COMMUNITY ECOLOGY

Bumblebees experience landscapes at different spatial scales: possible implications for coexistence

Catrin Westphal · Ingolf Steffan-Dewenter · Teja Tscharntke

Abstract Coexistence in bumblebee communities has largely been investigated at local spatial scales. However, local resource partitioning does not fully explain the species diversity of bumblebee communities. Theoretical studies provide new evidence that partitioning of space can promote species coexistence, when species interact with their environment at different spatial scales. If bumblebee species possess specific foraging ranges, different spatial resource utilisation patterns might operate as an additional mechanism of coexistence in bumblebee communities. We investigated the effects of the landscape-wide availability of different resources (mass flowering crops and semi-natural habitats) on the local densities of four bumblebee species at 12 spatial scales (landscape sectors with 250–3,000 m radius) to indirectly identify the spatial scales at which the bumblebees perceive their environment. The densities of all bumblebee species were enhanced in landscapes with high proportions of mass flowering crops (mainly oilseed rape). We found the strongest effects for *Bombus terrestris* agg. and *Bombus lapidarius* at large spatial scales, implying foraging distances of 3,000 and 2,750 m, respectively. The densities of *Bombus pascuorum* were most strongly influenced at a medium spatial scale (1,000 m), and of *Bombus pratorum* (with marginal significance) at a small spatial scale (250 m).

The estimated foraging ranges tended to be related to body and colony sizes, indicating that larger species travel over larger distances than smaller species, presumably enabling them to build up larger colonies through a better exploitation of food resources. We conclude that coexistence in bumblebee communities could potentially be mediated by species-specific differences in the spatial resource utilisation patterns, which should be considered in conservation schemes.

Keywords *Bombus* spp. · Pollination · Foraging ranges · Coexistence · Resource partitioning

Introduction

Pollination systems are diverse and widespread and often involve species-rich pollinator guilds competing for access to floral resources (nectar and pollen) (Waser et al. 1996). Different and often multiple mechanisms lead to coexistence of ecologically similar species within these mutualist guilds (Palmer et al. 2003). One important mechanism that facilitates species coexistence is resource partitioning (Schoener 1974; Tilman 1982). Resource partitioning is most likely to occur in spatially or temporally heterogeneous environments, where different species can specialise on distinct resources, exploit resources at different times, or use resources in different locations (Amarasekare 2003). If space is partitioned, more species can potentially occupy various niches from the local scale of single resource patches to the regional scale of heterogeneous landscapes containing multiple patches of different resources. Thus, more species may coexist across different spatial scales (Kneitel and Chase 2004).

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In North America and Europe bumblebee communities (*Bombus* spp.) consist of a number of ecologically similar species (Pekkarinen 1984), which are important generalist pollinators in temperate agricultural landscapes (Williams 1995; Kearns et al. 1998; Corbet 2000). Early studies on coexistence of bumblebees indicate that differences in the proboscis lengths of the species lead to resource partitioning by differential use of floral resources (Heinrich 1976b; Ranta and Lundberg 1980). Long-tongued bumblebee species (e.g. *Bombus pascuorum*) tend to exploit flowers with long corollas, whereas short-tongued species (e.g. *Bombus terrestris* agg., *Bombus lapidarius*, and *Bombus pratorum*) prefer more open shallow flowers (Brian 1957; Teräs 1985; Dramstad and Fry 1995; Meek et al. 2002).

However, proboscis length alone does not fully explain coexistence in bumblebee communities, as locally co-occurring species differ only slightly in proboscis lengths (Ranta 1982). Thus, additional mechanisms may enable species coexistence in bumblebee communities (Pekkarinen 1984). Such additional mechanisms might be the use of different nesting sites (subterranean versus ground nesting species) (Kells and Goulson 2003), and variation in the phenology of the species' life cycles (early- versus late-season species) (Pekkarinen 1984). Apart from food plant preferences attributed to differences in the proboscis lengths, bumblebee species also exhibit different degrees of specialisation. Most species are polylectic, but some are specialised on few or even single food plants (e.g. *Bombus gerstäckeri*) (von Hagen 1994). Long-tongued species (e.g. *B. pascuorum*, *Bombus hortorum*) usually collect both nectar and pollen on their foraging bouts, whereas short-tongued species (e.g. *Bombus lucorum*) perform foraging bouts on which they only collect pollen (Brian 1957; Heinrich 1979). This behavioural dissimilarity may also result in the partitioning of floral resources, as only short-tongued species exploit flowers that do not provide any nectar. Ranta and Vepsäläinen (1981) advocated spatio-temporal heterogeneity as primary mechanism for coexistence of bumblebee species: stationary bumblebee colonies rely on patchily distributed foraging sites that change seasonally. Because of the continuously changing energy available for colony growth, the competitive relations between the colonies may be reversed temporarily resulting in larger numbers of species in one region.

Coexistence in such heterogeneous environments may also be attributed to different foraging strategies (e.g. Kotler and Brown 1988; Chase et al. 2001). The short-tongued bumblebee species *B. terrestris* and *B. lapidarius* prefer the exploitation of large foraging patches with a copious supply of food plants (Sowig 1989; Walther-Hellwig and Frankl 2000). In contrast, the long-tongued species *B. pascuorum* forages more often in small foraging patches or in habitats with sparsely distributed food plants (Sowig 1989; Walther-Hellwig and Frankl 2000). Additionally, Teräs (1985) suggested that short-tongued species happen to find rewarding foraging sites more successfully than long-tongued species, which might be due to a more efficient communication and recruitment system in short-tongued species (Dornhaus and Chittka 1999, 2001).

As bumblebees are central place foragers all foragers rely on resources within their foraging range (Hamilton and Watt 1970). Hence, differences in the size of the species' foraging ranges might also favour coexistence, in this case via different patterns of spatial resource utilisation (Ritchie and Olff 1999; Kneitel and Chase 2004). It has long been assumed that bumblebees forage close to their nests, as long as food is locally abundant (Heinrich 1976a). In recent times there has been increasing evidence that bumblebees forage over large distances, even if resources are available close to their nests (Dramstad 1996; Osborne et al. 1999; Chapman et al. 2003). Furthermore, the foraging ranges of bumblebees seem to be species specific (Walther-Hellwig and Frankl 2000; Darvill et al. 2004). However, sound estimates of the specific foraging distances are difficult to obtain. Most studies are limited in sample size at large spatial scales, as the area in which a bee might forage increases with the square of the foraging distance (Walther-Hellwig and Frankl 2000; Darvill et al. 2004), and homing experiments probably do not reveal the actual foraging ranges (Hedtke 1994; Goulson and Stout 2001).

Potential foraging ranges seem to correspond with ecological traits of the bumblebee species. The large species *B. terrestris* and *B. lapidarius* are assumed to forage over long distances (Walther-Hellwig and Frankl 2000), and they establish colonies with numerous workers (von Hagen 1994). The smaller *B. pascuorum* and *B. pratorum* presumably have small foraging ranges (Mauss and Schindler 2002), and they establish smaller colonies (von Hagen 1994).

We assume that not only food plant or patch preferences, but also different patterns of spatial resource utilisation might favour coexistence in bumblebee communities, if the foraging ranges of bumblebees are in fact species-specific. An important prerequisite for the verification of this additional mechanism of coexistence in bumblebee communities is the identification of the spatial scales at which bumblebee species interact with their resource environment (see also Bronstein 1995; Kneitel and Chase 2004). Consequently, the main

objective of our study was to indirectly identify the specific foraging ranges of coexisting bumblebee species. We used a multiple spatial scale approach to reveal the scales at which the different bumblebees perceive their resource environment. Since foraging distances are presumably affected by resource availability (Potts et al. 2003), we incorporated this factor in our study. Based on the recent finding that bumblebees benefit from the availability of highly rewarding resources at regional spatial scales (Westphal et al. 2003), we tested the specific effects of the availability of different food resources (i.e. semi-natural habitats and highly rewarding mass flowering crops) on the densities of four bumblebee species across 12 spatial scales (i.e. circular landscape sectors with different radii).

Materials and methods

Study region and landscape sectors

The study was carried out in 2001 within an area of 42 km east–west and 35 km north–south around the city of Göttingen (Germany). Within the study region we selected 16 independent circular landscape sectors each with a radius of 3,000 m, which represented a gradient of resource availability owing to different proportions of mass flowering crops and semi-natural habitats. The southern Lower Saxony region comprises mainly intensively farmed areas with annual crops $51.0 \pm 5.1\%$ and grasslands $13.6 \pm 2.1\%$ (mean $\pm$ SE, $n=16$). In addition to these main agricultural land use types, forests, different amounts of settlement, and various scattered fragments of semi-natural habitats are found.

For each landscape sector the current land use was mapped using land register maps with a scale of 1:5,000, which were transferred into Geographical Information Systems (GIS; Topol 4.506, Gesellschaft für digitale Erdbeobachtung und Geoinformation, Göttingen and ARC/View 3.1, ESRI Geoinformatik, Hannover) for landscape analysis.

The influence of resource availability on the densities of bumblebee species was studied at multiple spatial scales. Each circular landscape sector was subdivided into 12 nested subsectors with radii from 250 to 3,000 m representing 12 spatial scales from local to landscape level. We chose the maximum scale, i.e. a radius of 3,000 m, to cover a larger range than the reported maximum foraging distance of bumblebees (1,750 m) (Walther-Hellwig and Frankl 2000). For all 12 subsectors (i.e. spatial scales) of the 16 study sites the proportions of mass flowering crops and semi-natural habitats were calculated separately using GIS (Table 1). Between both landscape factors (arcsin transformed to achieve normality) we did not find any significant correlation at any spatial scale ($P>0.1$).

The landscape factor "proportion of mass flowering crops" summarized the amounts of oilseed rape (*Brassica napus*, 4–5), clover (*Trifolium* spp., 6–9), *Phacelia tanacetifolia* (6–10), field beans (*Vicia faba*, 6–7), potatoes (*Solanum tuberosum*, 6–7), mustard (*Sinapis arvensis*, 5–6), and sunflowers (*Helianthus annuus*, 7–9); the numbers in parentheses indicate the months of the main flowering period of the crops (following Oberdorfer 1994). Queens of *B. terrestris* and *B. pratorum* emerge early in the season (mid March), *B. lapidarius* and *B. pascuorum* queens follow at the beginning of April. Nest-seeking queens of all species are found until mid May (von Hagen 1994). Thus, these common bumblebee species could benefit from the availability of flowering oilseed rape during the founding stage of their colonies, which was the most prevalent flowering crop in our study region. After the flowering period of

Table 1 Percent area of mass flowering crops and semi-natural habitats for all 12 spatial scales across the 16 landscape sectors

Radius of landscape sector (m)	Mass flowering crops			Semi-natural habitats		
	Mean $\pm$ SE	Minimum	Maximum	Mean $\pm$ SE	Minimum	Maximum
250	14.7 ± 3.9	0.0	54.5	15.9 ± 1.6	8.5	29.6
500	11.6 ± 2.7	0.4	43.9	8.4 ± 1.4	3.1	21.6
750	10.0 ± 1.5	0.9	24.6	7.9 ± 1.2	1.6	16.3
1,000	8.5 ± 1.2	2.0	19.7	6.8 ± 1.0	1.5	13.4
1,250	8.1 ± 1.0	1.9	16.1	6.3 ± 0.8	1.3	13.7
1,500	7.8 ± 0.9	2.6	15.1	5.9 ± 0.7	1.8	13.0
1,750	7.5 ± 0.7	3.8	13.8	5.7 ± 0.6	1.9	12.2
2,000	7.4 ± 0.6	3.8	11.9	5.6 ± 0.6	2.9	11.5
2,500	6.9 ± 0.6	3.1	10.6	5.5 ± 0.4	3.6	9.7
2,750	6.6 ± 0.6	2.9	9.9	5.5 ± 0.4	3.8	9.1
3,000	6.4 ± 0.6	2.8	10.2	5.6 ± 0.4	3.6	8.8

oilseed rape, only small amounts of other mass flowering crops could be found in our landscape sectors, which bloomed consecutively throughout the flight season of the bumblebee species (von Hagen 1994). Mass flowering crops without oilseed rape covered only 0.84±0.22% of the landscape sectors with 1,500 m radius (mean ± SE; range 0–3.37%). All studied bumblebee species could benefit from these resources, if they were available within their foraging ranges.

The landscape factor "proportion of semi-natural habitats" summarized the amounts of fallows, calcareous grasslands, orchard meadows, woods, hedgerows, grassy banks, and ditches. In contrast to mass flowering crops that flower only over short periods of time, semi-natural habitats provide different food plant species that flower continuously throughout the flight season.

Experimental design

On an old fallow in the centre of each landscape sector a 1.5 m × 3 m plot of *P. tanacetifolia* (Hydrophyllaceae) was established to implement a standardised foraging habitat with a single food plant and a uniform flower density for bumblebee observations. After removing the vegetation cover the experimental plots were dug, and *P. tanacetifolia* was sown between 16 May and 22 May 2001 with 3 g *Phacelia* seeds/m^2. To standardise the nutrient supply of the soil each plot was covered with 2 cm commercial garden soil prior to sowing. Commercial fertilizer with 8% P_2O, 15% K_2O, 6% MgO was applied every 2 weeks.

P. tanacetifolia is a very attractive food plant for bumblebees (particularly for the short-tongued species), as the open and shallow flowers provide great amounts of pollen and nectar (Williams and Christian 1991). Although the long-tongued *B. pascuorum* generally prefers flowers with long corollas (Teräs 1985; Sowig 1989; Dramstad and Fry 1995; Meek et al. 2002), we observed substantial numbers of *B. pascuorum* foraging on *P. tanacetifolia* (see below). As *B. pascuorum* was found to even dominate *P. tanacetifolia* plots in mid to late summer (Williams and Christian 1991), we think that the standardised *P. tanacetifolia* plots represented an appropriate method to assess differences in bumblebee densities among landscapes.

Bumblebee observations

During the flowering period of *P. tanacetifolia* flower-visiting non-parasitic bumblebees were recorded from 0900 to 1900 hours in suitable weather conditions. In total 62 observations (each lasting 15 min) were conducted between 13 July and 2 August 2001. The observational period concurred with the main flight season of *B. terrestris*, *B. lapidarius*, and *B. pascuorum*. However, the flight season of *B. pratorum* ceases at the end of July (von Hagen 1994). In each landscape sector successive observations took place at different times of the day to avoid biased data. Depending on the length of the flowering period and weather conditions three to four observations were made per study site.

Owing to differences in flower densities, the area of the plot covered by *Phacelia* flowers was estimated after each observation. We calculated the average flower cover across all observations for each of the 16 plots. During the study period 50.5±2.2% of the plots were covered with *Phacelia* flowers (mean ± SE, range 33.3–63.3%, n=16). Taking these differences into account, the densities of the bumblebee species were calculated as numbers of flower-visiting bees per square metre *Phacelia* flowers. We took an average of these weighted bumblebee densities for all observations per study site. Bumblebee species were identified in the field. Since the ecologically similar species *B. lucorum* and *B. terrestris* (von Hagen 1994) are difficult to distinguish in the field, we treated them as a group denoted as *B. terrestris* agg. Nomenclature follows Mauss (1996).

Statistical analyses

Statistical analyses were performed with SPSS 11.0 for Windows (SPSS Software, Munich). Effects of the proportion of mass flowering crops and of the proportion of semi-natural habitats on the mean weighted densities of the bumblebee species were examined for all 12 spatial scales separately using simple linear regression models. We applied logarithmic transformation to the dependent variables (i.e. weighted species-specific densities) in order to achieve normality. As a measure for the strength of the correlations (Zar 1984), the coefficients of determination were plotted for each spatial scale (i.e. radius of landscape sectors) to reveal scale-dependent and species-specific patterns of the relationships (Bowers 1985b; Steffan-Dewenter et al. 2002). Arithmetic means ± 1 SE for the non-transformed data are given in the text.

Results

Flower-visiting bumblebees

In total 3,340 non-parasitic bumblebee visits were observed in the *Phacelia* plots. The overall bumblebee density was 12.1±1.2 individuals/m^2 flowers

(mean ± SE, range 5.4–20.7, *n*=16 plots). We recorded seven non-parasitic species: *B. terrestris* agg. (1,874 individuals), *B. lapidarius* (1,155), *B. pascuorum* (242), *B. pratorum* (52), *Bombus hypnorum* (11), *Bombus sylvarum* (4), and *B. hortorum* (2). Since the sample sizes for *B. hypnorum*, *B. sylvarum*, and *B. hortorum* were tiny, we excluded these species from statistical analyses. The small number of observed *B. pratorum* individuals might be due to the fact that the flight season of this common and ubiquitous species was already ceasing during the observation period (von Hagen 1994).

Scale-dependent and species-specific effects of mass flowering crops

We did not find any significant influence of the proportion of semi-natural habitats on the densities of *B. terrestris* agg., *B. lapidarius*, *B. pascuorum*, and *B. pratorum* at any spatial scale. However, the densities of all bumblebee species, except for *B. pratorum*, were significantly influenced by the availability of mass flowering crops (mainly oilseed rape) in the landscape sectors. For *B. pratorum* we only found a marginally significant effect (Fig. 1e–h). In general, all correlations were positive for every spatial scale and species, yet only some regression models were statistically significant (Table 2). For *B. terrestris* agg. we found the strongest positive effect of the proportion of mass flowering crops on the species' densities at the largest spatial scale. The pattern of the coefficients of determination in the scatter plot revealed that the positive effects of mass flowering crops on *B. terrestris* agg. densities were strengthened with increasing spatial scales (Fig. 1a). Great amounts of highly rewarding food resources in landscape sectors with 3,000 m radius enhanced the densities of *B. terrestris* agg. significantly (Fig. 1e). Since our analysis did not include landscape sectors with radii larger than 3,000 m, it was not possible to investigate whether the spatial scale at which *B. terrestris* agg. perceives the landscape might be even bigger.

For *B. lapidarius* we found a similar pattern: with increasing spatial scale the positive relationships between the proportion of flowering crops and the densities of *B. lapidarius* individuals became stronger (Fig. 1b). The strongest correlation between the proportion of flowering crops and *B. lapidarius* densities occurred for landscape sectors with 2,750 m radius (Fig. 1f). Thus, *B. lapidarius* presumably experiences landscapes at similar spatial scales as *B. terrestris* agg. does.

The availability of highly rewarding resources was most influential on *B. pascuorum* densities in landscape sectors with 1,000 m radius (Fig. 1g). The scale-dependent pattern of the plotted coefficients of determination described a plateau at medium spatial scales (Fig. 1c), indicating smaller foraging ranges than we found for *B. terrestris* agg. and *B. lapidarius*.

Even smaller foraging distances could be assumed for *B. pratorum*, as we found the strongest effect of the mass flowering crops on the species' densities at a small spatial scale (for landscape sectors with 250 m radius; Fig. 1h). Compared to the other species, this effect was weaker and only marginally significant (*P*=0.100). The influence of the mass flowering crops on the densities of *B. pratorum* attenuated with increasing spatial scale (Fig. 1d).

Moreover, the potential foraging ranges tended to be related to the body and colony sizes of the bumblebee species. The wingspan, which strongly correlates with the size of the bumblebee species (Alford 1975; Schmid-Hempel et al. 1990), seems to affect the potential foraging distance: the larger the species the larger were their potential foraging ranges (Fig. 2). Likewise, we found a positive trend between the potential foraging ranges and the species-specific colony size, i.e. the number of individuals that are present in a colony at the peak of its development (von Hagen 1994). The species maintaining large colonies (*B. terrestris* agg. and *B. lapidarius*) exhibited the largest potential foraging ranges, whereas the species with smaller colonies (*B. pascuorum* and *B. pratorum*) foraged presumably over smaller distances (Fig. 3).

Discussion

Availability of highly rewarding resources

Food plants in semi-natural habitats, such as field margins or fallows, are generally sparsely or patchily distributed. Thus, bumblebees have to spend more time and energy collecting the same amounts of pollen and nectar than in highly rewarding mass flowering crops (Heinrich 1979; Dukas and Edelstein-Keshet 1998). We found enhanced densities of different bumblebee species in landscape sectors with high proportions of mass flowering crops, whereas we did not find any significant effect of the availability of semi-natural habitats on the species-specific densities of bumblebees. The availability of highly rewarding resources (mainly oilseed rape) apparently promoted the bumblebees' colony growth, so that we could record substantially increased bumblebee densities in the *Phacelia* plots 2 months after the bloom of oilseed rape ceased. Since oilseed rape was most prevalent, highly rewarding resources seemed particularly

Fig. 1a–h Species-specific and scale-dependent effects of the availability of mass flowering crops on weighted bumblebee densities. **a–d** Coefficients of determination for simple regression models at all 12 spatial scales (i.e. radii of landscape sectors) demonstrate the species-specific patterns of scale effects for **a** *Bombus terrestris* agg., **b** *Bombus lapidarius*, **c** *Bombus pascuorum*, and **d** *Bombus pratorum*. **e–h** Relationships between the proportions of mass flowering crops (%) and number of bees/m² flowers for the simple regression models with highest coefficients of determination (r^2) indicating the most influential spatial scale for each species: **e** *B. terrestris* agg. [$\log(y + 1) = 0.040x + 0.852$, $r^2 = 0.272$, $F_{1,15} = 5.235$, $P = 0.038$], **f** *B. lapidarius* [$\log(y + 1) = 0.066x + 0.438$, $r^2 = 0.313$, $F_{1,15} = 6.386$, $P = 0.024$], **g** *B. pascuorum* [$\log(y + 1) = 0.033x + 0.565$, $r^2 = 0.277$, $F_{1,15} = 5.371$, $P = 0.036$] and **h** *B. pratorum* [$\log(y + 1) = 0.004x + 0.083$, $r^2 = 0.181$, $F_{1,15} = 3.099$, $P = 0.100$]
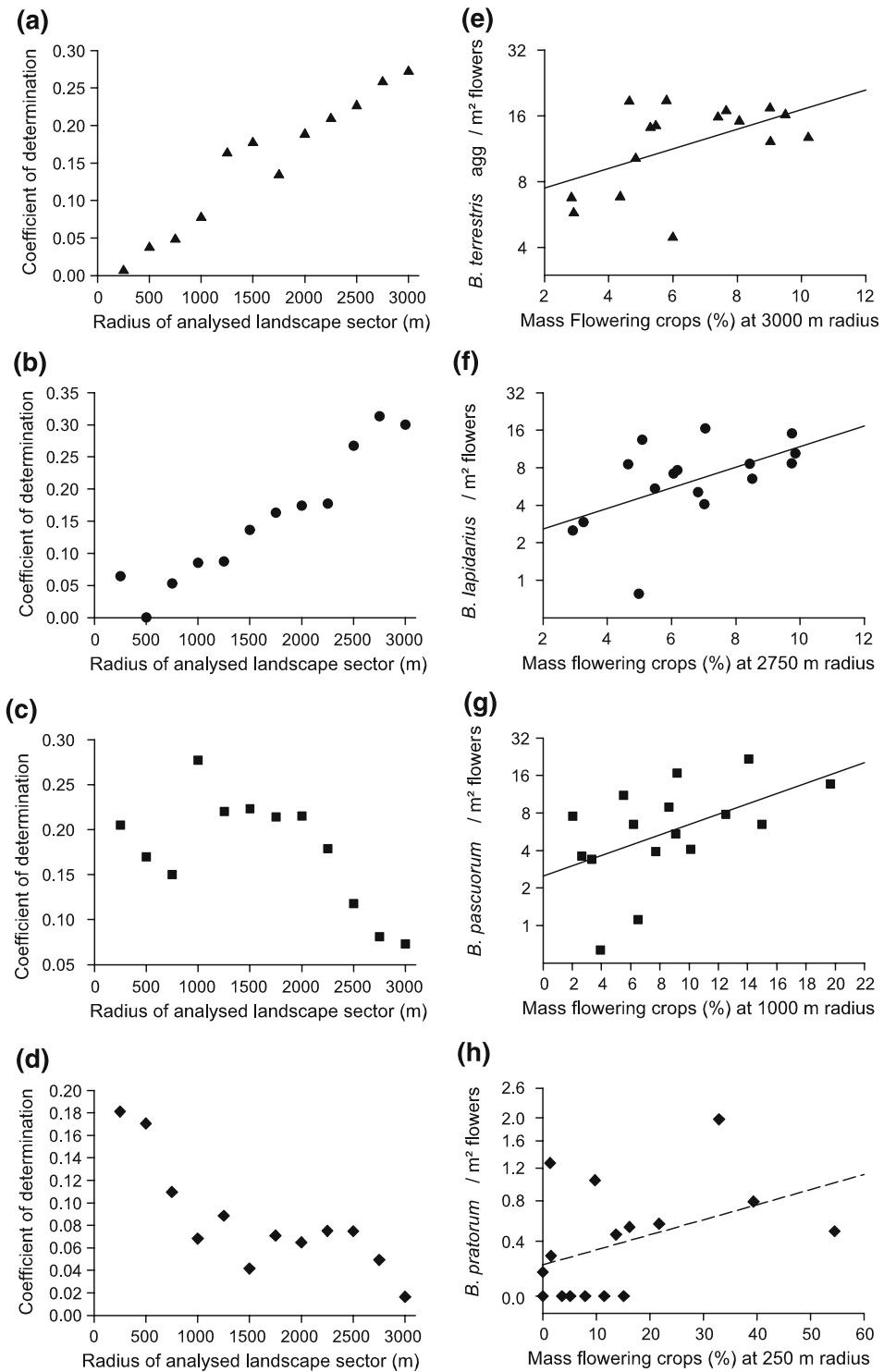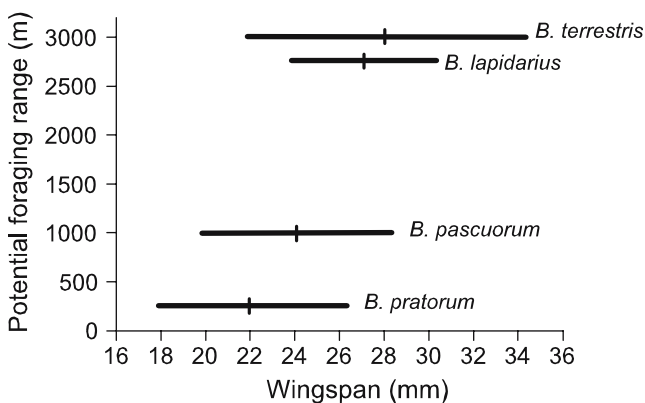

important in spring, i.e. at the time of colony founding, when only the queen or a few workers care for the brood (von Hagen 1994). Other mass flowering crops which bloomed during the bumblebees' flight season presumably had not such a strong effect on the bumblebees' densities, as they occurred only in small proportions and were not available in all landscape sectors.

Regardless of their different foraging strategies (Teräs 1985; Sowig 1989; Walther-Hellwig and Frankl 2000), the four dominant bumblebee species profited from mass flowering crops (Fig. 1e–h). Even *B. pascuorum*, which usually forages on patchily or sparsely distributed food plants with relatively long corollas (Teräs 1985; Walther-Hellwig and Frankl 2000), seemed to

Table 2 *P*-values for all relationships[a] between the weighted bumblebee densities and the proportion of mass flowering crops for all 12 spatial scales (i.e. landscape sectors with different radii)
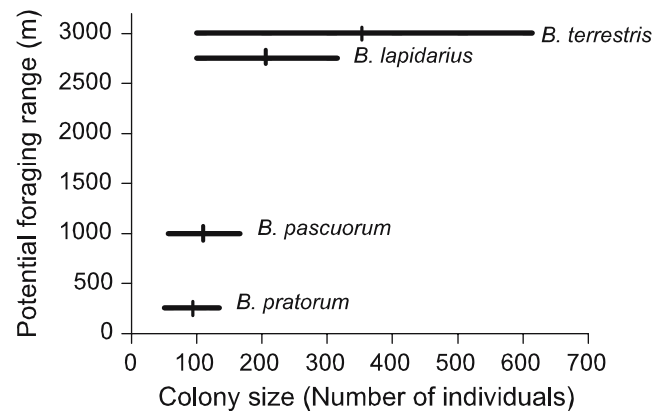
Radius of landscape sector (m)	*P*-values			
	*Bombus terrestris*agg.	*Bombus lapidarius*	*Bombus pascuorum*	*Bombus pratorum*
250	0.771	0.344	0.078	0.100
500	0.476	0.946	0.112	0.112
750	0.416	0.391	0.138	0.210
1,000	0.298	0.273	0.036	0.328
1,250	0.120	0.269	0.067	0.263
1,500	0.105	0.159	0.065	0.448
1,750	0.163	0.121	0.071	0.319
2,000	0.093	0.108	0.071	0.341
2,250	0.075	0.105	0.102	0.305
2,500	0.063	0.040	0.193	0.305
2,750	0.045	0.024	0.286	0.409
3,000	0.038	0.028	0.312	0.635

[a] Coefficients of determination of the corresponding regression models are shown in Fig. 1a–d

Fig. 3 Relation between the colony size (von Hagen 1994) and the potential foraging ranges (m) of four different bumblebee species. *Horizontal bars* represent the ranges of the species' colony sizes, *vertical lines* indicate the centres of the ranges

Fig. 2 Relation between the wingspan of workers (Alford 1975) and the potential foraging ranges (m) of four different bumblebee species. *Horizontal bars* represent the ranges of the species' wingspans, *vertical lines* indicate the centres of the ranges

exploit the open shallow flowers of the highly rewarding oilseed rape. This behaviour might be due to the fact that interspecific competition in the oilseed rape fields was low, as only queens or few workers forage during this time of the year. In contrast to *B. pascuorum*, the short-tongued species *B. terrestris* agg., *B. lapidarius*, and *B. pratorum* usually prefer food plants with open shallow flowers (Teräs 1985; Walther-Hellwig and Frankl 2000), like oilseed rape (Free and Ferguson 1980). Additionally, *B. terrestris* agg. and *B. lapidarius* show a preference for mass abundant resources (Walther-Hellwig and Frankl 2000).

Irrespective of our finding that the proportions of semi-natural habitats did not affect bumblebee densities at any spatial scale, semi-natural habitats represent important habitats for foraging (Bäckman and Tiainen 2002; Carvell et al. 2004) and nesting in agricultural landscapes (Svensson et al. 2000; Kells and Goulson 2003). Particularly after the flowering of oilseed rape and other mass flowering crops ceases, bumblebees rely on semi-natural habitats as their main food resources, as they provide a continuous supply of food plants throughout the flight season (von Hagen 1994).

Species-specific foraging ranges

We found species-specific patterns of the plotted coefficients of determination over the 12 spatial scales, indicating large foraging ranges for *B. terrestris agg*. (3,000 m) and *B. lapidarius* (2,750 m), and smaller foraging ranges for *B. pascuorum* (1,000 m) and *B. pratorum* (250 m; Fig. 1a–d).

Similar to a recent mark–recapture study our results revealed differences in the foraging distances of *B. terrestris* agg. (maximum 1,750 m), *B. lapidarius* (maximum 1,500 m), and *Bombus muscorum* (maximum 500 m, this species is assumed to have a foraging range similar to that of *B. pascuorum*) (Walther-Hellwig and Frankl 2000). However, the possibility of detecting marked bees over large distances is limited in mark–recapture studies, since the area within which the bees forage increases with the square of the distance from the nest (Osborne et al. 1999). Experiments testing homing ability also showed that over a distance of 3 km *B. terrestris* and *B. lapidarius* returned in significantly higher proportions than *B. pascuorum* (Hedtke 1994). Yet, the homing ability does not represent the bees'

natural foraging ranges. Mark–recapture studies, harmonic radar, and homing experiments are often limited in their significance, because of the usually low sample sizes (Osborne et al. 1999). Unfortunately, we did not find any study focussing on the foraging range of *B. pratorum*.

Compared to the mark–recapture study of Walther-Hellwig and Frankl (2000), our results imply larger foraging ranges for *B. terrestris* agg., *B. lapidarius*, and *B. pascuorum*. A genetic analysis of the spatial foraging patterns of *B. terrestris* and *B. pascuorum* provides further evidence that bumblebees might forage over several kilometres (Chapman et al. 2003, but see Darvill et al. 2004). In addition, theoretical studies indicate that, depending on food quality and abundance, foraging flights up to several kilometres could be energetically rewarding (Dukas and Edelstein-Keshet 1998; Cresswell et al. 2000). Since mass flowering crops represent a highly rewarding resource, the bumblebee species probably chose to forage over larger distances to gather a greater reward per unit time (Heinrich 1979; Hill et al. 2001). We assume that bumblebees (like honeybees) respond to landscape structure when making foraging decisions (Steffan-Dewenter and Kuhn 2003). Our results indicate the spatial scales at which common bumblebee species perceive agricultural landscapes. However, studies that are conducted in other types of landscapes (i.e. in areas dominated by semi-natural habitats) might reveal deviating foraging distances.

Relation between foraging range and body or colony size

The spatial scales at which the bumblebees perceived their environment were related to their body size. We found large potential foraging ranges for the large bumblebee species *B. terrestris* agg. and *B. lapidarius*, and small potential foraging ranges for the smaller species *B. pascuorum* and *B. pratorum* (Alford 1975; von Hagen 1994) (Fig. 2). These findings are consistent with other studies that demonstrated positive correlations between the body size and foraging ranges of bee species (van Nieuwstadt and Iraheta 1996; Gathmann and Tscharntke 2002). In addition, our results provide further evidence that changes in landscape structure might affect species differentially depending on their body size (Roland and Taylor 1997).

Interestingly, we could also demonstrate a positive trend between the species-specific foraging ranges and the colony size of the different species, i.e. *B. terrestris* agg. and *B. lapidarius* have larger colonies and larger potential foraging ranges than *B. pascuorum* and

B. pratorum. (Alford 1975; von Hagen 1994; Walther-Hellwig and Frankl 2000) (Fig. 3).

Coexistence in bumblebee communities

Earlier studies on coexistence could not fully explain the diversity patterns in bumblebee communities, perhaps because they mainly focussed on mechanisms at the local spatial scale (Heinrich 1976b; Ranta and Lundberg 1980). Local scale trade-offs in bumblebee communities emerge from the differential use of resources due to different flower, patch, or nesting site preferences of the respective species. Additionally, differences in the phenology of the species' life cycles might favour their coexistence (see Table 3 for references). However, if coexistence in bumblebee communities is not only viewed within a local but also a regional context, other mechanisms of coexistence could become more important (e.g. spatio-temporal heterogeneity) (Ranta and Vepsäläinen 1981). Taken together the mechanisms operating from local to regional spatial scales might explain more comprehensively, why so many species can coexist in bumblebee communities (Kneitel and Chase 2004).

At regional spatial scales additional trade-offs can be incurred when species respond differently to heterogeneous environments (Amarasekare 2003; Kneitel and Chase 2004). Using a multiple spatial scale analysis, we could demonstrate that bumblebee species respond differently to scale-dependent variation in resource abundance. Hence, we assume that additional mechanisms of coexistence might operate across multiple spatial scales contributing to coexistence in bumblebee communities. Mechanisms operating at regional spatial scales could be related to trade-offs regarding the species' degree of resource specialisation, their resource utilisation patterns, or trade-offs in their competitive, and colonisation abilities (Palmer et al. 2003; Amarasekare 2003; Kneitel and Chase 2004).

Considering allometric relationships between animals' body sizes and their foraging ranges or metabolic requirements (Peters 1983), we hypothesise that coexistence in bumblebees might be favoured by different patterns of spatial resource utilisation (Ritchie and Olff 1999). This hypothesis is supported by a conceptual model, which demonstrates that differences between the body sizes of species could result in a differential use of space, and therefore lead to species' coexistence (Basset 1995). The underlying trade-off in the model is that large species are inefficient when exploiting resources within large foraging ranges, and thus leave enough resources behind for more efficient smaller

Table 3 Hypothesised mechanisms of coexistence in bumblebee communities in heterogeneous environments: different traits and associated trade-offs lead to coexistence at local or regional spatial scales

Spatial scale	Differing species traits	Trade-offs among species	Mechanism of coexistence	Empirical or theoretical evidence
Local	Proboscis length	Flower-specific foraging efficiency, competitive ability	Resource partitioning	Brian (1957); Heinrich (1976b); Morse (1977); Inouye (1978); Ranta and Lundberg (1980); Harder (1985)
	Patch size or density preference	Foraging rates in large vs. small patches, or dense vs. sparse patches	Resource partitioning	Johnson and Hubbell (1975); Sowig (1989); Walther-Hellwig and Frankl (2000)
	Nesting site preference	Subterranean vs. ground nesting	Habitat selection	Kells and Goulson (2003)
	Phenology of the species' life cycles	Early- vs. late-season species	Resource partitioning, asymmetric competition due to differences in the numbers of workers	Pekkarinen (1984); Bowers (1985a)
	Pollen-collection behaviour	Collection of both nectar and pollen vs. collection of pollen only	Resource partitioning	Brian (1957); Heinrich (1979)
Regional	Foraging ranges, body and colony sizes	Foraging efficiency[a]	Size-related spatial scaling of resource utilisation patterns[a]	Bowers (1985a); Brown et al. (1994); Basset (1995); Ritchie and Olff (1999), this paper
	Foraging ranges, body and colony sizes	Predation risk or differences in the susceptibility to natural enemies[a]	Habitat selection, resistance[a]	Brown et al. (1994)

[a] Hypothesised trade-offs and mechanisms that need further investigation

species with small foraging ranges. The inefficiency of larger species can be explained by diminishing returns due to the continued exploitation of a resource patch, i.e. large species will experience critical resource levels earlier because of greater metabolic requirements, and thus leave a patch at higher levels of residual resources than a small species. Owing to this patch-departure behaviour, the more efficient, smaller species can meet their metabolic requirements by the exploitation of residual resources within smaller foraging ranges.

Not only individual metabolic requirements related to body size, but also costs related to colonial existence might affect the hypothesised trade-off between the foraging efficiencies of differently sized species and the extent of their foraging ranges, as the relationship between the foraging ranges and colony sizes of bumblebees might indicate (Fig. 3). Large colonies need more energy than small colonies, because of the higher energetic costs for the production of numerous workers and reproductives (Schaffer et al. 1979). The enhanced energetic requirements are more likely fulfilled within large foraging ranges, where the species can find sufficient resources to sustain large colonies (Heinrich 1979).

Based on Basset's model (1995) and the relationships between the foraging ranges and the body and colony sizes of the different bumblebee species, we propose a novel mechanism of coexistence in bumblebee communities, which could be based on a trade-off in the species' foraging efficiencies. Large bumblebee species (*B. terrestris* agg., *B. lapidarius*) with large colonies possibly need extensive foraging ranges in which they can find enough rewarding resource patches to meet their individual and colonial energetic requirements (Heinrich 1979; Peters 1983). Owing to their comparatively high energetic requirements, these species are assumed to exploit the most rewarding resource patches within their foraging ranges, and depart from exploited patches at relatively high levels of residual resources (Basset 1995). Because of their smaller body and colony sizes, the small bumblebee species (*B. pascuorum*, *B. pratorum*) presumably have lower energetic requirements (Heinrich 1979; Peters 1983). Additionally, they are assumed to forage with a

greater efficiency. The small bumblebee species should therefore be able to rely on the availability of less rewarding or already exploited resource patches within smaller foraging ranges (Basset 1995).

In contrast to the hitherto recognised, locally operating mechanisms of coexistence (Table 3), our proposed mechanism of coexistence is related to species-specific foraging ranges. Considering the possibility of different patterns of spatial resource utilisation, coexistence in bumblebee communities could be determined by various mechanisms, which involve trade-offs that are associated with different spatial scales (Table 3; see also Palmer et al. 2003; Kneitel and Chase 2004).

The mechanism of coexistence suggested here is based on several assumptions and theoretical considerations, which need to be verified in future studies. In particular, the hypothesised trade-off between the bumblebee species' foraging efficiencies, and the energetic costs and benefits related to the different foraging ranges, body and colony sizes need further investigation. As different mechanisms of coexistence (Table 3) might operate simultaneously at different spatial scales (e.g. the bumblebee species might exhibit the same food plant or patch preferences at local and regional spatial scales) (Kneitel and Chase 2004), future analyses should consider multiple spatial scales to identify the relevant scales at which different coexistence mechanisms operate. Furthermore, the relative importance of single mechanisms structuring bumblebee communities should be assessed.

Differences in the quality of resources, which are available within the species' foraging ranges, might favour additional trade-offs. For example, bumblebees might trade-off the exploitation of highly rewarding versus marginally rewarding resource patches in relation to their foraging ranges and energetic requirements (Johnson and Hubbell 1975; Schaffer et al. 1979). Other trade-offs, which might be associated with differences in the bumblebees' foraging ranges, their body or colony sizes, could be related to different travel costs, predation risks, or differences in the susceptibility to natural enemies (Brown et al. 1994). Based on a multiple spatial scale approach, potential effects of these trade-offs on the diversity patterns of bumblebee communities should be examined.

Conclusions

In contrast to the long-standing assumption that the foraging range, and therewith the spatial ecology of bumblebee species is similar (Goulson 2003, but see Walther-Hellwig and Frankl 2000), our results indicate that different bumblebee species perceive their sur-

roundings at different spatial scales. Species-specific differences in the spatial resource utilisation patterns of bumblebees could potentially mediate coexistence and should be acknowledged when designing conservation schemes (Hartley and Kunin 2003). Particularly, the smaller species rely on the limited resources within their more restricted foraging ranges.

Additional multiple spatial scale studies are needed to investigate the potential trade-offs that might be associated with the different foraging ranges, body and colony sizes of the bumblebee species. Furthermore, the relative impact of the different coexistence mechanisms on the diversity of bumblebee communities, and the spatial scales at which these mechanisms operate need to be identified.

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