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Interacting effects of farming practice and landscape context on bumble bees

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ABSTRACT

Organic farming has been suggested to counteract declines in farmland biodiversity, but comparisons to conventional farming have produced variable outcomes. To examine whether this is due to the landscape context farms are situated in and traits of the studied organisms, we surveyed bumble bees in cereal field borders and margins at 12 pairs of matched organic and conventional farms, with half the pairs located in heterogeneous farmland and the remaining in homogeneous plains. Species richness and abundance of bumble bees were significantly positively related to both organic farming and landscape heterogeneity. However, there was an interaction effect between farming practice and landscape context so that species richness and abundance were only significantly higher on organic farms in homogeneous landscapes. The higher abundance of bumble bees on organic farms was partly related to higher flower abundance on these sites. The effect of landscape context on bumble bee abundance was stronger for species with medium sized colonies than for those with smaller and larger colony sizes. These patterns may reflect that species with medium sized foraging ranges are most affected by fragmentation of foraging habitat, because colony size reflects the spatial scale at which bumble bees utilize resources. We conclude that both organic farming and landscape heterogeneity can be used to increase bumble bee species richness and abundance, but that organic farming has a larger effect in homogeneous landscapes and landscape heterogeneity a larger effect on conventional farms. The effects differed between species, suggesting that a single prescription to increase pollinator abundance may not be valid.

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1. Introduction

During the past 50 years, farming practices in most industrial countries have undergone major modernizations. Old farming traditions, such as the cultivation of many different locally adapted crops and diversified crop rotations, have been abandoned by most farmers resulting in highly specialized farms relying on intensive use of external inputs (Björklund et al., 1999; Krebs et al., 1999; Shrubbs, 2003). The changed agricultural practices have resulted in higher harvest yields, but

also in a decline of farmland biodiversity (Krebs et al., 1999; Tilman et al., 2001; Donald et al., 2001; Kremen et al., 2002). Two important reasons for the loss of biodiversity in agricultural landscapes are thought to be the removal and fragmentation of semi-natural habitats (Kremen et al., 2002; Ricketts, 2004; Tschardt et al., 2005; Greenleaf and Kremen, 2006) and intensification of farming practices, e.g. increased use of pesticides and fertilizers (agrochemicals) which directly and indirectly affect organisms both in the fields and in near-by habitats (Kevan, 1975; Chamberlain et al., 2000; Kremen

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et al., 2002; Roy et al., 2003; Carvell et al., 2006). These two factors may influence habitat suitability for organisms at both the farm scale and the landscape scale.

In Europe, both the European Union (EU) and individual countries have adopted new agricultural policies aimed at reducing or reversing the negative environmental effects caused by modern agricultural practices (Kleijn and Sutherland, 2003). One course of action is the financial support of organic farming by governmental subsidies (Kleijn and Sutherland, 2003; Sjö Dahl and Söderberg, 2004). Organic farming practices, which include the prohibition of most agrochemicals (EEC regulation 2092/91) and rely on a varied crop rotation (Stockdale et al., 2001), are believed to enhance farmland biodiversity (Hole et al., 2005; Bengtsson et al., 2005). However, so far the effect of organic farming is poorly investigated and the outcomes of the studies that have been made are varied (Bengtsson et al., 2005). Furthermore, many studies lack proper replication and do not control for bias in the spatial variation in use of subsidies (Kleijn and Sutherland, 2003). The cost to farmers of converting to organic farming practices may differ depending on factors such as climate, soil characteristics and crop types. For example, in Sweden organic farming is geographically unevenly distributed with a larger fraction of the arable land under organic farming in mixed agricultural landscapes compared to the more intensively farmed areas such as plains (Sjö Dahl and Söderberg, 2004; Rundlöf and Smith, 2006). These landscape types differ in habitat heterogeneity (Rundlöf and Smith, 2006) and it has been shown that habitat heterogeneity is a key factor in maintaining biodiversity (Weibull et al., 2000; Steffan-Dewenter, 2002; Benton et al., 2003). It is therefore crucial to understand how organic farming practice interacts with landscape heterogeneity in its effect on biodiversity.

Wild pollinators have been particularly negatively affected by modern agricultural practices, despite their importance in providing an essential ecosystem service (Steffan-Dewenter et al., 2005). Among the pollinators, bumble bees possess qualities which make them particularly important for pollination of wild flora and crops in areas within their distribution range in the northern hemisphere (Ranta, 1982; Fussell and Corbet, 1992). The decline in bumble bee populations that has been reported from different areas around the world during the last decades (Kearns et al., 1998; Steffan-Dewenter et al., 2005; Thorp, 2005; Benton, 2006; Biesmeijer et al., 2006) is cause for great concern. Several of the less common species are today endangered or locally and regionally extinct from agricultural landscapes, while the more common species have stable or increasing populations (Benton, 2006). The cause of this difference in rarity between bumble bee species is not clear, but has been attributed to differences in species traits such as diet (Goulson and Darvill, 2004), tongue length (Goulson et al., 2005), range size (Williams, 2005), foraging range (Benton, 2006) and emergence time (Fitzpatrick et al., 2007). Most of the specific species traits of European bumble bees are uncertain or unknown, but the existing literature suggests that the species differ markedly in traits such as tongue length, colony size, foraging range, niche breadth, nest position, colony dispersal and length of season (Walther-Hellwig and Frankl, 2000; Goulson and Darvill, 2004; Goulson et al., 2005; Benton, 2006).

In this study, we investigated the consequences of farming practice and landscape context on bumble bee diversity in the province of Skåne in southern Sweden. In Skåne the number of bumble bee species is thought to have declined from 19 species in the middle of the 20th century to the 14 species found here today (Holmström, 2002), with two additional species being very rare and localized (Holmström, 2002). By studying bumble bees on matched organic and conventional farms in landscapes of different habitat heterogeneity, we could not only test if farming practice and landscape context affected bumble bees, but also if the two interact such that the effect of organic farming on biodiversity depends on the landscape context.

We also used our data to study the effects of farming practice and landscape context on bumble bee species groups differing in colony size. The difference in colony size between bumble bee species (Benton, 2006) has been shown to be associated with the size of their foraging ranges (Westphal et al., 2006), so that bumble bee species with large colonies have larger foraging ranges compared to those with smaller colonies (Walther-Hellwig and Frankl, 2000; Goulson, 2003; Darvill et al., 2004; Westphal et al., 2006). This difference in foraging range has been suggested to affect the spatial scales at which species perceive the landscape (Westphal et al., 2006). Our study design allows us to investigate how these different bumble bee species, differing in foraging range, respond to differences in habitat quality at two spatial scales, the farm and the landscape.

2. Methods

2.1. Study design

We designed a study system consisting of twelve pairs of matched organic and conventional farms, located in landscapes differing in habitat heterogeneity. Six organically managed farms (with at least 50% of their arable land under organic management) with cereal cultivation were selected from each of two contrasting landscape types; heterogeneous mixed farmland or intensively farmed homogeneous plain (see Rundlöf and Smith, 2006). We used proximity, field size, crop type and occurrence of landscape features (e.g. stone walls, tree rows and small habitat islands) to carefully match the selected twelve organic farms with conventional farms, to as far as possible eliminate all differences not directly linked to the farming practice. Landscape characteristics and farming practice were determined using spatially explicit information on agricultural land-use (from the Swedish Board of Agriculture) interpreted in Arc View GIS 3.2. Organic farms were identified through the occurrence of EU subsidised organically managed fields (according to EEC regulation 2092/91). The habitat heterogeneity in a landscape with a 1 km radius surrounding the farm was characterized using the proportion of arable land (i.e. annually tilled fields with annual crops) and the occurrence of grasslands (field borders and pastures) (Purtauf et al., 2005; Roschewitz et al., 2005). The heterogeneous landscapes held a significantly lower proportion of arable land ($t_{22} = -8.83$, $P < 0.0010$), smaller fields ($t_{22} = -3.16$, $P = 0.0016$) and a significantly larger proportion

of pasture ($t_{13,6} = 4.92$, $P < 0.0010$) than the homogeneous landscapes (Table 1). The three landscape measures (proportion of arable land, field size and proportion of pasture) did not differ between organic and conventional farms within a pair (paired t-test; arable land $t_{11} = 1.31$, $P = 0.22$; field size $t_{11} = 0.79$, $P = 0.44$; pasture $t_{11} = 1.67$, $P = 0.12$; Table 1). Details about the selection process and landscape characteristics can be found in Rundlöf and Smith (2006).

2.2. Bumble bee recording

Bumble bees (*Bombus* spp.) were counted using a modified version of the standard line transects method developed for butterfly surveys (Pollard, 1977). The transect length differed between years and was 200 m along one cereal field in 2003 and 400–750 m along 2–3 cereal fields in 2004. Transects were located between the field and the uncultivated field border, and were divided into segments of 50 m each.

The bumble bee counts were made by walking slowly along the 2 m wide transects (1 m into the field and 1 m of the uncultivated field border). All bumble bees (no discrimination was made between workers, queens and males) visiting flowers along transects were visually identified to species and recorded. To prevent bias because of multiple recordings of the same bumble bee, the continued movement of a recorded bumble bee was monitored until it either left the transect or was lost from sight. Bumble bees that could not be immediately identified to species were caught with a hand net and determined following identification keys in Prýs-Jones and Corbet (1986) and Holmström (2002). In case of uncertainty, the bumble bee was noted as the most common species. Two bumble bee species, *Bombus lucorum* and *B. terrestris*, were pooled, because of documented difficulties in distinguishing them in the field (Svensson, 2002).

Each farm was visited four times between June 18th and August 8th in 2003, and five times in 2004, between May 23rd and August 11th. Farms within a pair were visited on the same day and the time interval between visits to the same pair of farms was at least one week. To prevent bias because of possible fluctuations in bumble bee occurrence during the day, the visits to each farm were rotated between morning and afternoon. Bumble bee counts were conducted between 9 a.m. and 5 p.m. on days when ambient temperature was 15 °C or above and there was no rain or strong winds.

Bumble bee species were grouped by their colony sizes according to Benton (2006) as being large, medium or small (Table 2). Two species, *B. hypnorum* and *B. subterraneus*, could not be classified due to lack of information.

2.3. Forage plant survey

The abundance of forage plants (flowering plants preferred by bumble bees; Appendix A) was surveyed during two visits, 19th June to 9th August, to each farm in 2004. The survey was conducted in the same transects as the bumble bee counting and was intended to reflect the local resources of forage available to the bumble bees. The abundance of forage plants flowering at the survey occasion were counted in two inventory squares per 50 m segment, with one square placed in the field and one in the uncultivated field border. Inventory squares measured 0.5 × 0.5 m and were divided into 25 equally sized sections. Total abundance of flowering forage plants was estimated on a scale from 0 to 25 based on how many sections flowering forage plants occurred in. Flower identification follows Mossberg et al. (1992).

2.4. Data analysis

Bumble bee species richness was analysed at the visit level (200 m of transect in 2003 and the first 400 m of transect in 2004) using Generalized Linear Mixed Models (SAS macro Glimmix; Littell et al., 1996) with Poisson error and log link function. The results of the analyses on species richness were qualitatively the same if analysed at farm level (results not shown). Bumble bee abundance (individuals per 50 m of transect) and abundance of flowering forage plants were log-transformed ($\ln(x + 0.1)$) and analysed using General Linear Mixed Models with normal error distribution. Bumble bee data was not pooled across years, because of differences in number of visits, timing of visits and weather conditions between years. We included year, visit, farm type, landscape type and the interaction between farm type and landscape type as fixed factors in the basic model. To account for the hierarchical study design we included the random factors farm pair (farm pair nested within landscape type), farm (the interaction between farm type and farm pair), and farm within year (c.f. Quinn and Keough, 2002). Survey visits within segments each year were treated as repeated measurements, with covariance structure selected to minimize the Akaike Information Criterion (AIC) of the model. The selected covariance structures were first-order autoregressive for the species richness data and compound symmetry for the abundance data. The denominator degrees of freedom were estimated with the Satterthwaite method or, when at least one covariance component was negative and therefore was set to zero, the containment method (Littell et al., 1996).

Table 1 – Measured landscape variables used to identify the two contrasting landscape types

Landscape type	Farm type	Field size (ha)	Proportion arable land	Proportion pasture
Heterogeneous	Organic	3.11 ± 0.68	0.15 ± 0.05	0.16 ± 0.05
Heterogeneous	Conventional	3.21 ± 0.69	0.16 ± 0.06	0.23 ± 0.03
Homogeneous	Organic	5.75 ± 0.72	0.64 ± 0.08	0.03 ± 0.02
Homogeneous	Conventional	6.29 ± 1.13	0.76 ± 0.05	0.03 ± 0.02
Mean (± SEM) field size, proportion of annually tilled arable land and proportion of grazed pasture in the landscapes (radius 1 km) surrounding the organic and conventional farms.				

Table 2 – Colony size classifications for the recorded bumble bee species according to Benton (2006), how frequently the different species occurred on organic ($f_{q_{org}}$) and conventional ($f_{q_{conv}}$) farms (max = 12) and the mean abundance (individuals 100 m^{-2}) of the different species per farm and year on organic (X_{org} (mean \pm SEM)) and conventional (X_{conv}) farms

Bumble bee species	Colony size	$f_{q_{org}}$	$f_{q_{conv}}$	X_{org}	X_{conv}
<i>Bombus hortorum</i>	Medium	9	5	1.30 \pm 0.51	0.23 \pm 0.16
<i>Bombus hypnorum</i>	?	4	3	0.59 \pm 0.38	0.29 \pm 0.20
<i>Bombus lapidarius</i>	Large	12	9	8.70 \pm 3.24	1.88 \pm 0.70
<i>Bombus lucorum/terrestris</i>	Large	12	10	20.03 \pm 5.62	9.78 \pm 4.43
<i>Bombus muscorum</i>	Small	3	0	0.16 \pm 0.12	0
<i>Bombus pascuorum</i>	Medium	9	7	4.43 \pm 2.00	3.38 \pm 1.83
<i>Bombus pratorum</i>	Small	9	5	0.90 \pm 0.40	0.78 \pm 0.52
<i>Bombus ruderarius</i>	Small	12	9	3.57 \pm 1.90	1.36 \pm 0.63
<i>Bombus soroeensis</i>	Medium	4	4	0.23 \pm 0.22	0.23 \pm 0.15
<i>Bombus subterraneus</i>	?	8	2	0.71 \pm 0.38	0.05 \pm 0.05
<i>Bombus sylvarum</i>	Small	10	5	1.88 \pm 0.75	0.26 \pm 0.23

Worker, queen and male bumble bees were not discriminated, but were all included in the bumble bee survey?, Colony sizes for *B. hypnorum* and *B. subterraneus* are not specified by Benton (2006).

We additionally wanted to test if the effects of farming practice and landscape heterogeneity on bumble bee abundance differed between groups of bumble bee species differing in colony size. We therefore calculated the total abundance of all individuals of each colony size group (large, medium or small colony size), summarized over visits within years. The statistical test was performed by adding the following factor and interactions; colony size, colony size \times landscape type and colony size \times farm type, as fixed factors to the basic model. The random structure of our statistical model, which in addition to the factors mentioned above included the interactions between colony size and farm pair and farm, respectively, ensured that the abundances of the colony size groups were not treated as independent estimates. We subsequently analysed the effects of farming practice, landscape context and their interaction on the abundances of bumble bees in each colony size category separately.

We also selected matching bumble bee and plant survey occasions (two visits to each farm in 2004) to test whether the residual variation, after controlling for visit and abundance of currently flowering forage plants, could be explained by farm type or landscape type and if the effect differed between groups of bumble bees. We ran the basic model with and without including log-transformed abundance of flowering forage plants as a covariate with the species richness and abundance of all bumble bees and abundances in the colony size groups as dependent variables.

All statistical analyses were performed in SAS 9.1 for Windows (Littell et al., 1996).

3. Results

We found in total 1838 foraging bumble bees of 11 species. All 11 species occurred in both farming practices and landscape types, except *B. muscorum* which was not detected on any conventional farm (Table 2). We found on average 7.67 ± 0.58 (mean \pm SEM) bumble bee species on organic farms, 4.92 ± 0.67 on conventional farms, 7.25 ± 0.49 on farms in heterogeneous landscapes and 5.33 ± 0.85 on farms in homogeneous landscapes.

3.1. Farming practice and landscape context

When not considering landscape type, both species richness and abundance of foraging bumble bees were significantly higher if the farm was under organic management (species richness $F_{1,14.3} = 24.75$, $P < 0.0010$; Fig. 1a; abundance $F_{1,9.9} = 21.15$, $P = 0.0010$; Fig. 1b). Similarly, if not considering farming practice, species richness ($F_{1,14.9} = 14.61$, $P = 0.0017$; Fig. 1a) and possibly abundance ($F_{1,10} = 4.96$, $P = 0.050$; Fig. 1b) were higher if the farm was located in a heterogeneous landscape. There were however significant interactions between farming practice and landscape type in their effect on both species richness ($F_{1,14.3} = 9.25$, $P = 0.0087$; Fig. 1a) and abundance ($F_{1,9.9} = 11.77$, $P = 0.0066$; Fig. 1b). This was because the effect of organic farming was stronger in more homogeneous landscapes. In fact, the effect of farming practice was only significant in homogeneous landscapes (species richness $F_{1,8.2} = 24.23$, $P = 0.0011$; abundance $F_{1,4.9} = 22.75$, $P = 0.0052$), but not in heterogeneous landscapes (species richness $F_{1,5.1} = 2.65$, $P = 0.16$; abundance $F_{1,4.9} = 1.21$, $P = 0.32$), although the trend was the same in both landscapes.

3.2. Bumble bee colony size

There was a significant interaction between colony size and landscape type on the abundance of foraging bumble bees ($F_{2,20} = 3.66$, $P = 0.044$). Abundance of bumble bees having large ($F_{1,10} = 2.51$, $P = 0.14$; Fig. 2) and small ($F_{1,10} = 2.01$, $P = 0.19$; Fig. 2) colonies were unaffected by landscape type, while bumble bees having medium size colonies were significantly more abundant in heterogeneous landscapes compared to homogeneous ones ($F_{1,10} = 19.85$, $P = 0.0012$; Fig. 2). Bumble bees were significantly more abundant on organic farms than on conventional ones (large $F_{1,11} = 12.35$, $P = 0.0049$; medium $F_{1,11} = 5.11$, $P = 0.045$; small $F_{1,11} = 13.51$, $P = 0.0037$) independent of colony class (interaction between colony size and farm type $F_{2,20} = 1.68$, $P = 0.21$). Although the interaction between colony size, farming practice and landscape context was non-significant ($F_{2,20} = 0.42$, $P = 0.66$), bum-

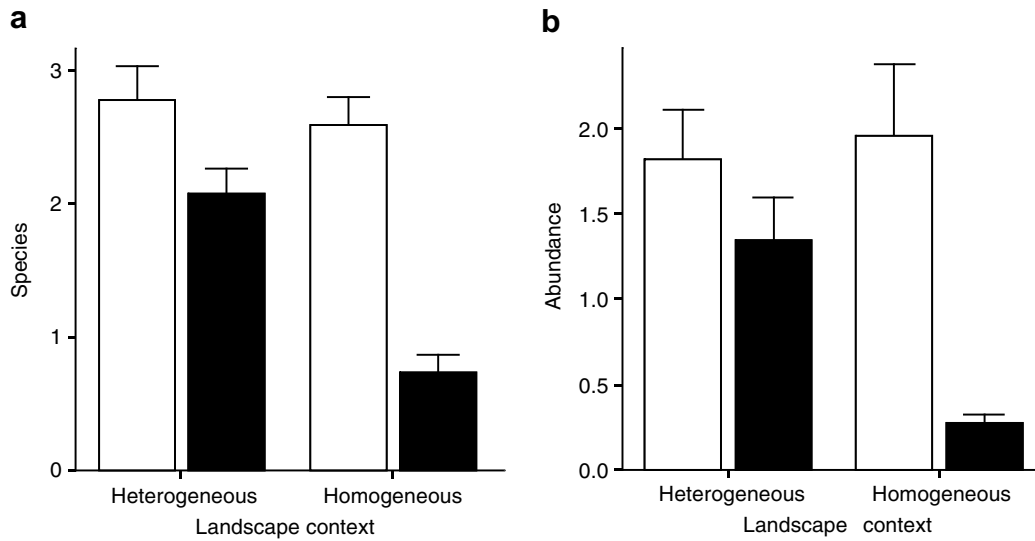


Fig. 1 – Bumble bee species richness and abundance in relation to farm practice (open bars – organic; filled bars – conventional) and landscape context. (a) Mean number of foraging bumble bee species per farm, visit and year. (b) Mean foraging bumble bee abundance (individuals per 50 m transect) per farm, visit and year. Error bars represent SEM and n equals 6 farms per regime and landscape type.

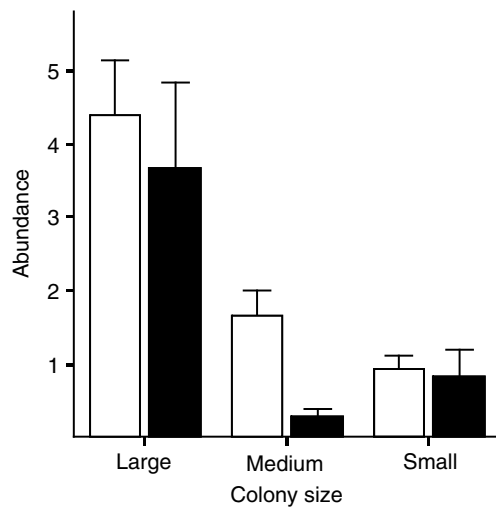


Fig. 2 – Abundance of foraging bumble bees per 50 m of transect, farm and year grouped by their colony size (large, medium, small) in relation to landscape context (open bars – heterogeneous landscapes; filled bars – homogeneous landscapes). Error bars represent SEM and n equals 12 farms per landscape type.

ble bee species having large colonies were more abundant on organic farms only in homogeneous landscapes, but not in heterogeneous (interaction $F_{1,10} = 6.16$, $P = 0.033$; homogeneous landscapes $F_{1,5} = 15.18$, $P = 0.012$; heterogeneous landscapes $F_{1,5} = 1.51$, $P = 0.27$), while no such interaction between farming practice and landscape context was present for species of either medium ($F_{1,10} = 1.33$, $P = 0.28$) or small ($F_{1,10} = 4.01$, $P = 0.073$) colony sizes. Consequently the general pattern, with the interaction between farming practice and

landscape context, for all bumble bees seems to be governed by bumble bee species having large sized colonies.

3.3. Bumble bees and forage plant abundance

The abundance of flowering forage plants showed a similar pattern as did the bumble bees, with a significant interaction between farming practice and landscape context ($F_{1,10} = 7.94$, $P = 0.018$) and higher abundance on organic farms ($F_{1,10} = 7.58$, $P = 0.020$), but no significant main effect of landscape type ($F_{1,11} = 2.81$, $P = 0.12$). Therefore, to investigate if the effects of farming practice, landscape context and their interaction was explained by forage plant abundance, we separately analysed data from those visits where we had matching forage plant surveys (two visits to each farm in 2004).

Bumble bee species richness was not significantly related to the local abundance of forage plants and the significant interaction between farming practice and landscape context remained also when including forage plant abundance as a covariate (Table 3). For bumble bee abundance, the effect of local forage plant abundance differed between the different colony size categories. Higher abundance of all bumble bees and abundance of bumble bees from large colonies were significantly associated with higher abundance of flowering forage plants (Table 3). The significant interaction between farm practice and landscape context did however persist for all bumble bees (Fig. 3a), but showed only a non-significant tendency to an interaction for bumble bees from large colonies (Fig. 3b), after including abundance of flowering forage plants in the model (Table 3). Bumble bees from neither medium nor small sized colonies were significantly associated with local abundance of flowering forage plants (Table 3). Bumble bees from medium sized colonies were significantly affected

Table 3 – Effect of farming practice and landscape context and their interaction on species richness and abundance of all bumble bees and on bumble bee abundance in the different colony size groups

	Basic model						Basic model including forage plant abundance as a covariate								
	Farm type		Landscape type		Interaction		Farm type		Landscape type		Interaction		Forage plants		
	F _{df}	P	F _{df}	P	F _{df}	P	F _{df}	P	F _{df}	P	F _{df}	P	F _{df}	P	
<i>Species richness</i>															
All bumble bees	18.11 _{1,10}	0.0017	6.48 _{1,10}	0.030	9.59 _{1,10}	0.0051	14.80 _{1,10}	0.0032	6.38 _{1,10}	0.030	7.67 _{1,10}	0.011	0.15 _{1,22}	0.71	
<i>Abundance</i>															
All bumble bees	8.64 _{1,10}	0.015	0.40 _{1,9,3}	0.54	13.37 _{1,10}	0.0044	2.79 _{1,12,7}	0.12	0.00 _{1,9,9}	1.0	5.49 _{1,12,8}	0.036	5.98 _{1,28}	0.021	
Large colony	8.20 _{1,10}	0.017	0.15 _{1,9,5}	0.71	12.47 _{1,10}	0.0054	2.06 _{1,12,4}	0.18	0.08 _{1,9,9}	0.78	4.37 _{1,12,5}	0.058	8.39 _{1,24,7}	0.0078	
Medium colony	0.01 _{1,10}	0.93	7.49 _{1,10,3}	0.020	1.24 _{1,10}	0.29	0.03 _{1,11,9}	0.86	5.15 _{1,11,2}	0.044	0.63 _{1,12}	0.44	0.61 _{1,31,8}	0.44	
Small colony	10.39 _{1,10}	0.0091	0.10 _{1,10,9}	0.75	0.05 _{1,10}	0.83	7.29 _{1,12,3}	0.019	0.01 _{1,11,4}	0.94	0.00 _{1,12,4}	0.97	0.37 _{1,26,8}	0.55	

Statistical results for the basic model, including only fixed and random factors, and for the basic model also including the abundance of flowering forage plants as a covariate. Bold numbers are for significant factors ($P < 0.05$). The denominator degrees of freedom were estimated with the containment method for the species richness model and the Satterthwaite method for the abundance models.

by the landscape context (Fig. 3c) and bumble bees from small colonies by farming practice (Fig. 3d) also after including abundance of flowering forage plants in the models (Table 3).

4. Discussion

Both farming practice and landscape heterogeneity significantly affected species richness and abundance of foraging bumble bees, with higher species richness and abundance on organic farms compared to conventional farms and in heterogeneous landscapes compared to homogeneous landscapes. Thus, both organic farming and landscape heterogeneity seem to provide more of one or several of the bumble bees' essential resources and thereby influence their occurrence. Large wild bees, like the bumble bees, have been shown to prefer patches surrounded by a diversity of habitat types (Hirsch et al., 2003), such as our farms in heterogeneous landscapes. These farms are surrounded by semi-natural grasslands, forest edges and other edge habitats that can offer forage and nest and hibernation sites for bumble bees (Svensson et al., 2000; Kells and Goulson, 2003). Heterogeneous landscapes might also provide temporal stability in resources which is of particular importance to bumble bees, because they are, in contrast to honey bees, only able to store nectar and pollen for a few days (Goulson, 2003; Benton, 2006). The bumble bee colony is therefore dependent on a continuous availability of resources in its surroundings during the whole season (Goulson, 2003; Benton, 2006).

Organic farming has been suggested to increase heterogeneity and thereby benefit biodiversity (Benton et al., 2003), but organic farming may also have more direct effects. The two major factors that may favour bumble bees on organic farms, compared to conventional ones, are the prohibition of agrochemicals and the larger proportion of leys (as green manure) (Sjödahl and Söderberg, 2004) that provide bumble bee forage (Risberg, 2004). The use of agrochemicals can affect bumble bees with direct lethal or sub-lethal effects (Kevan, 1975; Thompson and Hunt, 1999) or indirectly by altering habitat quality (Hyvönen et al., 2003; Aude et al., 2004). An environment free from agrochemicals favours a richer flora in and around arable fields (Hyvönen et al., 2003; Aude et al., 2004), resulting in more forage resources for bumble bees.

However, the effect of farming practice on bumble bees was not as simple as it first appeared, because species richness and abundance were significantly higher on organic farms in homogeneous landscapes, but not in heterogeneous landscapes. The same pattern, with a landscape dependent effect of organic farming, has also been found for arable weeds (Roschewitz et al., 2005) and butterflies (Rundlöf and Smith, 2006). This interacting effect between farming practice and landscape context might be caused by a larger difference between farming practices in homogeneous landscapes or because organic farming practices recreate some of the lost landscape heterogeneity in plain landscapes, or both (Benton et al., 2003; Rundlöf and Smith, 2006). The local abundance of flowers, which were higher on our studied organic farms, has also been shown to have a larger positive influence on bee species richness in homogeneous landscapes with a low

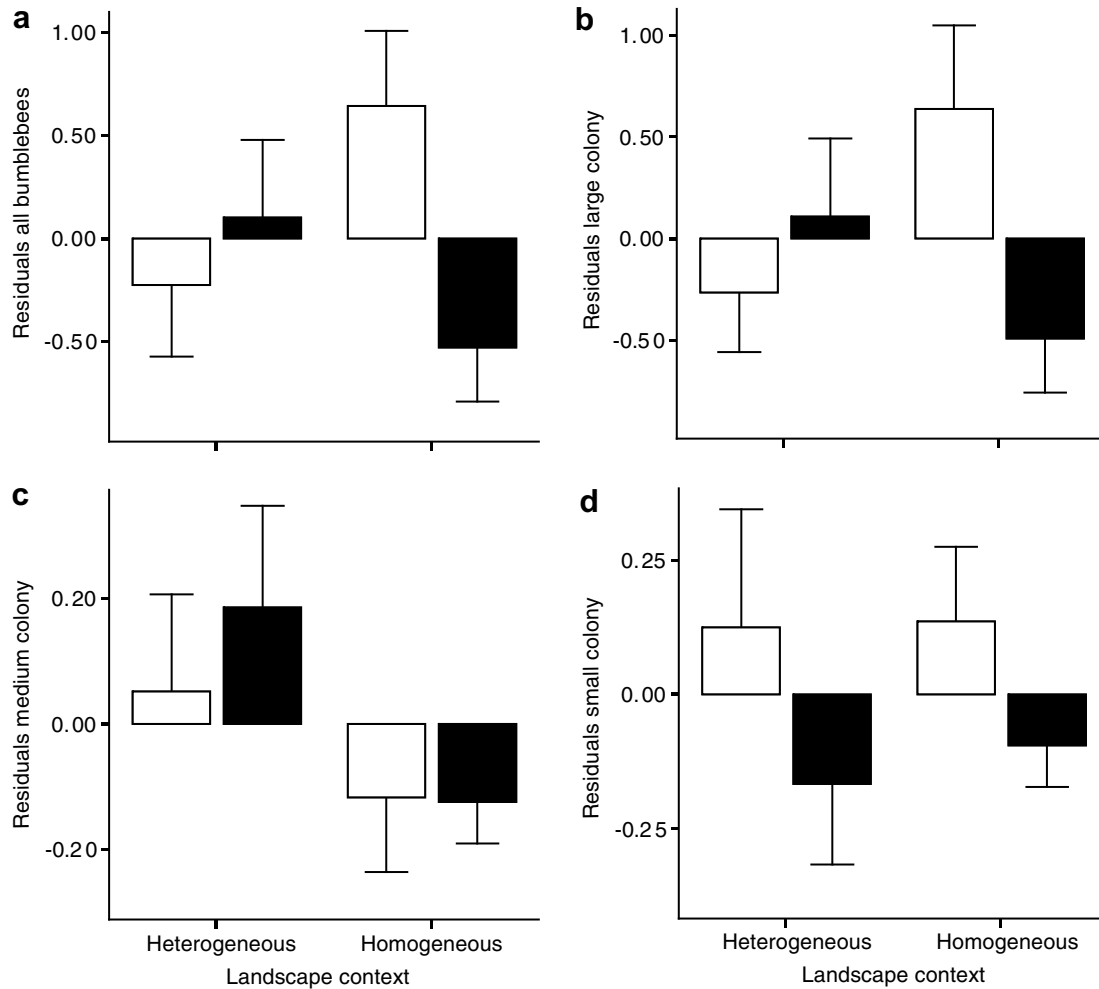


Fig. 3 – Residual variation in bumble bee abundance for (a) all bumble bee species and for bumble bee species with (b) large, (c) medium and (d) small colonies, after controlling for visit and abundance of flowering forage plants, in relation to farm practice (open bars – organic; filled bars – conventional) and landscape context. Error bars represent SEM and n equals 6 farms per regime and landscape type.

proportion of semi-natural habitats (Kleijn and van Langevelde, 2006). The context dependent value of resources might further enhance the difference in bumble bee species richness and abundance between organic and conventional farms in homogeneous landscapes.

Bumble bee abundance was significantly associated with local abundance of forage resources (Dreisig, 1995; Carvell, 2002; Meek et al., 2002; Bäckman and Tiainen, 2002; Pywell et al., 2005). In contrast, bumble bee species richness was unrelated to our measure of local forage resources and related to farming practice and landscape context also after statistically controlling for this factor. These partly different patterns indicate that different bumble bee species might be differently affected by their surroundings, independent of local flower resources.

Bumble bee species differing in their colony sizes, and as a consequence at which spatial scale they perceive the landscape (Westphal et al., 2006), were differently affected by local abundance of forage plants, farming practice and landscape context. Bumble bee species with large colonies were associ-

ated with organic farming primarily in homogeneous landscapes, largely reflecting the distribution of available forage resources. These species can fly longer to utilise scattered and temporary forage resources (Walther-Hellwig and Frankl, 2000), such as locally rich patches of flowers at organic farms or mass-flowering crops in homogeneous landscapes (Westphal et al., 2003). Bumble bee species with small colonies were also associated with organic farming, but this effect was independent of landscape context. Species with small colonies may find sufficient forage resources for colony persistence in field borders within the vicinity of their nest (Walther-Hellwig and Frankl, 2000). Our finding that bumble bees with small colonies were not influenced by the landscape context may be due to our study design where transects were not located randomly, but instead along a habitat that was part of the definition of landscape heterogeneity (field borders). In contrast to species with large and small colony sizes, the ones with medium sized colonies were significantly associated with heterogeneous landscapes. These bumble bee species may be unable to survive on ephemeral food resources in homogeneous

landscapes, because forage resources within their foraging range exhibit too large spatio-temporal variation in availability to allow colony persistence. We therefore suggest that bumble bees with medium sized colonies are most affected by loss of landscape heterogeneity in agricultural landscapes. A similar pattern of sensitivity to fragmentation, based on mobility, has been suggested for butterflies (Thomas, 2000).

The outcomes of the analysis of how different bumble bee species groups respond to habitat quality at different spatial scales are dependent on accurate identification of the bumble bee species. The species identification in our study was conservative, as uncertain specimens (<5%) were recorded as the most common species. The abundances in the three colony size classes could thus be slightly altered if some bumble bees were misidentified. However, as the number of misidentified specimens is low, this would probably not alter the results from the analysis.

We suggest that the findings of how the different bumble bee species groups integrate the landscape may partly shed light on why some bumble bee species have gone extinct or are currently decreasing in distribution and abundance, while others are still thriving. Studies in UK have shown that the bumble bee species that have survived in reasonable abundance in arable landscapes are the two species *B. terrestris* and *B. lapidarius* with large colony sizes (Goulson, 2003), which might indicate that species with this trait are more resistant towards the changes that have occurred and are occurring in agricultural landscapes.

4.1. Conservation implications

We conclude that both organic farming and landscape heterogeneity can be used as tools to increase species richness and abundance of bumble bees in agricultural landscapes. In the case of bumble bee abundance one contributing factor appears to be an increased abundance of forage plants on organic farms, while the pattern for species richness is more complex, possibly because other factors such as spatio-temporal variation of resources and nest site availability also are important (Walther-Hellwig and Frankl, 2000; Kells and Goulson, 2003). Since the effect of local forage resources, farm practice and landscape context differed between groups of bumble bees it might be risky to suggest a single solution to increase pollinator abundance. Organic farming does however appear to be a more efficient tool in homogeneous agricultural landscapes than in heterogeneous ones, independent of the local forage resource abundance. Due to the distribution of organic farming, with a higher proportion of arable land under organic management in heterogeneous landscapes in Sweden (Sjödahl and Söderberg, 2004; Rundlöf and Smith, 2006), the net benefit of organic farming may be reduced. The current design of the subsidy scheme for organic farming, with higher incentives to convert in marginal agricultural areas, does not fully make use of organic farming as a tool to increase biodiversity in intensively farmed homogeneous areas. Our results indicate that the benefit to bumble bees in Swedish agricultural landscape can be increased by promoting organic farming in these intensively farmed homogeneous landscapes. If the pattern is the same in other

parts of Europe, which is indicated by the lower uptake of agri-environment schemes in general in extensive regions (Kleijn and Sutherland, 2003), this may reduce the intended biodiversity benefits of organic farming considerably.

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Appendix A

Nectar and pollen plants recorded in the forage plant survey. Mean abundance (number of 10 × 10 cm sections the species occurred in per 50 m transect segment and farm) of the forage plant species, or group of species, on organic and conventional farms.

Species/group of species	Mean abundance	
	Organic	Conventional
<i>Aegopodium podagraria</i>	0.58	0.13
<i>Anchusa</i> spp.	0	0
<i>Arctium</i> spp.	0	0
<i>Brassica/Sinapis</i> spp.	0.07	0.01
<i>Centaurea cyanus</i>	0.09	1.08
<i>Centaurea jacea</i>	0	0
<i>Centaurea scabiosa</i>	0.06	0
<i>Cirsium acaule</i>	0	0.03
<i>Cirsium arvense</i>	3.05	1.00
<i>Cirsium helenioides</i>	0.03	0
<i>Cirsium palustre</i>	0	0
<i>Cirsium vulgare</i>	0.08	0
<i>Cytisus scoparius</i>	0	0
<i>Dipsacus strigosus</i>	0.08	0
<i>Echium vulgare</i>	0	0
<i>Epilobium angustifolium</i>	0.01	0.12
<i>Galeopsis</i> spp.	0.63	0.31
<i>Hypericum</i> spp.	0.58	0.87
<i>Knautia arvensis</i>	0.02	0
<i>Lamium album</i>	0.08	0.04
<i>Lamium</i> spp. (other than above)	0.41	0.32
<i>Lathyrus linifolius</i>	0	0.03
<i>Lathyrus pratensis</i>	0.28	0
<i>Leontodon autumnalis</i>	0.01	0.45
<i>Lotus corniculatus</i>	0	0.02
<i>Lupinus</i> spp.	0	0
<i>Medicago</i> spp.	0.15	0
<i>Persicaria</i> spp.	1.42	2.20
<i>Rubus idaeus</i>	0.72	1.20
<i>Rubus</i> spp. (other than above)	0.82	0.74
<i>Symphytum officinale</i>	0	0
<i>Succisa pratensis</i>	0	0
<i>Trifolium pratense</i>	4.21	0.54
<i>Trifolium repens</i>	1.75	0.29
<i>Trifolium</i> spp. (other than above)	0.49	0.02
<i>Vicia cracca</i>	0.56	0.90
<i>Vicia hirsuta</i>	1.05	0
<i>Vicia</i> spp. (other than above)	0.07	0.01

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