinator diversity and abundance independently from soil conditions and habitat quality, we established patches of potted flowering plants in the center of each of the 15 landscape sections (Fig. 1b). To cover a broad spectrum of flower morphology and flowering time we used four perennial plant species, *Anthyllis vulneraria* (Fabaceae), *Campanula rotundifolia*, *Campanula rapunculoides* (Campanulaceae), and *Centaurea jacea* (Asteraceae), and two annual plant species, *Raphanus sativus* (Brassicaceae) and *Borago officinalis* (Boraginaceae). Seeds from wild plant populations were obtained from a commercial seed grower (Conrad Appel, Abteilung Wildpflanzensamen, Darmstadt, Germany). The perennial species were sown in November 1996 in a glasshouse, pricked out in mid-December (*Anthyllis vulneraria*) and mid-January (*Campanula rotundifolia*, *C. rapunculoides*, and *Centaurea jacea*), respectively, and planted in upper compartments (pots of 3.5 L, 24 cm diameter) with standardized garden soil (Einheitserde Typ T; Archut/Hawita, Vechta, Germany) of larger pots (8.5 L, 24 cm diameter) in March. The lower part of the pot was used as a water supply (5 L) and was connected with wicks to the upper part, which contained the garden soil. Annuals were sown in mid-March 1997 (*R. sativus*) and mid-May (*B. officinalis*). Two of the experimental plant species were placed into each pot using the following combinations: *A. vulneraria* with *Campanula rotundifolia*, *R. sativus* with *Centaurea jacea*, and *Campanula rapunculoides* with *B. officinalis*. Four pots of each of the three plant species combinations were placed on grassy field margins adjacent to cereal fields in each of the 15 landscapes between 13 and 16 May 1997 to establish experimental patches of flowering plants, i.e., 12 pots per study site and 180 pots altogether. Distance between each conspecific pot was 1 m. To prevent damage by rabbits or deer, the plants were fenced with wire (6 m × 1.20 m, 1 m height). Depending on weather conditions, plants were watered every 5–10 d.

Flower-visitor observations

Flower visitation was observed between 0900 and 1700 during June–August 1997 in typical weather conditions, i.e., at least 18°C, 70% sunshine, and low wind velocity. The four individuals of each plant species were observed simultaneously, recording all flower-visiting insects for 15 min (Plate 1). Bees were identified to genus level in the field. After each observation period, flower-visiting bees were captured during a further 15-min period for identification in the laboratory. To obtain unbiased data, on each field day, observations were made in different landscape types, and time of day was varied at a given study site for successive observations. The number of observation periods per plant species depended on the flowering period and weather conditions and varied between two and five observations per study site. Altogether 314 flower-visitor record periods (15-min observation and 15-min capture) were made. *A. vulneraria* flowered between 18 June and 25 July, *Campanula rotundifolia* between 25 June and 8 August, *Campanula rapunculoides* between 29 June and 4 August, *Centaurea jacea* between 29 July and 25 August, and *B. officinalis* between 6 and 25 August 1997. *R. sativus* plants could not be observed, because they did not grow well and developed only few flowers.

Statistical analyses

The statistical analyses of the data were performed using Statgraphics plus for Windows 2.1 (Statgraphics 1995). All data were tested for normality and transformed where necessary. Arcsine transformation ($\arcsin\sqrt{p}$ where p is a proportion) was used to achieve normal distribution for percentages (Sokal and Rohlf 1995).

Pollinator abundance per study site was the mean number of observed flower-visiting bee individuals per 15 min over all five plant species. Species richness per landscape represents the total number of bee species captured in the second part of each observation period. The effect of landscape context on pollinators was assessed using simple linear regressions. We analyzed each of the eight nested landscape sectors (radius from 250 to 3000 m) separately and tested for each radius how the species richness and abundance of all wild bees, solitary wild bees, bumble bees, and honey bees responded to the proportion of seminatural habitats. Mean individual body size of solitary wild bees was calculated using a database of German bee species (Steffan-Dewenter and Tscharntke 1999). Scatterplots

TABLE 2. Correlations between percentage of seminatural habitats (rows) and the diversity of habitat types (H', columns) at different spatial scales.

Percentage of seminatural habitats at scale	Scale for H'							
	250 m	500 m	750 m	1000 m	1500 m	2000 m	2500 m	3000 m
250 m	0.870***	0.783**	0.727**	0.535*	0.474	0.348	0.310	0.325
500 m	0.758**	0.753**	0.743**	0.565*	0.479	0.409	0.396	0.479
750 m	0.726**	0.677**	0.723**	0.569*	0.527*	0.407	0.449	0.448
1000 m	0.783**	0.718**	0.741**	0.595*	0.558*	0.419	0.526*	0.451
1500 m	0.745*	0.630*	0.644**	0.494	0.438	0.346	0.559*	0.477
2000 m	0.653**	0.528*	0.520*	0.389	0.385	0.44	0.636*	0.556*
2500 m	0.578*	0.436	0.445	0.352	0.410	0.471	0.608*	0.539*
3000 m	0.548*	0.378	0.398	0.329	0.364	0.415	0.550*	0.510

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

were used to illustrate scale-dependent changes of r^2 values for the correlation between landscape context and pollinators. Arithmetic means ± 1 SD are given in the text.

RESULTS

Characteristics of landscape context

Landscape context was characterized by the proportion of each habitat type and by the diversity of habitat types at eight spatial scales. Field inspections allowed us to distinguish 11 different habitat types, whereas the digital thematic maps only differentiated between 6 habitat types (Table 1). Dominant habitat types were arable land, forest, and grasslands. The proportions of these habitat types were similar in the field inspections and the maps (Table 1a and b). For example, the mean percentage of seminatural habitats in a radius of 750 m was 10.5 ± 9.3% for field data and 12.8 ± 9.7% for data from digital maps and varied between 1.4–28.0% and 0.1–36.6%, respectively.

The proportion of seminatural habitats and the diversity of habitat types were significantly correlated at most spatial scales (Table 2). Due to this close intercorrelation, we focused our analyses on the proportion of seminatural habitats. Furthermore, the proportion of seminatural habitats of landscape sectors of different size were only closely correlated when radii of landscape sectors were similar (Fig. 2).

Flower-visiting insects

A total of 865 wild bee individuals was observed in the field, and 475 individuals were caught for species identification. Altogether, we found 36 bee species from nine genera. The most species-rich genera were *Lasioglossum* (10 species), and *Bombus* (8 species) followed by *Halictus* (4), *Megachile* (4), *Hylaeus* (3), *Chelostoma* (2), *Andrena* (2), *Psithyrus* (2), and *Melitta* (1). Additionally, 467 honey bees (*Apis mellifera*) were observed. The mean number of observed wild bee species was 11 ± 3.9 per landscape sector, and the mean number of observed individuals per 15 min was 2.69 ± 2.01 for all wild bees (Table 3). Solitary wild bees were more abundant than honey bees and bumble bees. These three pollinator guilds varied considerably in species richness and/or abundance between the 15 study sites (Table 3). Species richness and abundance of flower-visiting wild bees were closely correlated ($r^2 = 0.733$, $n = 15$, $P < 0.001$).

Scale-dependent effects of landscape context

The focus of this study was on the effects of landscape context on pollinators at different spatial scales.

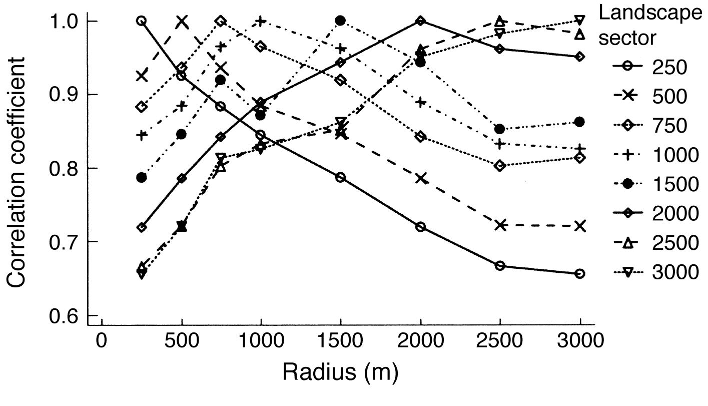

FIG. 2. Correlation coefficients between the proportion of seminatural habitats at different spatial scales. Proportions of seminatural habitats are extracted from digital thematic maps (see *Material and methods*).

TABLE 3. Species richness and species abundance for all wild bees, solitary wild bees, bumble bees, and honey bees.

Factor	Species group	Mean ±1 SD	Minimum	Maximum
Species richness	all wild bees	11 ± 3.85	6	17
	solidary wild bees	7.73 ± 3.83	3	15
	bumble bees	3.27 ± 1.5	1	6
Abundance (no. individuals per 15 min)	all wild bees	2.69 ± 2.01	0.81	7.59
	solitary wild bees	1.84 ± 2.03	0.2	6.47
	bumble bees	0.85 ± 0.53	0.23	2.14
	honey bees	1.24 ± 0.89	0.1	3.37

Note: Means ±1 SD, minimum, and maximum are given for 15 study sites.

For small scales up to 750 m we could rely on our own field data. Both species richness and abundance of wild bees significantly increased with the proportion of seminatural habitats at all three scales (Table 4). The strongest correlation between species richness and abundance of all wild bees and the proportion of seminatural habitats was found for the 750 m radius (Fig. 3a and b). Similarly, the number of species and the abundance of solitary wild bees were closely correlated with the proportion of seminatural habitats, whereas bumble bees and honey bees did not show a relationship with landscape context at scales up to 750 m (Table 4). Total pollinator abundance (including all wild bees and honey bees) declined with decreasing proportion of seminatural habitats ($y = 0.47 + 0.22 \arcsin\sqrt{x}$; $r^2 = 0.722$, $F = 33.83$, $n = 15$, $P < 0.001$), i.e., the general pattern was determined by the distribution of solitary wild bees. The mean body size of solitary flower-visiting bees showed a tendency to increase in landscapes with lower proportions of seminatural habitats ($r^2 = 0.238$, $n = 15$, $P = 0.065$).

In the next step, we analyzed the effects of landscape structure at multiple spatial scales on pollinator distribution using data from digital thematic maps. For each of eight landscape sectors between 250 and 3000 m radius, we tested how species richness and abundance of all wild bees, solitary wild bees, bumble bees, and honey bees was related to landscape structure. For scales between 250 and 750 m, the results were similar to those from the field inspections, indicating that the less detailed data from digital maps were similarly useful in predicting the distribution of bees (Table 5). Again, species richness and abundance of solitary wild bees were a positive function of the proportion of seminatural habitats, whereas the bumble bees and honey bees did not show a significant correlation. However, the best correlations for the distribution of species richness or abundance of all wild bees or solitary wild bees was found in a radius of 250 m and explained ~25% less of the variation than the detailed data from our field inspections (see Tables 4 and 5).

A scatterplot of r^2 values for solitary wild bees, bumble bees, and honey bees with the proportion of seminatural habitats over all landscape sectors indicated that each pollinator group depended on landscape structure at different spatial scales. The amount of variation in solitary wild bee abundance explained by the proportion of seminatural habitats in the surrounding landscape decreased with increasing spatial scale (Fig. 4a and b). The dependence of bumble bees on landscape context was weak and not significant at any scale (Fig. 4c and d). In clear contrast, the significance of land-

TABLE 4. Relationship between species richness and abundance of pollinator groups and the proportion of seminatural habitats at three spatial scales.

	Scale					
	250 m		500 m		750 m	
Species group	Corr. Coef.	*P*	Corr. Coef.	*P*	Corr. Coef.	*P*
Species richness (no.)						
All wild bees	0.710	0.003	0.770	<0.001	0.820	<0.001
Solitary wild bees	0.804	<0.001	0.870	<0.001	0.856	<0.001
Bumble bees	−0.286	NS	−0.286	NS	−0.071	NS
Abundance (no. individuals per 15 min)						
All wild bees	0.746	0.001	0.824	<0.001	0.859	<0.001
Solitary wild bees	0.787	<0.001	0.822	<0.001	0.842	<0.001
Bumble bees	−0.224	NS	−0.094	NS	0.040	NS
Honey bees	−0.017	NS	−0.037	NS	0.086	NS

Notes: Correlation coefficients (Corr. Coef.) and significance levels are given for simple linear regressions. Landscape structure was quantified by field inspections (see *Material and methods*).

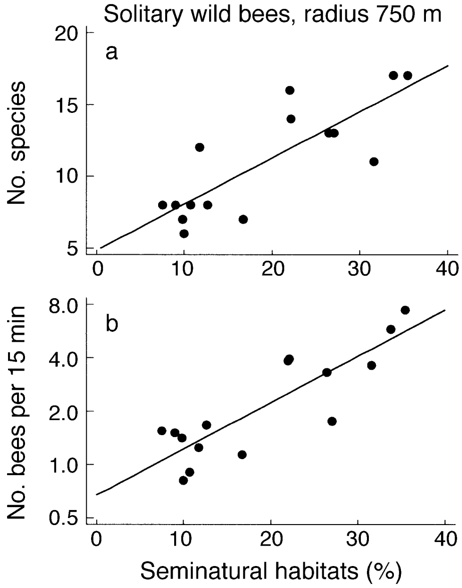

FIG. 3. Relationship between the species richness and abundance of flower-visiting wild bees on five experimentally exposed potted plant species and the proportion of seminatural habitats in a radius of 750 m. (a) Relationship between the number of species and the proportion of seminatural habitats: $y = 4.865 + 0.396 \times \arcsin\sqrt{x}$; $r^2 = 0.673$, $F = 26.75$, $n = 15$, $P < 0.001$. (b) Relationship between the number of flower-visiting bees per 15 min and the proportion of seminatural habitats: $\ln(y) = -0.40 + 0.0748 \times \arcsin\sqrt{x}$; $r^2 = 0.738$, $F = 36.58$, $n = 15$, $P < 0.001$. Note the logarithmic scale for bee abundance.

scape context for the distribution of honey bees increased with the tested spatial scale (Fig. 4e). Interestingly, the abundance of flower-visiting honey bees increased with decreasing proportion of seminatural habitats at the largest spatial scale (Fig. 4f).

DISCUSSION

Our results show that landscape context significantly influences pollinator diversity and abundance. Furthermore, the three main pollinator groups, solitary wild bees, bumble bees, and honey bees responded to landscape context at different spatial scales.

We focused on one parameter to quantify landscape structure, the proportion of seminatural habitats in a landscape. This parameter was correlated with other potential indicators of landscape structure such as the diversity of habitat types, mean habitat size, and habitat isolation for both the data from digital thematic maps and the field data (see Thies and Tscharntke 1999). Similarly, Gustafson (1998:150) argues that ''knowing the proportion of a type of interest tells you almost as much as knowing many other measures of heterogeneity.'' We conclude that for our study system it is better to use a simple and ecologically relevant factor instead of difficult-to-interpret indices that combine multiple components. However, not only the proportion of seminatural habitats but also changes in habitat diversity and habitat isolation may have influenced the observed patterns. Depending on the proportion of suitable habitat, either the amount of habitat or the habitat isolation may be more important (Andrén 1994).

The overall diversity and density of flower-visiting bees linearly declined with decreasing proportion of seminatural habitats. Thus, we did not find a critical threshold of habitat destruction beyond which diversity drastically drops as some models suggest (Kareiva and Wennergren 1995, With and Crist 1995, Andrén 1999, Keitt et al. 1997), although the proportion of seminatural habitats was <5% in seven landscapes due to intensive agricultural land use. Our empirical data suggest a much simpler relationship, as Kareiva and Wennergren (1995:302) formulate: ''species are steadily lost in direct proportion to habitat destruction (without hidden thresholds. . .).'' Nonetheless, our data show an alarming loss of pollinator diversity and abundance in structurally simple landscapes. In these landscapes, pollinator services mainly depend on some bumble bee species and honey bees.

Solitary wild bees, bumble bees, and honey bees

TABLE 5. Relationship between species richness and abundance of pollinator groups and the proportion of seminatural habitats at eight spatial scales.

	Scale							
	250 m		500 m		750 m		1000 m	
Species group	Corr. Coef.	*P*	Corr. Coef.	*P*	Corr. Coef.	*P*	Corr. Coef.	*P*
Species richness (no.)								
All wild bees	0.696	0.004	0.6187	0.014	0.521	0.046	0.533	0.041
Solitary wild bees	0.686	0.005	0.620	0.014	0.552	0.033	0.582	0.023
Bumble bees	0.048	0.864	0.010	0.972	0.083	0.767	−0.142	0.614
Abundance (no. individuals per 15 min)								
All wild bees	0.779	0.001	0.729	0.002	0.715	0.003	0.755	0.001
Solitary wild bees	0.621	0.014	0.601	0.018	0.502	0.056	0.538	0.038
Bumble bees	0.361	0.186	0.368	0.177	0.407	0.132	0.403	0.137
Honey bees	0.013	0.964	−0.068	0.810	−0.199	0.476	−0.238	0.394

Notes: Correlation coefficients (Corr. Coef.) and significance levels are given for simple linear regressions. Proportions of seminatural habitats are extracted from digital thematic maps (see *Material and methods*).

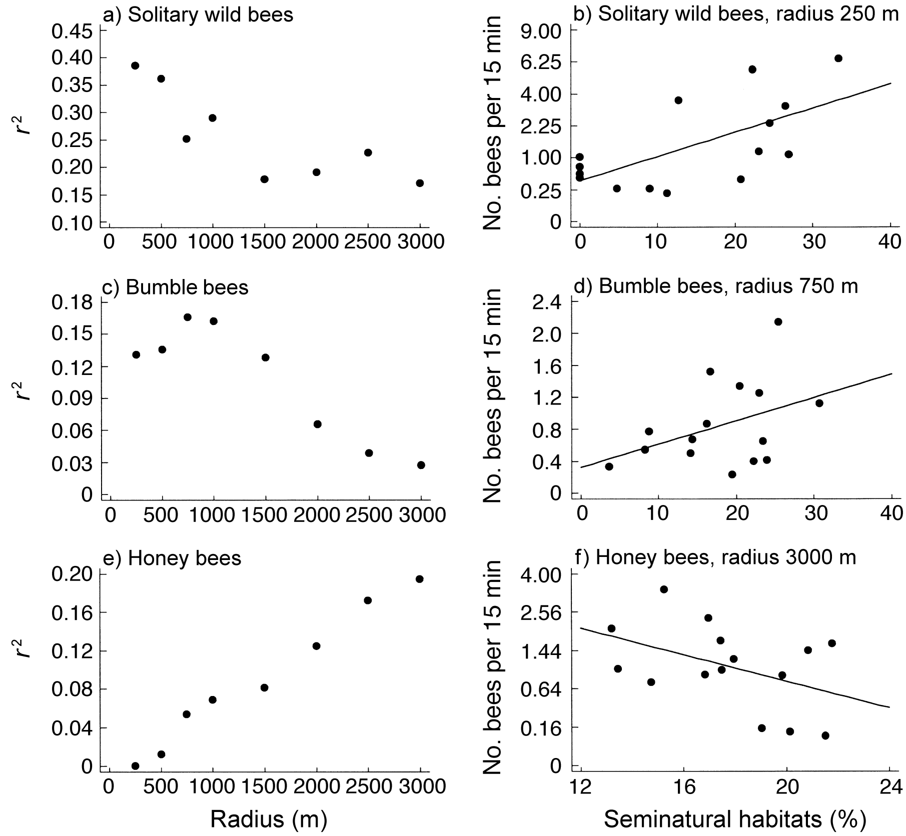

FIG. 4. Scale-dependent effects of landscape structure on flower-visiting solitary wild bees, bumble bees, and honey bees. In panels (a, c, e), for eight landscape sectors of 250–3000 m radius, r^2 values for simple linear regressions between the proportion of seminatural habitats and the number of flower-visiting bees per 15 min are presented. In panels (b, d, f), the relationships between bee abundance per 15 min and the proportion of seminatural habitats are presented. Simple linear regressions for the spatial scale with the highest r^2 value are shown. Solitary wild bees: $\sqrt{y} = 0.641 + 0.038 \times \arcsin\sqrt{x}$; $r^2 = 0.413$, $F = 9.15$, $n = 15$, $P = 0.010$. Bumble bees: $r^2 = 0.162$, $F = 2.51$, $n = 15$, $P = 0.137$. Honey bees: $\sqrt{y} = 2.27 - 0.069 \times \arcsin\sqrt{x}$; $r^2 = 0.194$, $F = 3.13$, $n = 15$, $P = 0.100$. Note the square-root scale for bee abundance in panels (d) and (f). Proportions of seminatural habitats are extracted from digital thematic maps (see *Material and methods*).

revealed different degrees of dependence on landscape structure. This may have two reasons: First, solitary wild bees have specific habitat requirements and can be assumed to be more restricted to seminatural habitats such as calcareous grasslands or orchard meadows than bumble bees and honey bees (Osborne et al. 1991, Banaszak 1992, O'Toole 1993). Second, foraging ranges of solitary wild bees are smaller than those of bumble

TABLE 5. Extended.

Scale							
1500 m		2000 m		2500 m		3000 m	
Corr. Coef.	*P*	Corr. Coef.	*P*	Corr. Coef.	*P*	Corr. Coef.	*P*
0.376	0.168	0.296	0.284	0.284	0.305	0.236	0.397
0.448	0.094	0.357	0.188	0.337	0.220	0.283	0.307
−0.218	0.436	−0.192	0.493	−0.159	0.571	−0.142	0.614
0.604	0.017	0.571	0.026	0.599	0.018	0.461	0.084
0.422	0.117	0.437	0.117	0.476	0.073	0.414	0.125
0.358	0.190	0.256	0.357	0.197	0.482	0.169	0.557
−0.273	0.324	−0.322	0.241	−0.375	0.169	−0.408	0.131

bees and honey bees, although concrete data are still lacking in many cases (Eickwort and Ginsberg 1980, Visscher and Seeley 1982, Wesserling and Tscharntke 1995, Dramstad 1996, Osborne et al. 1999). The importance of foraging ranges is supported by the observed increase in mean body size of solitary wild bees in landscapes with lower proportion of suitable habitat and higher patch isolation, because larger species are assumed to have better flight capabilities and larger foraging distances (see Gathmann et al. 1994, van Nieuwstadt and Iraheta 1996, Steffan-Dewenter and Tscharntke 1999). Solitary wild bees and honey bees showed contrasting responses when we analyzed different spatial scales. The distribution of solitary wild bees could be best explained by the percentage of seminatural habitat at small spatial scales whereas honey bees responded to landscape structure only at large scales. This supports the view that species perceive the landscape structure at different spatial scales depending on their dispersal abilities or foraging ranges (Keitt et al. 1997, With et al. 1999). Interestingly, the densities of honey bees visiting the experimental patches of flowering plants increased when the proportion of seminatural habitats decreased. The predictive power of the larger scales in our study fit well with the foraging range of honey bees of 2.5–3 km and indicates that a colony selects the most profitable flower patches in this range (Visscher and Seeley 1982, Steffan-Dewenter and Tscharntke 2000*b*). In landscapes dominated by crop fields, alternative food sources were presumably rare, and therefore, honey bees visited the experimental patches more intensively than in landscape sectors with a higher proportion of seminatural habitats. The local distribution and density of foraging honey bees clearly depends also on the location of apiaries. We have not yet a complete database of apiaries in all studied landscapes, but beekeepers often use seminatural habitats to place their colonies, possibly resulting in a positive correlation between the proportion of seminatural habitats and the density of honey bee colonies (Steffan-Dewenter and Tscharntke 2000*b*). Therefore, from the distribution of honey bee colonies we would expect the opposite pattern to the one we found, i.e., higher densities of flower-visiting honey bees in structurally rich landscapes. To summarize, the spatial pattern of bee foraging may be affected by: the spatial arrangement of additional flower patches, which are predicted to be more abundant in structurally rich than poor landscapes; the spatial scale at which the flower visitor perceives variation in flower abundance depending on species-specific foraging ranges; and by the distribution of nesting sites, which should be more important for solitary wild bees than for social bees.

Our results may have implications for both competitive interactions between bees and mutualistic interactions between plants and pollinators. The higher foraging density of honey bees in landscapes with lower proportions of seminatural habitat suggest a higher foraging pressure by honey bees on isolated habitat fragments in such landscapes. Thus, the potential of mosaic landscapes to lower competitive pressure (Hanski 1995) may be lost in very simple landscapes with few alternative food resources. Although landscape structure has been suggested to influence competition between honey bees and wild bees under certain conditions (e.g., Steffan-Dewenter and Tscharntke 2000*b*), we are not aware of any empirical studies to date showing contrasting foraging patterns related to landscape context at different spatial scales.

Our data suggest that small plant patches are well connected in structurally rich landscapes, whereas connectivity in landscapes with low proportions of seminatural habitats is maintained only by a few social species (bumble bees and honey bees) with large foraging ranges. The decline of these remaining species would have severe effects on allogamous plant species (Corbet 1997). Furthermore, the loss of pollinator diversity and the dominance of bumble bees and honey bees in landscapes with low proportions of seminatural habitats may favor plant species that require only generalist pollinators with the possible long-term loss of more specialized plant species relying on more specialist solitary bees (Rathcke and Jules 1993, Kearns et al. 1998). However, lower proportions of seeds damaged by seed predators in landscapes with few seminatural habitats may counterbalance the negative effects of pollinator limitation on the number of remaining seeds (Steffan-Dewenter et al. 2001).

Most published studies on the effects of landscape context, dealing almost always with vertebrates not insects, analyzed species occurrence in native habitat fragments and asked for additional matrix effects (e.g., Aberg et al. 1995, Stouffer and Bierregaard 1995, Gascon et al. 1999, Norton et al. 2000). In these studies, community changes depend on fragment size or quality and matrix composition. In contrast, our experimental patches were placed in the nonhabitat matrix and thereby allow for an assessment of landscape effects independent from local habitat effects. By exposing potted plants of identical origin, growing in one soil type with the same nutrient and water availability, we were able to minimize possible confounding factors. For example, landscape structure correlated with nutrient richness of soils, but not with insecticide application (I. Roschewitz, *unpublished data*). Diversity of butterflies in a Swedish agricultural landscape depended on landscape heterogeneity but no differences between organic and conventional farms were found (Weibull et al. 2000). In a recent study on the biodiversity of moths in a fragmented agricultural landscape in Costa Rica, Ricketts et al. (2001) mapped moths in agricultural habitats and quantified, at different radii in the surrounding landscape, the cover of the forest habitat. Correlations between species richness of moths and forest cover were low for small neighborhood scales, but dramatically increased when neighborhood scales of 1.0

and 1.4 km were used, indicating that landscape context at larger spatial scales was more important than at smaller scales.

We conclude (1) that landscape destruction affects solitary wild bees more than social bees, which possibly leads to changes in mutualistic and competitive interactions and (2) that only analyses of multiple spatial scales may detect the importance of landscape context for pollinator communities.

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