**LETTER**

Mass flowering crops enhance pollinator densities at a landscape scale

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**Abstract**

To counteract the decline of pollinators in Europe, conservation strategies traditionally focus on enhancing the local availability of semi-natural habitats, as supported by the European Union’s Common Agriculture Policy. In contrast, we show that densities of bumblebees, an important pollinator group in agroecosystems, were not determined by the proportion of semi-natural habitats in agricultural landscapes. Instead, bumblebee densities were positively related to the availability of highly rewarding mass flowering crops (i.e. oilseed rape) in the landscape. In addition, mass flowering crops were only effective determinants of bumblebee densities when grown extensively at the landscape scale, but not at smaller local scales. Therefore, future conservation measures should consider the importance of mass flowering crops and the need for management schemes at landscape level to sustain vital pollination services in agroecosystems.

**Keywords**

Agri-environment schemes, Bombus spp., bumblebees, conservation measures, foraging habitats, landscape structure, landscape-scale study, mass flowering crops, nesting sites, pollination.


**INTRODUCTION**

Pollination is an ecosystem service of major economic and societal value, which is endangered by recent declines in pollinators (Daily 1997). Destruction and fragmentation of habitats through agricultural intensification create structurally poor landscapes (Tilman et al. 2001), which adversely affect the diversity and abundance of solitary wild bees and bumblebees (Williams 1995; Kremen et al. 2002; Steffan-Dewenter et al. 2002). Furthermore, serious declines of managed honeybees have been documented (Williams et al. 1991; Watanabe 1994). However, the declines of managed honeybees and solitary wild bees may be compensated by generalist and mobile pollinators such as bumblebees (Corbet 2000; Kremen et al. 2002).

Bumblebees pollinate a wide range of wild plants and crops in agroecosystems (Corbet et al. 1991). For the development of their annual colonies they require a continuous supply of food plants from early spring to late summer, as usually is provided in perennial semi-natural habitats (Fussell & Corbet 1991; Corbet 1995). In addition, semi-natural habitats represent suitable nesting sites in agricultural landscapes (Svensson et al. 2000; Kells & Goulson 2003). Flowering crops are assumed to be of little value for bumblebees because of their short flowering period (Corbet 2000). However, empirical evidence is still missing for this assumption, as far as we know.

To enhance pollinator diversity and abundance, semi-natural habitats are traditionally implemented within the framework of conservation measures and agri-environment schemes (Banaszak 1992; Institute for European Environmental Policy 2002). However, pollinators benefit only marginally from the current European Union’s agri-environment schemes (Kleijn et al. 2001). This deficiency of the agri-environment schemes might be due to the implementation of various habitats (at a local scale) without considering the landscape context (see Addicott et al. 1987; With et al. 1999). Therefore, future sustainable management of European agroecosystems will depend on the identification of key factors enhancing landscape-wide pollinator densities and appropriate spatial scales at which pollinators perceive the landscape (Kareiva & Wennergren 1995).

We tested the effects of two landscape factors determining bumblebee densities in agricultural landscapes: first, the availability of nesting sites and continuously flowering food plants (i.e. proportion of semi-natural
habitats), and second the availability of short flowering, but highly rewarding mass resources (i.e. proportion of flowering crops) (Fussell & Corbet 1991; Banaszak 1992; Steffan-Dewenter et al. 2002). The influence of either landscape factor on bumblebee densities was examined from local to regional spatial scales to identify the appropriate spatial scale for the implementation of conservation schemes (Kareiva & Wennergren 1995; Steffan-Dewenter et al. 2002).

**MATERIAL AND METHODS**

The study was conducted in 2001 in the vicinity of the city Göttingen (Germany) in an agricultural landscape representing typical land use types for southern Lower Saxony (Table 1). Within an area of 42 km east–west and 35 km north–south around Göttingen we selected 16 independent circular landscape sectors each with a radius of 3000 m. These landscape sectors represented a gradient of landscape complexity ranging from structurally rich to poor landscapes (Table 1). Landscape complexity did not correlate with the geographical north–south and east–west gradients.

To study scale-dependent effects of landscape complexity each circular landscape sector was subdivided into 12 nested sectors with radii from 250 to 3000 m, representing 12 different spatial scales (Tischendorf & Fahrig 2000; Steffan-Dewenter et al. 2002). We chose the maximum scale (radius of 3000 m) larger than the reported potential foraging distances of bumblebees (Osborne et al. 1999; Walther-Hellwig & Frankl 2000; but see below). Two landscape factors – the proportion of semi-natural habitats and the proportion of flowering crops – were calculated for all 12 subsectors (i.e. spatial scales) of the 16 landscape sectors separately using Geographic Information Systems (GIS; Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany).

Bumblebee densities were recorded during 15-min observations (between 13 July and 2 August 2001) in experimental *Phacelia tanacetifolia* (Hydrophyllaceae) patches (4.5 m²), which we had established on old fallows (1.8 ± 0.2 ha, *n* = 16) in the centre of each landscape sector. Compared with the low cover of flowers on the fallows (4.89 ± 0.95%), the *Phacelia* plots were largely covered with flowers (50.5 ± 2.2%; minimum 33.3%, maximum 63.3%), and thus bumblebees were likely to be attracted (Williams & Christian 1991). Depending on weather conditions and flowering periods three to four observations were made per study site. The plots were sown between 16 May and 22 May 2001 with 3 g *Phacelia* seeds per m². To standardize nutrient supply, the plots were covered with 2 cm standard garden soil and fertilized every 2 weeks (c. 80 g m⁻²). We used standard fertilizer with 8% P₂O₅, 15% K₂O and 6% MgO. The area of *Phacelia* flowers covering the plot was estimated after each observation. Bumblebee densities were calculated as number of individuals per square metre *Phacelia* flowers.

Data were analysed with SPSS 11.0 for Windows (SPSS GmbH Software, Munich, Germany). In simple regression models the effects of both landscape parameters on bumblebee densities were tested individually for each spatial scale (i.e. landscape sector). For all regression models the coefficients of determination (*R²*) were plotted to demonstrate the influence of spatial scale on the correlations between the landscape factors and bumblebee densities (Bowers 1985; Steffan-Dewenter et al. 2002). Arcsine square-root transformation was used to achieve normality for the proportions of semi-natural habitats (Zar 1984). Arithmetic means and standard errors of the non-transformed data are given in the text.

**RESULTS**

We observed a total of 3340 non-parasitic bumblebee visits in the *Phacelia* plots during sixty-two 15-min observations. The bumblebee density was on average 23.2 ± 1.8 bumblebee individuals per m² flowers (minimum 10.4, maximum 33.5; *n* = 16). We found seven *Bombus* species out of (presumably) nine in the region. The prevalent species were *B. terrestris* agg. (a group of *B. terrestris* and *B. lucorum*, which are difficult to distinguish in the field), *B. lapidarius* and *B. pascuorum*.

In contrast to our expectations the proportion of semi-natural habitats did not significantly influence bumblebee

### Table 1 Landscape characteristics for medium landscape sectors with 1500 m radius (*n* = 16)

<table>
<thead>
<tr>
<th>Land use type</th>
<th>Mean area (%) ± 1 SEM</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual crops</td>
<td>51.01 ± 5.09</td>
<td>14.72</td>
<td>83.23</td>
</tr>
<tr>
<td>Mass flowering crops*</td>
<td>7.80 ± 0.87</td>
<td>2.55</td>
<td>15.12</td>
</tr>
<tr>
<td>Oilseed rape</td>
<td>6.95 ± 0.92</td>
<td>2.28</td>
<td>14.87</td>
</tr>
<tr>
<td>Grasslands</td>
<td>13.55 ± 2.06</td>
<td>1.86</td>
<td>27.42</td>
</tr>
<tr>
<td>Semi-natural habitats†</td>
<td>5.91 ± 0.75</td>
<td>1.77</td>
<td>13.02</td>
</tr>
<tr>
<td>Settlements</td>
<td>4.46 ± 0.80</td>
<td>0.23</td>
<td>14.08</td>
</tr>
<tr>
<td>Forests</td>
<td>17.55 ± 3.87</td>
<td>0.00</td>
<td>53.77</td>
</tr>
</tbody>
</table>

*Brassica napus* (oilseed rape, 4–5), *Trifolium* spp. (clover, 6–9), *Phacelia tanacetifolia* (6–10), *Vicia faba* (field bean, 6–7), *Solanum tuberosum* (potato, 6–7), *Sinapis arvensis* (wild mustard, 5–6) and *Helianthus annuus* (sunflower, 7–9). Crops that require bee pollination for seedset or increased yields (following Free 1993) are printed in bold letters. Numbers indicate the months of the main flowering period of the crops (following Oberdorfer 1994).

†fallows, calcareous grasslands, orchard meadows, woods, hedges, rows, grassy banks and ditches.

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densities at any of the 12 spatial scales ($P > 0.3$ in all cases; Fig. 1). Even the strongest regression model, for landscape sectors with 2750 m radius ($F_{1,15} = 0.979$, $P = 0.339$, $r^2 = 0.065$). (b) $r^2$ values for positive simple linear regressions between the proportion of semi-natural habitats and bumblebee densities for 12 landscape sectors with 250–3000 m radius. Regressions are not statistically significant ($P > 0.300$, $n = 16$).

Figure 1 Effects of the proportion of semi-natural habitats on bumblebee densities. (a) Relationship between the proportion of semi-natural habitats (%) and the bumblebee density for the regression with the highest $r^2$ in landscape sectors with 2750 m radius ($F_{1,15} = 0.979$, $P = 0.339$, $r^2 = 0.065$). (b) $r^2$ values for positive simple linear regressions between the proportion of semi-natural habitats and bumblebee densities for 12 landscape sectors with 250–3000 m radius. Regressions are not statistically significant ($P > 0.300$, $n = 16$).

In contrast, the availability of mass flowering crops (mainly oilseed rape, *Brassica napus*; Table 1) had strong positive effects on bumblebee densities (Fig. 2). The strongest correlation between the proportion of mass flowering crops and bumblebee densities was found for landscape sectors with 3000 m radius (Fig. 2a). The positive influence of mass flowering crops on bumblebee densities strengthened with spatial scale, as the coefficients of determination were increasing with the area of the landscape sectors (Fig. 2b). Simple linear regressions were significant for landscape sectors with radii >1250 m ($P < 0.050$, except for 1750 m radius: $P = 0.055$, $n = 16$).

Figure 2 Scale-dependent effects of the proportion of mass flowering crops on bumblebee densities. (a) Proportion of mass flowering crops (%) in landscape sectors with 3000 m radius in relation to bumblebee densities (numbers per m$^2$ flowers; $y = 2.25x + 8.74$, $F_{1,15} = 13.64$, $P = 0.002$, $r^2 = 0.493$). (b) $r^2$ values for positive simple linear regressions between the proportion of mass flowering crops and bumblebee densities for 12 landscape sectors with 250–3000 m radius. Regressions are statistically significant for landscape sectors with radii >1250 m ($P < 0.050$, except for 1750 m radius: $P = 0.055$, $n = 16$).

**DISCUSSION**

As semi-natural habitats serve as nesting sites and offer a continuous as well as diverse supply of food plants throughout the season, they are considered to be of great importance for solitary wild bees and bumblebees in agricultural landscapes (Corbet 1995; Dramstad & Fry...
Therefore, they are traditionally implemented within the framework of conservation measures and agri-environment schemes (Banaszak 1992; Kleijn et al. 2001). However, we did not find any beneficial effect of the availability of semi-natural habitats on bumblebee densities in our landscape sectors. In agricultural landscapes with at least 2% semi-natural habitats the numbers of bumblebees were apparently not limited by the availability of nesting sites and food plants in semi-natural habitats. In contrast to bumblebees, solitary wild bees significantly profited from the availability of semi-natural habitats at small spatial scales (Steffan-Dewenter et al. 2002). This difference may be due to larger foraging distances, less restricted nesting site requirements and the more generalized use of food plants by bumblebees (Prys-Jones & Corbet 1991; Walther-Hellwig & Frankl 2000; Gathmann & Tscharntke 2002). However, we cannot infer from our data whether the rare bumblebee species, which contributed little to our results, are more dependent on semi-natural habitats than the three prevalent species. Although our study area is typical for many agricultural landscapes in central Europe, bumblebee densities might be enhanced in other landscape types by much larger amounts of semi-natural or natural habitats than provided in our human-altered landscape sectors.

Deviating from the general assumption that social wild bees do not profit from annual crops such as oilseed rape because of the short flowering time (Corbet 2000), we report here great benefits in terms of bumblebee densities. The strong positive effects of the availability of mass flowering crops (mainly oilseed rape) on bumblebee densities at medium to large spatial scales indicate that mobile and generalist pollinators like bumblebees exploit mass resources over large distances. Bumblebees apparently perceive their surroundings over large distances. Furthermore, they seem to require a sufficient supply of food plants at a regional and not at a local level. The strongest correlation found at the largest spatial scale (i.e. landscape sectors with 3000 m radius) provides evidence that bumblebees have large foraging ranges and serve as efficient pollinators at a landscape level. This differs somewhat from foraging distances up to 1750 m found in recent mark-recapture experiments (Walther-Hellwig & Frankl 2000). However, due to the exceptionally high effort required to recapture individuals over large areas, mark-recapture experiments have limited ability to detect large foraging ranges. In addition, theoretical studies indicate foraging ranges exceeding several kilometres (Dukas & Edelstein-Keshet 1998; Cresswell et al. 2000).

We found various mass flowering crops in our landscape sectors, which could provide pollen and nectar continuously until October. But only oilseed rape occurred in all landscape sectors in substantial proportions (Table 1). Hence, we consider oilseed rape to be the major mass flowering crop influencing bumblebee densities.

Oilseed rape flowers in May at the time of colony founding, when only the queen or few workers care for the brood (Alford 1975). Compared with the sparsely distributed wild plants in semi-natural habitats mass flowering crops represent energetically much more rewarding resources (Dukas & Edelstein-Keshet 1998), which seem to be particularly beneficial for colony-founding bumblebees. We assume that highly rewarding resources promote early colony growth, resulting in higher pollinator densities later in the season, when our observations took place. As the capability to reproduce is enhanced by the availability of resources (Bowers 1985), population densities might also increase due to higher numbers of young queens founding more numerous colonies in the next spring. Nevertheless, semi-natural habitats represent important nesting sites and continuous forage resources for bumblebees (Corbet 2000) and solitary wild bees (Steffan-Dewenter et al. 2002) when no flowering crops are available.

Irrespective of the indispensable priority on the conservation of all remaining semi-natural habitats, we conclude that the importance of mass resources and the necessity to manage landscapes, and not just local habitats, should be considered in future agri-environment schemes to improve pollination services in agroecosystems. Furthermore, our results emphasize the need to broaden perspectives of ecological research to the landscape level (Kareiva & Wennergren 1995).

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