Effects of Forest Habitats on the Local Abundance of Bumblebee Species: a Landscape-scale Study

ISABEL DIAZ-FORERO[1]*, VALDO KUUSEMETS[1], MARIKA MÄND[1], AVE LIIVAMÄGI[1], TANEL KAART[2] AND JAAN LUIG[1]

[1]*Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, Tartu, 51014, Estonia; *e-mail: isabel.diaz@emu.ee, isadiazf@gmail.com*

[2]*Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, Kreutzwaldi 62, Tartu, 51014, Estonia*

Diaz-Forero, I., Kuusemets, V., Mänd, M., Liivamägi, A., Kaart, T. and Luig J. 2011. Effects of Forest Habitats on the Local Abundance of Bumblebee Species: a Landscape-scale Study. *Baltic Forestry* 17(2): 235–242.

Abstract

The main objective of our study was to analyse how different bumblebee species are influenced by the presence of forest habitats in the surrounding landscape. The local abundance of bumblebee species was studied in 22 semi-natural meadows located in Northeast Estonia. The proportion of forest cover and brushwood cover, the mean patch area of forest and the edge density of forest were calculated at four spatial scales (i.e., radii of 250 m, 500 m, 1000 m and 2000 m). In total, we found 597 individuals of bumblebees belonging to 24 species (gen. *Bombus*), including five species of cuckoo bumblebees (subgen. *Psithyrus*). Our study shows that some bumblebee species seem to have different preferences in terms of the structure of the landscape. Some species may benefit from a heterogeneous landscape with a high proportion of forest habitats (e.g., *B. schrencki*), whereas others seem to prefer open areas (e.g., *B. veteranus*). We also found that some bumblebee species that have large foraging distances (e.g., *B. terrestris*) seem to be negatively affected by forest, as the presence of a high quantity of forest patches in the surrounding landscape could narrow their foraging area. The joint effects of the set of landscape variables related with forests appear to be important for some bumblebee species, specially, but not only, at the largest spatial scale. Overall, our results indicate that the presence of forest is very important for bumblebees, even for some species that prefer open areas, as forest habitats and edges may offer overwintering sites and nesting places for them. In countries like Estonia, where forests are widely distributed and represent a relevant part of the landscape mosaic, this type of habitat should be preserved if conservation of biodiversity is desired. In addition, conservation efforts targeting particular species of bumblebees should consider the landscape preferences of the species under study, and these efforts should aim to maintain the habitat types that are suitable for most bumblebee species.

Key words: *Bombus*, forest cover, brushwood, edge density, mean patch area, landscape indices

Introduction

Bees are considered a vital element of global biodiversity and an important pollinator group in agroecosystems. Their activities support both crops and the diversity of wild plants (Sepp et al. 2004, Goulson et al. 2006, Rundlöf et al. 2008, Knight et al. 2009, Potts et al. 2010). However, mainly due to the intensification of farming practices in agriculture, bumblebees and other pollinators are at risk (Mänd et al. 2002, Goulson et al. 2006, Holzschuh et al. 2008, Xie et al. 2008).

The decline of pollinators, particularly bees, has been widely recognised based on evidence from many countries worldwide (Mänd et al. 2002, Kells and Goulson 2003, Goulson et al. 2006, Williams and Osborne 2009, Potts et al. 2010). Bumblebees are considered the best-documented group in the existing literature on the topic (Potts et al. 2010). However, according to Goulson et al. (2006), very little is known about the habitat requirements of bumblebees. Many bumblebee species in Europe and North America have declined and become extinct at local levels, whereas other species are still common and widely distributed (Ahrné et al. 2009). The causes of these differences in response are not clear, but they appear to involve particular characteristics of single species such as diet and foraging distances (Ahrné et al. 2009). Williams (2005) suggested that some species have more specific habitat, but Goulson et al. (2006) argued that bumblebees are generally not habitat specialists because all the bumblebee species that they studied were found in more than one biotope; moreover, most species were found across a broad range of biotopes. However, data from monitoring in Finland have shown that some species prefer particular types of habitats (Söderman 1999). According to Goulson et al. (2011), bumblebees have been well-studied in modern agricultural landscapes of Western Europe, the United Kingdom, Asia and North America. These areas usually consist of large monoculture fields separated by field margins and patches of woodlands. However, very little is known about the distribution and ecology of bumblebees elsewhere. It seems important to study the associations between bumblebee species and landscape-scale factors, particularly in areas that have mosaic landscapes with high proportions of forest and natural habitats. In addition, Jones (2011) argues that the abundance and distribution of species are impacted by processes that occur at multiple spatial scales. For this reason, multiple-scale studies are currently needed (Jones 2011). Generally, bumblebees are studied in regions having warmer climates and open landscapes. Therefore, studies conducted on bumblebee populations on the northern areas and in more forested landscapes are of great interest.

Different kinds of relationships have been found between forest cover and bees: e.g., Taki et al. (2007) found that bee abundance and species richness were positively related to forest cover (at a radius of 750 m), whereas Winfree et al. (2007) found negative relationships between similar variables (at a radius of 1600 m). Other authors have found differences in the behaviour between some species of bumblebees. There is the case of *B. pascuorum* and *B. terrestris* that were studied by Kreyer et al. (2004); they found that although forest cover did not represent a barrier for both species, *B. terrestris* seems to prefer open landscapes. However, there is still little knowledge about the influence of forest on bumblebees and species-specific studies are currently needed (Kreyer et al. 2004). Estonia is a country with a landscape dominated by forest; for this reason, it is important to know how this land cover type influences bumblebees and whether forest could serve as a potential habitat for some bumblebee species.

We analysed how the local abundance of different bumblebee species is influenced by the presence of forest cover in the surrounding landscape. Our study was carried out in Northeast Estonia, where forests dominate the landscape. Our main objective was to study the relationships of every single species of bumblebees to a set of landscape variables related to forest and calculated at various spatial scales. In addition, we performed multiple regression analysis for each bumblebee species with more than 20 individuals using the landscape variables at different spatial scales as predictors; this was done to explain the joint effects of the landscape variables on the abundance of individual species.

Materials and methods

Study area

Our research was carried out in Ida-Virumaa County, Northeast Estonia. The total area of the county is 336,400 ha, approximately 7.4% of the total area of Estonia. The landscape in the region is generally dominated by forests, which occupy an area of 195,245 ha (approximately 58% of the total area of Ida-Virumaa). The region is also covered to a lesser extent by brushwoods having a total area of 21,701 ha (approximately 6.5% of the area of the county). The most common types of forests in the study area are coniferous and mixed and are dominated by pines and spruce trees. We selected 22 semi-natural meadows in the region as study sites. The areas of these meadows range from 0.10 to 3.83 ha.

Survey

Field work was done in 2008 and 2009, during June, July and August, the warmest months of the year. The visits were made twice each year. The first visit was made in early summer in June and the second in late summer, during the end of July or at the beginning of August. We used a systematic walking survey to count bumblebees (Kumar et al. 2009). The counting of individuals and identification of bumblebee species were done by sight, mainly on the wing or by the colour of the bumblebee when they were standing on the flowers. When the observer could not identify the bumblebee species on site, some individuals were captured with an insect net for later identification in the laboratory. The surveys took approximately 45 min or more per visit per study site, until all the species present in the site were recorded. Our method was based on Goulson et al. (2006). Individuals and species of bumblebees were counted between 10:00 h and 16:00 h when the weather conditions were appropriate (i.e., temperature more than 18ºC and wind speed less than 5 by the Beaufort scale). Our source for the nomenclature of bumblebees was the Fauna Europaea Web Service (2004). The average air temperature in Ida-Virumaa County during summer (including June, July and August) was a bit higher in 2009 than in 2008 (15.1ºC and 14.9ºC, respectively).

Proportion of forest and brushwood

We determined the percentage of forest cover and brushwood cover within a radius of 250 m, 500 m, 1000 m and 2000 m around the centre of each study site. The forest cover in our study region is mainly composed of managed mixed forest; birches, pines and spruces are among the dominant trees. The brushwood cover is characterized by the presence of deciduous trees, woody seedlings, shrubs and young trees, primarily willows, maples, birches, among others, which have become established on abandoned agricultural land, in overgrown meadows or in forest clearings. Calculations were performed using the digital Estonian Basic Map at a scale of 1:10,000 provided by the Estonian Land Board. We used the software ArcGIS 9.3.

Landscape indices

In addition to the proportion of forest and brushwood, we used two Fragstats indices in our study: mean patch area of forest (AREA_MN) and edge density of forest (ED). AREA_MN equals the sum, across all patches of the corresponding patch type (here, forest) of the area of the patches, divided by the total number of patches of the same type (McGarigal et al. 2002). We used "mean patch size" because it gives information about the size of the patches and the number of patches at the same time. ED equals the sum of the lengths of all edge segments involving the corresponding patch type, divided by the total landscape area and multiplied by 10,000 (to convert to hectares) (McGarigal et al. 2002). These variables were also calculated at four spatial scales, i.e., radii of 250 m, 500 m, 1000 m and 2000 m. We used the software Fragstats, version 3.3.

Statistical analysis

Data on bumblebees were collected during two years, but we used the total numbers of species and individuals in our analyses. Spearman rank order correlation analysis was applied to describe the relationships between the landscape variables (i.e., proportion of forest, proportion of brushwood, mean patch area of forest and edge density of forest) at various spatial scales (at radii of 250 m, 500 m, 1000 m and 2000 m) and local abundance of different bumblebee species. For each landscape variable and species combination the scale corresponding to the strongest relationship was selected and the statistical significance of the selected relationships was tested, considering 24 tests (one for every species) performed with a single landscape variable (at the most suitable scale) and the species abundance as one experiment, and applying the Benjamini-Hochberg correction to the p values. The relationships with corrected p value < 0.05 were considered statistically significant. When the correlation coefficient (r_s) was between 0.0 and ±0.3, the correlation was considered to be weak; when r_s was between ±0.3 and ±0.6, the correlation was medium; and when r_s was between ±0.6 and ±1, the correlation was strong. Additionally, multiple regression analysis was performed to study the joint effect of the four landscape variables at different scales on the local abundance of individual species, using only the bumblebee species with more than 20 individuals. STATISTICA 9 software was used for all the statistical analyses.

Results

Local abundance of bumblebee species

A total of 24 species of bumblebees (gen. *Bombus*), including five species of cuckoo bumblebees (subgen. *Psithyrus*), were found in Ida-Virumaa. Currently, 29 species of bumblebees, including seven species of cuckoo bumblebees, occur in Estonia. The total number of individuals recorded was 597, including 150 males, 84 queens and 363 workers. The bumblebee species with the highest number of individuals were *B. pascuorum*, *B. lucorum* and *B. ruderarius* with 140, 70 and 58 individuals, respectively. In contrast, *B. muscorum* and *B. distinguendus* were the bumblebee species having the lowest abundance (Table 1).

Table 1. Total number of individuals of bumblebees per species found in 2008 and 2009

Species	Number of individuals	
	2008	2009
Bombus cryptarum (Fabr.)	13	11
Bombus distinguendus Morawitz	1	0
Bombus hortorum (L.)	5	6
Bombus hypnorum (L.)	3	6
Bombus jonellus (Kirby)	2	16
Bombus lapidarius (L.)	5	21
Bombus lucorum (L.)	18	52
Bombus muscorum (L.)	1	0
Bombus pascuorum (Scopoli)	70	70
Bombus pratorum (L.)	6	9
Bombus ruderarius (Müller)	26	32
Bombus semenoviellus Skorikov	0	7
Bombus schrencki Morawitz	6	10
Bombus soroeensis ssp. Soroeensis (Fabr.)	9	5
Bombus soroeensis ssp. Proteus (Fabr.)	1	15
Bombus soroeensis ssp. soroeensis x proteus (Fabr.)	8	13
Bombus sylvarum (L.)	5	13
Bombus terrestris (L.)	2	16
Bombus veteranus (Fabr.)	3	24
Psithyrus bohemicus Seidl.	6	27
Psithyrus campestris (Panzer)	3	13
Psithyrus norvegicus (Sparre-Schneider)	3	8
Psithyrus rupestris (Fabr.)	9	9
Psithyrus sylvestris (Lep.)	2	7
Total	207	390
Average per meadow	9.41	17.73
Standard error	0.90	1.87

Relations between bumblebees and proportion of forest

We found that two species of cuckoo bumblebees have medium positive correlations with the proportion of forest: *P. bohemicus* and *P. norvegicus* at 250 m (r_s = 0.54, p = 0.04; r_s = 0.57, p = 0.04, respectively). Among the bumblebee species known to prefer forest and forest margins, we found that *B. schrencki* was positively associated with the proportion of forest at 500 m (r_s = 0.58, p = 0.04). In addition, the most abundant species in the study area, *B. pascuorum*, was medium positively correlated with this variable at 250 m, but the relationship was nearly statistically significant (r_s = 0.49, p = 0.07).

In contrast, negative correlations were found between some species of bumblebees and the proportion of forest. *B. veteranus* and *B. terrestris*, both species have negative relationships with the proportion of forest in a similar progressive trend, i.e., the larger the spatial scale, the stronger the relationship between the variables (Figure 1); the strongest relationship was found at the spatial scale of 2000 m (in the case of *B. veteranus*, r_s = -0.63, p = 0.03; and in the case of *B. terrestris*, r_s = -0.55, p = 0.04). On the contrary, *B. ruderarius* and *B. lapidarius* had nearly significant negative correlations with the proportion of forest at the smallest spatial scale, i.e., 250 m (r_s = -0.46, p = 0.09; r_s = -0.50, p = 0.06, respectively).

Relations between bumblebees and proportion of brushwood

We found a medium positive correlation between *B. schrencki* and the proportion of brushwood at a large spatial scale (at 1000 m, r_s = 0.60, p = 0.03). *B.*

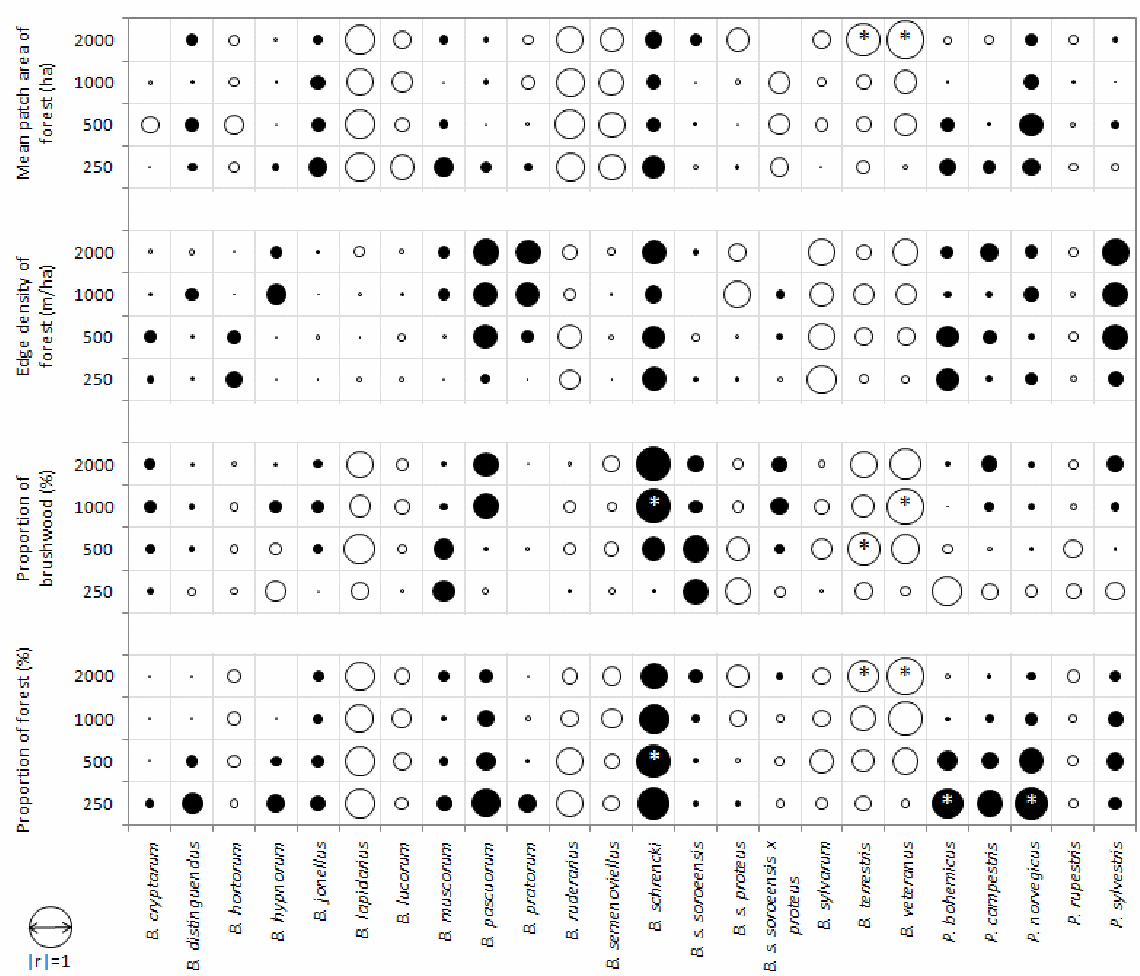

Figure 1. Relationships between the local abundance of bumblebee species and the studied landscape characteristics at various spatial scales based on the Spearman rank correlation coefficients (r_s). The width of the circle indicates the strength of the relationship (the bigger the circle, the stronger the relationship between the variables) and the colour determines the direction of the relationship (black circles correspond to positive relationships and white circles to negative relationships). The stars (*) inside the circles indicate the statistically significant correlations, after Benjamini-Hochberg correction (p < 0.05), for the spatial scale with the strongest relationship

pascuorum was also positively correlated with this variable at 1000 m, but this correlation did not remain statistically significant after Benjamini-Hochberg correction (r_s = 0.44, p = 0.12). In addition, we found that the subspecies *B. s. soroeensis* and *B. s. proteus* showed opposing relationships with the proportion of brushwood (Figure 1): *B. s. soroeensis* was positively correlated at 500 m, whereas *B. s. proteus* was negatively correlated at 250 m; however, these correlations were not statistically significant after the correction (r_s = 0.44, p = 0.12; r_s = -0.45, p = 0.12, respectively). Other negative correlations were detected between the proportion of brushwood and some species of bumblebees, i.e., *B. terrestris* at 500 m (r_s = -0.56, p = 0.04), *B. veteranus* at 1000 m (r_s = -0.63, p = 0.03), and *B. lapidarius* with a nearly significant correlation at 500 m (r_s = -0.54, p = 0.05). Also, *P. bohemicus* appeared to have a nearly significant negative correlation with the proportion of brushwood at 250 m (r_s = -0.52, p = 0.06); in contrast, this species was found to be positively correlated with the proportion of forest at the same spatial scale (see previous section) (Figure 1).

Relations between bumblebees and landscape indices

Some bumblebee species showed significant positive relationships with edge density, i.e., *B. pascuorum*, *B. pratorum* and *P. sylvestris* at 2000 m; however, none of these correlations remained statistically significant after Benjamini-Hochberg correction (r_s = 0.45, p = 0.15; r_s = 0.43, p = 0.15; r_s = 0.46, p = 0.15, respectively). In addition, medium negative relationships were detected between the edge density of forest and some bumblebee species (but these correlations were not statistically significant after the correction): *B. sylvarum* at 250 m (r_s = -0.49, p = 0.15), *B. s. proteus* at 1000 m (r_s = -0.46, p = 0.15) and *B. veteranus* at 2000 m (r_s = -0.46, p = 0.15).

We found medium negative relationships between the mean patch area of forest and some bumblebee species: *B. terrestris* and *B. veteranus* at 2000 m (r_s = -0.59, p = 0.04; r_s = -0.65, p = 0.02, respectively). There were other nearly significant negative correlations between this variable and two bumblebee species at 500 m, i.e., *B. ruderarius* (r_s = -0.51, p = 0.09) and *B. lapidarius* (r_s = -0.52, p = 0.09).

Joint effects of landscape variables on individual species

The joint effects of landscape variables on the abundance of individual species had the best fit at different spatial scales (Table 2). The highest association for two of the most abundant species, *B. pascuorum* and *B. ruderarius*, was found at the scale of 2000 m; for both species the models were statistically significant and explained 51% and 43% of the variation in their abundance, respectively (Table 2). Other species that showed the best fit at the largest spatial scale were *B. cryptarum* and *B. veteranus*, and their models explained 50% and 30%, respectively; however, only the regression model for *B. cryptarum* was statistically significant (Table 2). In contrast, *P. bohemicus* was mostly influenced by the landscape variables at the smallest spatial scale (250 m); this model explained 62% of the variation and it was statistically significant (Table 2).

Previously, the bumblebee species *B. cryptarum* was not significantly associated with any of the single landscape variables (Figure 1). However, this species showed strong associations with the combination of landscape variables at the largest spatial scale, as it was mentioned above. In addition, *B. cryptarum*

Table 2. Results of the multiple regression analyses. For each bumblebee species with over 20 individuals, four models corresponding to the different spatial scales were fitted; regression coefficients and model fit characteristics of the best model (with the highest R^2 and the smallest p-value) are presented

Species	Scale with the best fit	Model intercept	Regression coefficients				R^2	Model p value
			Proportion of forest (%)	Proportion of brushwood (%)	ED[a] (m/ha)	AREA_MN[b] (ha)		
B. cryptarum	2000	3.231	0.081*	0.049	-0.066*	-0.061*	0.500	0.014
B. lapidarius	500	2.354	-0.070	-0.103	0.019	0.030	0.370	0.081
B. lucorum	250	4.247	0.028	-0.084	-0.001	-0.533	0.290	0.189
B. pascuorum	2000	2.032	0.061	0.359	0.040	-0.109*	0.508	0.013
B. ruderarius	2000	11.368	0.202*	0.321	-0.210*	-0.181*	0.427	0.041
B. s. soroeensis x proteus	1000	1.505	-0.023	0.208	0.002	-0.019	0.295	0.179
B. veteranus	2000	2.555	-0.005	-0.058	-0.005	-0.028	0.297	0.177
P. bohemicus	250	-1.215	0.087*	-0.103*	0.007	-0.471*	0.618	0.002

[a] Edge density of forest; [b] Mean patch area of forest
* Regression coefficients significant at p < 0.05

showed some significant associations inside the regression model: a positive relationship with the proportion of forest, and negative relationships with edge density and mean patch area of forest (Table 2).

Discussion

Our results showed that the presence of forest in the surrounding landscape of the habitat is an important factor for some species of bumblebees. In our study, *B. pascuorum* (the most abundant and widely distributed species in the study area), *B. schrencki* and particularly two species of cuckoo bumblebees (i.e., *P. bohemicus* and *P. norvegicus*) seemed to prefer landscapes having high proportions of forest in the surrounding areas. This finding is consistent with a study on bumblebees in Finland that recognised these species of cuckoo bumblebees as forest species (Bäckman and Tiainen 2002). On the other hand, *B. pascuorum* seemed to be positively influenced by the presence of forest cover at a small spatial scale. A possible explanation for this positive association was given by Goulson et al. (2010). They argued that *B. pascuorum* tends to nest above the ground in areas of leaf litter and thickets, and woodland areas are likely to offer these types of nesting sites (Goulson et al. 2010). In addition, we found clear indications that *B. schrencki* was positively influenced by the presence of forest. This species is said to prefer forest and forest margins (Söderman 1999). According to Söderman (1999), the expansion of this bumblebee in the Baltic countries was promoted by the rapid afforestation of open fields.

Other bumblebee species, particularly *B. terrestris*, *B. veteranus*, *B. lapidarius* and *B. ruderarius*, showed negative trends with the proportion of forest. These species seemed to prefer open areas. Mänd et al. (2002) found that the species *B. lapidarius*, *B. veteranus* and *B. lucorum* were particularly numerous in agricultural habitats, which are open areas. The bumblebee *B. lapidarius* belongs to a group of specialists on Fabaceae, a large family of flowering plants that are commonly found in grasslands (Goulson et al. 2005). Also, species such as *B. terrestris* and *B. lapidarius* are considered spatial generalists because they have large foraging distances (Walther-Hellwig and Frankl 2000a, Walther-Hellwig and Frankl 2000b). In a recent study, Hagen et al. (2011) found that some bumblebee species are able to flight long distances (maximum distances of 1.3 – 2.5 km) and to use large areas (0.25 – 43.53 ha); e.g., they found that *B. terrestris* can flight a maximum distance of 2.5 km. These bumblebee species may prefer an open landscape to have more freedom for their long-distance flights. Similarly, Bäckman and Tiainen (2002) classified *B. ruderarius*, *B. lapidarius* and *B. veteranus* as species preferring open habitats. Other species, such as *B. pascuorum*, are considered ubiquitous as they can be found in different types of habitats (Bäckman and Tiainen 2002, Goulson et al. 2006).

Medium and strong relationships involving brushwood were found for some bumblebees. Some species were positively related with the proportion of brushwood, i.e., *B. schrencki* and *B. pascuorum*, whereas others were negatively related, i.e., *B. terrestris*, *B. veteranus*, *B. lapidarius* and *P. bohemicus*. In addition, we found that the subspecies *B. s. soroeensis* and *B. s. proteus* seem to be ecologically different: *B. s. soroeensis* appears to prefer brushwoods, whereas *B. s. proteus* does not. Positive relationships may occur because many patches of brushwood have grown in areas that were former meadows. The soil of these areas is rich in calcium and can therefore support more flowering plant species. Additionally, brushwood areas are dominated by willows that offer food during their spring flowering period. However, brushwood areas dominated by willows might also represent an ecological trap for bumblebees. Food resources would become scarce in summer and these areas would no longer be able to provide good forage places for bumblebees.

Relationships involving edge density of forest seem to be positive for some species of bumblebees, i.e., *B. pascuorum*, *B. pratorum* and *P. sylvestris*, whereas negative relationships were found for *B. sylvarum*, *B. s. proteus* and *B. veteranus*. A positive relationship between *B. pascuorum* and edge density may occur because this species prefers bell-shaped flowers. Flowers having this shape occur commonly in berry-bearing plants, and these plants often grow close to forests or in forest margins. In general, edges may support a greater abundance and diversity of flowering plants. The species *B. pratorum* was also positively associated with forest edges. This finding is consistent with Goulson et al. (2005); they suggested that early-emerging species like *B. pratorum* are related to woodland and woodland edges. Sepp et al. (2004) suggested that edges are particularly important in April and May as bumblebee queens forage from the flowering willows that are commonly found in the forest edges of Estonia.

Negative associations were found between the mean patch area of forest and some species of bumblebees (i.e., *B. terrestris*, *B. veteranus*, *B. lapidarius* and *B. ruderarius*). Kreyer et al. (2004) have found that even though forest did not seem to represent a barrier for the bumblebee *B. terrestris*, this species seems to prefer open areas. Overall, mean patch area of forest showed a negative pattern of relationships with the local abundance of the bumblebee species that were significantly associated with this variable, even when the joint effects of the landscape variables were analysed in multiple regression. Moreover, this landscape index appears to be important for the bumblebee species that seem to prefer open areas, judging from the negative relationships found with the proportion of forest. One possible explanation is that a high number of patches of forest may be seen as potential obstacles in the landscape for some species of foraging bumblebees (Kreyer et al. 2004, Goulson et al. 2010), particularly for those like *B. lapidarius* and *B. terrestris* that have large foraging distances (Walther-Hellwig and Frankl 2000a, Walther-Hellwig and Frankl 2000b).

The joint effects of the set of landscape variables related with forests appear to be important for some bumblebee species (i.e., *B. pascuorum*, *B. ruderarius*, *B. cryptarum* and *P. bohemicus*), specially, but not only, at the largest spatial scale.

Conclusions

Our study shows that some bumblebee species seem to have preferences related to the structure of the landscape. Some species may benefit from a heterogeneous landscape with a high proportion of forest habitats (e.g., *B. schrencki*), whereas others seem to prefer open landscapes (e.g., *B. veteranus*). Some bumblebee species that have large foraging distances (e.g., *B. terrestris*) also seem to prefer open landscapes because the presence of many forest patches in the surrounding landscape could narrow their foraging area, affecting their long-distance flights. Other studies have also found differences in behaviour and preferences between some bumblebee species (e.g., Kreyer et al. 2004).

In general, our results indicate that the presence of forest is very important for bumblebees, even for those species that seem to prefer open areas, because forest habitats may provide overwintering sites and nesting places. Similarly, Taki et al. (2007) concluded in their study on potential pollinators that forest loss at the landscape scale may cause negative impacts on bee communities. In countries like Estonia, where forests are widely distributed and represent a relevant part of the landscape mosaic, forest habitats seem to be very important for some species of bumblebees and therefore should be preserved if conservation of biodiversity is desired. In addition, conservation efforts intended to protect particular species of bumblebees should consider their preferences for surrounding landscapes. These efforts should aim to maintain the habitat types that are suitable for the target species.

Acknowledgements

This research was funded by targeted financing of the Estonian Ministry of Education and Research (SF1090050s07, SF0170057s09), Estonian Science Foundation Grant No. 7391 and by an applied research project of the Estonian Ministry of Agriculture (T8014PKPK). We greatly thank the two anonymous referees whose comments greatly improved the manuscript.

References

Ahrné, K., Bengtsson, J. and Elmqvist, T. (2009) Bumble Bees (*Bombus* spp) along a Gradient of Increasing Urbanization. *PLoS ONE* 4 (5): e5574.

Bäckman, J.C. and Tiainen, J. 2002. Habitat quality of field margins in a Finish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture, Ecosystems and Environment* 89: 53–68.

Fauna Europaea Web Service. 2004. Fauna Europaea version 1.1. http://www.faunaeur.org.

Goulson, D., Hanley, M.E., Darvill, B. and Ellis, J.S. 2006. Biotope associations and the decline of bumblebees (Bombus spp.). *Journal of Insect Conservation* 10 (2): 95–103.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. and Knight, M.E. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122: 1–8.

Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L. and Darvill, B. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology* 47 (6): 1207–1215.

Goulson, D., Rayner, P., Dawson, B. and Darvill, B. 2011. Translating research into action; bumblebee conservation as a case study. *Journal of Applied Ecology* 48 (1): 3–8.

Hagen, M., Wikelski, M. and Kissling, W.D. 2011. Space use of bumblebees (*Bombus* spp.) revealed by radio tracking. *PLoS ONE* 6 (5): e19997.

Holzschuh, A., Steffan-Dewenter, I. and Tscharntke, T. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117: 354–361.

Jones, J.P.G. 2011. Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* 48 (1): 9-13.

Kells, A.R. and Goulson, D. 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation* 109: 165–174.

Knight, M.E., Osborne, J.L., Sanderson, R.A., Hale, R.J., Martin, A.P. and Goulson, D. 2009. Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conservation and Diversity* 2: 116–124.

Kreyer, D., Oed, A., Walther-Hellwig, K. and Frankl, R. 2004. Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biological Conservation* 116 (1): 111–118.

Kumar, S., Simonson, S.E. and Stohlgren, T.J. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. *Biodiversity and Conservation* 18 (3): 739–763.

Mänd, M., Mänd, R. and Williams, I.H. 2002. Bumblebees in the agricultural landscape of Estonia. *Agriculture, Ecosystems and Environment* 89: 69–76.

McGarigal, K., Cushman, S.A., Neel, M.C. and Ene, E. 2002. FRAGSTATS, Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the website: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Natural History Museum. 2011. Research and curation. Available at the website: http://www.nhm.ac.uk.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* 25 (6): 345–353.

Rundlöf, M., Nilsson, H. and Smith, H.G. 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation* 141 (2): 417–426.

Sepp, K., Mikk, M., Mand, M. and Truu, J. 2004. Bumblebee communities as an indicator for landscape monitoring in the agri-environmental programme. *Landscape and Urban Planning* 67: 173–183.

Söderman, G. 1999. Diversity of pollinator communities in Eastern Fennoscandia and Eastern Baltics. Results from pilot monitoring with yellow traps in 1997 - 1998. Finnish Environment Institute 355, Nature and Natural Resources, Edita Ltd, Helsinki, Finland, 69 pp.

Taki, H., Kevan, P.G. and Ascher, J.S. 2007. Landscape effects of forest loss in a pollination system. *Landscape Ecology* 22: 1575–1587.

Walther-Hellwig, K. and Frankl, R. 2000a. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology* 124 (7-8): 299–306.

Walther-Hellwig, K. and Frankl, R. 2000b. Foraging distances of *Bombus muscorum, Bombus lapidarius,* and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behavior* 13 (2): 239–246.

Winfree, R., Griswold, T. and Kremen, C. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21 (1): 213–223.

Williams, P.H. 2005. Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biological Conservation* 122: 33–43.

Williams, P.H. and Osborne, J.L. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40: 367–387.

Xie, Z., Williams, P.H. and Tang, Y. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation* 12: 695–703.

Received 03 March 2011
Accepted 16 November 2011

ВЛИЯНИЕ ЛЕСНЫХ МЕСТООБИТАНИЙ НА ЛОКАЛЬНОЕ ОБИЛИЕ ВИДОВ ШМЕЛЕЙ: ИССЛЕДОВАНИЕ С ИСПОЛЬЗОВАНИЕМ РАЗНОМАСШТАБНОГО АНАЛИЗА

И. Диаз-Фореро, В. Куусеметс, М. Мянд, А. Лиивамяги, Т. Каарт и Я. Луиг

Резюме

Главной целью нашего исследования был анализ влияния наличия лесных местообитаний в окружающем ландшафте на различные виды шмелей. Обилие видов шмелей было исследовано на 22 полуприродных лугах в Северо-Восточной Эстонии. Доля лесов и кустарников, средняя площадь облесенных участков и густота опушки оценивались в четырех масштабах: в радиусе 250 м, 500 м, 1000 м и 2000 м. Всего было обнаружено 597 особей шмелей, принадлежащих к 24 видам (gen. *Bombus*), включая 5 видов шмелей-кукушек (subgen. *Psithyrus*). Наше исследование показало, что некоторые виды шмелей, очевидно, имеют разные предпочтения в отношении структуры ландшафта. Некоторые виды могут получать преимущество от обитания в гетерогенном ландшафте с большой долей лесных местообитаний (например, *B. schrencki*), тогда как другие, похоже, предпочитают открытые пространства (например, *B. veteranus*). Мы обнаружили также отрицательное влияние леса на наличие некоторых видов, совершающих далекие вылеты за кормом (например, *B. terrestris*) – наличие в ландшафте большого числа облесенных участков сокращает площадь их кормовых угодий.

Общее влияние связанных с лесом параметров оказалось важным для некоторых видов шмелей, особенно в случае максимального масштаба, но не только. В целом, наши результаты показывают, что лес очень важен для шмелей, даже для некоторых видов, предпочитающих открытый ландшафт, так как лесные местообитания и опушки предоставляют им места для зимовки и устройства гнезд. В таких странах как Эстония, где леса широко распространены, и составляют значительную часть ландшафтной мозаики, для сохранения биоразнообразия следует сохранять этот тип местообитаний. Кроме того, усилия, направленные на сохранение определенных видов шмелей, должны учитывать их ландшафтные предпочтения. Вместе с тем, эти усилия должны быть направлены и на сохранение местообитаний, пригодных для большинства видов шмелей.

Ключевые слова: шмель, лесное местообитание, структура ландшафта