Pollination, seed set and seed predation on a landscape scale

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We analysed the combined effects of pollination and seed predation on seed set of *Centaurea jacea* in 15 landscapes differing in structural complexity. In the centre of each landscape, a patch of *Centaurea* plants was established for standardized measurements of flower visitation, seed predation and seed set. Both the number of flower-visiting bees and the proportion of flower heads damaged by seed predators increased with landscape complexity, which was measured as the proportion of semi-natural habitats. The mean number of seeds per flower head did not increase with the proportion of semi-natural habitats, presumably because of the counterbalancing effects of pollination and seed predation. For a subset of undamaged flower heads, the number of seeds per flower head was positively correlated with the number of flower visits. Further reasons for the unexpected failure to detect a correlation between landscape complexity and seed set appeared to be changes in flower-visitor behaviour and the contrasting responses of honeybees and wild bees to habitat context. Landscape analyses at eight spatial scales (radius of landscape sectors, 250–3000 m) showed that different groups perceived the landscape at different spatial scales. Changes in pollinator numbers could be explained only at small scales (up to 1000 m), while the seed predators also responded to large scales (up to 2500 m).

Keywords: landscape structure; biotic interactions; habitat fragmentation; foraging behaviour; bees; spatial scale

1. INTRODUCTION

The seed set and fruit set of a plant are critical elements of its reproductive success, and may determine the distribution and size of its populations (Eriksson & Ehrlén 1992; Louda & Potvin 1995; Turnbull *et al.* 2000). Seed set depends on interactions with animals that result in pollination, seed predation and foliar herbivory, as well as on nutrient availability and microclimatic site conditions (Bierzychudek 1981; Louda 1982; Schemske & Horvitz 1988; Rathcke & Jules 1993). Despite the fact that these plant–insect interactions are likely to act together in many cases, few studies have analysed the combined effects of pollinators and seed predators or herbivores on seed set with a focus on the relative importance and spatio-temporal variability of each interaction type (Heithaus *et al.* 1982; Schemske & Horvitz 1988; Herrera 1993, 2000; Brody 1997; Juenger & Bergelson 1997; Cunningham 2000*a*).

To our knowledge, no large-scale study has been performed to analyse the combined effects of pollination and seed predation in the context of landscape complexity at different spatial scales. Destruction and fragmentation of habitats, and the resulting changes in landscape complexity, may alter or even disrupt such biotic interactions (Rathcke & Jules 1993; Bronstein 1995; Kareiva & Wennergren 1995; Kearns *et al.* 1998). Because many biotic interactions act on spatial scales much larger than a single habitat, it is important to analyse the effects of habitat fragmentation not only in terms of habitat size or isolation but also by including further features of landscape structure (Andren 1994; With & Crist 1995; Keitt *et al.* 1997; Hanski 1998).

Allogamous plants need pollinators to act as pollen vectors for a high fruit set (Burd 1994). In central Europe, solitary and social wild bees (Hymenoptera: Apoidea) and managed honeybees (*Apis mellifera*) are the most important pollinators (Corbet *et al.* 1991; Williams 1996). The local abundance of pollinators on a plant can be partly explained by the plant's relative attractiveness to pollinators. On a larger spatial scale, the availability of nesting sites and flower resources in a habitat may determine the structure of the pollinator community. In central Europe, potential bee habitats are, in most cases, semi-natural man-made habitats, because natural primary bee habitats have been destroyed (Osborne *et al.* 1991). On a landscape scale, the proportion of potential bee habitats and the diversity of habitat types in a landscape can be expected to influence the diversity and abundance of pollinators (Steffan-Dewenter *et al.* 2002). Similarly, population dynamics of herbivores and host–parasitoid interactions have been shown to depend on landscape complexity (Durrer & Schmid-Hempel 1995; Solbreck 1995; With & Crist 1995; Thies & Tscharntke 1999).

Here, we analysed the combined effects of plant–pollinator and plant–seed-predator interactions along a gradient of increasing landscape complexity on seed set of *Centaurea jacea* (Asteraceae). We selected 15 independent landscape sectors to establish a gradient from structurally simple to structurally rich landscapes. For each landscape sector, we quantified landscape structure at eight spatial scales with radii between 250 m and 3000 m. We experimentally placed a single patch of flowering *Centaurea* plants in the centre of each landscape to analyse the diversity and abundance of flower visitors, seed set and seed predation with a focus on the following questions:

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(i) Do the abundance and diversity of flower-visiting bees and the impact of seed predators change with landscape structure?

(ii) Does foraging behaviour change with landscape structure?

(iii) Is seed-set pollinator limited in structurally simple landscapes?

(iv) How important is the relative impact of seed predators and pollinators on seed set?

(v) Does landscape structure affect pollination and seed predation at different spatial scales?

2. MATERIAL AND METHODS

(a) *Study region and landscape sectors*

The study was carried out in 1997 in an agricultural landscape in southern Lower Saxony (Germany) around Göttingen. The region is characterized by intensively managed agricultural areas with annual crops and patchily distributed fragments of forest and semi-natural habitat types. We selected 15 independent sites in an area of about 32 km east–west by 22 km north–south around Göttingen, which covered different levels of complexity from structurally simple to structurally rich landscapes. There was no geographical gradient (north–south or east–west) in landscape complexity. For each site, landscape structure was quantified at radii of 250 m, 500 m, 750 m, 1000 m, 1500 m, 2000 m, 2500 m and 3000 m, representing a nested set of landscape sectors at eight spatial scales. Landscape structure was quantified using commercially available official digital thematic maps (ATKIS-DLM 25/1, Landesvermessung & Geobasisinformationen Niedersachsen, Postfach 510450, 30634 Hannover, Germany, 1991–1996) covering the habitat types: arable land, grassland, hedgerows, garden land, forest and settled area. For each of the eight nested spatial scales the proportion of semi-natural habitats (intensively and extensively used grasslands, calcareous grasslands and orchard meadows, hedgerows and garden land) was quantified using the Geographical Information Systems ARC/View 3.1 (ESRI Geoinformatik GmBH, Hannover, Germany) and Topol 4.506 (Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany). Arable land, forest and settled area were not considered to be semi-natural. By using the proportion of semi-natural habitats, our measurement of landscape structure was rather simple. However, this factor has been shown to be a robust and useful parameter for characterizing landscape complexity because of its close correlation with other landscape metrics such as habitat diversity, habitat isolation and patchiness (Gustafson 1998; Thies & Tscharntke 1999).

(b) *The experimental species*

The focal plant used in this study was *C. jacea* L. (Asteraceae), a perennial European native. The bee-pollinated protandrous flowers of the genus *Centaurea* are known to be mostly obligate outcrossers (Harrod & Taylor 1995). Our experiments also demonstrate that *C. jacea* depends on pollinators: 42 bagged flower heads on four plants showed a significantly reduced seed set, with only mean ± s.e.m. = 0.8 ± 0.1 seeds per flower head compared with open pollinated flower heads with mean-± s.e.m. = 41.6 ± 1.3 seeds per flower head (*n* = 376).

(c) *The experimental design*

In the centre of each landscape sector we established a patch of four potted *C. jacea* plants. Seeds were obtained from a seed grower, sown in November 1996, picked out in mid-January and planted in pots (8.5 l) of standardized garden soil in March. The potted plants were placed on grassy field margins adjacent to cereal fields in each of the 15 landscapes between 13 May and 16 May 1997. The distance between conspecific plants was 1 m. To prevent damage by rabbits or deer, the plants were fenced in with wire (6 m × 1.20 m, 1 m high). Depending on weather conditions, plants were watered every five to ten days.

(d) *Flower-visitor observations*

Flower-visitor observations were conducted between 09.00 and 17.00 during the flowering time of *C. jacea* in suitable weather conditions, i.e. at least 18 °C, 70% sunshine and low wind. Flowering of *C. jacea* occurred between 29 July and 25 August 1997. The four pots were observed simultaneously for 15 min and all flower-visiting insects were recorded. The number of consecutively visited experimental plants per individual bee was noted. Bees were identified to genus level in the field. After each observation period, the number of flower heads per plant was recorded and flower-visiting bees were captured for further species identification in the laboratory. To obtain unbiased data, landscape types and time of day were varied for successive observations. Depending on the flowering period and weather conditions, between five and eight observations were made per site.

(e) *Analyses of flower heads*

All ripened flower heads were collected from the experimental plants between 13 August and 15 September 1997. They were stored in plastic tubes, which were closed with fine-mesh gauze. For each flower head, we determined the number of fully developed undamaged seeds (achenes) and the diameter and weight of the flower head. Each flower head was classified as undamaged or damaged by seed predators. Emerged adults of seed predators were used to assess species composition. The major seed predators were larvae of tephritid flies and microlepidoptera.

(f) *Statistical analyses*

The statistical analyses of the data were performed using 'Statgraphics plus for Windows 2.1' (Statgraphics 1995). As necessary, we used logarithmic or square-root transformation of the variables to achieve normality of the residuals from statistical models. The arcsine–square-root of p was used for proportions (Sokal & Rohlf 1995). Simple linear-regression analyses were carried out to examine the possible effects of landscape structure on pollination and seed predation at each of the eight spatial scales. To examine plant–insect interactions at different spatial scales, we plotted correlation coefficients considering landscape complexity at each of the eight scales for each of the 15 landscapes. We do not give statistics for these scale-dependent patterns because the eight nested scales were not independent and we failed to find an appropriate statistical procedure. The significance of the effect of pollinator visitation rates on seed set was tested using an s-curve model because the dependence of reproductive output on pollination is intrinsically a non-linear phenomenon (Kunin 1993). Arithmetic means ± s.e.m. are given in the text. The mean number of flower visitors per 15 min per flower head was used for each patch to exclude possible effects of differences in resource availability. For the separate analyses of pollinator and seed–predator effects we used subsets of undamaged and damaged flower heads, respectively. For these analyses we had to exclude, for statistical reasons, four sites and one site, respectively, with fewer than five flower heads. Altogether, we collected and analysed 1151 flower heads, with a
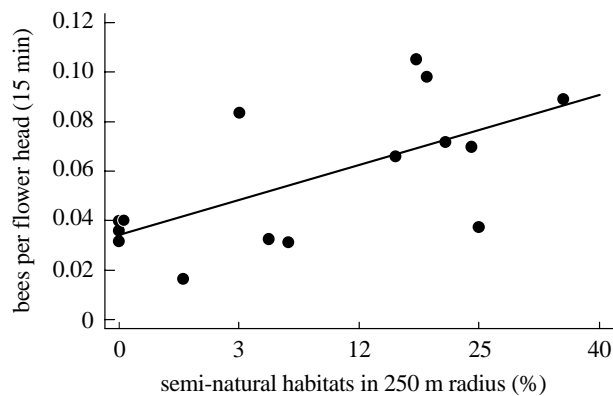
Figure 1. Relationship between the number of flower-visiting bees per 15min per flower head on *Centaurea jacea* and the proportion of semi-natural habitat (%) within a radius of 250 m: $y = 0.034 + 0.0014 \arcsin \sqrt{x}$, $r^2 = 0.418$, $n = 15$, $p = 0.009$.
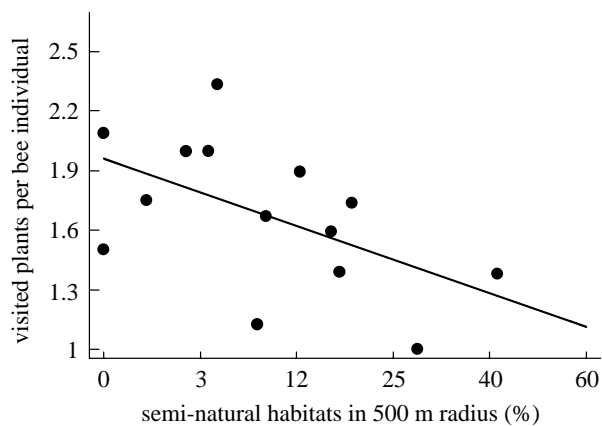

Figure 2. Relationship between the number of consecutively visited experimental plants per individual bee and the proportion of semi-natural habitat (%) within a radius of 500 m: $y = 1.96 - 0.017 \arcsin \sqrt{x}$, $r^2 = 0.290$, $n = 14$, $p = 0.047$.

mean of 76.5 ± 8.6 flower heads per study site. There was no correlation between the number of flower heads and landscape structure ($p = 0.566$).

3. RESULTS

(a) *Flower visitors*

Altogether, 233 individual wild bees (Hymenoptera: Apoidea) and 227 individual honeybees (*A. mellifera*) were observed. The wild bees were represented by the genera *Bombus* (126 bees), *Lasioglossum* (81 bees), *Halictus* (22 bees), *Megachile* (3 bees) and *Andrena* (1 bee). The total abundance of flower-visiting bees significantly increased with the proportion of semi-natural habitat in a landscape sector (figure 1). This pattern was determined by the abundance of solitary wild bees, which significantly increased with the proportion of semi-natural habitat ($y = -0.001 + 0.001 \arcsin \sqrt{x}$, $r = 0.566$, $n = 15$, $p = 0.028$). In contrast, bumble-bees ($r = 0.266$, $p = 0.338$) and honeybees ($r = 0.164$, $p = 0.560$) did not respond significantly to landscape structure at a spatial scale of 250 m. The number of experimental plants consecutively visited by an individual bee significantly decreased in landscapes with increasing proportions of semi-natural habitat (figure 2).
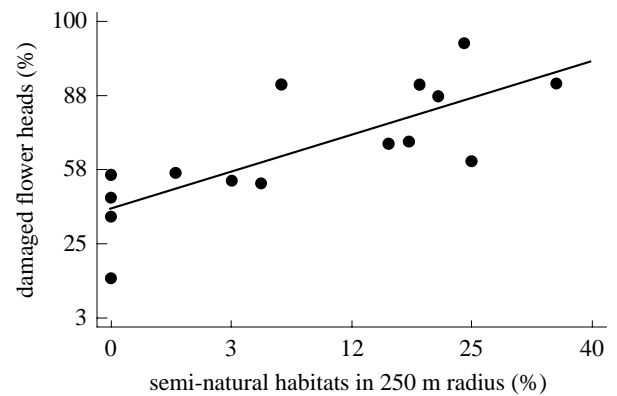

Figure 3. Relationship between the proportion of damaged flower heads (%) and the proportion of semi-natural habitat (%) within a radius of 250 m: $\arcsin \sqrt{y} = 39.3 + 1.0 \arcsin \sqrt{x}$, $r^2 = 0.604$, $n = 15$, $p = 0.0007$.

(b) *Seed set and seed predation*

In contrast to the expectation that higher pollinator abundance would result in higher seed set, the mean number of seeds per flower head did not increase with the proportion of semi-natural habitat at any spatial scale (e.g. $r = -0.309$, $p = 0.263$ for a radius of 250 m). The reason for this appeared to be the large impact of insect seed predators, especially microlepidoptera and the larvae of tephritid flies (Diptera: Tephritidae, mainly *Chaetostomella cylindrica*, *Urophora quadrifasciata* and *Acanthophilus helianthi*). Altogether, 775 flower heads were attacked by seed predators. The percentage of damaged flower heads increased significantly with the proportion of semi-natural habitat in a landscape (figure 3). Further analyses showed that the number of seeds per flower head for a subset of 376 undamaged flower heads was positively correlated with the flower-visitation rate of bees ($y = e^{(4.49 - 0.043/x)}$, $r^2 = 0.539$, $n = 11$, $p = 0.01$), whereas the mean number of seeds per flower head for a subset of 775 damaged flower heads significantly decreased with the percentage of damaged flower heads per study site ($y = 34.16 - 0.24x$, $r^2 = 0.331$, $n = 14$, $p = 0.031$) indicating more damage per flower head in severely attacked patches.

(c) *Scale-dependent effects on pollinators and seed predators*

Up to now, we have discussed only relationships between pollinator abundance, pollinator behaviour or seed predation and landscape structure at relatively small spatial scales, at which the predictive power was highest. However, it is not, *a priori*, clear at which spatial scale landscape complexity has the strongest effect. Furthermore, different plant–animal interactions may operate at different spatial scales. Therefore, we tested how the correlation coefficients changed with the analysed spatial scale for the relationship between pollinator abundance or the percentage of damaged flower heads and the proportion of semi-natural habitat (figure 4a). At all spatial scales, the effects of landscape complexity on seed predators were stronger than those on pollinators. Changes in pollinator numbers could be explained only at small scales (up to 1000 m), while seed predators also responded to large scales (up to 2500 m). The different
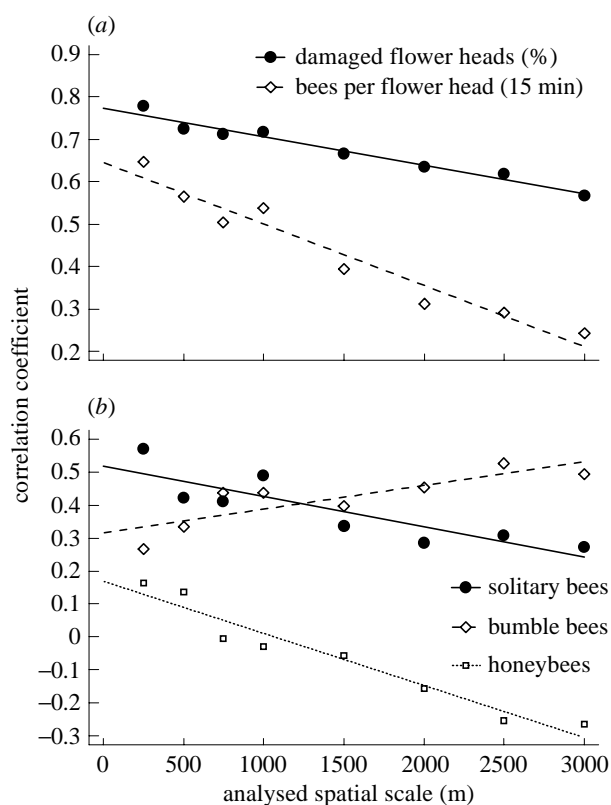
Figure 4. Correlation coefficients on eight spatial scales. Each point represents the result of a simple linear regression of *Centaurea* parameters on landscape structure. Lines were fitted to illustrate the contrasting patterns. Relationships between (*a*) seed predators or pollinators and landscape structure (see figures 1 and 3) and (*b*) solitary bees, bumble-bees or honeybees and landscape structure.

slopes indicate a lesser correlation between landscape structure and pollinator abundance than between landscape structure and seed predators at larger spatial scales. This was presumably due to the different responses of the three main pollinator groups to different spatial scales (figure 4*b*). Solitary bees depended significantly on landscape structure only at small spatial scales, whereas bumble-bees showed a positive relationship with landscape structure only at very large spatial scales. The fitted line for honeybees suggests a negative correlation between abundance and landscape complexity at larger spatial scales (figure 4*b*).

4. DISCUSSION

In this study, we analysed the combined effects of pollinators and seed predators on seed set in relation to landscape structure. Our results show that the abundance of pollinators and the impact of seed predators both increase significantly with landscape complexity. Much of the unexplained spatial variation in pollen limitation and seed predation found in earlier studies (e.g. Heithaus *et al.* 1982; Herrera 1988; Ehrlén 1996) may be related to such large-scale effects of landscape structure on plant–animal interactions.

The combined analysis of pollinator abundance, seed set and seed predation rates allowed us to assess the relative importance of pollination and seed predation for seed

set. The lower abundance of pollinators in landscapes with fewer semi-natural habitats should result in an overall lower seed set if pollinator limitation is an important factor (Schemske & Horvitz 1988; Burd 1994; Cunningham 2000*b*). Although we found a weak correlation between flower-visitation rate and seed set for undamaged flower heads, there was no direct relationship between mean overall seed set and landscape complexity. We see three possible explanations: first, the increasing impact of seed predators in more complex landscapes; second, the differing and opposing responses of solitary wild bees, bumble-bees and honeybees to landscape structure at different spatial scales; and third, the changed foraging behaviour of flower visitors with increasing landscape complexity.

The landscape-related effects of seed predators were stronger than those of pollinators; 67% of all flower heads were damaged by seed predators and the damage increased significantly with landscape complexity at all spatial scales. This clear relationship is presumably due to the distribution of natural populations of *C. jacea*, which mainly occur on semi-natural grasslands. The isolation distances of the experimental patches from naturally occurring *Centaurea* populations could be expected to increase, and the regional density of natural populations to decrease, with decreasing landscape complexity. The unexpected failure to find a positive correlation between the number of undamaged seeds per flower head and landscape complexity appeared to be partly caused by the counterbalancing effects of pollination and predation. Subsamples of flower heads showed that pollination per se (enhanced seed numbers in undamaged flower heads) and seed predation per se (reduced seed numbers when only damaged flower heads were considered) had significant effects on seed production. The relative importance of pollination and seed predation on seed set may vary with landscape complexity, as suggested by the different slopes in figure 4*a*. Thus, the degree of landscape complexity may change the selective pressures exerted by pollinators and seed predators (Armbruster 1997; Strauss 1997).

Solitary bees, which have small foraging ranges, were significantly correlated with landscape structure at small spatial scales, whereas bumble-bees and honeybees were not correlated with landscape structure at these spatial scales. At very large scales (radius, 3 km) honeybee densities increased in flower patches in structurally simple landscapes with few alternative flowers. Thus, although total bee abundance (and diversity) significantly decreased in simple landscapes due to the loss of solitary bees, the few social-bee species appeared to compensate partially for the loss of the solitary bees. Severe effects of pollinator limitation may occur only if plant species depend exclusively on solitary bees as pollinators (e.g. Aizen & Feinsinger 1994; Steffan-Dewenter & Tscharntke 1999; Cunningham 2000*b*). The number of plants visited per individual bee decreased with increasing landscape complexity. Thus, flower patches in structurally simple landscapes with few alternative flower resources received more flower visits per individual bee than patches in complex landscapes. Similarly, a higher flower-visitation rate per individual (but a lower total number of visitors) was found in small fragments compared with large control plots (Goverde *et al.* 2001; Schulke & Waser 2001).

Such changes in foraging behaviour with landscape structure may enable seed set of isolated plant populations but, in the long run, a higher proportion of biparental inbreeding (and selfing in self-compatible species) may disrupt gene flow and increase inbreeding depression (Waser & Price 1991; Kwak *et al.* 1998).

As far as we know, only a few other studies have analysed biotic interactions on a landscape scale (e.g. Roland & Taylor 1997; Thies & Tscharntke 1999), and none have examined the combined effects of plant–pollinator and plant–seed-predator interactions. Our experimental approach allowed us to exclude other factors that could potentially influence seed set, such as nutrient availability (e.g. Schemske & Horvitz 1988; Burd 1994; Juenger & Bergelson 1997), genetic variability (e.g. Oostermeijer *et al.* 1994) and patch size (e.g. Ågren 1996), which were equal at all study sites. Flower and leaf herbivory (Petterson 1991; Karban & Strauss 1993; Strauss *et al.* 1996; Brody 1997; Strauss 1997; Herrera 2000) and interactions between herbivores and their natural enemies (Roland & Taylor 1997; Thies & Tscharntke 1999) may show similar dependencies on landscape complexity, but we did not analyse these interactions in our study. In conclusion, there is a need for experimental studies that take into account the real complexity of plant–insect interactions and approaches at a landscape level in order to better understand the role of large-scale changes of biotic interactions as shaping factors of local population and community dynamics.

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