Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context

ANDREA HOLZSCHUH,* INGOLF STEFFAN-DEWENTER,* DAVID KLEIJN† and TEJA TSCHARNTKE*

*Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany; and
†Nature Conservation and Plant Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, the Netherlands

Summary

1. Agri-environment schemes promote organic farming in an attempt to reduce the negative effects of agricultural intensification on farmland biodiversity and ecosystem services such as pollination. Farming system, landscape context and regional differences may all influence biodiversity, but their relative impact and possible interactions have been little explored.

2. The study was performed in three regions (150 km apart, 400–500 km$^2$ per region) differing in land use intensity. Within each region, seven pairs of conventionally and organically cultivated wheat fields (mean size 4 ha, 42 study fields) were selected to encompass a gradient from heterogeneous to homogeneous landscapes within a 1-km radius around each field.

3. Farming system had the greatest influence on biodiversity. Higher bee diversity, flower cover and diversity of flowering plants were recorded in organic compared with conventional fields. Bee diversity was related both to flower cover and diversity of flowering plants, suggesting plant-mediated effects of the farming system.

4. Differences in bee diversity between organic and conventional fields increased with the proportion of arable crops in the surrounding landscape, indicating that processes at the landscape level modified the effectiveness of organic farming in promoting biodiversity. Similar patterns for flower cover and diversity of flowering plants suggested that landscape effects on bee diversity were mainly resource-mediated. After statistically removing the variance explained by flower parameters, residual bee diversity increased with increasing landscape heterogeneity.

5. Bee diversity differed between the three regions, but the effects of farming systems and landscape context were independent of regional differences.

6. Synthesis and applications. Bee diversity in wheat fields was mainly influenced by farming system, but an understanding of local bee diversity needs to incorporate both landscape and regional perspectives. The consistency of the results in three regions provides a reliable basis for management decisions. Agri-environment schemes that promote organic farming in homogeneous landscapes where there are few remaining flower-rich habitats could have the highest relative impact. However, while organic farming could help to sustain pollination services by generalist bees in agricultural landscapes, other measures are required to conserve more specialized bee species in semi-natural habitats.

Key-words: agri-environment schemes, biodiversity, flowering plants, landscape structure, organic farming, pollination, spatial scales, weeds, winter wheat

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Correspondence: Andrea Holzschuh, Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany (fax + 49 551 398806; e-mail a.holzschuh@agr.uni-goettingen.de).
Agricultural intensification at different spatial scales has caused a significant decline in farmland biodiversity (Krebs et al. 1999). During recent decades, cultivation of annual crops has expanded at the cost of non-crop habitats such as extensive grasslands, fallows, hedges and field margins (Tilman et al. 2001; Benton, Vickery & Wilson 2003). Non-crop habitats provide dispersal corridors for wildlife and habitat islands required by many species as refuges and feeding areas (Stoate et al. 2001; Öckinger & Smith 2007). Several studies have shown habitat fragmentation and decreasing landscape heterogeneity to be associated with a loss of biodiversity in agricultural landscapes (Jonsen & Fahrig 1997; Steffan-Dewenter & Tscharntke 1999; Steffan-Dewenter et al. 2002; Weibull, Östman & Granquist 2003). Additionally, ecological functions, such as predation of pest insects and pollination of crops, suffer from decreasing landscape heterogeneity (Thies & Tscharntke 1999; Richards 2001; Kremen, Williams & Thorp 2002; Tilman et al. 2002; Kremen et al. 2004; Tscharntke et al. 2005).

At the field scale, agricultural intensification has affected biodiversity by changing farming practices (Benton, Vickery & Wilson 2003). High-input arable systems, with increased applications of fertilizers and pesticides, have adverse effects on biodiversity (Wilson et al. 1999). More extensive systems, such as organic farming, aim to mitigate the negative impacts of modern agriculture and to enhance biodiversity (Krebs et al. 1999; Reganold, Glover & Andrews 2001; Tybirk, Alroe & Frederiksen 2004). Several studies have shown positive effects of organic farming relative to conventional agriculture in terms of botanic diversity (Hald 1999; Hyvönen et al. 2003; Bengtsson, Ahnström & Weibull 2005) whereas arthropods appear to respond ambiguously to organic cropping (reviewed in Hole et al. 2005). Contrasting findings may arise when differences between farming systems result from associated differences in landscapes rather than directly from farming practices (Bengtsson, Ahnström & Weibull 2005). Although Krebs et al. (1999) suggest that biodiversity in agro-ecosystems depends on both landscape heterogeneity and farm management, studies that take landscape variables into account are rare. The few studies performed at a large enough scale found that the landscape context can modify the influence of organic farming on plants (Roscchwitz et al. 2005) or may be even more important for the diversity of bees, butterflies, carabids and spiders than the local farming system (Weibull, Bengtsson & Nohlgren 2000; Kremen, Williams & Thorp 2002; Weibull, Östman & Granquist 2003; Schmidt et al. 2005). In homogeneous landscapes, differences in biodiversity between organic and conventional fields may be larger because organic fields compensate for the missing non-crop habitats (Bengtsson, Ahnström & Weibull 2005). On the other hand, the isolation of organic fields in homogeneous landscapes may be too high and the species pool too small to allow a response of biodiversity to organic farming (Tscharntke et al. 2005). In the latter scenario, the positive impact of organic farming will be smaller in the most intensively used homogeneous landscapes (Kleinig & Sutherland 2003). Modifications of local patterns may not only result from surrounding landscapes but also from even larger spatial scales (Schweiger et al. 2005; Knop et al. 2006). Geographical regions might differ regarding the regional species pool, large-scale patterns of land use, and climatic and soil conditions. Further, political and administrative regulations that differ among regions might affect the implementation of agri-environment schemes and agricultural management practices (Wilson 1994).

Solitary and social wild bees are considered to be important pollinators in central Europe (Corbet, Williams & Osborne 1991; Williams 1996). A decline in bee diversity will affect the pollination of wild plant species and many insect-pollinated crops. Pollinator populations cannot be maintained by short-flowering crops alone but also need a continuous supply of nectar and pollen in the surrounding agricultural landscapes.

The objective of our study was to examine if organic farming is efficient in promoting the diversity of bees as a functionally important and threatened species group in agricultural landscapes. We surveyed bees in winter wheat 

\[Triticum aestivum\] L., which is the most important arable crop in Germany. Although wheat itself does not contain pollen or nectar, wheat fields can provide flower resources when they also support a species-rich non-crop flora (Roscchwitz et al. 2005). Using a paired-field approach (organic vs. conventional), we incorporated a landscape scale and a regional scale into the study. We compared different regions to examine whether patterns generated by processes acting at local and landscape scales were robust across regions. In particular, we were interested in the relative contribution of effects mediated by changes in flower resource availability compared with other effects related to farming system and landscape context.

**Methods**

**STUDY REGIONS AND STUDY SITES**

The study was conducted in 2003 in three regions about 150 km apart in three different federal states in Germany (Soester Boerde/North Rhine-Westphalia, Leine Bergland/Lower-Saxony and Lahn-Dill-Bergland/Hesse). The regions were between 400 and 500 km² in size and differed in large-scale land use intensity as well as a number of other factors (Table 1). The Soester Boerde (51°35'00"N, 008°07'00"E) is characterized by intensive agriculture on fertile loess soils that are mainly used for producing wheat and sugar beet \[Beta vulgaris\] L. The Leine Bergland (51°32'00"N, 009°56'00"E) has very productive areas on fertile soils in flat parts of the region that alternate with more diverse agricultural landscapes in hilly parts. The Lahn-Dill-Bergland...
Table 1. Altitude, climate factors, land use and crop data for the three regions Leine Bergland, Lahn-Dill-Bergland and Soester Boerde in 2003. Large-scale land use (% arable land, % grassland, % forest) was calculated for circular areas with a 10-km radius around the study sites. Average percentage crop fields, semi-natural habitats and annual fallows were calculated for the 14 landscape sectors per region (1-km radius). Minimum and maximum altitudes of the study sites are shown.

<table>
<thead>
<tr>
<th></th>
<th>Leine Bergland</th>
<th>Lahn-Dill-Bergland</th>
<th>Soester Boerde</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Altitude (m)</strong></td>
<td>155–340</td>
<td>100–496</td>
<td>70–320</td>
</tr>
<tr>
<td><strong>Precipitation (mm year</strong></td>
<td>550</td>
<td>704</td>
<td>693</td>
</tr>
<tr>
<td>¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean temperature (°C)</strong></td>
<td>8.7</td>
<td>9.4</td>
<td>9.3</td>
</tr>
<tr>
<td><strong>% grassland</strong></td>
<td>5–3</td>
<td>16–8</td>
<td>8–9</td>
</tr>
<tr>
<td><strong>% forest</strong></td>
<td>31–3</td>
<td>42–8</td>
<td>16–2</td>
</tr>
<tr>
<td><strong>% arable land</strong></td>
<td>52–1</td>
<td>23–5</td>
<td>61–8</td>
</tr>
<tr>
<td><strong>% crop fields in 1-km radius</strong></td>
<td>62–7</td>
<td>46–8</td>
<td>64–1</td>
</tr>
<tr>
<td><strong>% semi-natural habitats</strong></td>
<td>2–6</td>
<td>1–5</td>
<td>4–4</td>
</tr>
<tr>
<td><strong>% annual fallows</strong></td>
<td>5–1</td>
<td>1–8</td>
<td>3–2</td>
</tr>
<tr>
<td><strong>Mean winter wheat yield (100 kg ha⁻¹)</strong></td>
<td>62–0</td>
<td>58–1</td>
<td>62–8</td>
</tr>
</tbody>
</table>

Table 2. Agricultural practices and yields in the study year, field sizes and landscape characteristics for 21 conventional and 21 organic winter wheat fields (42 farmers). Means ± SD, minima and maxima are given.

<table>
<thead>
<tr>
<th></th>
<th>Conventional</th>
<th>Organic</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Use of insecticides</strong></td>
<td>Nine farmers</td>
<td>–</td>
</tr>
<tr>
<td><strong>Use of herbicides against broadleaves</strong></td>
<td>All farmers</td>
<td>–</td>
</tr>
<tr>
<td><strong>Weed control by harrowing or hoeing</strong></td>
<td>One farmer</td>
<td>17 farmers</td>
</tr>
<tr>
<td><strong>Use of synthetic fertilizer</strong></td>
<td>20 farmers</td>
<td>–</td>
</tr>
<tr>
<td><strong>Use of organic fertilizer</strong></td>
<td>Nine farmers</td>
<td>Eight farmers</td>
</tr>
<tr>
<td><strong>Legumes in crop rotation</strong></td>
<td>–</td>
<td>15 farmers</td>
</tr>
<tr>
<td><strong>Length of crop rotation (years)</strong></td>
<td>3–45 ± 0.69 (2–5)</td>
<td>4.25 ± 1.25 (3–7)</td>
</tr>
<tr>
<td><strong>Fertilization (kg N ha⁻¹)</strong></td>
<td>175±1 ± 34.01 (125–260)</td>
<td>38.4 ± 55.63 (0–180)</td>
</tr>
<tr>
<td><strong>Winter wheat yield (100 kg ha⁻¹)</strong></td>
<td>75.9 ± 18.4 (42–98)</td>
<td>45.9 ± 10.2 (25–60)</td>
</tr>
<tr>
<td><strong>Field size (ha)</strong></td>
<td>5.1 ± 3.5 (0.7–11.3)</td>
<td>3.3 ± 3.0 (0.6–12.5)</td>
</tr>
<tr>
<td><strong>% crop fields in 1-km radius</strong></td>
<td>58.1 ± 19.9 (17–85)</td>
<td>57.6 ± 19.2 (17–86)</td>
</tr>
</tbody>
</table>

(50°49’00”N, 008°46’00”E) is divided into a large hilly area with a high proportion of grassland and rather small fields, and a flat and homogeneous part supporting intensive agriculture. Characteristically, as for many other agricultural regions in Germany and other European countries, organic and conventional fields were interspersed with one another rather than being organized into large contiguous blocks.

In total, 42 winter wheat fields were studied, with seven organic and seven conventional fields in each region. About 60% of the total arable area in Germany is cultivated with cereals, and 45% of this area is cultivated with wheat (Statistisches Bundesamt 2004). Cereals were the only annual crops in our study regions that were managed in the same landscapes both conventionally and organically. The 21 organic farmers cultivated winter wheat according to European Union (EU) regulation 2092/91/EEC, which prohibits, among others, the use of synthetic fertilizers and pesticides (Council of the European Communities 1991) (Table 2). Each organic field was paired with the closest conventional winter wheat field for a comparison that controlled for differences in abiotic conditions and landscape context.

Distances between fields within a pair ranged from 0 to 600 m. Field sizes did not differ between the two farming types (t-tests for paired samples; Table 2).

SURVEYING BEES AND FLOWERING PLANTS

Bees (Apiformes) were recorded for 15 min transect⁻¹ (95 × 1 m) on four occasions between May and July along transects in the field centre and at the field edge (15 min × 2 × 4 = 120 min field⁻¹). The edge transects were located 1 m into the cereal field along the field edge. All bees were collected for subsequent identification in the laboratory. Fields of a pair were sampled directly one after the other, between 10:00 and 18:00 under sunny weather conditions (temperature > 18 °C, cloud cover < 30%, low wind speeds < 3 Bft). The number of bee species used for statistical analysis was the accumulated number caught within the study period. Data from the field centre and the field edge were pooled for analysis. There was no significant difference in bee diversity between the field centre and edge in organic fields (t-test for paired samples, P = 0.074). In conventional fields, bee diversity was higher at the field edge than in the field centre (P = 0.009). The field edge represented a relatively small area of the total field only. Thus we overestimated the value of conventional fields for bees.

All plant species flowering during the survey and flower cover were recorded during each sampling period in a 1-m wide sector along the bee transects. The number of
flowering plant species in our analyses was the accumulated number recorded within the study period. Flower cover was the percentage cover of flower corollas per ground surface area; values were summarized for each transect and averaged over transects and the four surveys.

QUANTIFYING LANDSCAPE CONTEXT

The surrounding landscape was characterized for each field within a circle of 1 km radius around the field centre. This radius was chosen because solitary wild bees, which comprise most of the recorded bee species, are known to be influenced by the landscape at small spatial scales up to 1 km (Gathmann & Tscharntke 2002; Steffan-Dewenter et al. 2002). Field inspections were made to record the areas of different habitat types in these landscape sectors on the basis of official topographical maps (Deutsche Grundkarte 1 : 5000). The proportions of different habitat types, and the Shannon index of habitat diversity were calculated for the landscape sectors using geographic information systems (GIS; Topol 4·506, Gesellschaft für digitale Erdbewachung und Geoinformation mbH, Göttingen, Germany, and ArcView 3·2, ESRI Geoinformatik GmbH, Hannover, Germany). Sectors of different field pairs did not overlap as the distance between pairs within a region ranged from 3 km to 45 km. We used the proportion of annual crop fields as a homogeneous indicator for landscape complexity because of its negative correlation with the Shannon index of habitat diversity and the proportions of grassland and forest (Spearman rank correlations, \( n = 21, P < 0·01 \)). The proportion of crop fields did not differ significantly between the three study regions (Table 1; \( t \)-test, \( P = 0·174 \)) nor between landscape sectors around organic and conventional fields (Table 2; \( t \)-test for paired samples, \( P = 0·770 \)). The proportion of crop fields was negatively related to the altitude of study sites, but initial analyses did not show any relationship between altitude and bee diversity or flower availability.

STATISTICS

We used linear mixed-effects models to determine effects acting at three spatial scales on flower cover, diversity of flowering plants and bee diversity (Pinheiro & Bates 2000). We tested for significance of fixed effects (region; landscape context, proportion of crop fields; farming system, organic vs. conventional) and their interactions. Neighbouring organic and conventional fields were grouped within pairs by adding a random block factor. The landscape parameter was tested at the level of the field pairs (\( n = 21 \)) because landscape sectors of neighbouring fields were not independent. Wald-type \( F \)-tests (type I) were used for the factor selection. Fixed factors and interactions that did not contribute to the model with \( P < 0·05 \) were removed by a stepwise backward procedure from the full model. Non-significant factors that were part of significant interactions were not removed (Crawley 2002). We also referred to ecologically meaningful marginally significant factors (0·05 < \( P < 0·10 \)). Differences between regions were further inspected using one-way ANOVA and Tukey HSD post-hoc tests on the data averaged over field pairs.

Multiple linear regression models were used to analyse the relative importance of flower cover and diversity of flowering plants for bee diversity. By including diversity of flowering plants and flower cover into the linear mixed-effects model for bee diversity, we tested for other effects of farming system, landscape context and region after accounting for the variance explained by flower parameters. We transformed the number of bee species [\( \log_{10}(x + 1) \)] and the percentage values of flower cover (arcsine square-root transformation; Sokal & Rohlf 1995). All statistical analyses were performed using R (R Development Core Team 2004).

Bee diversity was correlated with individual numbers in organic and conventional fields. We checked for a possible bias of sample size in our analysis of diversity by computing first-order jack-knife estimates of species richness, which are independent of the number of sampled individuals (EstimateS; Colwell 2005). Estimates were based upon data from the four sample dates. Despite season-dependent species turnover, the observed bee species richness was 66% of the estimated species richness in conventional fields and 79% in organic fields. Results of analyses performed on species richness estimates did not differ from results based on raw data. In addition, we computed estimates based upon data from five subsamples of the fourth sample date to avoid effects of season-dependent species turnover. Sampling effort proved to be sufficient, with observed bee species richness being between 100% of the estimated species richness in conventional fields and 87% in organic fields.

We partitioned the total observed species richness (\( \gamma \) diversity) in organic and conventional fields into its diversity components at the landscape scale using the additive partitioning approach: \( \alpha \) diversity + \( \beta \) diversity = \( \gamma \) diversity or \( \beta \) diversity = \( \gamma \) diversity – \( \alpha \) diversity (\( \alpha \) diversity, mean species richness per organic or conventional field; \( \beta \) diversity, species turnover between organic or conventional fields) (Lande 1996).

Results

SPECIES RICHNESS OF BEES AND FLOWERING PLANTS

In total, 1507 bee individuals were recorded (167 solitary bees, 693 bumblebees and 647 honeybees). We identified 37 bee species from 12 genera. The most species-rich genera were Anthophora (15 species), Bombus (seven species), Nomada (four species) and Lastioglossum (three species). We found 1326 individuals of 31 bee species in organic fields and 181 individuals of 16 bee species in conventional fields (\( \gamma \) diversity at the landscape scale). The
mean abundance was $63.1 \pm 11.9$ (mean $\pm$ SE) in organic fields and $8.6 \pm 4.0$ in conventional fields. The $\alpha$ diversity at the landscape scale (mean bee species richness per field) was 2-1 species for conventional fields and 6-9 species for organic fields; the $\beta$ diversity at the landscape scale (between-field species turnover) was 13.9 species for conventional fields and 24.1 for organic fields. We observed only polylectic bee species using pollen resources from different plant families and no specialized bee species depending on certain plant families as pollen resources. We recorded 51 species of plants flowering during the study period.

**EFFECTS OF FARMING SYSTEM, LANDSCAPE CONTEXT AND REGION**

Bee diversity was related to factors at all three spatial scales (local, landscape and regional). The local-scale factor farming system (organic vs. conventional) had the highest impact on bee diversity (Table 3). Bee diversity was generally higher in organic than in conventional fields (Fig. 1a). A significant interaction between farming system and landscape context showed that differences in bee diversity between organic and conventional fields depended on landscape context (Table 3). The positive effect of organic farming was highest in homogeneous landscapes (Fig. 1b). Bee diversity was significantly higher in the region Leine Bergland than in Soester Boerde. Lahn-Dill-Bergland did not differ significantly in bee diversity from the other regions. Regional differences did not interact with the effects of farming system or landscape context.

Diversity of flowering plants and flower cover were higher in organic than in conventional fields (Table 3 and Fig. 1c, e). Differences in the diversity of flowering plants and flower cover between organic and conventional fields were largest in homogeneous landscapes (Fig. 1d, f). Flower cover increased significantly in homogeneous landscapes mainly because of three dominant species, *Matricaria chamomilla* L., *Tripleurospermum inodorum* (L.) Schultz Bip. and *Sinapis arvensis* L.

**RELATIVE IMPORTANCE OF PLANT-MEDIATED AND OTHER EFFECTS ON BEE DIVERSITY**

Diversity of flowering plants and flower cover were correlated in conventional but not organic fields (Spearman rank correlation; conventional fields, $R = 0.618$, $P = 0.006$; organic fields, $R = 0.166$, $P = 0.457$). In multiple regression analyses, we tested the importance of diversity and cover of flowering plants for bee diversity. Bee diversity in conventional fields mainly depended on the diversity of flowering plants ($\text{diversity of flowering plants}, F_{1,19} = 12.63, P = 0.002$; flower cover, $F_{1,19} = 3.94$, $P = 0.063$). Bee diversity in organic fields depended on flower cover only ($\text{diversity of flowering plants}, F_{1,19} = 0.27, P = 0.613$; flower cover, $F_{1,19} = 9.81$, $P = 0.006$). All significant relationships between bee diversity, diversity of flowering plants and flower cover from simple regressions are shown in Fig. 2.
Additionally, we tested for the relative importance of flower resource availability and other effects of farming practice and landscape context for bee diversity. In a linear mixed-effects model we included first diversity of flowering plants and flower cover and then farming system, landscape context and region. After removing the variance explained by the flower parameters (diversity of flowering plants, $F_{1,16} = 88·12, P < 0·001$; flower cover, $F_{1,16} = 12·10, P = 0·003$), the other factors contributed significantly or marginally significantly to the model (farming system, $F_{1,16} = 3·27, P = 0·090$; landscape context, $F_{1,16} = 4·74, P = 0·045$, region: $F_{2,16} = 7·21, P = 0·006$).

**Discussion**

The main objective of our study was to evaluate the effectiveness of a widespread agri-environment scheme in promoting diversity of bees as a functionally important insect group. In addition to a comparison of farming systems, our approach took the landscape and regional contexts of fields into account. Our results indicated that organic farming increases bee diversity by enhancing flower availability. In addition to the effect of farming system, both bee diversity and flower resources were influenced by the landscape context. Although regions differed in total bee diversity, effects of farming system and landscape context were consistent over the three regions.

**EFFECTS OF FARMING SYSTEMS ON PLANT AND BEE DIVERSITY**

The diversity of flower-visiting bees in wheat fields depended greatly on the farming system, with higher bee diversity in organic than conventional fields. An obvious reason for the differences between farming systems is the absence of agrochemical applications in organic fields. Herbicides reduce the cover and diversity of flowering weed species in conventional fields (Bengtsson, Ahnström & Weibull 2005; Roschewitz et al. 2005) and therewith the resource availability for flower-visiting insects. Flower cover and diversity of flowering plants were positively related to bee diversity in our study, and have also been shown to benefit other species groups (Hole et al. 2005).

Thus organic farming converted wheat fields into insecticide-free and richer foraging habitats. Other studies have suggested that arable fields might provide richer food resources than semi-natural habitats, thereby complementing habitat requirements of bees settling in non-arable habitats (Banaszak 1992). For example, bumblebee densities have been shown to be enhanced by a high proportion of mass-flowering crops in the landscape (Westphal, Steffan-Dewenter & Tscharntke 2003). The total number of bee species recorded in our wheat fields (37 bee species) was very similar to the bee species richness on old field margins in the same study regions (36 bee species; Steffan-Dewenter et al. 2002) as well as to the bee species richness in a grassland study on ecological compensation areas in Switzerland (49 bee species; Knop et al. 2006). The high relative contribution of the $\beta$ diversity to the total observed bee species richness ($\beta$ diversity represented 77·7% of the $\gamma$ diversity) indicates large between-field species turnover between organic fields. Thus organic wheat fields promoted over larger spatial scales may contribute to a considerably greater number of bee species in agricultural landscapes, provided that sufficient semi-natural areas for nesting are available (Steffan-Dewenter et al. 2002; Kremen et al. 2004).

Flower cover and diversity of flowering plants may both have contributed to the observed pattern of bee diversity. Bee diversity often benefits from a high diversity of flowering plants, whereas abundance is correlated with flower cover (Steffan-Dewenter & Tscharntke 2001). In our study, bee diversity depended on diversity of flowering plants in conventional fields but was related to flower cover in organic fields. The absence of a relationship...
between bee and plant diversity in organic fields may have been a consequence of the generally high diversity of flowering plants in organic fields. Provided that a threshold of plant diversity is exceeded, bee species adapted to crop-dominated environments may benefit from high flower cover. This is supported by the fact that all recorded bee species were classified as polylectic (Westrich 1989). We cannot rule out the fact that bee diversity in conventional fields was also influenced by flower cover because diversity and cover of flowering plants were correlated in conventional fields.

EFFECTS OF LANDSCAPE CONTEXT ON PLANT AND BEE DIVERSITY

Landscape context influenced bee diversity in organic and conventional fields to a different extent, resulting in larger differences between farming systems in homogeneous than heterogeneous landscapes. We found the same pattern for flower cover and diversity of flowering plants, suggesting that the effects of the landscape context on flowering plants were relayed to the pollinators. Similar results for relationships between landscape context and plant diversity were reported by Weibull, Östman & Granquist (2003) and Roschewitz et al. (2005), with negative effects of landscape homogeneity generally more pronounced in conventional than organic fields. Plant diversity in conventional fields probably suffers from a reduced area and smaller variety of permanent refuges for weed populations in homogeneous landscapes, whereas plant diversity in organic fields is self-sustaining to a certain extent (Roschewitz et al. 2005).

The flower cover in organically managed fields was higher in homogeneous landscapes, whereas the cover in conventionally fields remained constantly low. The high flower cover in organic fields in homogeneous landscapes resulted from three major weed species (Matricaria chamomilla, Tripleurospermum inodorum and Sinapis arvensis). These species mainly occur on cultivated land and rank among the most abundant and economically important weeds in German winter cereals (Hanf 1990). Matricaria chamomilla and T. inodorum have spread in the last decades because chemical and mechanical control of these weeds has proved to be difficult (Arlt, Hilbig & Illig 1991; Hinz & McClay 2000). Perennial or ruderal sites contribute little to their overall population size (Fogg 1950; Kay 1994). Thus seed rain of these weeds can be expected to be higher in homogeneous landscapes.

STRUCTURAL EFFECTS OF THE LANDSCAPE CONTEXT ON BEE DIVERSITY

In addition to the variance of bee diversity explained by the cover and diversity of flowering plants, landscape context contributed further to bee diversity. This structural effect of landscape context resulted in higher bee diversity in heterogeneous landscapes. Presumably, study fields in homogeneous landscapes were more isolated from semi-natural nesting habitats. Compared with other studies that found strong positive effects of a heterogeneous landscape on local arthropod diversity (Weibull, Bengtsson & Nohlgren 2000; Steffan-Dewenter et al. 2002; Clough et al. 2005), the effects in this study were only marginal. This might be because of a lack of landscapes with extremely high or low proportions of semi-natural habitats and the absence of more specialized bee species that depend on certain nesting sites and foraging plants (Banaszak 1992; Westrich 1996).

REGIONAL DIFFERENCES

Bee diversity was significantly influenced by regional differences. The study regions differed in a variety of aspects, for example the regional species pool, large-scale patterns of land use and climatic and soil conditions. Our study design did not enable us to identify the factors causing regional differences in bee diversity. The motivation for addressing bee diversity in more than one region was to identify possible interactions between region and the other factors under investigation. The positive effect of organic farming and its modifications by the landscape context were robust across different regions, suggesting that our results provide a reliable basis for management decisions. Regions were situated in different federal states of Germany. Our results are remarkable because the governments of the German federal states play a significant role in the selection and development of their own agri-environment schemes. Directives of the EU are interpreted by the federal states, and programmes and subsidies depend on regions. Thus the effectiveness of agri-environment schemes may not be evaluated at a national scale but a regional perspective is needed (Wilson 1994).

CONCLUSIONS

Farming system, landscape context and regional context were involved in determining bee diversity. Organic wheat fields proved to be valuable foraging habitats, providing diverse and abundant flower resources for a variety of bee species. The effectiveness of organic farming was greatest in homogeneous landscapes. This interaction between farming system and landscape context clearly shows that evaluations of agri-environment schemes have to incorporate a landscape perspective. Agri-environment schemes should aim to sustain heterogeneous landscapes because of their structural (i.e. not mediated by plants) positive effects on bee diversity. In homogeneous landscapes, organic farming greatly compensates for the negative effects of landscape simplification. Thus incentives for conversion to organic farming or the retention of non-intensive farming practices should be most cost-effective in such intensively managed landscapes. The benefits arising from organic farming may even be enhanced if agri-environment schemes explicitly promoted flowering plants by restricting mechanical weeding. From a conservation
perspective, organic farming may not benefit the specialized and threatened bee species occurring mainly in semi-natural habitats but it does help to sustain the diversity of bees in agro-ecosystems.

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