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Diversity partitioning of wild bee assemblages (Hymenoptera: Apoidea, Apiformes) and species preferences for three types of refuge habitats in an agricultural landscape in Poland

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ABSTRACT. Patterns in bee assemblages consisting of 52 core (most abundant) species in farmland in the Wielkopolska region of W Poland were analysed. The entomological material was assessed during earlier research in 1978-1993 from 18 plots in three habitat types: shelterbelts, roadsides and forest patches. At the scale of the refuge habitat size analysed here, an increase in area only slightly enhanced bee species richness. The bee assemblage structures of roadsides and forest patches differ significantly, but their indicator species do not form any well-defined ecological groups. In non-linear forest patches, the bee community structure was more homogeneous than on roadsides. These two habitat types differed significantly in their species composition. Nine significant indicator species were found, but they did not share any ecological characteristics. Three factors were found to affect significantly the responses of individual bee species in the agricultural landscape: the degree of isolation of the refuge habitat, the edge ratio, and roadsides as a refuge habitat type. A large part of the regional diversity is due to the heterogeneity of habitats within the landscape. Habitat area has little influence on the diversity of wild bees, at least within the size range analysed here. We concluded from this study that, regardless of the habitat type, the density of bees from the summer phenological period is affected by the number of food plant species. Point forest patches are habitats where summer species from the genus *Andrena* and the cleptoparasitic genera *Nomada* and *Sphecodes* achieve their highest abundances. Roadsides negatively affected abundances of wild bees and there were no characteristic species for this type of habitat. We hypothesised that this might be related to the specific ecological part played by this type of habitat.

KEY WORDS: wild bees, habitat islands, shelterbelts, forest patches, roadsides, Western Poland.

INTRODUCTION

Bees play a major role as pollinators in the agricultural landscape. The yields of many fruit and seed crops depend to a large extent on pollinating insects. For bees, crop fields are only temporary sources of food. Because farming activities are frequent, fields are not favourable nesting sites for them. Consequently, bees spend most of the growing season in remnants of natural ecosystems (habitat islands), which are diversity reservoirs of these insects (BANASZAK 1983, HANNON & SISK 2009, MANDELIK et al. 2012). It is thought that good crop pollination is ensured by high densities and diversities of pollinators. Thus, it is important to maintain near arable fields some refuge habitats, rich in herbaceous and woody vegetation, as they have a positive effect on the above features of pollinating insect communities (CIERZNIAK 2003, LOWENSTEIN et al. 2012). Consequently, one of the basic recommendations for shaping the agricultural landscape is to leave some unmanaged patches, which become refuge habitats for many animal species, including bees (BANASZAK 1983). The functionality of the resulting habitat islands in the matrix of cultivated fields depends to a large extent on their spatial relationships (BANASZAK 1992, WINFREE 2010). In the farming landscape, the number of habitat islands, their quality and spatial distribution may vary widely (PYWELL et al. 2006). An increase in the percentage contribution of semi-natural habitats near crop fields has a positive effect on bee communities in the flowering season (STEFFAN-DEWENTER et al. 2002).

The value of refuges for bees can be determined by the refuge habitat type (distinguished from the human standpoint) (BANASZAK 1983, STEFFAN-DEWENTER et al. 2002, HANNON & SISK 2009) or by its characteristics, like total area (BOMMARCO et al. 2010, HINNERS et al. 2012) or abundance of bee forage plants (BANASZAK 1984, POTTS 2003). The spatial distribution of some habitat islands may, in turn, cause them to become isolated and, consequently, may affect the species composition of the insects occurring there (CALVILLO et al. 2010, SCHÜEPP et al. 2011). LE FÉON et al. (2013) noted that the bee fauna of some habitats, even those apparently very similar to one another, may be very distinct. Bees are a highly diverse group and because of differences between species, they respond in various ways to local conditions in habitat islands. The question arises as to what the network of refuge habitats should look like if it is to support the desired structure and abundance of pollinating insects in the landscape. So far there has been no clear answer to this question.

Many long-term effects of shaping the agricultural landscape, such as fragmentation and the associated change in metapopulation dynamics (GYLLENBERG & HANSKI 1997, CASAGRANDI & GATTO 2002), have not yet been described (AIZEN & FEINSINGER 2003), and the functioning of pollinators in a network of refuge habitats has been little studied. The facts and suggested hypotheses concerning these issues show that this problem should be viewed from a very broad perspective. Bees vary in their intensity of migration between patches of favourable habitat (FRANZÉN et al. 2009, DORCHIN et al. 2013), and some components of the environment may hamper their spread (ZURBUCHEN et al. 2010). A high diversity of bees in the agricultural landscape may be much more favourable if the hypothesis concerning the functional complementarity of plants and their pollinators proves to be true. It assumes that pollination success depends on the proper sequence of pollinators that complement one another (BLÜTHGEN & KLEIN 2011). Another potentially important problem for pollinators in the agricultural landscape is neophobia – the unwillingness of bees to switch to another species of forage plants – and a shortage of additional food sources. A rise in the number or area of refuge habitats may increase the density of pollinators in the landscape, thus reducing the bees' exclusive dependence on abundantly flowering crops (RANDS & WHITNEY 2010, 2011). In view of all this, research into pollinators in the agricultural landscape remains a challenge, both theoretical and practical. One of the first steps should be to identify the factors responsible for the occurrence of individual bee species in refuge habitats.

In this study, we analysed the 52 most frequent (up to 0.1% of the total bee density) bee species (*vide* Appendix 1) and their relations with selected characteristics of refuge habitats in the agricultural landscape. Three questions are addressed in this paper: 1) What is the species turnover within and between the two agricultural landscapes analysed? 2) Are different types of refuge habitats similar to each other as regards species composition? 3) How do different bee species react to specific characteristics of particular types of refuge habitat? We took into consideration the most common habitat types in the agricultural landscape of the Wielkopolska region of W Poland: roadsides, point forest patches and shelterbelts. They are described using their geometric characteristics and foraging suitability.

METHODS

Field studies

In this study we used entomological material collected by the first author during the growing season (April-September) in 1978-1980 (Wierzenica), 1987-1990 and 1991-1993. Some of the results, particularly those concerning species diversity, were published in monographs on wooded islands in the farming landscape (BANASZAK 2000, BANASZAK & CIERZNIAK 2002). Here we attempt to synthesise those earlier studies and focus on diversity partitioning , community structure and responses of individual bee species to changes in the characteristics of refuge habitats.

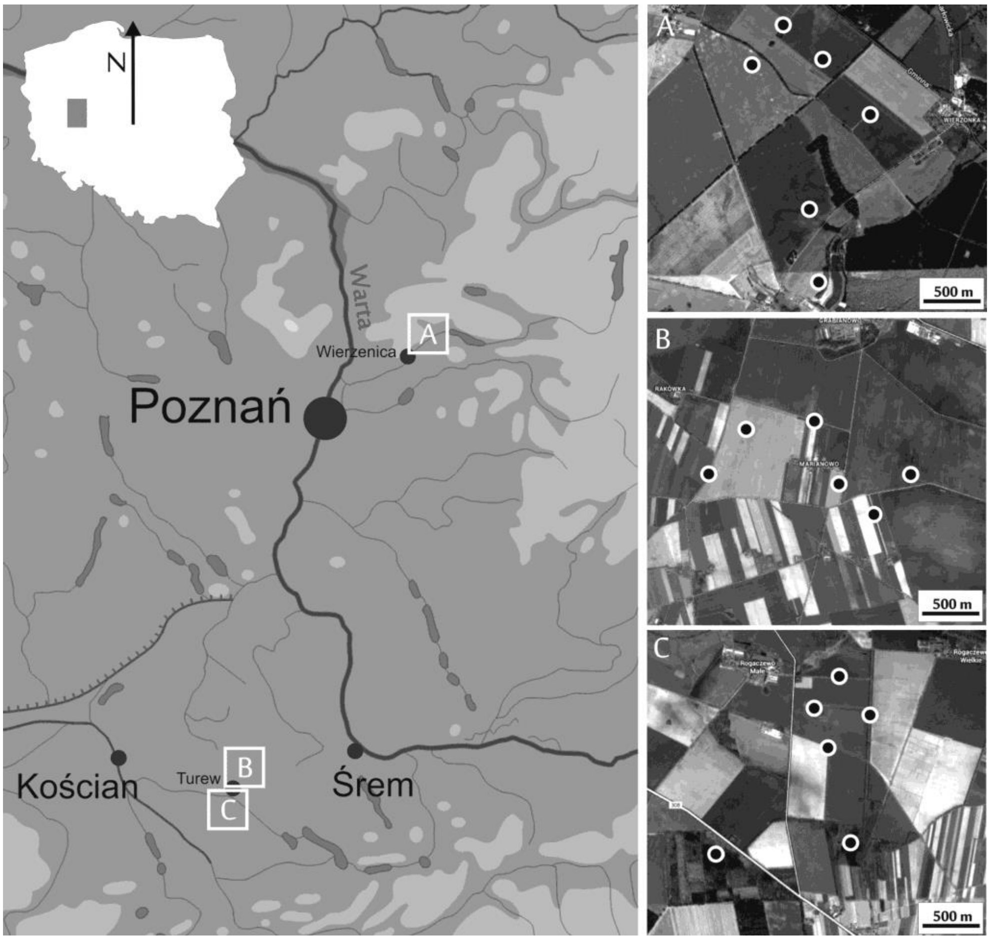

Fig. 1. Map of the 18 refuge habitats in two agricultural landscapes: A – near Wierzenica (10 km NE of Poznań); B, C – near Turew (50 km S of Poznań). The filled black circles indicate the sampling plots in the landscapes.

Data on species composition and diversity were obtained for 18 refuge habitats in two agricultural landscapes (Fig. 1): near Turew (50 km S of Poznań) and near Wierzenica (10 km NE of Poznań) in the Wielkopolska region (English: Great Poland) of western Poland. They included 7 forest patches (non-linear), 4 shelterbelts, and 7 roadsides. We regarded the forest areas as small patches (points) of wooded habitats surrounded by cultivated fields, usually in sites inaccessible to farming equipment. Shelterbelts are forest and shrub communities forming belts 5-30 m wide. Roadsides are dominated by herbaceous vegetation formed along rarely used roads. They vary in width from 2 to 14 m (both sides jointly). A detailed description of the study sites can be found in BANASZAK (2000), BANASZAK & CIERZNIAK (2002). Both landscapes are similar with respect to their geology, geomorphology and climate. The soils are brown or grey-brown podzols. The annual precipitation is about 500 mm. The potential vegetation is oak-hornbeam forest (*Galio-Carpinetum*). The landscape near Turew is devoid of extensive woodlands, whereas that near Wierzenica consists of farmland surrounded by extensive forests, with small islands of woodland. The characteristics of these refuge habitats are listed in Tab. 1.

Table 1. Characteristics of refuge habitats in two agricultural landscapes in western Poland. Edge area is the area covered by herbaceous forest edge vegetation in a given habitat. Edge ratio is the edge area of a habitat divided by its total area. Degree of isolation is computed according to the formula $I_i=\Sigma d_{ij}*n^{-1}$, where d_{ij} denotes distance from habitat *i* to habitat *j*, and *n* is the number of habitats. Abbreviations: HC – habitat code, A – area [ha], EA – edge area [ha], ER – edge ration, DI – degree of isolation, CP – cover of bee forage plants [%], NCPS – number of bee forage plants species, HT – habitat type, L – landscape.

HC	A	EA	ER	DI	CP	NCPS	HT	L
F1	0.50	0.14	0.280	417	15	17	forest patch	Wierzenica
F2	0.10	0.03	0.300	469	11	10	forest patch	Wierzenica
F3	0.09	0.04	0.444	456	25	13	forest patch	Wierzenica
F4	0.14	0.06	0.429	464	12	7	forest patch	Wierzenica
F5	0.35	0.08	0.229	388	5	12	forest patch	Wierzenica
S1	0.53	0.25	0.472	203	35	25	shelterbelt	Wierzenica
F6	1.61	0.23	0.143	260	50	18	forest patch	Turew
F7	0.23	0.01	0.043	400	35	16	forest patch	Turew
S2	2.25	0.90	0.400	198	10	14	shelterbelt	Turew
S3	3.60	0.40	0.111	260	5	24	shelterbelt	Turew
S4	0.30	0.01	0.033	422	10	18	shelterbelt	Turew
R1	0.16	0.16	1.000	228	5	11	roadside	Turew
R2	0.12	0.12	1.000	171	15	23	roadside	Turew
R3	0.35	0.35	1.000	88	25	31	roadside	Turew
R4	1.40	1.40	1.000	207	40	26	roadside	Turew
R5	0.40	0.40	1.000	148	30	29	roadside	Turew
R6	0.14	0.14	1.000	172	15	21	roadside	Turew
R7	0.08	0.08	1.000	188	20	11	roadside	Turew

Bee densities were assessed by the transect method (BANASZAK 1980). This involved counting and catching bees with an entomological net while walking along a strip 1 m wide and 200 m long in weather conditions favourable to bees (little or no wind, temperature >20ºC). A single sample consisted of the insects collected as described above, from an area of 200 m^2. Additionally, during each sample collection from a transect, the flowering bee forage plant species and their cover were recorded with 5% accuracy. In each refuge habitat, 19-45 quantitative samples were collected (mean – 29.22), depending on habitat size, to avoid the negative effects of excessive sampling on the local bee communities. Next, the bee density was expressed per 1 hectare. All together 526 samples and 6343 specimens were collected. Using high-resolution aerial photographs, we calculated for each habitat: total area; edge area covered by herbaceous forest edge vegetation (in the case of roadsides, total area was classified as edge); edge ratio (i.e. ratio of edge area to total area); degree of isolation, according to the formula $I_i=\Sigma d_{ij}*n^{-1}$, where d_{ij} denotes distance from habitat i to habitat j, and n is the number of habitats (KING 1969); number of bee forage plant species; and cover (%) of bee forage plants, in relation to total area.

Data analysis

Additive partitioning was used to assess the contribution of various levels of landscape organisation to total species diversity (gamma) in the whole study area (STEVENS 2009). It is based on the simple assumptions that alpha and beta diversity sum up to gamma diversity ($\alpha + \beta = \gamma$), and that species diversity can be partitioned in all cases when samples at the j level are nested within samples at the j+1 level, e.g. habitats (lower level j) within the landscape (higher level $j+1$) or landscapes within regions. For additive partitions of nested sampling design the β-component is calculated as $\beta_m = \gamma - \alpha_m$ at the highest sampling level, and as $\beta_i = \alpha_{i+1} - \alpha_i$ for each lower sampling level (WAGNER et al. 2000; CHRIST et al. 2003). Based on the above assumptions, gamma diversity was partitioned into mean species richness within a single landscape (β_1) and between the landscapes (β_2). It is also possible to apply additive partitioning to species–area relationships (CRIST & VEECH 2006). β_{area} is then defined as the mean deviation between the species richness of the largest habitat patch and the species richness of smaller patches. Because in isolated habitats species richness is highly variable, the maximum species richness (the species richness of the largest habitat) was obtained from values predicted from the species curve in the area ($S = c*A^z$), calculated from the collected data. Expected values and curve fitting was conducted in STATSTICA 10 software (STATSOFT 2012).

Nonmetric multidimensional scaling (NMDS) was used to analyse the similarity of bee assemblages in individual habitats. The Bray-Curtis index was applied as a measure of similarity. To assess statistical significance, differences in structure of bee communities between groups of habitats were then subjected to the multi-response permutation procedure (MRPP) (MIELKE & BERRY 2001). MRPP tests the null hypothesis that there are no differences between the groups described by multidimensional variables. Pair-wise comparisons between groups were made if the overall test detected significant differences.

To identify which species were responsible for the observed differences, we analysed indicator values (IndVal) (DUFRENE & LEGENDRE 1997). The indicator value is also often used to identify species that are closely related to given group of habitats (based on species specificity and fidelity). The values range from 0 to 1. They are high for a species when all individuals are found in the given habitat type and the species is present in all samples from the given habitat type. Statistical significance was assessed using a permutation test with 1000 replications. Indicator species were regarded as significant if their significance was confirmed statistically and their IndVal exceeded 0.25. Calculations were made in the R software environment (RDCT 2011) with the use of *vegan* (OKSANEN et al. 2011) and *labdsv* libraries (ROBERTS 2010).

Next, we attempted to relate individual species' abundances to specific characteristics of the target habitats. We used canonical correspondence analysis (CCA) to enable ordination of the species observed in refuge habitats and their connection with the variables describing individual habitat islands. Earlier, we had applied detrended correspondence analysis (DCA) to assess gradient lengths (JONGMAN et al. 1995). As these were greater than 4 standard deviations, we assumed a unimodal response of the species to the measured factors. CCA with forward selection was then performed to determine the best set of variables describing variation in the bee community structure. Species with negligible densities (lower than 0.1% of the total catch) were excluded from the analyses and a matrix of 52 bee species abundances from 18 habitats were used as input. The remaining densities were log transformed $\log_{10}(x+1)$. Statistical significance was assessed by using a permutation test with 500 replications. Ordination analysis and permutation tests were done using CANOCO 4.5 software (TER BRAAK & ŠMILAUER 2002).

RESULTS

In total, 109 species were recorded in the 18 habitats (BANASZAK & CIERZNIAK 2002). The number of species numbers in individual landscapes was 80 near Turew and 78 near Wierzenica. Thus, more than 70% of the species from the whole study area were found in each of the landscapes. Additive partitioning showed that refuge habitat size only slightly affected total species diversity (Fig. 2). Moreover, values for two habitats were outliers. Shelterbelt S1 had a small area but supported a large number of species. By contrast, a relatively small number of species was observed in the largest habitat S3.

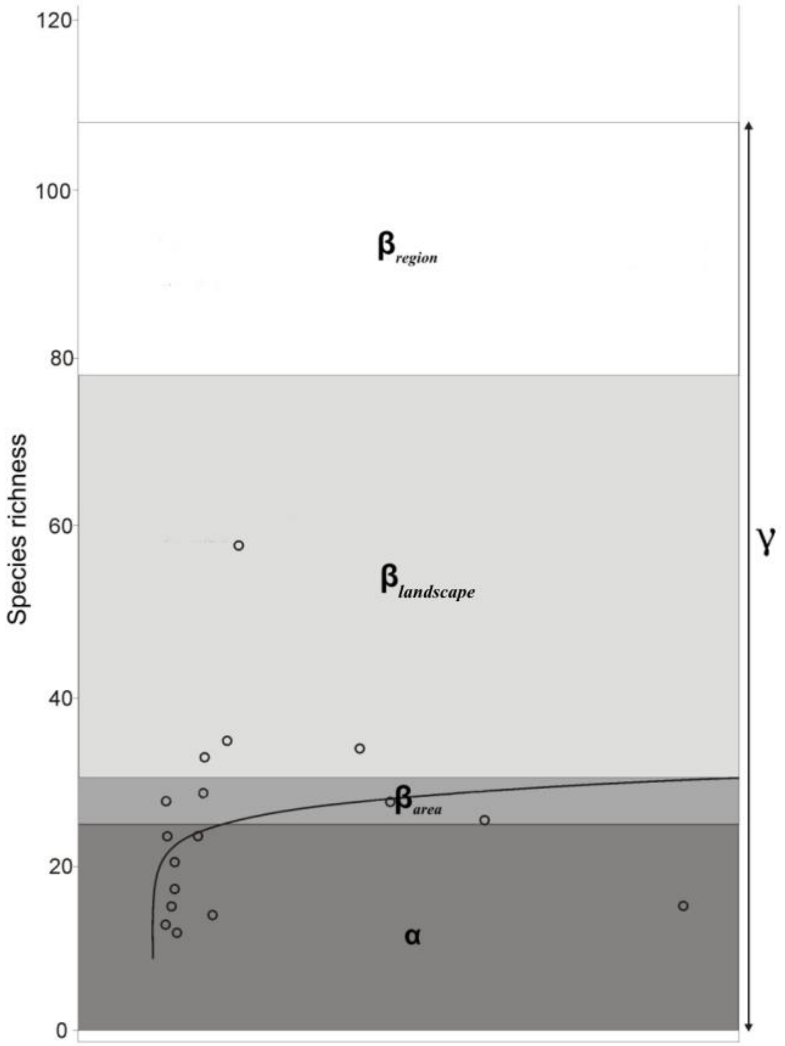

Fig. 2. Additive partitioning of species richness for the habitats studied in two agricultural landscapes in western Poland. Diversity: α = mean species richness in a habitat; β_{area} = species richness explained by the species-area curve; $\beta_{ecoregion}$ = mean number of species not recorded in individual habitats but present in the landscape; $\beta_{georegion}$ = mean number of species not recorded in individual landscapes but present in the total study area. The estimated parameters of the species-area curve function $S=C*A^{Z}$, including outliers, are c=27.15 (P<0.001) and z=0.089 (not significant) respectively. When outliers (S1 and S3) were excluded from the analyses, the corresponding values were c=27.72 (P<0.001) and z=0.15 (P=0.01). The expected number of species for the largest island did not then differ markedly: 30.5 and 31.0 respectively.

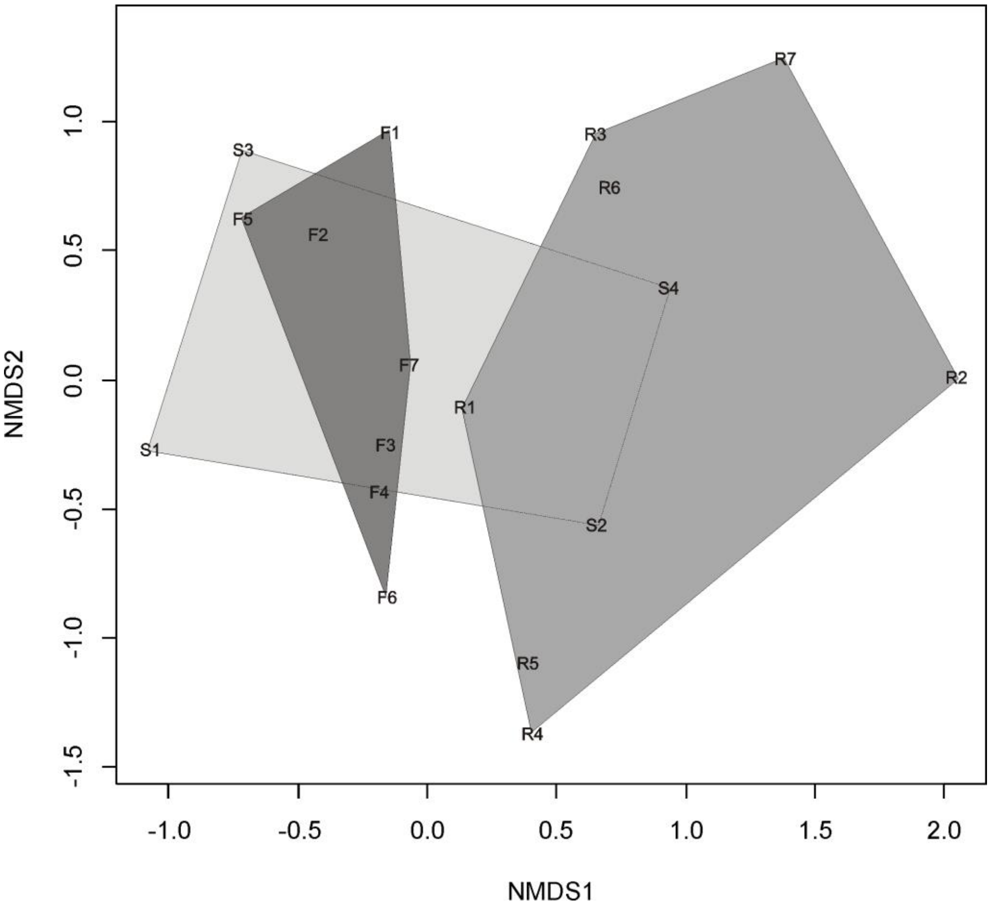

Fig. 3. Nonmetric multidimensional scaling (NMDS) diagram, showing the similarity (Bray-Curtis index) of the bee community structure in individual types of refuge habitats: F = forest patches; S = shelterbelts; R = roadsides.

The beta diversity for the geographical region (comprising two landscapes) made only a small contribution to the total species diversity. It is that part of the species richness which is explained by the differences between the landscapes near Turew and Wierzenica. The beta diversity β_{region} is the mean number of species absent from one of the landscapes but present in the total species pool (109). About 30 out of the total of 109 species would not have been recorded if only one landscape had been studied. Diversity due to variation within landscapes ($\beta_{landscape}$) is a major contributor to the gamma diversity of the region (Fig. 2). About 50 species would not have been recorded within a landscape if only a single locality had been studied. Thus a major role in increasing the number of recorded species in a study area can be attributed to target habitat heterogeneity. The mean number of species not observed (= 5) because of small habitat island size (β_{area}) was relatively low. The mean species richness of a single site (α) was close to 25.

Next we analysed the similarity of bee communities in individual types of refuge habitats, distinguished mostly on the basis of their shape. The NMDS diagram (Fig. 3) shows clear differences in community structure between roadside habitats (R) and forest patches (F). However, shelterbelts (S) are not distinct from them with respect to community structure and overlap both the other groups. This suggests that various factors are responsible for the species composition of wild bees found in shelterbelts. Pair-wise comparisons (MRPP) confirm the significance of differences between forest patches and roadsides (999 permutations, P=0.015). Roadside bee communities are highly heterogeneous, with large differences between individual habitats. Some of them are more similar to those of a number of forest patches and shelterbelts.

In order to focus on indicator species, IndVal analysis was performed on individual refuge habitats (Tab. 2) (DUFRENE & LEGENDRE 1997). In total, 9 species with high indicator values were recorded: 5 for forest patches and 4 for shelterbelts. Roadsides did not have any bee species typical of them, which confirms the high heterogeneity of this group of habitats, visible in the NMDS diagram. Relatively high indicator values, from 0.5607 to 0.8585 for forest patches and from 0.4361 to 0.5916 for shelterbelts, show that these species are strongly associated with the given types of refuge habitats.

Table 2. Significant indicator species and their IndVal values for the studied refuge habitats in the agricultural landscapes of mid-western Poland. The indicator value identifies species that are closely related to a given group of habitats. The probability is the statistical significance assessed using a permutation test with 1000 replications.

Species	Type	Indicator value	Probability
Andrena nigroaenea	Forest patch (F)	0.8585	0.003
Nomada goodeniana	Forest patch (F)	0.7143	0.004
Anthophora furcata	Forest patch (F)	0.6492	0.021
Nomada fucata	Forest patch (F)	0.5714	0.039
Andrena flavipes	Forest patch (F)	0.5607	0.040
Evylaeus nitidulus	Shelterbelt (S)	0.5916	0.017
Andrena fucata	Shelterbelt (S)	0.4741	0.049
Evylaeus albipes	Shelterbelt (S)	0.4409	0.039
Nomada marschamella	Shelterbelt (S)	0.4361	0.047

Wild bee species varied in their response to refuge habitat type and some other properties. Canonical correspondence analysis (CCA) detected non-random preferences for individual habitat types. CCA combined with forward selection detected 3 statistically significant environmental variables associated with species' responses. These include the degree of isolation of a refuge habitat (*P*=0.004), the edge ratio (*P*=0.004), and one habitat type – roadsides (*P*=0.002). The response of species to roadsides is evidently negative, as most of them generally avoid roadsides or occur there irregularly. This may be due to the instability of such habitats or their role as an intermittent food source. The diagram shows correlations between variables describing individual habitat types. Forest patches were isolated to a large degree, while roadsides were the habitats with the highest edge ratio and cover (%) of bee forage plants. Parasitic species, such as *Nomada fucata*, *N. goodeniana*, *Sphecodes ferruginatus*, and *S. monilicornis*, mostly preferred forest patches. Only one species of unspecialised nest parasite of wild bees, *S. ephippius*, was very abundant in the less isolated shelterbelt S1. Less abundantly but more frequently, it was also recorded in non-linear forest patches. Some species located at the centre of the ordination diagram can be classified as generalists, which do not respond clearly to the studied environmental factors.

Species preferring roadsides and significantly associated with an increase in edge ratio included *Apis mellifera*, *Evylaeus calceatus* (a common species of the family Halictidae), and the bumblebees *Bombus sylvarum*, *B. lapidarius*, *B. terrestris* and *B. ruderarius*. Two other species, *Seladonia tumulorum* and *Lasioglossum quadrinotatum*, were also recorded on roadsides, but their occurrence was more closely associated with the cover of bee forage plants than with any habitat type. Nevertheless, most species avoid roadsides or their occurrence in this habitat type is irregular.

Of the 52 species included in the analysis (after the exclusion of species with negligible densities, <0.1% of the total catch), as many as 31 (59%) were present in all the refuge habitats. Another 13 species (25%) were found exclusively in wooded habitats (shelterbelts or non-linear forest patches) and were absent from roadsides. About 5% of species (3 parasitic species) were recorded only in non-linear forest patches. Another 3 species were absent from this habitat type: *Lasioglossum quadrinotatum*, *Halictus rubicundus*, and *Evylaeus albipes*. Only single species were found exclusively on roadsides (*Osmia aerulenta*) and in non-linear forest patches (*Hylaeus communis*). All 52 species except *Anthophora furcata* were polylectic.

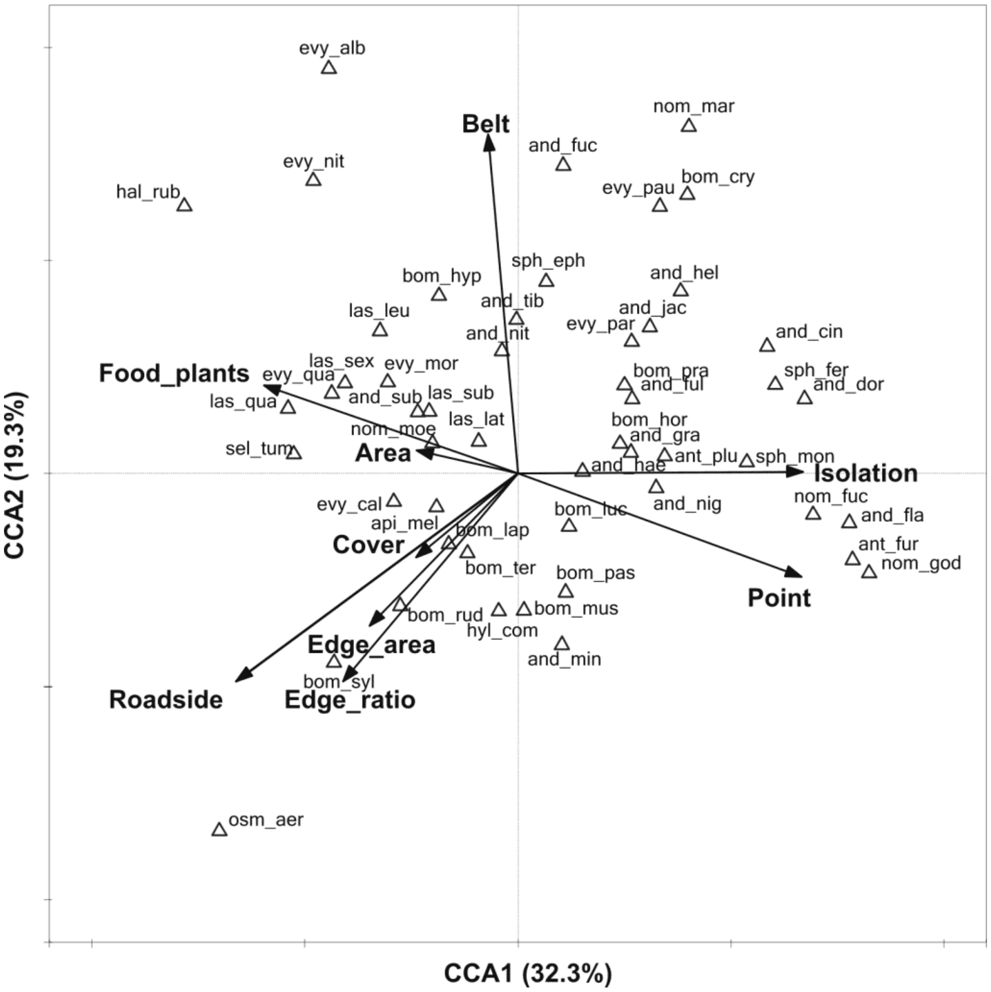

Fig. 4. Canonical correspondence analysis (CCA) diagram with given % of variation in species composition explained by the first two axes. The species codes are explained in Appendix 1. Statistical significance was detected by a permutation test with forward selection for three variables: degree of isolation of refuge habitat (Isolation, *P*=0.0040), edge ratio (Edge_ratio, *P*=0.0040), and roadside habitat (Roadside, *P*=0.0020). The diagram also shows non-significant variables.

CCA indicates that *Osmia aerulenta* is associated with the roadside type of habitat. However, it was found in only 2 of the studied roadsides and its density was low, so it was not a significant indicator species. *Bombus sylvarum*, because of its high density on roadside R3, also shows some preference for this habitat type.

The results obtained using the IndVal method can also be seen on the ordination diagram (Fig. 4). The species strongly associated with a given refuge habitat type exhibit a high correlation with dummy variables for that type. Species from the genera *Sphecodes* LATR., *Nomada* SCOP. (cleptoparasitic species) and *Andrena* FABR. are more abundant in isolated forest patches. They show a negative correlation with the number of food plants or increasing patch area. Many halictid bees (from the genera *Lasioglossum* CURT., *Seladonia* ROB., *Evylaeus* ROB., *Halictus* LATR.) increased their abundances in accordance with available food plants and patch area and were not abundant in isolated forest point habitats.

DISCUSSION

In the landscapes analysed here, the number of bee species increased slightly with increasing refuge habitat size. Their z value of 0.15 (for the species-area curve function $S=C*A^{z}$, P = 0.036, CI: 0.011 – 0.291) was within the range typical of terrestrial habitat islands (MCARTHUR & WILSON 1967). However, the value was lower than those reported in other publications regarding the dependence of bee species numbers on refuge habitat size (STEFFAN-DEWENTER 2003). This may indicate a greater exchange between our two refuge habitats and a greater homogeneity of the bee community structure within the landscapes. The largest part of the landscape diversity was partitioned between different habitats (both from the same and different types of habitats), as the beta diversity at the landscape level was relatively high. Thus, differentiation of habitat types by increasing food resources, nesting sites and nesting material has the greatest influence on diversity in the two landscapes.

The species composition differed between roadsides and forest patches. This non-randomness suggests that a number of factors favourable to some species in these types of habitat are present. Comparison of the bee community structure in shelterbelts and non-linear forest patches revealed several characteristic species. However, the species typical of one habitat type do not seem to share any specific features. For instance, in shelterbelts we found *Andrena fucata* and *Nomada marschamella,* which are common spring species, as well as *Evylaeus nitidulus* and *E. albipes* which are active during spring and summer. The forest patches are "marked" by three species of early spring bees (*Andrena nigroaenea*, *Andrena flavipes*, *Anthophora furcata*) and three cleptoparasitic species (*Nomada goodeniana, N. fucata*). In older wooded patches, species characteristic of forests prevail. Long-term processes taking place in such a habitat also result in a greater contribution of parasites to the bee fauna (CIERZNIAK 2003). A similar trend is also observed in the agricultural landscapes that we studied. The ordination diagram (Fig. 4) shows that parasitic bees (*Nomada* and *Sphecodes* species) were not found in roadside habitats. Roadsides do not have any characteristic species. This might be related to unstable environmental conditions or some specific ecological role of this type of refuge habitat (for example, sink habitats in metapopulation dynamics). Roadsides may have a high immigration rate, but these habitats are not suitable to sustain a population for a long time.

Only 3 of the refugee habitat characteristics analysed proved to be significant: edge ratio (ratio of edge area to total habitat area), degree of isolation, and the group of roadside habitats. The response of most bees to roadsides was negative and was modified by other properties of this habitat. Since roadsides were completely covered by vegetation typical of edge habitats, the edge ratio (as well as edge area) was correlated with this type of habitat. The area covered with food plants was also correlated with edge area. Edges are parts of habitats with high levels of food resources for wild bees. Nevertheless, this is not correlated with the richness of food plant species. Isolation was high within the forest point habitat group. There were some species, mainly cleptoparasites and early spring species, the abundance of which responded positively to this factor. SCHÜEPP et al. (2011) reported that the degree of isolation did not have any significant effect on bees nesting in nest traps. These are mostly species of the family Megachilidae. The most significant factor for this family was the area of adjacent wooded habitats. Only one species of this family occurred in the communities analysed in this study: *Osmia aerulenta*. As expected, in a landscape with a small total area of wooded habitats, megachilid species are present in low densities. Habitat size, as shown by SOWIG's (1989) research, has an effect on community structure, at least in the case of bumblebees. Probably at the level of families or ecological groups, the response to this factor would be more conspicuous or it would vary widely.

From our results we can imply that, regardless of the type of habitat, there is a close relation between food plant cover and the density of many species from the summer phenological period (genera *Halictus*, *Evylaeus*, *Lasioglossum*, *Seladonia* and some bumblebee species). The point forest patches were preferred mainly by summer species from the genus *Andrena*, and these were followed by their cleptoparasites *Nomada* and *Sphecodes*. The possibility also exists that, for example, factors like flowering plant cover and area have a multiplicative effect on diversity.

As stated in MANDELIK et al. (2012), complementarity in resources is important for bees that are active for much of the year. In our study these were bumblebees and some species of halictid bees, which were more abundant in habitats where rich food resources were available. A greater specificity to habitat type is evident in species with shorter flying periods starting at the beginning of the season.

The results of this study draw more attention to roadsides and similar refuge habitats, where edge flora account for a high proportion or even 100% of the total area. It is still unclear how bee communities function in habitats like these. We know that in some periods they may provide bees with forage, but the quality of habitats of this type with regard to other requirements of these insects is still poorly understood. The occurrence of insects on roadsides, field edges, etc. may thus be linked only indirectly with the properties of these habitats, and the populations found in them may in fact be the net result of supply from neighbouring habitats.

This study focused on wooded habitats and their edges. Bees, however, are insects that evolved in open, dry habitats, and can thus be expected to be most diverse there. In the light of the results of this study, remnants of open habitats, represented by herbaceous roadside vegetation, are not an effective reservoir of diversity for many solitary bee species. These can be found there but their density is low, so their populations in such habitats may be vulnerable (FRANZÉN et al. 2009). Wooded habitats have a specific fauna, unlike open habitats in an agricultural landscape. A lot of information is available on the functioning of bee communities in agricultural landscapes, also in the open habitats of hay meadows and wastelands as well as anthropogenic habitats, which to some extent may also increase the diversity of wild bees (CIERZNIAK 2003). The spatial and seasonal dynamics of bees in the whole landscape is certainly important but equally difficult to analyse. It could provide many interesting data on the use of individual types of habitats by pollinating insects and on methods of agricultural landscape management.

Based on our results, we suggest diversification of the agricultural landscape by creating or maintaining different refuge habitats, as they significantly increase the beta diversity of wild bees. As regards their configuration, it is best to create connections between different refuge habitat patches (physically or by decreasing distance) to prevent isolation and diversity loss, which leads to the simplification of wild bee assemblages. We also recommend diversifying habitat types (hedgerows, copses, shelterbelts and arable lands) rather than increasing their area; at the landscape scale, the latter adds but little to the overall species richness of wild bees. Edges are the most suitable foraging sites for bees because they support flowers that bloom later in the season, whereas forest flowers and shrubs are usually the main food resources in spring. Therefore, a rich edge vegetation should be allowed to develop.

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Appendix 1. List of species and density (ind·ha^{-1}) of bees from 18 research plots from two agroecological landscapes (Turew and Wierzenica) in Wielkopolska, Poland (after Banaszak 1983, Cierzniak 1994, Banaszak & Cierzniak 1998).

Species	Code	Habitat																		%
		F1	**F2**	**F3**	**F4**	**F5**	**S1**	**F6**	**F7**	**S2**	**S3**	**S4**	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**	**R7**	
Andrena alfkenella Perk.	and_alf	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
A. barbilabris (Kby.)	and_bar	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
A. bicolor Fabr.	and_bic	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0	0.014
A. cineraria (L.)	and_cin	1.8	0	0	4.2	4.2	9.5	0	0	0	0	0	0	0	0	0	0	0	0	0.178
A. denticulata (Kby.)	and_den	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.009
A. dorsata (Kby.)	and_dor	3.6	2.8	0	2.1	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.118
A. falsifica Perk.	and_fal	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2.1	0	0.046
A. flavipes Panz.	and_fla	123.2	255.3	247.2	204.2	0	7.1	0	0	0	0	2	0	0	0	0	0	0	0	7.570
A. fucata Sm.	and_fuc	1.8	0	0	0	0	11.9	0	0	0	6.9	0	0	0	0	0	0	0	0	0.186
A. fulva (Müll.)	and_ful	16.1	7.9	12.5	0	6.3	23.8	1.7	1	1.5	6	0	0	0	1.5	0	0	2.1	0	0.725
A. gelriae Vecht	and_gel	0	0	0	0	0	0	0	0	0	0	0	0	5.5	0	0	0	0	0	0.050
A. gravida Imh.	and_gra	0	10.5	1.4	0	0	4.8	0	0	0	0	0	0	0	3	0.8	0	0	0	0.185
A. haemorrhoa (Fabr.)	and_hae	7.1	7.9	8.3	2.1	6.3	11.9	0	0	3	21.7	0	0	0	0	6.8	8.3	2.1	0	0.771
A. helvola (L.)	and_hel	0	0	1.4	0	6.3	7.1	0	0	6	0	0	0	0	0	0	0	0	0	0.188
A. jacobi Perk.	and_jac	0	0	1.4	0	2.1	9.5	0	0	0	0	0	1.2	0	0	0	0	0	0	0.128
A. labiata Fabr.	and_lab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.9	5.8	0	0	0.078
A. minutula (Kby.)	and_min	0	0	0	4.2	0	4.8	0	0	0	0	0	0	0	0	12.5	0	0	0	0.194
A. minutuloides Perk.	and_mul	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0.036
A. nigroaenea (Kby.)	and_nig	112.5	94.7	161.1	277.1	43.8	57.1	16.7	62.5	7.5	0.7	2	0	0	1.5	1.6	4.2	0	1.6	7.621
A. nitida (Müll.)	and_nit	0	0	0	0	4.2	2.4	0	0	0	0	0	0	5.5	0	0	0	0	0	0.109
A. subopaca Nyl.	and_sub	0	0	1.4	0	0	4.8	0	0	0	0	4	1.2	0	0	4.3	0	0	0	0.142
A. synadelpha Perk.	and_syn	0	0	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019
A. tibialis (Kby.)	and_tib	0	0	0	0	0	7.1	5.6	0	0	0	0	0	0	0	0	0	0	0	0.115
A. varians (Rossi)	and_var	0	0	0	0	0	7.1	0	0	0	0	0	0	0	0	0	0	0	0	0.064
A. wilkella (Kby.)	and_wil	0	0	0	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019

Appendix 1. Continued.

Species	Code	Habitat																		%
		F1	**F2**	**F3**	**F4**	**F5**	**S1**	**F6**	**F7**	**S2**	**S3**	**S4**	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**	**R7**	
Anthidium manicatum (L.)	ant_man	0	0	0	2.1	0	2.4	0	0	0	0	0	0	0	0	1	0	0	0	0.050
Anthophora furcata (Panz.)	ant_fur	3.6	7.9	12.5	16.7	0	2.4	1.2	0	0	0	0	0	0	0	0	0	0	0	0.400
A. plumipes (Pall.)	ant_plu	7.1	5.3	12.5	4.2	0	14.3	0	13.5	3	0	0	0	0	0	0	1.7	2.1	0	0.575
Apis mellifera L.	api_mel	89.3	39.5	298.6	68.8	39.6	457.1	388.7	798.8	16	470.9	78	102.8	293	303	112.8	405	169.5	678.1	43.395
Bombus cryptarum Fabr.	bom_cry	1.8	0	0	0	2.1	14.3	0	0	0	0	0	0	0	0	0	0	0	0	0.164
B. hortorum (L.)	bom_hor	5.4	0	2.8	2.1	4.2	11.9	2.4	0	4.5	0	0	1.2	0	3	0.6	0	0	0	0.344
B. hypnorum (L.)	bom_hyp	0	0	0	0	2.1	4.8	0	0	0	3.1	0	0	0	1.5	0	0	3.1	0	0.132
B. lapidarius (L.)	bom_lap	3.6	7.9	65.3	18.8	83.3	40.5	281.3	24.5	7.5	3.1	6.5	5	5.5	54.5	211.8	155.8	25	27.6	9.271
B. lucorum (L.)	bom_luc	28.6	26.3	20.8	25	6.3	23.8	39.2	9.4	0	31.2	0	4.7	0	9	34.1	0	0	0	2.331
B. muscorum (L.)	bom_mus	1.8	2.6	18.1	4.2	10.4	0	3.8	3.1	6	0	0	0	0	1.5	9.2	3.3	6.2	7.8	0.704
B. pascuorum (Scop.)	bom_pas	14.3	15.8	61.1	29.2	31.3	14.3	40.5	0	16	0	0	16.9	0	0	50	38.3	3.1	3.1	3.013
B. pomorum (Panz.)	bom_pom	0	0	0	0	0	0	1.2	0	0	0	0	0	0	0	0.5	0	0	0	0.015
B. pratorum (L.)	bom_pra	5.4	0	2.8	0	6.3	7.1	0	0	0	2.1	0	0	0	0	0.5	0	2.1	0	0.237
B. ruderarius (Müll.)	bom_rud	0	0	9.7	0	35.4	2.4	5.5	0	3	0	0	1.2	5.5	12	47.7	20.8	1	12.5	1.414
B. sylvarum (L.)	bom_syl	0	0	1.4	0	2.1	0	7.5	0	0	0	2	0	0	3	47.5	0	0	1.6	0.587
B. terrestris (L.)	bom_ter	41.1	52.6	19.4	29.2	0	4.8	42.1	49	9	24.6	4	5.3	22	39.5	188.8	4.2	2.1	15.1	4.988
Ceratina cyanea (Kby.)	cer_cya	0	0	0	0	0	0	1.2	0	0	0	0	0	5.5	0	0	0	0	0	0.060
Colletes daviesanus Sm.	col_dav	1.8	5.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.064
C. fodiens (Fourcr.)	col_fod	3.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.1	0.051
C. similis Schenck	col_sim	5.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.049
Dasypoda hirtipes (Harr.)	das_hir	0	0	0	0	0	4.8	1.4	0	0	0	0	0	0	0	0	0	0	0	0.056
Evylaeus aeratus (Kby.)	evy_aer	1.8	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0.030
E. albipes (Fabr.)	evy_alb	0	0	0	0	0	4.8	0	0	0	0	8	0	0	3	0	0	0	0	0.143
E. calceatus (Scop.)	evy_cal	26.8	0	1.4	2.1	4.2	9.5	72	0	3	0	30	1.2	22	68	47.6	11.7	2.1	3.1	2.749
E. intermedium (Schenck)	evy_int	0	0	0	0	2.1	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.041
E. leucopus (Kby.)	evy_leuc	0	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0.022

Appendix 1. Continued.

Species	Code	Habitat																		%
		F1	**F2**	**F3**	**F4**	**F5**	**S1**	**F6**	**F7**	**S2**	**S3**	**S4**	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**	**R7**	
Evylaeus lucidulus (SCHENCK)	evy_luc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0.005
E. minutissimus (KBY.)	evy_min	0	0	0	0	0	2.4	0	4.2	0	4.2	0	0	0	0	0	0	0	0	0.097
E. morio (FABR.)	evy_mor	0	0	0	0	6.3	4.8	14.9	0	0	1	4	0	0	4.5	2.5	0	0	0	0.343
E. nitidisculus (KBY.)	evy_nit	0	0	0	0	0	0	0	18.7	4.5	9.4	26	0	0	0	0	0	0	0	0.529
E. nitidulus (FABR.)	evy_nul	0	0	0	0	0	0	0	0	0	3.1	0	0	0	0	0	0	0	0	0.028
E. parvulus (SCHENCK)	evy_par	50	10.5	0	16.7	0	219	1.7	0	4.5	0	10	1.2	0	3	0	0	0	0	2.857
E. pauxillus (SCHENCK)	evy_pau	0	0	0	0	6.3	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.100
E. punctatissimus (SCHENCK)	evy_pun	0	2.6	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.045
E. quadrinotatulus (SCHENCK)	evy_qua	3.6	0	0	0	0	0	0	9.4	0	0	6	0	0	3	2.7	0	0	0	0.223
E. semilucens (ALFK.)	evy_sem	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0.072
E. setullosus (STRAND)	evy_set	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1.6	0.023
E. sexstrigatus (SCHENCK)	evy_sex	0	0	0	0	0	0	1.2	0	1.5	0	2	0	0	0	0	0	0	0	0.042
E. villosulus (KBY.)	evy_vil	0	0	0	0	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.043
Halictus maculatus SM.	hal_mac	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0.027
H. rubicundus (CHRIST)	hal_rub	0	0	0	0	0	0	0	0	0	0	16	1.2	0	7.5	0	0	0	0	0.223
Heriades crenulatus NYL.	her_cre	0	0	0	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019
H. truncorum (L.)	her_tru	0	0	0	0	0	0	0	0	0	0	0	0	5.5	0	0	0	0	0	0.050
Hylaeus brevicornis NYL.	hyl_bre	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0.014
H. communis NYL.	hyl_com	0	0	4.2	0	4.2	0	0	0	0	0	0	0	0	6	4.3	0	0	0	0.169
H. confusus NYL.	hyl_con	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0.005
H. gracilicornis (MORAW.)	hyl_gra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.3	0	0	0	0.039
Lasioglossum lativentre (SCHENCK)	las_lat	1.8	0	2.8	0	0	0	1.2	0	1.5	0	2	0	0	1.5	0	0	4.2	0	0.135
L. leucozonium (SCHRANK)	las_leu	3.6	0	0	0	0	4.8	0	0	0	0	6	0	5.5	1.5	0	0	0	3.1	0.221
L. quadrinotatum (KBY.)	las_qua	0	0	0	0	0	0	0	0	7.5	0	4	0	11	10.5	0.6	6.2	0	0	0.339
L. sexnotatum (KBY.)	las_sex	3.6	0	0	0	2.1	4.8	2.8	6.2	0	0	26	0	5.5	12	3.1	0	8.3	0	0.671
L. subfasciatum (IMH.)	las_sub	7.1	5.3	0	0	0	14.3	36.1	25	4.5	22.7	4	0	0	2.5	3.8	0	17.4	0	1.279

Appendix 1. Continued.

Species	Code	Habitat																		%
		F1	F2	F3	F4	F5	S1	F6	F7	S2	S3	S4	R1	R2	R3	R4	R5	R6	R7	
Lasioglossum xanthopus (Kby.)	las_xan	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0	1.6	0	0	0	0.028
Megachile versicolor Sm.	meg_ver	0	0	2.8	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0.030
M. willughbiella (Kby.)	meg_wil	0	0	0	0	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.043
Nomada fabriciana (L.)	nom_fab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.1	0	0	0	0.028
N. flava Panz.	nom_fla	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
N. flavoguttata (Kby.)	nom_fvg	0	0	0	0	0	2.4	0	1	1.5	0	0	0	0	0	0	0	0	0	0.044
N. fucata Panz.	nom_fuc	3.6	10.5	1.4	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.159
N. goodeniana (Kby.)	nom_god	1.8	5.3	1.4	6.3	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.152
N. marshamella (Kby.)	nom_mar	1.8	0	0	0	0	26.2	0	0	0	0	0	0	0	0	0	0	0	0	0.253
N. moeschler Alfk.	nom_moe	0	0	0	0	0	2.4	7.2	0	1.5	0	0	0	0	0	0	2.8	0	0	0.125
N. ochrostoma Zett.	nom_och	0	0	0	0	0	7.1	0	0	0	0	0	0	0	0	0	0	0	0	0.064
N. panzeri Lep.	nom_pan	0	0	0	0	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.043
N. ruficornis (L.)	nom_ruf	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0.027
N. sheppardana (Kby.)	nom_she	0	0	0	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019
N. signata Jur.	nom_sig	0	0	4.2	0	0	4.8	0	0	0	0.7	0	0	0	0	0	0	0	0	0.088
Osmia aerulenta (Panz.)	osm_aer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.8	4.2	0	0	0.108
O. brevicornis (Fabr.)	osm_bre	0	0	0	0	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019
O. rufa (L.)	osm_ruf	0	2.6	0	0	2.1	0	1.4	0	1.5	0	0	2.8	0	0	0	0	0	0	0.094
Psithyrus bohemicus (Seidl.)	psi_boh	0	0	0	0	0	4.8	2.4	0	0	0	0	0	0	0	0	0	0	0	0.065
P. rupestris (Fabr.)	psi_rup	0	0	0	0	0	0	0	0	0	0	0	0	5.5	0	0	0	0	0	0.050
P. vestalis (Fourcr.)	psi_ves	0	0	0	2.1	0	0	0	0	0	0	0	0	5.5	0	0	0	0	0	0.069
Seladonia tumulorum (L.)	sel_tum	0	0	1.4	0	0	0	12.3	0	1.5	0	14	0	5.5	25.5	0.9	10	4.2	0	0.679
Sphecodes ephippius (L.)	sph_eph	1.8	2.8	0	0	2.1	7.1	0	0	0	0	4	0	0	0	0	0	0	1.6	0.173
S. ferruginatus Hag.	sph_fer	14.3	10.5	0	0	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.267
S. miniatur Hag.	sph_min	0	0	0	0	0	0	0	0	1.5	0	0	0	0	0	0	0	0	0	0.014
S. monilicornis (Kby.)	sph_mon	0	5.3	0	0	6.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0.105

Appendix 1. Continued.

Species	Code	Habitat																		%
		F1	**F2**	**F3**	**F4**	**F5**	**S1**	**F6**	**F7**	**S2**	**S3**	**S4**	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**	**R7**	
Sphecodes pellucidus SM.	sph_pel	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
S. puncticeps THOMS.	sph_pun	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
S. reticulatus THOMS.	sph_ret	1.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.016
Sphecodes sp. 1	sph_sp1	0	0	0	0	0	4.8	0	0	0	0	0	0	0	0	0	0	0	0	0.043
Sphecodes sp. 2	sph_sp2	0	0	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0.022
Stellis punctulatissimus (KBY.)	ste_pun	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0	0	0	0.005
No. of species		35	24	28	21	33	58	28	14	26	16	24	13	16	29	34	15	18	14	Σ = 109