

GUEST EDITORIAL

The interplay of pollinator diversity, pollination services and landscape change

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Summary

1. Pollinators are a functional group with high relevance for ensuring cross-pollination in wild plant populations and yields in major crops. Both pollinator declines and losses of pollination services have been identified in the context of habitat destruction and land use intensification.
2. This editorial synthesizes and links the findings presented in seven papers in this Special Profile, focusing on pollinator diversity and plant–pollinator interactions in natural habitats and agricultural landscapes.
3. The results contribute to our understanding of local and landscape scale effects of land use intensification on pollinator densities and diversity, and pollination functions in wild plant communities and crops.
4. *Synthesis and applications.* We emphasize the exceptional coverage in pollination ecology ranging from basic ecological relationships to applied aspects of ecosystem services and ecosystem management, and conclude with identifying gaps in current knowledge and challenging research areas for the future.

Key-words: agri-environment schemes, bees, butterflies, ecosystem services, gene flow, habitat fragmentation, habitat management, land use intensification, spatial scales

Introduction

Research on pollinators and plant–pollinator interactions in a spatial context has significantly expanded since seminal articles illustrated the effects of habitat fragmentation and landscape structure on pollinator diversity (Banaszak 1992; Aizen & Feinsinger 1994), revealed related reductions of seed set in fragmented native plant populations (Jennersten 1988), and addressed the importance of wild pollinators for crop pollination (Corbet, Williams & Osborne 1991). Recent publications on large-scale parallel declines of plants and pollinators reinforce the concern that pollination as an important ecosystem service is at risk (Biesmeijer *et al.* 2006). Generally, in this context two major threats for pollinator diversity can be distinguished: first, the destruction and fragmentation of natural or semi-natural habitats is expected to cause reduced species richness and abundance as well as changes in species composition of pollinators in these habitats (Fig. 1). As a consequence, pollination and seed set of wild plant populations might be reduced in small or isolated populations (Rathcke & Jules 1993). Secondly, land use

intensification in agricultural landscapes might have significant effects on pollinator communities and crop pollination services (Fig. 1; Tschardt *et al.* 2005; Kremen *et al.* 2007). Importantly, the two topics are linked with natural habitats providing pollinators for crops and agricultural landscapes potentially impacting pollinator communities in their natural or semi-natural habitats (e.g. Steffan-Dewenter 2003). Over the last 20 years, the progress in research and the appearance of synthesis articles indicate the consolidation of an emerging research area. Recent reviews quantify that *c.* 35% of the crop production volume and *c.* 70% of major global crops rely on animal pollination (Klein *et al.* 2007). Overall, crop visitation rates decline with increasing distance from pollinator habitats, as demonstrated in a meta-analysis of 16 case studies in tropical and temperate regions illustrating the potential threat for an important ecosystem service (Ricketts *et al.* 2008). Similarly, a meta-analysis for wild plants illustrates more significant pollination limitation in small, fragmented compared to large, continuous plant populations (Aguilar *et al.* 2006). However, many basic questions remain unanswered or are controversial: in particular, the relevance of species traits for predicting the sensitivity to habitat change, the efficiency of agri-environmental schemes such as organic farming in enhancing pollinator

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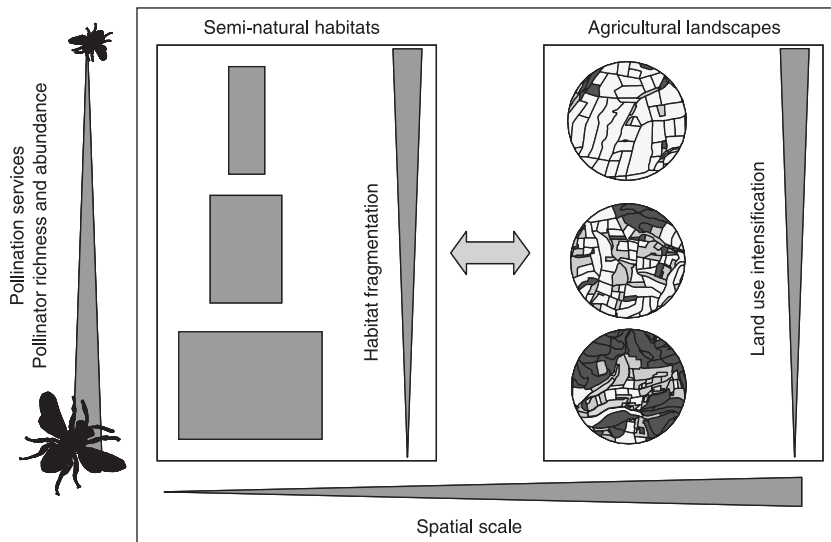


Fig. 1. Interplay of pollination services, pollinator richness and abundance and land use changes (habitat fragmentation and land use intensification). Both habitat fragmentation and land use intensification affect pollinator communities at different spatial scales and interact with each other.

densities (Bengtsson, Ahnström & Weibull 2005; Kleijn *et al.* 2006) and the dependence of crops on pollination services (Ghazoul 2005; Steffan-Dewenter, Potts & Packer 2005). The papers in this Special Profile cover several of these topics: two papers address the impact of habitat fragmentation and semi-natural landscape elements for population densities, species richness and community composition of bees (Brosi *et al.* 2008; Osborne *et al.* 2008). The next three papers focus on the combined effects of local and landscape-scale land use intensity and semi-natural or natural landscape elements on pollinators (Kohler *et al.* 2008; Rundlöf, Bengtsson & Smith 2008; Winfree *et al.* 2008). The last two papers focus on pollination functions and consider cross-pollination rates in a major crop (Devaux *et al.* 2008) and plant–pollinator networks in heathlands (Forup *et al.* 2008). The papers mainly deal with bees (Hymenoptera: Apiformes) as the most important pollinator taxa in temperate ecosystems, but butterflies and syrphid flies are also considered in three papers.

HABITAT FRAGMENTATION

The loss and fragmentation of natural or semi-natural habitats is considered as a major threat for biodiversity (Fahrig 2003). Generally, species numbers and species densities are expected to decline according to a species-area or species-density relationship, with higher trophic levels and food or habitat specialists being more sensitive to habitat reduction and increasing habitat isolation than lower trophic levels (Tscharrntke & Brandl 2004). For pollinators very few studies in subtropical and temperate regions exist (e.g. Cane *et al.* 2006).

Here, Brosi *et al.* (2008) present the first study of the effects of tropical forest fragmentation on entire bee communities. Using 22 forest fragments differing in size, shape and isolation in southern Costa Rica they did not find effects on species numbers but report strong effects on bee community composition, with opposing responses of native stingless bees

and introduced honeybees. An innovative aspect of this fragmentation study is the inclusion of the landscape context at multiple spatial scales. They found that stingless bee abundance is enhanced by the proportion of forested area in the surrounding landscape with the most significant scale of response providing an estimate of average foraging distances. Compiling such data for different bee guilds and biomes will provide a better understanding of potential foraging distances of pollinators in the future.

While tropical stingless bees use tree cavities as nesting sites and are therefore limited to forest habitats, the key nesting habitats of bumblebees in temperate regions are not well understood, because nests are difficult to locate. Osborne *et al.* (2008) realized an unusual and impressive approach to circumvent these problems. In 2004 a national bumblebee survey with standardized questionnaires was carried out by 719 trained volunteers in the UK. Using this significant man-power, nest densities of bumblebees in different habitat types could be quantified. They found that nest densities were highest in gardens and linear countryside habitats. Besides the few studies using genetic kinship of randomly collected bumblebees to calculate nest densities (e.g. Knight *et al.* 2005), these data provide the only estimates of colony densities in agricultural landscapes. It is worth noting that simply counting flower visiting bumblebees as a proxy for nest densities can be biased by flower resource availability and landscape-dependent differences in colony size (Herrmann *et al.* 2007). The authors conclude that their results will help to enhance the efficiency of habitat management for bumblebees and stress the value of volunteer surveys for increasing public interest in environmental issues.

LAND USE INTENSIFICATION

Land use intensification is seen as a further important cause for biodiversity losses in agricultural landscapes (Tscharrntke *et al.* 2005). At local scales, intensification is characterized by machine-driven farming and increased input of fertilisers and

pesticides that directly kill pollinators or reduce nest and flower resources. At landscape scales, typical consequences of agricultural intensification are large field sizes, a reduced amount of edge habitats and a low number of different land use types (Tschardt *et al.* 2005). To mitigate the negative effects of land use intensification for diversity, agri-environmental schemes (AES) such as organic farming have been implemented. AES enhance pollinator diversity and density at local scales in different cropping systems and countries (Kremen, Williams & Thorp 2002; Kleijn *et al.* 2006). The efficiency of AES depends on the landscape context with stronger positive effects in simple landscapes with a low proportion of natural or semi-natural habitat compared to complex landscapes with a higher proportion and diversity of non-agricultural habitats (Holzschuh *et al.* 2007). However, only recently it has been shown that a high proportion of low-intensity organic farming enhances pollinator diversity at a landscape scale (Holzschuh, Steffan-Dewenter, & Tschardt 2008).

Rundlöf *et al.* (2008) used an elegant and well replicated design to separately address local and landscape effects of organic farming on butterfly assemblages in southern Sweden. They found that at a local scale butterfly species richness and abundance was higher on organic compared to conventional fields, and additionally show that a large proportion of organic fields in the surrounding landscape positively affected butterfly richness and abundance. The authors argue that the spatial distribution of AES must be taken into account to maximize their potential to improve farmland biodiversity.

Along similar lines, Winfree *et al.* (2008) studied bee visitation to four vegetable crops in relation to land use intensity at local and landscape scales. The results were different: they did not find an association between bee visitation and land use intensity at any spatial scale. In contrast to previous findings (Klein *et al.* 2007), neither farming practice at the local scale (organic vs. conventional) nor regional land use intensity (measured as proportion of natural woodlands) had a significant effect on bee visitation rates. The authors explain their contradictory findings on the basis of the great similarity between the studied organic and conventional farms that did not differ in field size, crop diversity and weedy flower density, and with the great habitat heterogeneity in their study region. This study (Winfree *et al.* 2008) indicates that both local habitat characteristics (e.g. habitat size or flower density) and regional habitat heterogeneity could be more important factors than farming practice in influencing the diversity and abundance of pollinators in agricultural landscapes, and thus should be considered when implementing AES (Benton, Vickery & Wilson 2003; Tschardt *et al.* 2005).

Not only overall landscape heterogeneity plays an important role in promoting biodiversity in agricultural landscapes, but also the spatial arrangement of high-quality habitats, which can act as source of species (Banaszak 1992). However, only a few studies have quantified the extent to which species disperse from high-quality habitats into intensively used agricultural landscapes (Steffan-Dewenter & Tschardt 1999; Albrecht *et al.* 2007). This question was

addressed by Kohler *et al.* (2008), who investigated at what spatial scales high-quality habitats enhance the diversity of three functional groups (forbs, bees and hover flies). The spatial scales at which the species-rich source habitats increased biodiversity in the surrounding intensively used agricultural landscape were relatively small. Thus, the effects of high-quality habitats are likely to be more effective in enhancing pollinator diversity and abundance, when ecological restoration sites or fields under AES are available in the close vicinity. Taken together, the three studies (Kohler *et al.* 2008; Rundlöf, Bengtsson & Smith 2008; Winfree *et al.* 2008) in this Special Profile emphasize that the effectiveness of AES will be greatest in homogeneous landscapes with low habitat heterogeneity and where the spatial arrangement of habitats in the landscape is taken into account.

CONSEQUENCES FOR POLLINATION FUNCTIONS

Land use intensification and habitat fragmentation do not only affect pollinator diversity and abundance, but also pollination services (Jennersten 1988; Cunningham 2000). Moreover, the distance of insect-pollinated plant populations to high-quality habitats for pollinators affects their pollination and reproductive success (Steffan-Dewenter & Tschardt 1999; Albrecht *et al.* 2007; Kohler *et al.* 2008). However, the effect of landscape composition on large-scale foraging routes of pollinators, and hence landscape-wide pollen dispersal and cross-pollination rates, are largely unknown. Since studies on insect-mediated pollen flow are difficult to conduct at a landscape-scale, modelling approaches can provide some insight (Shaw *et al.* 2006; Hoyle, Hayter & Cresswell 2007). Considering the implementation of transgenic crops in agricultural landscapes, this topic is of great importance and of public interest (Rieger *et al.* 2002).

In their innovative study, Devaux *et al.* (2008) combined both empirical studies and modelling of landscape-wide cross-pollination rates using dispersal kernels. The authors report that dispersal kernels that were fitted at the local scale, but also dispersal kernels that were fitted at the landscape scale, tend to underestimate the observed pollen dispersal. The model predictions of cross-pollination rates at the landscape-scale could be further improved by including the pollen dispersal by insects, and mechanisms that describe temporal, environmental, and spatial variations in agricultural landscapes. Yet, it should be noted that another study came to the conclusion that the wind, not pollinators, is the main vector of long-distance gene flow in oilseed rape (Hoyle, Hayter & Cresswell 2007).

The pollination success of insect-pollinated plant species is usually not dependent on single, highly specialized pollinator species, but rather on a diverse community of pollinators. Plant–pollinator interactions, their functionality and robustness can be characterized using an ecological network approach (Bascompte *et al.* 2003; Blüthgen *et al.* 2007). In this Special Profile, Forup *et al.* (2008) demonstrate that the ecological network approach can also be used to evaluate the outcome of restoration programmes. The authors used

visitation and pollen transport networks to characterize both the pollinator communities and the importance of individual species for pollen transportation in ancient and restored heathlands. Although visitation networks varied considerably among study sites, the most important pollinators, which were represented by a few widespread species, were present in both the ancient and restored sites assuring full pollination services. In contrast to the findings of Kohler *et al.* (2008), the adjacent ancient and restored heaths did not have more species in common than distant sites, suggesting that the regional species pool might be determined by landscape effects that potentially act across different spatial scales.

Conclusions

This Special Profile adds significantly to the progress made in landscape-based research on pollinators and plant–pollinator interactions over the last decade. However, to understand and counteract the ongoing declines of pollinators and insect-pollinated plant species more comprehensively (Biesmeijer *et al.* 2006), future studies should build on this progress to reach a more general understanding of the effects of landscape components and their arrangement at different spatial scales on pollinator diversity. Not much is currently known about the effects of corridors connecting isolated habitats (Haddad *et al.* 2003). In this context, a promising approach for future studies is the consideration of species traits as an explanatory factor. Moreover, the spatial and temporal population dynamics of pollinators are the basis for a causal understanding of their occurrence in fragmented agricultural landscapes, but little is known about the relative importance of driving factors such as food and nesting resources, or natural antagonists. Another challenging research area is the interplay between managed and natural/semi-natural habitats (Rand, Tylianakis & Tschardt 2006). For example, spillover effects from agricultural habitats might swamp natural systems with generalist pollinators or predators. On the other hand, mass flowering crops might outcompete populations of rare plants in conservation areas for pollinators (Westphal, Steffan-Dewenter & Tschardt 2003). The little known functional consequences of such interactions for reproduction and gene flow of plant populations are highly relevant for the long-term survival and adaptation of plant populations to changing environments. Furthermore, the economic value of pollination services for crops remains controversial. While Ricketts *et al.* (2008) demonstrate a general reduction in visitation rates, the quantification of reductions in yield quantity, quality and net revenues is still in its infancy. Interestingly, not only pollinator densities but also pollinator diversity has proved to be important for ensuring high yields, but mechanisms of biodiversity–functioning relationships need further exploration (Klein *et al.* 2007; Kremen *et al.* 2007). In conclusion, the study of pollinators and their interactions with its fascinating coverage from basic ecological questions to applied aspects of ecosystem services and ecosystem management will remain a fruitful and further expanding area of research.

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