



Agricultural landscapes with organic crops support higher pollinator diversity

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Pollinators are traditionally thought to perceive non-flowering crop fields as hostile landscape matrix. In this study, we show that landscapes composed of higher proportions of organic crop fields support more bee species at greater abundances in fallow strips. An increase in organic cropping in the surrounding landscape from 5% to 20% enhanced bee species richness in fallow strips by 50%, density of solitary bees by 60% and bumble bee density by 150%. Bee species richness and bumble bee density responded strongest to organic cropping in landscape sectors with 500 m radius, solitary bee density in landscape sectors with 250 m radius. The most likely source of these results is that crop and noncrop habitats are strongly connected via bee foraging at the landscape scale. It seems likely that bees depending on nesting sites in fallow strips benefited from the more abundant flower resources provided by broadleaved weeds in organic crop fields. We conclude that the incorporation of organic crop fields into conventionally managed agricultural landscapes can provide food resources needed to sustain greater pollinator species richness in noncrop habitats.

Processes occurring at the landscape scale have substantial influence on local diversity and dynamics (Kareiva and Wennergren 1995, Polis et al. 1997). Our ability to interpret and manipulate landscape patterns is critical for understanding species diversity (Bestelmeyer et al. 2003) and for applied issues such as the conservation of ecosystem services (Steffan-Dewenter et al. 2001, Kremen 2005, Tschardt et al. 2005a, Bianchi et al. 2006, Albrecht et al. 2007, Kremen et al. 2007). Dynamics at the landscape scale are coupled by metapopulations (Hanski 1999, Vandermeer and Carvajal 2001), by multi-habitat users, which move among habitats during their lifetime to meet their foraging, nesting or hibernating requirements (Duelli et al. 1990, Banaszak 1992, Westrich 1996), or by spillover of organisms from productive into less productive habitats (Pulliam 1988, Polis et al. 1997). The recognition of processes occurring at the landscape scale has resulted in increasing empirical research. High proportions of natural, seminatural, or noncrop habitats in agricultural landscapes have been shown to enhance diversity, offspring production and ecosystem services in noncrop habitats (Steffan-Dewenter et al. 2002) and in crop systems at the landscape scale (Kremen et al. 2004, Clough et al. 2005, Schmidt and Tschardt 2005, Williams and Kremen 2007). The inverse effect – crop systems enhance organisms in noncrop habitats – is nearly undocumented, and first evidence has been found for individual densities only (Tschardt et al. 2005b). Bumblebee densities in nesting habitats were enhanced by mass-flowering crops in the surrounding landscape, which provide huge densities of pollen and

nectar resources over short time periods (Westphal et al. 2003). Indirect evidence suggests that increasing predator and herbivore densities in productive crop fields might result in spillover effects which enhance population densities in adjacent seminatural habitats (Rand et al. 2006). Positive effects of crop systems on diversity in noncrop habitats at the landscape scale have never been documented, and the contribution of crop systems to conservation efforts in noncrop habitats is poorly known.

Crop production has been intensified in Western Europe during the recent decades by converting noncrop habitats into crop fields, and by increasing usage of agrochemicals (Krebs et al. 1999, Benton et al. 2003). Thus, conventionally managed crop systems are generally considered to contribute to the widespread decline in biodiversity in agricultural landscapes (Krebs et al. 1999, Firkbank 2005). To mitigate the negative consequences of agricultural intensification on diversity and ecosystem services, organic farming and other agri-environment schemes are applied worldwide and with rapidly growing importance because of the increasing interest of consumers, farmers and politicians in more sustainable farming (Kleijn et al. 2005). Organic fields are managed without herbicides, insecticides and synthetic fertilizers. Fertilization is achieved by organic farm manure and natural nitrogen fixation, and weeds are controlled by mechanical weeding and crop rotation. Numerous studies confirm higher species diversity of many species groups in organic compared with conventional fields (reviewed by Bengtsson et al. 2005, Holzschuh et al. 2007). However, recent studies suggest that positive effects of organic farming on

biodiversity are low compared to positive effects of landscape factors such as landscape diversity and the proportion of (semi-)natural or other noncrop areas (Weibull et al. 2000, 2003, Kremen et al. 2002, Clough et al. 2005). Cross-habitat fluxes may connect organic fields and noncrop habitats, which are little disturbed compared with arable crop systems. Noncrop habitats provide alternative foraging resources, nesting and hibernation sites, and diversity in organic fields may greatly benefit from heterogeneous landscapes with a high availability and diversity of alternative habitats. However, organic fields may themselves contribute to more heterogeneous landscapes, because local environment conditions are changed compared to conventional crop systems, resulting in a higher diversity and cover of noncrop vegetation (Bengtsson et al. 2005, Gabriel et al. 2006, Clough et al. 2007, Holzschuh et al. 2007). Thus, a high proportion of organic fields at the landscape scale may enhance biodiversity in other habitats at the landscape scale, but information about the impact of the landscape-scale distribution of organic fields on their effectiveness in promoting biodiversity at larger scales is completely missing.

The expansion of organic farming is stated as an explicit objective in the “European Action Plan for Organic Food and Farming” and the “Biodiversity Action Plan for Agriculture (European Communities 2006). Most EU member states have already set targets for the proportion of area under organic farming, often 10–20% in 2010 (from 3.7% on the average in 2002) (European Environment Agency 2005). However, the area covered by organic farming is considered only an indirect indicator of biodiversity conservation. Even if organic farming results in changed environmental conditions and higher biodiversity in organic crop systems (Bengtsson et al. 2005, Hole et al. 2005), the relationship between area under organic farming and biodiversity conservation is unknown. Such knowledge is of great political relevance, because otherwise basic ecological information about landscape-wide consequences of one of the fastest-growing agri-environmental scheme is missing (112% growth between 1998 and 2002, European Environment Agency 2005).

In this study, we examined whether organic cropping fulfils expectations on agri-environment schemes to enhance bees at the landscape scale, or whether positive effects are detectable at the local scale only. We focused on bee species richness and abundance in permanent fallow strips situated adjacent to organic or to conventional wheat fields. Bees, which are considered the most important pollinators in European agroecosystems, rely on nesting habitats in little disturbed perennial habitats to fulfil their reproduction cycle. Thus, fallow strips and seminatural habitats are generally assumed to be valuable habitats of bees in agricultural landscapes (Lagerlöf et al. 1992, Bäckmann and Tiainen 2002, Steffan-Dewenter et al. 2002, Pywell et al. 2005, 2006, Öckinger and Smith 2007). In addition, bees depend on nectar and pollen resources, which are often provided in spatially separated foraging habitats, resulting in cross-habitat fluxes between crop and noncrop habitats at the landscape scale (Steffan-Dewenter et al. 2002, Westphal et al. 2003, Kremen et al. 2004).

We tested determinants of bee species richness and abundance at the local scale (organic vs conventional management of the adjacent wheat field) and at four

landscape scales (proportion of organic crop fields and proportion of seminatural habitats in landscape sectors of 250–1000 m radius). Further, we tested the effect of the politically relevant factor “organic crop area per total crop area” on species richness and abundance of pollinators, and predicted landscape-wide consequences of an increase in percentage area under organic farming from in Germany current 5% to 20%, which was politically targeted in Germany to achieve by 2010 (European Environment Agency 2005). We expected that pollinator groups respond to landscape factors to different degrees and at different spatial scales depending on their habitat requirements and foraging ranges (Gathmann and Tschardt 2002, Steffan-Dewenter et al. 2002).

Methods

Study regions and study sites

In 2003, bees were monitored in 42 permanent field fallow strips in three regions in Germany (Soester Börde/North Rhine-Westphalia, Leine Bergland/Lower-Saxony and Lahn-Dill-Bergland/Hesse, 14 fallow strips per region). The regions were situated about 150 km from each other, and were between 400 and 500 km² in size. Twenty-one fallow strips were adjacent to organic winter wheat fields and 21 were adjacent to conventional winter wheat fields. Organic fields were managed according to the European Union regulation 2092/91/EEC. This regulation limits the amount of fertilizers and prohibits the use of synthetic fertilizers and pesticides. Each fallow strip adjacent to an organic field was paired with the nearest fallow strip adjacent to a conventional winter wheat field. These pairs allowed a comparison of fallow strips adjacent to fields differing in the farming system (organic vs conventional), but similar in abiotic conditions and landscape context. Distances between fallow strips within a pair ranged from 0 m to 600 m and between pairs within a region from 3 km to 45 km. All fallow strips were established between the wheat field and a farm track, had a naturally developed herb and grass layer, and mostly included a narrow ditch. The occurrence of a ditch and the management of fallow strips (mowing once a year) did not differ between the two farming types. Mean fallow strip width was 2.6 ± 1.4 m (SE) and did not differ in fallow strips adjacent to conventional or organic fields (t-test for paired samples: $t = 1.34$, $p = 0.196$).

Quantifying landscape context

For each fallow strip, the surrounding landscape was characterized in a circular landscape sector (radius 1000 m). Field inspections were made to record the areas of different habitat types in these landscape sectors on the basis of official topographical maps (DGK 1:5000). Crop fields were identified as organically managed by interviewing the organic farmers. To study scale-dependent effects of landscape factors each of the 42 circular landscape sectors was subdivided into four nested sectors (radii: 250 m, 500 m, 750 m, 1000 m). We calculated the proportion of organic crop fields (in the following referred to as “organic land

cover”) and the proportion of seminatural habitats (“seminatural land cover”) in each landscape sector individually for the four spatial scales using Geographic Information Systems (GIS; Topol 4.506 and ARC/View 3.2). We classified fallows and ruderal areas, allotment gardens, vegetation along inshore waters, non-intensively used calcareous grasslands, orchard meadows, hedgerows and forest edges (10 m deep boundary) as seminatural habitats.

The organic land cover did not differ between regions at any spatial scale, nor did the seminatural land cover at scales up to 500 m, which was the most relevant scale in our study (linear mixed-effects models, $p > 0.1$). The organic land cover was highly correlated at all spatial scales with the factor “organic crop area per total crop area” (Spearman rank correlations: all $R > 0.852$, $p < 0.001$, min: 0.6%, max: 46.1%, mean \pm SE: $16.1 \pm 12.0\%$). There were no correlations of organic land cover with seminatural land cover (Table 1) or other landscape parameters or elevation at any spatial scale, indicating that the uptake of organic management of fields by farmers did not depend on landscape context at these scales (Spearman rank correlations: all $p > 0.10$, $n = 21$).

The studied landscapes were made up of a patchwork of crop fields, intensively used grasslands, forests and seminatural habitats. All landscapes were farmland dominated, so the gradient of seminatural habitats was rather small (min: 0.6%, max: 15.5%, mean \pm SE: $7.1 \pm 4.1\%$, 500 m radius). Organic and conventional fields of different farmers were interspersed. The organic land cover ranged from 0.4% to 33.8% (mean \pm SE: $10.7 \pm 8.4\%$, 500 m radius), the conventional land cover from 24.4% to 76.0% (mean \pm SE: $53.3 \pm 3.4\%$, 500 m radius). Cereals were the dominant crop cultivated in both organic and conventional fields ($73.5 \pm 4.3\%$ of the organic crop field area and $70.3 \pm 2.6\%$ of the conventional crop field area, mean \pm SE, 500 m radius). Other crops were corn, oil seed rape, sugar beets, field beans, potatoes, carrots and lettuce. The proportion of flowering crops (oil seed rape, field beans and potatoes) did not differ between organic and conventional crop fields (organic: $22.4 \pm 4.8\%$, conventional: $18.6 \pm 3.0\%$, mean \pm SE, linear mixed-effects models, $p > 0.1$).

Surveys of bees and flowering plants

In four surveys between May and July 2003, all bees (Apiformes) sighted along 100-m transects in the fallow strips were collected. Transects spanned the full width of the fallow strips. Each survey was conducted for 15 min. We surveyed fallow strips of an organic-conventional-pair directly one after the other, between 10:00 and 18:00, when

Table 1. Spearman rank correlations between organic land cover and seminatural land cover at four spatial scales for landscape sectors around conventional and organic fallow strips ($n = 21$).

	Conventional		Organic	
	R	p	R	p
250 m radius	0.262	0.241	0.170	0.447
500 m radius	0.091	0.648	0.121	0.589
750 m radius	0.245	0.272	0.005	0.982
1000 m radius	0.314	0.160	0.240	0.283

wind speeds were below 3 Beaufort, temperature was at least 18°C and cloud cover was less than 30%. Solitary bees as well as bumble bee species that could not be identified to species level in the field were brought to the laboratory for identification. The species richness of bees is the total number of bee species caught within the study period. Bee abundances were calculated as numbers of individuals caught within 4×15 min per 100 m^2 fallow strip (total number of individuals/fallow strip width). Solitary bees, bumble bees and honey bees were expected to respond differently to the landscape context, because they differ in their habitat requirements and foraging distances (Steffan-Dewenter et al. 2002). Therefore, bee abundances were calculated separately for these three pollinator groups.

All plant species flowering during the survey and flower cover were recorded during each sampling period in the bee transect in the fallow strip and in two transects in the centre and the edge of the adjacent wheat field. Field transects were 100 m long and 1 m wide. The edge transects were located 1 m into the cereal field along the field edge. Flower cover was estimated by sight as the percentage cover of actual flower corollas per area ground surface. Flower cover values were averaged over both field transects and over the four surveys. Flower cover was correlated with species richness of flowering plants in both fields and fallow strips (Spearman rank correlation $R > 0.51$, $p < 0.02$). Flower cover in fields was correlated with flower cover in fallow strips, as well as species richness of flower plants in fields with species richness of lowering plants in fallow strips (Spearman rank correlation $R > 0.38$, $p < 0.02$).

Statistics

For analysing landscape scale effects, we followed a two part procedure: In the first set of analyses, we identified the relevant landscape scale through single-factor linear mixed-effect models (Pinheiro and Bates 2000). We separately tested the effects of the landscape parameters organic land cover and seminatural land cover for the four landscape scales. Response variables were species richness of bees and abundances of bumble bees, solitary bees and honey bees in fallow strips. Fallow strips adjacent to neighbouring organic-conventional field pairs were nested within landscapes by using a random factor. Landscape parameters were tested at the level of pairs, because landscape sectors of fallow strips within a field pair were not independent. The four spatial scales per landscape sector were analysed separately. For all models, the F-values of the tested landscape parameters were plotted to demonstrate the influence of the spatial scale on the correlation between landscape parameters and species richness and abundances of bees, respectively (Steffan-Dewenter et al. 2002, Kremen et al. 2004).

In the second set of analyses, we used the most relevant landscape scale (i.e. that with the highest F-value) defined in the first set of analyses for each response variable. We developed multi-factor linear mixed-effect models to examine the relative importance of the local factor farming system of the adjacent field (organic vs conventional) and the landscape factors seminatural land cover and organic land cover. Wald-type F-tests (type I) were used for the factor selection. Effects of region and fallow strip width

were tested in the full model, but had no additional explanatory power and thus were excluded. Independent variables that did not contribute to the model with $p < 0.05$ were removed in a backward stepwise procedure from the full model. Models with bee species richness and abundances as response variables, landscape as random factor and the political relevant variable “organic crop area per total crop area” as fixed factor were calculated. Finally, we tested which flower variable (flower cover field/fallow strip, species richness of flowering plants in fields/fallow strips) was most important in determining bee species richness and abundances in fallow strips and is the best replacement of the categorical fixed factor “farming system” (flower variable with the highest p -value). We transformed the number of bee species ($\log_{10}(x+1)$) and the percentage values of flower cover (arcsine-square-root-transformation). All statistical analyses were performed using R (R Development Core Team 2004).

We checked for a possible bias of sample size by computing first-order jackknife estimators (Jack1), which are independent from the number of sampled individuals (EstimateS, Colwell 2005). Estimates were based upon data from the four sample dates. Despite season-dependent species turnover, observed bee species richness was 68% of the estimated species richness in conventional fallow strips, and 72% in organic fallow strips. Results of analyses performed on species richness estimates did not differ from results based on original data.

Results

In total, 1612 bee individuals were caught (302 solitary bees, 932 bumble bees, 378 honey bees). We identified 40 bee species from thirteen genera. The most species-rich genera were *Andrena* (17 species), *Bombus* (7 species), *Nomada* (4 species) and *Lasioglossum* (3 species). We found 16 species exclusively in fallow strips adjacent to organic fields, and three species exclusively in fallow strips adjacent to conventional fields.

First, we tested in single-factor models at what landscape scales correlations between landscape parameters and bee response variables were strongest. The plotted F-values revealed that the effect of organic land cover on bee species richness and abundances of bumble bees and honey bees was strongest in landscape sectors with 500 m radius (Fig. 1a, 1c, 1d; bee species richness: $F_{1,21} = 10.85$, $p = 0.004$; bumble bee abundance: $F_{1,21} = 13.61$, $p = 0.001$; honey bee abundance: $F_{1,21} = 4.67$, $p = 0.043$). The abundance of solitary bees responded most strongly to organic land cover in landscape sectors with 250 m radius (Fig. 1b; $F_{1,21} = 17.82$, $p < 0.001$). The seminatural land cover had a significant effect on solitary bees, and in landscape sectors with 250 m radius only (Fig. 1b; $F_{1,21} = 11.88$, $p = 0.002$).

In the second step, we examined in multi-factor analyses the relative importance of the local factor farming system and the landscape parameters in landscape sectors with 500 m radius for bee species richness and abundances of

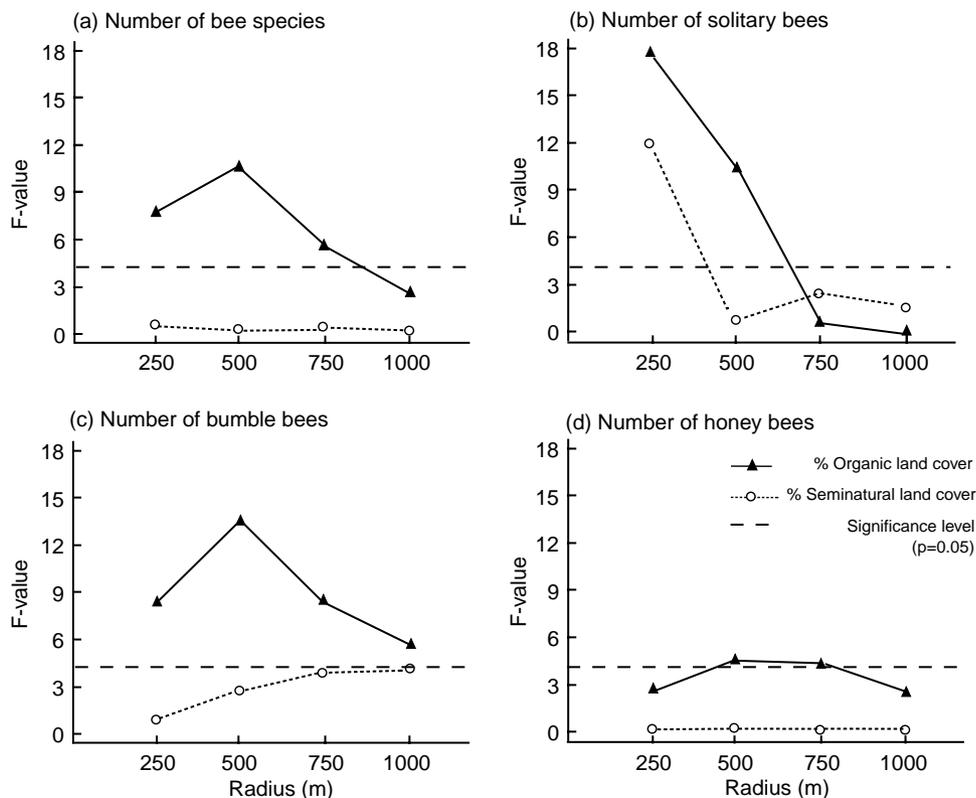


Fig. 1. Effects of organic and seminatural land cover on bee species richness and the abundance of solitary bees, bumble bees and honey bees in fallow strips. F-values are from single-factor linear mixed-effects models with the organic land cover and the seminatural land cover separately for the four landscape sectors of 250–1000 m radius. The dashed line shows the critical $F_{1,21}$ -value for the significance level $p = 0.05$.

bumble bees and honey bees, and with 250 m scale for the abundance of solitary bees. Organic farming in the adjacent fields enhanced species richness of bees in fallow strips by 60% (from average 3.95 to 6.33 species, Fig. 2), the abundance of bumble bees by 130% (from average 3.7 to 8.5 individuals per 100 m²) and the abundance of solitary bees by 136% (from average 1.1 to 2.6 individuals per 100 m²). Abundances of honey bees were not significantly higher in fallow strips adjacent to organic than in fallow strips adjacent to conventional fields (Table 2). As in the single-factor models, a high organic land cover enhanced the species richness of bees and the abundances of solitary bees, bumble bees and honey bees (Table 2). Seminatural habitats enhanced the abundance of solitary bees only (Table 2). The positive impact of a high organic land cover influenced species richness of bees in both organic and conventional fallow strips similarly (Fig. 2).

Because of the high correlation between organic land cover and the factor “organic crop area per total crop area”, organic land cover can be replaced in all models by “organic crop area per total crop area” without changing results of the analysis. According to our models, an increase in the organic crop area per total crop area from the current 5% to 20% may enhance species richness of bees in fallow strips by 50% (Fig. 3), density of solitary bees by 60% and bumble bee density by 150% (x = organic crop area per total crop area; y = species richness: $\log_{10}(y + 1) = 0.010x + 0.562$, $F_{1,21} = 7.61$, $p = 0.012$; y = bumble bee abundance: $\log_{10}(y + 1) = 0.019x + 0.340$, $F_{1,21} = 14.63$, $p = 0.001$; y = solitary bee abundance: $\log_{10}(y + 1) = 0.006x + 0.193$, $F_{1,21} = 19.84$, $p < 0.001$).

Flower cover and species richness of flowering plants were significantly higher in organic than in conventional fields, and in fallow strips adjacent to organic than adjacent to conventional fields (Table 3). The fixed factor “farming system” was best replaced by the factor “species richness of flowering plants in the fallow strip” in the bee species richness model ($p < 0.001$), and the bumble bee abundance model ($p < 0.001$), and by the factor “flower cover field” in the solitary bee abundance model ($p = 0.008$). As all flower variables were correlated to each other, bee species richness

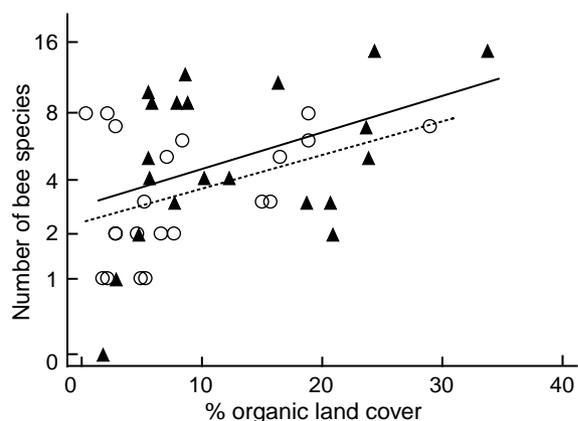


Fig. 2. Effect of the organic land cover in landscape sectors with 500 m radius on the species richness of bees in 42 fallow strips adjacent to organic wheat fields (triangles and solid line in) and conventional wheat fields (circles and dashed line). Results are from multi-factor mixed-effects models (Table 2).

Table 2. Final multi-factor linear mixed-effects models describing the effects of the farming system practiced in the adjacent wheat field (organic vs conventional) and of seminatural and organic land cover in the landscape sectors (scales selected by the comparison of F-values from one-factor linear mixed-effects models with one landscape factor at a time, see Fig. 1).

	DF	F	p
Bee species richness			
farming system	20	6.48	0.019
% organic land cover (500 m)	20	6.48	0.019
Abundance of solitary bees			
farming system	19	12.18	0.002
% seminatural land cover (250 m)	19	7.37	0.014
% organic land cover (250 m)	19	4.89	0.040
Abundance of bumble bees			
farming system	20	7.87	0.011
% organic land cover (500 m)	20	8.72	0.008
Abundance of honey bees			
% organic land cover (500 m)	21	4.67	0.042

and abundance generally increased with increasing flower cover and species richness of flowering plants in fields and fallow strips.

Discussion

In this study, we compared bee species richness and abundances in perennial fallow strips adjacent to organic and conventional crop fields, and in landscapes differing in their organic and seminatural land cover. Our results provide the first evidence that annual crop fields – although unsuitable for the completion of reproductive cycles – have positive effects on the richness of a species group in its perennial reproductive habitat. Benefits provided by organic farming were strong enough to enhance bee species richness and abundances in fallow strips not only at the local but also at the landscape scale.

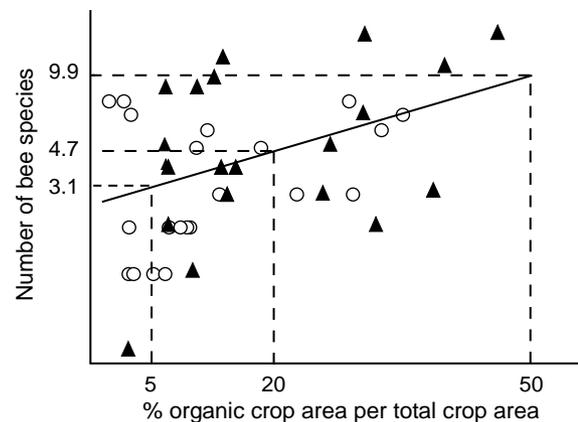


Fig. 3. Prediction of the increase of bee species richness with increasing organic crop area per total crop area in landscape sectors with 500 m radius, according to our data from 42 fallow strips adjacent to organic wheat fields (triangles) and conventional wheat fields (circles). Results are from multi-factor mixed-effects models (see Result section).

Table 3. Effects of farming system (organic vs conventional) on flower cover and species richness of flowering plants in fields and adjacent fallow strips. Results are from paired t-tests (n = 21).

	t	p	mean _{conv} ± SE	mean _{org} ± SE
Field				
flower cover (%)	2.82	0.011	0.09 ± 0.06	2.9 ± 1.1
species richness of flowering plants	9.39	<0.001	5.4 ± 0.8	12.6 ± 0.8
Fallow strip				
flower cover (%)	2.82	0.011	1.2 ± 0.4	3.3 ± 0.7
species richness of flowering plants	2.29	0.033	12.4 ± 1.7	16.9 ± 1.4

Local scale

Species richness of bees, abundances of solitary and bumble bees, species richness of flowering plants, and flower cover were higher in fallow strips adjacent to organic fields than in fallow strips adjacent to conventional fields. As organic and conventional fallow strips did not differ in their management (mowing once a year), differences in vegetation and bee fauna between organic and conventional fallow strips were apparently caused by differing management of the adjacent fields: in contrast to conventional fields, the organic fields were not sprayed with insecticides, herbicides and synthetic fertilizer. The negative effect of insecticides did not significantly contribute to the observed bee patterns. Conventional farmers applied insecticides in only nine of 21 wheat fields, and bee species richness or density did not differ in fallow strips adjacent to conventional fields with and without insecticide applications (unpubl.). Differences between organic and conventional fallow strips may be mainly based upon the absence of fertiliser and herbicide drift from the adjacent field resulting in a more diverse and flower-rich vegetation in organic than conventional fallow strips (mean species richness of flowering plants: 36% higher, mean flower cover: 175% higher) (also known from de Snoo and van der Poll 1999, Marshall and Moonen 2002, Aude et al. 2004), and subsequently in higher bee species richness and abundance.

A further explanation for differences in bee species richness and abundances is that flower resources in organic fields may have attracted bees, with subsequent positive effects on bees in the adjacent organic fallow strips providing nesting sites and additional food resources. Species richness of flowering plants in organic fields was more than twice as high, flower cover 32 times as high as in conventional fields. Corroborative positive effects on the density and species richness of noncrop vegetation in the absence of agrochemicals have been often shown (Bengtsson et al. 2005, Hole et al. 2005, Roschewitz et al. 2005, Gabriel et al. 2006, Clough et al. 2007, Holzschuh et al. 2007). Furthermore, organic wheat fields disproportionately enhance insect pollinated weed species, whereas non-insect pollinated weeds dominate in conventional wheat fields (Gabriel and Tscharrntke 2007), and bees may respond accordingly to the flower resources in organic fields.

As high weed densities reduce crop yields, organic farmers aim to control weeds by non-chemical methods such as mechanical weeding and suitable crop rotations. However, average yields are lower in organic than in conventional fields. To compensate for that, organic farmers get incentives within the framework of agri-environmental schemes, which encourage farmers to convert to less

intensive, diversity enhancing farming methods. In addition, an increasing number of consumers is willing to pay for nature friendly and chemical free produced products, even if prizes are higher to compensate for lower yields.

Landscape scale

A high organic land cover enhanced bee species richness and the abundances of solitary, bumble and honey bees in fallow strips. According to our data, an increase of organic crop area per total crop area from current 5% to 20%, which was set as a political target in Germany for 2010 (European Environment Agency 2005), enhanced species richness of bees in fallow strips by 50%, density of solitary bees by 60% and bumble bee density by 150%. Up to now, positive effects of organic farming on species richness have been considered in organic fields themselves, and in relation to conventional farming practices only (reviewed by Bengtsson et al. 2005, Hole et al. 2005). Crop-noncrop resource fluxes and effects of organic farming on habitats other than organic fields have remained unexplored.

Bees often depend on several spatially separated foraging habitats in addition to their nesting habitat, because nesting habitats do not always provide sufficient nectar and pollen for larvae provisioning (Westrich 1996, Kremen et al. 2007). Three mechanisms could have contributed to the positive landscape effects of organic farming on bees: Landscapes with higher organic land cover may benefit bees, (1) because total insecticide application may be lower, resulting in lower bee mortality; (2) because flower cover and species richness of flowering plants were higher in organic than in conventional fallow strips; (3) because flower cover and species richness of flowering plants were higher in organic than in conventional crop fields.

We do not suspect negative landscape scale effects of insecticides, because insecticides did not affect bees at the local scale (above). The total area covered by organic fields was more than thirty times as high as the area covered by organic fallow strips (calculated from 42 organic fields and adjacent fallow strips). Thus, organic fields contributed much more to a high availability of flower resources at the landscape scale than organic fallow strips, despite the slightly higher flower availability in organic fallow strips than in organic fields (14% higher flower cover, 34% higher species richness of flowering plants in organic fallow strips than in organic fields). We therefore suppose that benefits on bee species richness and density in noncrop nesting habitats at a landscape scale resulted from flower resources provided by noncrop vegetation in organic crop fields.

Resource fluxes from one habitat into another habitat arise when resources in a productive habitat enhance species

richness or abundance in other habitats (Polis et al. 1997), but are almost undocumented from human-dominated landscapes (Rand et al. 2006). Traditionally, unproductive fallow strips and seminatural habitats are considered to be sources of species richness in agricultural landscapes, because they provide refuges after disturbances, hibernation sites, and nesting sites (Banaszak 1992, Westrich 1996). Fields that are cultivated with non-flowering crops such as cereals cover the largest part of arable land (Statistisches Bundesamt 2006). They have been considered to form the landscape matrix, which is without value for pollinators and may even isolate habitats from each other, because nectar and pollen providing weeds are widely suppressed by agrochemicals (Westrich 1996). Our study indicates that the species richness and abundance of bees in fallow strips were apparently limited by foraging resources, and that fluxes from productive crop fields to unproductive noncrop habitats have the potential to reduce this limitation when fields are managed organically. However, we only found polylectic bees in the study fallow strips. Bees that are more specialized did obviously not benefit from fallow strips or organic fields, presumably because they were restricted to other remnant seminatural habitats such as calcareous grasslands. Thus, small strips of uncultivated land and low-intensity farming were not able to completely compensate for missing seminatural habitats, and measures other than fallow strips and organic farming are required for the conservation of specialist bees in agricultural landscapes. Positive effects of organic crop fields may be strongest in landscapes where noncrop habitats are rare, and converting crop land into noncrop area is difficult to implement.

The abundance of solitary bees, but not of bumble or honey bees, was additionally enhanced by high seminatural land cover. This suggests that solitary bees were more restricted by habitats providing nesting site than bumble and honey bees (Banaszak 1992, Westrich 1996, Steffan-Dewenter et al. 2002). A high seminatural land cover may offer a higher variety and availability of nesting that favour higher abundances of solitary bees. Due to their relatively low nesting requirements, bumble bees rather benefit from a high amount of flower resources than of nesting habitat, provided that a minimum of uncultivated land is available (Westphal et al. 2003). Honey bees may depend on other factors than seminatural cover such as the location of apiaries (Steffan-Dewenter and Tscharrntke 2000). Further, solitary bees obviously perceived the landscape at smaller spatial scales probably due to their smaller foraging distances (Gathmann and Tscharrntke 2002). Thus, foraging and nesting habitats of solitary bees have to be in closer proximity than habitats of bumble and honey bees.

Conclusions

Our results show that benefits of organic farming do not arise from a concentration effect which attracts bees from the surrounding landscape to food resources in organic fields without consequences for species richness and density at larger scales. As organic crop fields in the landscape benefited bee species richness even in conventional fallow strips, noncrop habitats were apparently connected with organic crop fields at the landscape scale. This may have

important consequences for understanding diversity patterns, as well as for the design and evaluation of conservation measures. Our study revealed that evaluations of organic farming and other agri-environment schemes have to incorporate also landscape scale effects on others than the target habitats to record the total benefits of the agri-environment schemes on diversity. A landscape perspective provides an insight into the spatial scales at which agri-environment schemes are likely to work most effectively in enhancing biodiversity. Therefore, financial support of farmers should be linked to the spatial arrangement of organic fields at the relevant landscape scale. As bees perceive their environment at landscape scales, it is apparently unnecessary to provide all requirements in close proximity. Pollination services can be expected to be enhanced within landscape sectors (Kremen et al. 2004). As solitary bees respond to landscape factors within a 250 m radius, populations at a distance of > 500 m from each other should be considered non-overlapping service-providing units (sensu Luck et al. 2003). The absence of the requirements of such a service-providing unit may result in the loss of pollination services within this landscape sector and negatively affect wild plant species as well as insect-pollinated crops (Luck et al. 2003, Klein et al. 2007). In conclusion, we have shown an important crop-noncrop relationship that need to be taken into account when designing management plans for the conservation of diversity and pollination in human dominated landscapes.

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