Bee Diversity and Plant–Pollinator Interactions in Fragmented Landscapes

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The worldwide destruction and fragmentation of natural habitats and the increasing dominance of highly disturbed anthropogenic habitats are considered major threats to biodiversity and ecosystem functioning (Harrison and Bruna 1999; Naeem et al. 1999). The loss of biodiversity may threaten essential ecological interactions in ecosystems such as decomposition, parasitism, predation, or pollination (Martinez 1996); however, most research on biodiversity and ecosystem functions has focused on more general, integrating ecosystem characteristics, such as productivity, stability, or resilience of ecosystems, and has neglected biotic interactions as important drivers of ecosystem functioning (Chapin et al. 1997; Loreau et al. 2001; Lundberg and Moberg 2003). Furthermore, most research has been done with plants in small experimental patches, whereas larger spatial scales and functional animal groups have rarely been considered in the context of biodiversity and ecosystem functioning (Naeem and Wright 2003).

Pollinators do not directly affect ecosystem processes but they have the potential to change the structure and diversity of plant communities, thereby indirectly affecting ecosystem properties (Lundberg and Moberg 2003). The loss of pollinators and consequent risks for pollination as an important ecosystem service has received much attention during past years (e.g., Rathcke and Jules 1993; Kearns et al. 1998; Wilcock and Neiland 2002). The actual impact of pollinator loss on pollination services depends greatly on the degree of specialization of plant–pollinator interactions (fig. 17.1). Assuming a close one-to-one relationship between a single pollinator species and a single plant species, this should result in the extinction of the remaining mutualistic partner in case of extinction of either the pollinator or the plant species. Unbalanced relationships where several plant species rely on one pollinator species or several pollinator species on one plant species also impose a high extinction risk for either the pollinator or the plant species. At the other extreme (generalized relationships where several pollinator species visit several plant species and vice versa), plant–pollinator systems should be resilient over a broad range of pollinator loss (fig. 17.1).
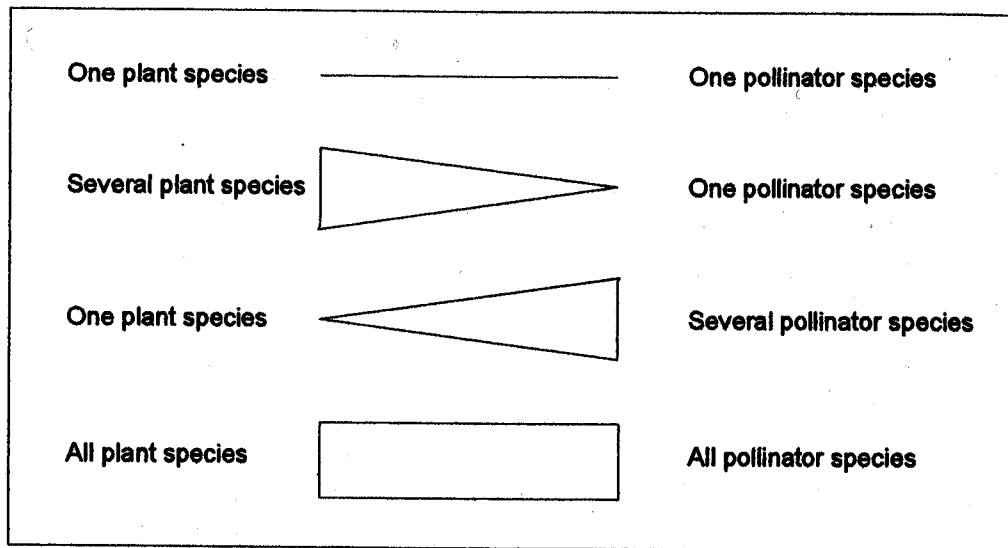
Figure 17.1 Four scenarios for the specialization of plant–pollinator interactions

The degree of specialization of plant–pollinator interactions is part of an on-going lively discussion (Waser et al. 1996; Johnson and Steiner 2000). Whereas traditional views favor the existence of specialized pollination syndromes, more recent concepts emphasize that most plant–pollinator interactions are generalized and variable in space and time (Herrera 1988; Waser et al. 1996). One possibility is that generalization is favored in human-dominated ecosystems, whereas natural systems show a higher degree of specialization (Johnson and Steiner 2000).

Interactions between plants and pollinators play a key role in the structure of terrestrial ecosystems and have attracted much attention since Darwin's pioneering evolutionary and behavioral research (e.g., Pellmyr 2002). However, remarkably little is known about the spatial and temporal variation of plant–pollinator interactions in response to habitat fragmentation and land-use change (e.g., Rathcke and Jules 1993; Bronstein 1995; Kearns et al. 1998). This may have several explanations. First, plant–pollinator interactions have usually been studied from a narrow botanical or zoological perspective rather than a broad perspective (Bronstein 1995; Waser and Price 1998). Second, plant–pollinator interactions may have been studied at an inappropriate local spatial scale (Bronstein 1995), not taking into account the considerable foraging distances of pollinators such as bees and others, which affect genetic, ecological, and evolutionary integration on greater scales (Gathmann and Tscharntke 2002; Steffan-Dewenter and Kuhn 2003). Third, other biotic interactions that may modulate plant–pollinator interactions (e.g., between plants and herbivores or seed predators) have rarely been taken into account (but see, e.g., Jennersten and Nilsson 1993; Kéry et al. 2001; Steffan-Dewenter et al. 2001; Gómez and Zamora, chap. 7 in this volume).

In this chapter, we consider plant–pollinator interactions from a landscape perspective, and from both botanical and zoological points of view. In the first

section, we attempt to summarize existing knowledge of how habitat fragmentation affects the diversity and community structure of pollinators. We present new data on species–area relationships for a diverse bee community in limestone quarries and test the hypothesis that higher trophic levels and specialized species groups respond more sensitively to habitat loss and isolation. In the second section, we ask how shifts in species richness and density of pollinators affect the seed set of rare plant populations in fragmented habitats. After reviewing existing evidence for pollination limitation, we present our own study on *Primula veris,* which is novel in that it separates subpopulation size and habitat fragment size and also considers seed predation. In the third section, we expand our perspective to a landscape scale: we argue that the analysis of multiple spatial scales is necessary for a more complete understanding of plant–pollinator interactions and we give a condensed overview of recent research on this topic from our group. In this section, we also consider biodiversity–function relationships in plant–pollinator interactions and present results from a study on coffee pollination in the tropics as rare evidence for a positive relationship. Such biodiversity effects should significantly depend on the degree of specialization or generalization of plant–pollinator interactions and may give new insights into the large-scale risks posed to these mutualistic interactions. Our main emphasis will be on the specialization and generalization of pollinators rather than of plant species. Furthermore, we focus on bees as an important pollinator group, at least in temperate ecosystems. Approximately 17,000 bee species worldwide are described and the total number has been estimated at 30,000 (Michener 2000). Bees exhibit a great diversity of habitat requirements and life histories, for example, solitary versus social organization, nesting in soil or above-ground cavities, specialized or generalized requirements for pollen (e.g., Cane and Sipes, chap. 5 in this volume), or even parasitic species that develop on the stored food of other bee species (Wcislo and Cane 1996; Michener 2000).

Bee Diversity in Fragmented Habitats

The process of habitat fragmentation mainly results in a smaller size and larger isolation of remaining habitat fragments and a reduced total area in a landscape. In most cases, species richness and population density increase with fragment or patch area: the so-called species–area and abundance–area relationships (Rosenzweig 1995; Connor et al. 2000). The relative importance of patch size and isolation is expected to differ at different levels of habitat loss. The impact of isolation is expected to increase below critical thresholds of habitat area in a landscape (Andren 1994; Bascompte and Sole 1996). An interesting but largely unknown aspect is the impact of the surrounding landscape matrix on the survival of species in habitat fragments (Ricketts 2001; Koptur, chap. 15 in this volume). Species with specialized nesting or food plant requirements, species of higher trophic levels, species with limited dispersal abilities, and species that depend

on obligate mutualists are expected to suffer most from habitat fragmentation (e.g., Holt et al. 1999; Davies et al. 2000; Tscharntke et al. 2002). Studies on habitat fragmentation are biased with respect to species groups (mainly birds and small mammals) and spatial dimension (mainly small-scale experimental arrays; Debinski and Holt 2000).

For insect communities generally and bees specifically, the response to habitat fragmentation is poorly understood (Steffan-Dewenter and Tscharntke 2002). For example, Cane (2001) found only four published studies dealing with habitat fragmentation and native bees and pointed out that none of these considered complete habitats including nesting sites. Aizen and Feinsinger (1994a) found reduced taxon diversity with decreasing fragment size but no effects on total visit frequency of two spring-flowering tree species. Bolger at al. (2000) did not find significant species–area relationships for bees sampled by pitfall traps and vacuum suction in urban habitat fragments. Steffan-Dewenter (2003) analyzed species richness and abundance of trap-nesting bees on 45 orchard meadows ranging in size from 0.08 to 5.8 ha and differing in habitat connectivity and the surrounding landscape matrix. Species richness of bees showed a steep positive species–area relationship. With a z value of 0.23 (the exponent of the log-log species–area relationship) species loss in small habitat fragments was considerably greater than for most other species groups in terrestrial habitats (e.g., Rosenzweig 1995).

In another recent study in central Germany, Alfert et al. (2001) selected 24 limestone quarries ranging in size from 0.01 to 25.1 ha and in age from 1 to 120 years. Because of their high habitat heterogeneity, limestone quarries provide diverse food-plant resources and nesting sites and are expected to be valuable secondary habitats for bees in the intensively used central European landscapes (Westrich 1989). Bees were monitored by standardized transect walks. We characterized each study site via the following habitat parameters: area, age, species richness, and cover of flowering plants. Each bee species was categorized with respect to social status (solitary or social), trophic status (nest building or parasitic), nesting sites (below- or above-ground nesting sites), and food-plant requirements (oligolectic or polylectic; Cane and Sipes, chap. 5 in this volume), following Westrich (1989).

A total of 6882 individuals were identified, representing 123 wild bee species (Hymenoptera, Apidae) from 20 genera. The outstanding value of this habitat type is supported by the fact that these comprise about 41% of all bee species occurring in this part of Germany (Theunert 2003). The total number of bee species significantly increased with habitat area (fig. 17.2A) but not with habitat age ($r^2 = 0.04, P = .36$). The species–area exponent (z) was 0.33, which is unusually high (Rosenzweig 1995). The density of bees measured as number of individuals per transect area also increased with habitat area (fig. 17.2B), thus providing rare empirical evidence that insect density may also increase with habitat area (Connor
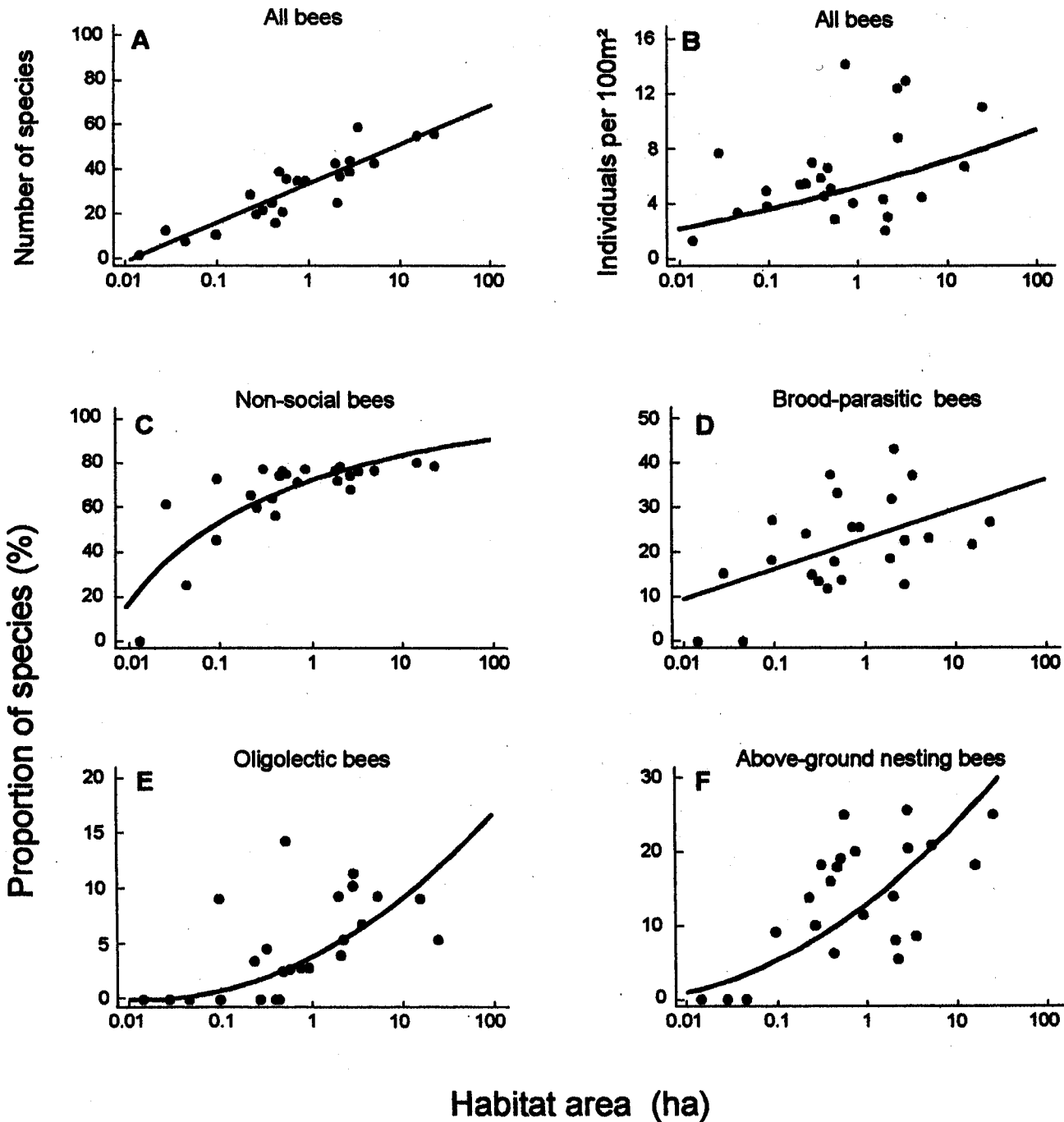
Figure 17.2 Effects of habitat area on species richness, density, and community structure of bees in limestone quarries: (A) total number of bee species in relation to habitat area ($r^2 = 0.82$, $N = 24$, $P < .001$); (B) bee density (number of individuals per 100 m²) in relation to habitat area ($r^2 = 0.25$, $N = 24$, $P = .013$); (C) proportion of nonsocial bee species in relation to habitat area ($r^2 = 0.66$, $N = 24$, $P < .001$); (D) proportion of parasitic bee species in relation to habitat area ($r^2 = 0.26$, $N = 24$, $P = .011$); (E) proportion of oligolectic bee species in relation to habitat area ($r^2 = 0.44$, $N = 24$, $P < .001$); and (F) proportion of above-ground-nesting bee species in relation to habitat area ($r^2 = 0.49$, $N = 24$, $P < .001$).

et al. 2000). Possible explanations for the bee communities' response to area come from correlations with other habitat parameters. The number of flowering plant species increased with habitat area ($r^2 = 0.61$, $P < .001$), thereby suggesting that higher resource diversity supported a greater number of different bee species. Furthermore, the percentage cover of flowering plants increased with area

($r^2 = 0.24, P = .015$), which possibly explains the higher density of bees in larger habitats.

Dividing the bee communities into species groups revealed considerable differences in responses to habitat area. Social (colony-building) bees represented about 19% of the pollen-collecting species and 73% of the individuals coming from the genera *Bombus, Halictus,* and *Lasioglossum,* whereas the remaining species were grouped as nonsocial and included solitary, colonial, and communal species. The species–area relationship was significantly steeper for nonsocial than for social bee species ($z = 0.42$ vs. 0.16) and, accordingly, the proportion of nonsocial bee species significantly increased with area (fig. 17.2C). This may be explained by the large foraging distances of at least bumblebees, the dominating group among the social species (Walter-Hellwig and Frankl 2000). An additional recent study suggests that the abundance of the three most common bumblebee species depends more on the availability of mass-flowering crops in agricultural landscapes than on the distribution of seminatural habitats (Westphal et al. 2003).

A total of 32 parasitic so-called cuckoo species from six genera were found, representing 26% of all species and 7.5% of all individuals. The slope of the species–area curve was steeper for parasitic than for pollen-collecting species ($z = 0.36$ vs. 0.29) and the proportion of brood parasitic species increased with habitat area (fig. 17.2D). These results confirm the hypothesis formulated by Holt et al. (1999) that higher trophic levels (here parasitic bees) are affected more by reduced habitat area than are lower trophic levels (here brood-provisioning bees).

Sixteen oligolectic species (13% of all species but only 3.8% of all individuals) with specialized food-plant requirements were recorded. The slope of species–area curves was similar for oligolectic and polylectic species ($z = 0.285$ vs. 0.273), but the proportion of oligoleges significantly increased with habitat area (fig. 17.2E). The results suggest that species with more specialized food-plant requirements suffer more from habitat loss than generalists.

The majority of the bee species found (67%) build their nests in the soil, 20% require above-ground nesting places (e.g., in dead wood), and 7% (mainly the bumblebee species) use both below- and above-ground nesting places. No information was available for the remaining 6%. The slope of species–area curves was not significantly different for ground-nesting species ($z = 0.317$) or above-ground cavity nesters ($z = 0.361$); however, the proportion of above-ground cavity nesters increased with area (fig. 17.2F). This may be due to the fact that above-ground nesting sites seem to be a limiting factor in most habitats; hence, these species have lower density and, thereby, should be more prone to extinction.

These results support the assumption that the destruction and fragmentation of potential bee habitats has significant effects on their species richness, population density, and community structure. The strongest impact of habitat frag-

mentation existed for solitary species with specialized pollen needs and for species of higher trophic levels. The reduced proportion of parasitic bees in small habitat islands suggests that not only mutualistic but also antagonistic biotic interactions might be lost. In the short term, brood-provisioning bee species could benefit from reduced parasitism, but in the long term, this may change competitive interactions and result in reduced local diversity of species and their interactions. The significant loss of oligolectic bee species in small habitats suggests that specialized plant–pollinator interactions are more threatened by habitat fragmentation than are generalized interactions.

Pollination Limitation in Fragmented Habitats

Recent reviews argue that pollination systems are under threat due to habitat fragmentation, agricultural intensification, and invasions (Rathcke and Jules 1993; Kearns et al. 1998; Richards 2001; Wilcock and Neiland 2002), but all emphasize the need for more field research. Indeed, the empirical case for pollination declines remains incomplete. The logical reasons to expect declines are that fully 91% of the estimated 240,000 plant species for which pollen vectors have been recorded are pollinated by animals (Renner 1998), and limitation of pollen receipt is a wide-spread phenomenon for animal-pollinated plant species: it occurs for 62% of 258 species surveyed in natural habitats (Burd 1994). Assuming that pollinators are often a limiting factor in intact habitats, reproductive success of plants should be even more limited by pollinator scarcity in landscapes disturbed and fragmented by human activities (Nabhan and Buchmann 1997).

To provide evidence for the existence of pollination failure due to habitat fragmentation, a study should (1) monitor the diversity and abundance of flower visitors as well as flower-visiting behavior, (2) quantify the seed set of open-pollinated flowers, and (3) perform pollination experiments to assess maximum seed set after cross-pollination and exclusion of pollinators, respectively. Evidence for pollinator limitation comes from a positive relationship between pollinator availability and fruit or seed set of open-pollinated flowers; the most direct evidence for pollinator limitation is provided by an increasing difference between seed set of open- compared to hand cross-pollinated flowers with decreasing pollinator availability or patch size. This approach also allows for the exclusion of external effects such as reduced resource availability or changed genetic structure in small habitat patches.

Several studies do show that small plant populations in fragmented habitats have reduced seed set, reduced genetic diversity and offspring fitness, and higher extinction risk (Oostermeijer et al. 1994; Fischer and Matthies 1997; Fischer and Stöcklin 1997; Morgan 1999; Hendrix and Kyhl 2000; Kéry et al. 2000; Luijten et al. 2000). However, relatively few studies include direct observations of flower visitation and experimentally test for pollinator limitation as the cause for lower seed set. Similarly, it is not well understood if such fragmentation effects are

exacerbated as plant–pollinator interactions become more specialized. Reduced seed set and more severe pollinator limitation have been found in small plant populations of *Dianthus deltoides* (Jennersten 1988), *Lythrum salicaria* (Ågren 1996), *Viscaria vulgaris* (Nielsen and Ims 2000), *Gentiana campestris* (Lennartsson 2002), *Nepeta cataria* (Sih and Baltus 1987), *Calystegia collina* (Wolf and Harrison 2001), *Acacia brachybotrya* and *Eremophila glabra* (Cunningham 2000), *Primula sieboldi* (Matsumura and Washitani 2000), and for most of 16 plant species in dry subtropical forests in Argentina (Aizen and Feinsinger 1994b). However, in other studies, reproductive success did not decline in fragmented or more isolated populations (e.g., Spears 1987; Costin et al. 2001).

We recently undertook a study of how pollinator limitation and seed predation influence seed output of *Primula veris* at different spatial scales. *Primula veris* is a perennial, insect-pollinated, self-incompatible spring-flowering herb, which is endangered in central Germany where it grows on calcareous grasslands (Garve 1994). We selected 15 calcareous grassland fragments covering a gradient from 0.03 to 5.15 ha area, each of which supported several spatially separated different-sized subpopulations of the plant. We focused on subpopulations of fewer than 200 individuals, because earlier studies did not find significant variation in seed set for larger populations (Kéry et al. 2000). On each grassland, we selected a small, an intermediate, and a large subpopulation, resulting in a total of 45 subpopulations ranging in size from 6 to 450 flowering individuals. Flower visitation was observed in each subpopulation over several days. In each subpopulation, 10 inflorescences were randomly selected and permanently marked; after ripening of fruits, these inflorescences were collected and the number of seeds per fruit and percentage of fruit set per plant were measured. Additionally, we quantified the proportion of fruits destroyed by seed-feeding insects. To experimentally test for pollinator limitation, five inflorescences per subpopulation were cross-pollinated by hand. The two spatial scales under consideration (i.e., subpopulation size and habitat fragment area) were not intercorrelated ($r = -0.20, P = .20$); therefore, it was possible to independently test for effects of subpopulation size and habitat area on flower visitation, seed set, and seed predation.

Overall, flower visitation rates on *P. veris* were low: only 35 observed individuals from 8 species (mainly bumblebee queens). In contrast to expectations, flower visitation rates did not respond to habitat area ($r = -0.12, N = 45, P = .45$) but tended to increase with subpopulation size ($r = 0.28, N = 45, P = .06$). In addition, the number of observed species significantly increased only with subpopulation size ($r = 0.34, N = 45, P = .02$). We can only speculate about the reasons for low flower visitation rates: perhaps parallel flowering oil seed rape in the surrounding agricultural landscape attracted most of the social bee species, or *P. veris* is pollinated mostly by moths visiting the flowers at night (Lehtilä and Syrjänen 1995).

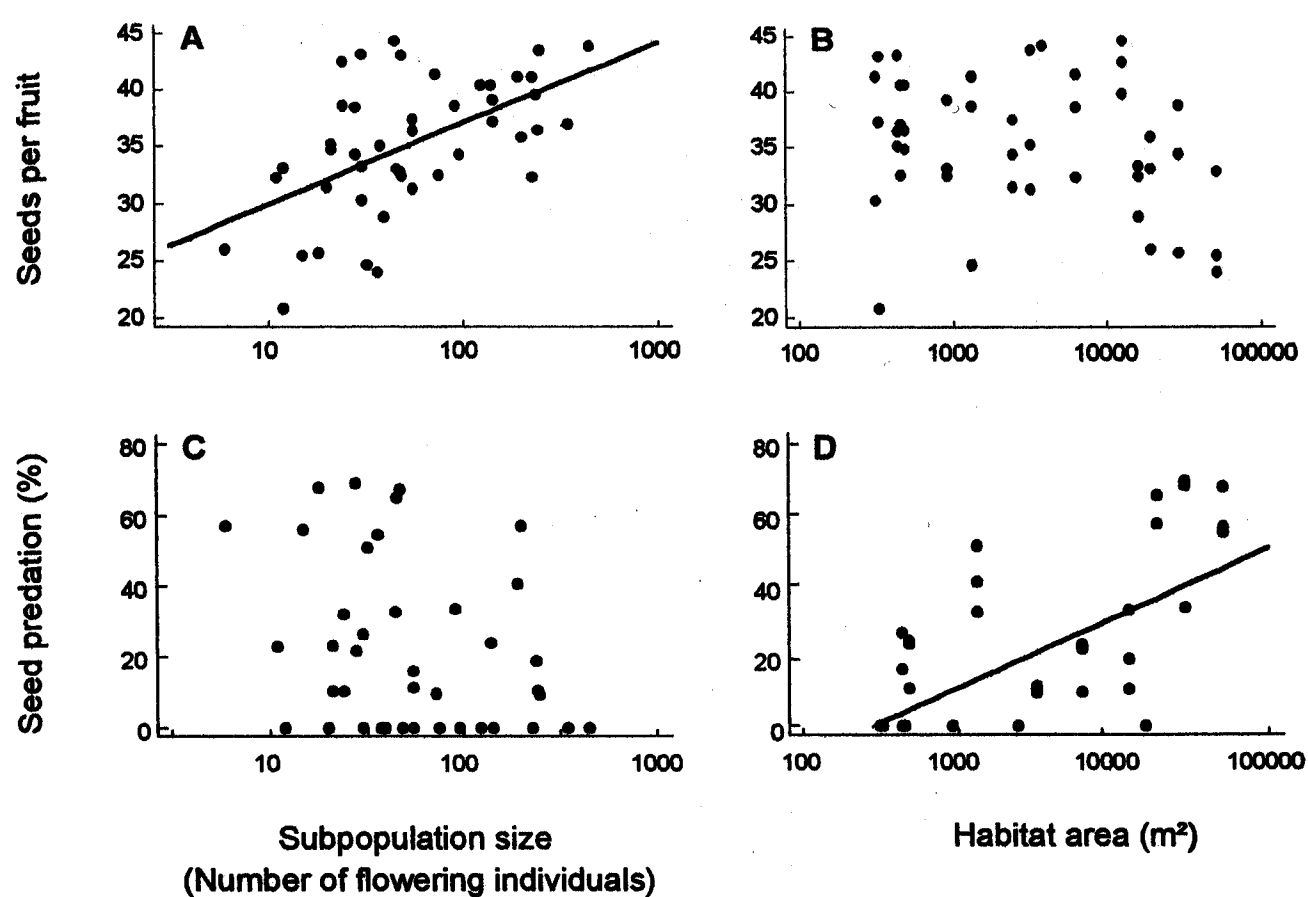Our results gave no evidence for actual pollinator limitation: the proportion

Figure 17.3 Seed set and seed predation of *Primula veris* in relation to subpopulation size and habitat area of calcareous grasslands: (A) number of seeds per fruit (only undamaged fruits) in relation to subpopulation size (number of flowering individuals; $r^2 = 0.30$, $N = 45$, $P < .0001$); (B) number of seeds per fruit (only undamaged fruits) in relation to habitat area (not significant); (C) proportion of fruits (arcsin $\sqrt{p}$ transformed) damaged by seed predators in relation to subpopulation size (number of flowering individuals; not significant); and (D) proportion of fruits (arcsin $\sqrt{p}$ transformed) damaged by seed predators in relation to habitat area ($r^2 = 0.38$, $N = 45$, $P < .0001$).

of flowers setting fruits was related neither to subpopulation size nor to habitat area. Nonetheless, the number of seeds per undamaged fruit significantly increased with subpopulation size (fig. 17.3A). This agrees with the results obtained by Kéry et al. (2000) and could be interpreted as evidence for pollinator limitation. However, for hand-pollinated inflorescences, the number of seeds per fruit also increased with subpopulation size ($r = 0.39$, $N = 45$, $P = .008$), indicating that other factors such as reduced genetic diversity, uneven distribution of flower morphs due to demographic stochasticity (Kéry et al. 2003), or less-suitable habitat conditions were responsible for reduced seed set in small subpopulations. Furthermore, habitat area had no significant effect on the number of seeds per fruit (fig. 17.3B), although this outcome was expected because this was the spatial scale at which the diversity and density of pollinators was influenced in the community-level study of bees discussed earlier in this chapter (figs. 17.2A, 17.2B).

Seed predation also played a significant role for *P. veris* and was found on 11

out of 15 study sites and in 27 out of 45 subpopulations. The main seed predator was *Phalonia ciliella* Hb. (Lepidoptera, Tortricidae), which destroyed all seeds in infested fruits. The proportion of damaged fruits did not depend on subpopulation size but significantly increased with habitat area (figs. 17.3C, 17.3D).

Our study illustrates how results may depend on the choice of spatial scale and the inclusion of both mutualistic and antagonistic interactions. If we had focused only on spatially separated subpopulations within the habitat fragments, we might have concluded that actual pollinator limitation does not seem to be important but would have had no explanation for the variation in seed predation. On the other hand, focusing only on habitat fragments and defining all subpopulations within a fragment as one population would have identified habitat area as the determinant of predispersal seed predation rate but would have obscured insights on pollinator visitation and seed set. More generally, many other factors might alter the outcome of plant–pollinator interactions such as herbivory (e.g., Strauss 1997; Herrera 2000), fungal infections (e.g., Jennersten 1985), and below-ground herbivores (Poveda et al. 2003); these have rarely been considered at multiple spatial scales in the context of habitat fragmentation (Brody 1997; Ettema and Wardle 2002; Pellmyr 2002).

It is still too early to reach conclusions with respect to general effects of habitat fragmentation on plant–pollinator interactions. Existing empirical data show that small plant populations may suffer from reduced seed set and genetic erosion, but the direct impact of pollinator limitation requires further research that should also take into account other biotic interactions, different spatial scales, and responses of plant species with different life-history traits (e.g., low or high pollinator specialization, or in different habitat types).

Effects of Landscape Context on Bees and Plant Reproduction

Important drivers such as habitat fragmentation, land-use change, climate change, and species invasions act on spatial scales much larger than single habitats; accordingly, population dynamics, species richness, and community interactions should also be affected on regional scales. However, ecologists have only recently become aware that such a landscape perspective is helpful (e.g., Kareiva and Wennergren 1995); until the past decade, they tended to consider habitat fragments in a matrix of nonhabitat and to focus on the effects of habitat area or isolation distance between neighboring habitats of the same type. But real landscapes are much more complex, and taking into account this complexity of the surrounding landscape context yields additional insights (e.g., Rickets 2001; Krauss et al. 2003, 2004; Steffan-Dewenter 2003).

The landscape approach in pollination studies takes into account that organisms such as bees depend on more than one habitat type during their life cycle (e.g., Westrich 1996) and that foraging and dispersal distances of bees are often larger than a single habitat fragment (e.g., Walter-Hellwig and Frankl 2000;

Gathmann and Tscharntke 2002; Steffan-Dewenter and Kuhn 2003). In this perspective, natural or seminatural habitats are recognized as sources for beneficial insects that spread over the surrounding landscape and supply services such as biological control of pest insects or pollination of crops (e.g., Daily 1997; Kremen et al. 2002; Thies et al. 2003). The response of different species to landscape features depends on their life-history traits, in particular foraging ranges and dispersal abilities, which emphasize the importance of considering multiple spatial scales for an understanding of ecosystems made up of interacting species (Kareiva 1990; Roland and Taylor 1997; Wiegand et al. 1999).

It is evident that ecological research on large spatial scales faces huge logistical problems. Estimating species richness in single habitat fragments with sufficient sample size and replications is already a challenge, but doing this in even larger landscapes is often impossible. Two previous solutions are the use of landscape models (Wiegand et al. 1999) or the creation of experimental fractal landscapes on a small spatial scale (With et al. 1999). Here we focus on an alternative approach: the use of large-scale experimental and observational data in a statistically meaningful number of independent real landscape units. We consider effects of landscape context on local species richness and density of pollinators, foraging distances and flower-visiting behavior of bees, and consequent effects on pollination services for wild plants and crops.

Our basic approach has been to select 15 independent circular landscape sectors in the area near Göttingen, central Germany, covering a gradient from structurally simple to complex landscapes (Steffan-Dewenter et al. 2002). In the center of each landscape unit, experimental patches were established that allowed for a standardized measurement of species richness and densities of functional groups and biotic interactions in relation to the surrounding landscape context. Landscape context was quantified within eight nested circles ranging from a 250 to a 3000 m radius. Using geographic information systems, the percentage land cover of seminatural habitats and habitat type diversity was calculated for each circular landscape sector. The parallel analysis of different spatial scales made it possible to identify "functional spatial scales," that is, the radius around experimental patches at which landscape structure most significantly influenced functional groups and their biotic interactions (Steffan-Dewenter et al. 2002; Thies et al. 2003).

To monitor species richness and density of bees independently from variation in resource quality, experimental patches with potted flowerings plants and trap nests were established in the center of each landscape unit (Steffan-Dewenter 2002; Steffan-Dewenter et al. 2002). We thereby provided both a standardized food resource for flower-visiting bees and a standardized nesting site for above-ground nesting bees (and wasps; Tscharntke et al. 1998). Consequently, variation between study sites should only be caused by differences in landscape context. Flower visitation was observed on six different plant species during

summer months. The species richness and abundance of solitary wild bees increased with the proportion of seminatural habitats in the surrounding landscape. This relationship was only significant for small spatial scales but not for circular landscape sectors larger than 1000 m. In contrast, honeybees were only affected by landscape structure at a large spatial scale (landscape units with 3000 m diameter) and showed a pattern opposite that of solitary bees; thus, flower-visitor densities of honeybees were higher in structurally simple than in complex landscape units. Presumably, alternative flower resources were scarcer in simple landscapes than in complex ones, thereby enhancing the relative attractiveness of the experimental patches in simple landscapes (Steffan-Dewenter et al. 2002). This suggests that honeybees partly compensate for the loss of other more specialized pollinator species in simple landscapes but may also indicate more severe competition for the remaining food resources.

The colonization of trap nests also depended on the landscape context. The total number of trap-nesting bees and wasps significantly increased with increasing proportion of seminatural habitats in the surrounding landscape. However, this pattern was mainly determined by increasing species richness of wasps, whereas, for bees alone, only a positive trend existed ($r = 0.44$, $N = 15$, $P = .10$). In contrast with expectations, neither the abundance of bees (number of brood cells) nor the higher trophic level of natural enemies responded to landscape structure. Again landscape effects were most significant for small landscape units, indicating restricted dispersal and foraging distances of solitary bees and wasps (Steffan-Dewenter 2002).

For one focal plant, *Centaurea jacea,* we analyzed whether the reduced species richness and abundance of flower-visiting bees had negative consequences for pollination and seed set (Steffan-Dewenter et al. 2001). In contrast with expectations, the mean number of seeds per flower head did not increase with the proportion of seminatural habitats. This was presumably caused by counterbalancing effects on flower-visitor behavior, on the one hand (see following discussion), and on seed predation, on the other. Seed predation by larvae of microlepidoptera and tephritid flies played a significant role. The percentage of damaged flower heads increased from 13 to 99% along the gradient from structurally simple to complex landscapes; in addition, the proportion of damaged seeds per flower head increased with the percentage of colonized flower heads. We failed in this study to experimentally test for pollinator limitation, but indirect evidence comes from a weak positive correlation between seed set of undamaged flower heads and flower visitation rates of bees.

The foraging behavior of pollinators on single plants or patches plays an important role in pollination efficiency (e.g., Kunin 1993; Goulson 2000), but this has rarely been considered in a landscape context. In our study on *Centaurea jacea,* we found that the number of plants consecutively visited by a single bee was higher in simple landscapes with low proportions of seminatural habitats

than in complex landscapes (Steffan-Dewenter et al. 2001). Simple landscapes presumably provide fewer alternative food resources, thereby changing economic constraints and increasing patch residence times (Dukas and Edelstein-Keshet 1998). As a result, a lower number of visitors provides similar flower visitation rates (see also Schulke and Waser 2001; Goverde et al. 2002). Such changes in foraging behavior possibly enhance the seed set of isolated plant populations but may incur ecological costs in terms of disrupted gene flow and increased inbreeding (Kwak et al. 1998). However, the actual gene flow via pollen dispersal in relation to changing landscape structure is difficult to assess, again because effects of foraging behavior may be counterbalanced by increased foraging distances of pollinators in structurally simple landscapes that should result in gene flow over larger distances (Schulke and Waser 2001). This may occur via shifts in pollinator community structure toward larger solitary bees, bumblebees, and honeybees, with foraging distances much larger than those of small solitary bees (Steffan-Dewenter and Tscharntke 1999; Walther-Hellwig and Frankl 2000; Gathmann and Tscharntke 2002). Foraging distances of pollen-collecting honeybees may also be significantly longer in simple landscapes than in complex ones (Steffan-Dewenter and Kuhn 2003).

We conclude that landscape context (1) affects species richness, community structure, and abundance of bees; (2) changes biotic interactions such as pollination and seed predation; and (3) modifies foraging behavior and foraging distances of pollinators. Interesting, and important, is that different species groups and interaction types are influenced at different "functional" spatial scales. Further studies are needed to assess the consequences that increasing dominance of generalist pollinators in simple landscapes have on plant–pollinator interactions.

In the studies discussed thus far, species richness and abundance of bees were closely correlated; diversity effects could not be unambiguously disentangled from pure abundance effects. Nonetheless, the results suggest that the diversity of bees may also contribute to intact pollination services in generalized, theoretically highly redundant plant–pollinator systems (Steffan-Dewenter and Tscharntke 1999; Steffan-Dewenter et al. 2001). We will expand this aspect by using a recently published case study, where we analyzed shifts of bee diversity and pollination services in tropical coffee agroforestry systems (Klein et al. 2003a, 2003b). The research was done in 2000 and 2001 in central Sulawesi (Indonesia) at the margin of the Lore-Lindu National Park. Two coffee species, lowland coffee (*Coffea canephora*) and highland coffee (*C. arabica*), which differ in pollination biology (Klein et al. 2003a), are grown in the region; here we focus on the latter species. Highland coffee has been assumed to be a self-compatible crop with no dependence on insect pollination; recently, however, Roubik (2002) published indirect evidence that honeybee pollination significantly improves coffee yields. We compared the fruit set of *C. arabica* after differ-

ent pollination treatments and could show that cross-pollination by hand significantly increased fruit set compared to wind pollination or self-pollination by hand (Klein et al. 2003a).

To assess the importance of bee diversity for highland coffee yields, we selected 24 coffee agroforestry fields covering an isolation gradient from the tropical rainforest margin to a human-dominated open agricultural landscape. We assumed that undisturbed rainforests are source habitats for social bee species nesting in old trees (Liow et al. 2001). As a second possible determinant of bee diversity, we analyzed the impact of local shade management, quantified as light intensity and local plant diversity. Reduced shading is generally expected to reduce biodiversity in tropical agroforestry systems (Perfecto et al. 1996), but it may also improve local nest-site quality for soil-nesting solitary bee species and cover of flowering herbs (Klein et al. 2002). We observed flower visitation rates and fruit set of coffee plants and additionally performed experimental cross-pollination by hand to test for pollinator limitation (Klein et al. 2003b). The numbers of both all flower-visiting bee species and fruit set of coffee increased with light intensity and decreased with distance to the forest margin. Social and solitary bees showed guild-specific differences in the response to these habitat parameters: species richness of social bees only depended on the distance from the forest margin, whereas the number of solitary bee species was determined by local factors and increased with light intensity and plant diversity.

We found a significant diversity–ecological function relationship: fruit set of open-pollinated coffee flowers increased with the species richness of flower-visiting bees but, interestingly, not with the abundance of flower visitors. Furthermore, the difference between fruit set of open insect-pollinated flowers and flowers cross-pollinated by hand was negative for sites with low bee diversity and increased with bee diversity, thereby providing experimental evidence for pollinator limitation (fig. 17.4A). Thus, our study provides empirical evidence for a positive relationship between pollination as an important ecosystem service and functional group diversity of bees. Because coffee is pollinated by several unspecialized bee species, the results indicate that diversity also matters for generalized plant–pollinator relationships; complementary effects and sampling effects can generally cause such diversity effects.

Complementary effects of diverse bee assemblages include (1) reduced spatial variability and (2) reduced temporal variability of pollination services and may act on very different spatial and temporal scales. Different bee species are known to prefer low- or high-placed flowers within an individual plant (Hambäck 2001), thereby contributing to more complete pollination. In our study, the variation of fruit set (CV) between four spatially separated coffee trees per study site was reduced when bee diversity increased (fig. 17.4B).

Thus, the complementary effects of a more diverse bee community appear to have contributed to a more constant and high pollination service in coffee agro-
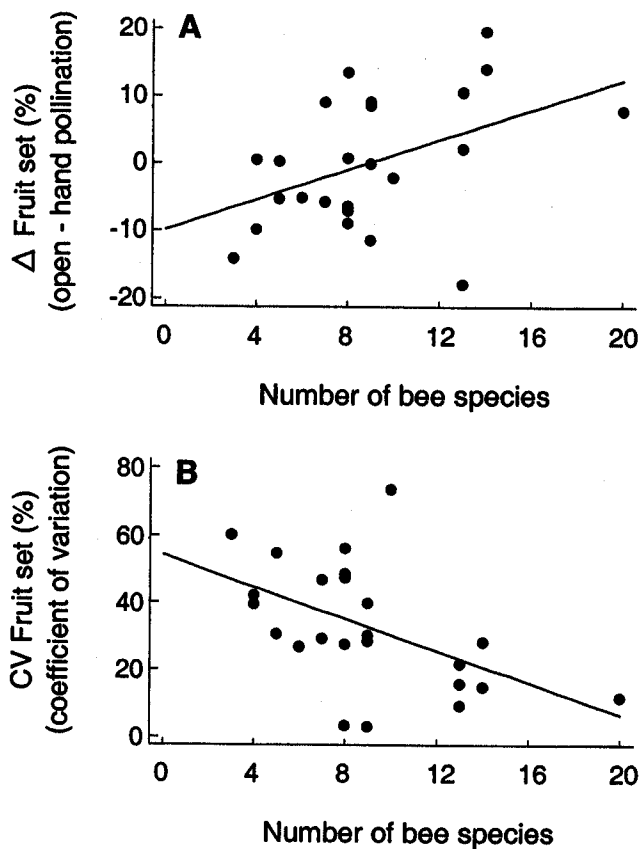
Figure 17.4 Diversity–ecological function relationship for bees and the pollination of highland coffee: (A) relationship between the difference of fruit set after open pollination minus fruit set after experimental cross-pollination, and the species richness of flower-visiting bees ($r^2 = 0.203$, $N = 24$, $P = .027$); (B) relationship between the coefficient of variation (CV) of mean fruit set after open pollination of four spatially separated coffee trees and the species richness of flower-visiting bees ($r^2 = 0.257$, $N = 24$, $P = .011$).

forestry systems. Activity patterns of bee species are also known to differ temporally: within days, between seasons, and between years (Herrera 1988; Stone et al. 1999; Kremen et al. 2002) and again diverse bee assemblages with corresponding phenological variation could act as a buffer for possible pollinator limitation.

Sampling effects suggest that within a diverse bee community there is a higher chance of a more efficient pollinator species being represented. In our coffee study, the pollination efficiency of different bee species varied significantly: single flower visits of the less abundant solitary bee community resulted in a higher probability in fruit set than for the more abundant social bee species (Klein et al. 2003b). Thus, a combination of complementary and sampling effects presumably contributed to a positive relationship between bee diversity and pollination in our generalized plant–pollinator system.

Conclusions and Future Directions

The studies we have discussed provide evidence for the decline of pollinator diversity as a result of human-induced habitat fragmentation and land-use intensification. Solitary bees, which represent the vast majority of wild bee species, are particularly threatened by reduced habitat area and increased isolation;

within this group, specialized and parasitic species are even more threatened. On a landscape scale, this translates to simplified, less-species-rich pollinator assemblages dominated by social generalist bee species. We are still far from understanding the driving forces of spatial and temporal variation in bee diversity and abundance. Bees depend on several key resources such as nesting sites, food resources, and nest-building material that are often spread over different habitat types (Westrich 1996); therefore, conservation and management activities for bees as key pollinators should take spatial scales larger than single habitat fragments into account, but further research is needed on the effects of landscape composition and the relative importance of different habitat types. Very little is known about spatial population dynamics of bees and the relative importance of bottom-up control by food or nesting resources compared with top-down control by natural enemies (Roubik 2001). The consideration of such trophic cascades is essential for understanding the mechanisms behind fragmentation- or landscape-related patterns of bee diversity and community structure.

Shifts in bee diversity and abundance associated with habitat fragmentation and land-use change are also assumed to strongly affect pollination. The limited empirical evidence suggests that plant–pollinator interactions are threatened by habitat fragmentation and land-use change, but comparative case studies for specialized and generalized plant–pollinator interactions or meta-analyses of existing data are still lacking in this context. Similarly, pollination requirements of many crop species are unknown and pollinator limitation may be much more important than at first recognized; only coarse and unsatisfying estimates of the economic value of pollination services exist (Kevan and Philips 2001). Finally, very limited insights exist for how gene flow is influenced by pollinator movement, landscape context, and the spatial arrangement of plant populations. This has profound implications for genetic erosion and inbreeding depression of plant populations in natural habitats and also for the escape of genes from genetically modified crop plants (Rieger et al. 2002).

Human-induced habitat fragmentation and shifts in landscape structure may also have evolutionary consequences for plant–pollinator interactions. We have shown that pollinator limitation presumably becomes more important in small and isolated habitat fragments and structurally simple landscapes and that species composition and foraging behavior is altered. On the other hand, herbivory and seed predation also seem to be reduced; thus, one could assume that targets and strength of natural selection are changed due to newly emerging landscape patterns. For example, this could lead to a reallocation of resources from herbivore defense to flower advertisement and rewards and could disrupt correlated evolution of mutualism- and antagonism-related traits (Herrera et al. 2002).

The threat of decreased pollination services due to loss of pollinator diversity has been considered to depend on the degree of specialization or generalization of plant–pollinator relationships (Bond 1995). Our results indicate that special-

ized pollinators are affected more by habitat loss and land-use change; consequently, specialized plant–pollinator relationships should be more threatened than generalized relationships. Nonetheless, our coffee study demonstrates that even generalized plant species may suffer from reduced pollinator diversity; therefore, an incomplete picture may be given when we only use the degree of specialization or generalization to judge future environmental risks for plant–pollinator interactions.

In conclusion, research on plant–pollinator interactions in changing landscapes remains a challenging topic with many possible applications. Although a beginning has been made, our understanding is still limited. Many more large-scale field experiments and multidisciplinary collaborations are called for to understand the real complexity of plant–animal interactions in their natural setting.

Acknowledgments

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Plant–Pollinator Interactions

From Specialization to Generalization

Edited by Nickolas M. Waser and Jeff Ollerton