



Are cities hotspots for bees? Local and regional diversity patterns lead to different conclusions

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Abstract

With the decline of natural habitats, there is an ongoing debate about the importance of the urban environment for pollinating insects. Our research assessed patterns in wild bee species composition, as well as α -, β - and γ -diversity patterns and the nestedness structure in urban, suburban and rural areas. For three years bees were collected along 18 sampling transects in the Poznań area in western Poland. The average species diversity (α -diversity) and the average number of specimens per sample (local abundance) did not differ significantly between the three classes of urbanization. The rarefaction analysis, however, was partly contradictory to the results recorded on the local scale. The highest dissimilarity in the species composition among the samples was observed in the rural areas, while the lowest (more homogenous) was in the urban areas. The differences were significant. This resulted in the highest γ -diversity (cumulative number of species) in the rural areas and the lowest in the urban areas. Furthermore, the bee community in the habitats studied was significantly nested, indicating that species-poor sites (sites with high rank) constituted subsets of species-rich sites (sites with low rank) and that this pattern was not random. Samples collected in urban areas had a significantly higher nestedness rank compared to samples from the other two classes of urbanization, thus suggesting that the urban bee community is a subset of the rural bee community. This is an important conclusion, which emphasises that different components of species diversity need to be screened to identify the real biological impact of urbanisation on bee communities.

Keywords Apoidea · Biotic homogenization · Hymenoptera · Pollinators · Urban-rural gradient

Introduction

In recent decades, the diversity of wild bees has declined markedly worldwide due to environmental changes (Biesmeijer et al. 2006; Fitzpatrick et al. 2007; Potts et al. 2010; Cameron et al. 2011; Ollerton et al. 2014). Among the main factors causing the decline in bee populations, two seem to be the most important: the intensification of agriculture and

the disappearance of natural habitats (Kremen et al. 2002; Le Féon et al. 2010). Locally, the cessation of management practices in some regions also contributes to the decline, as semi-natural habitats become overgrown with bushes and trees (Benayas et al. 2007). Moreover, the use of pesticides in agriculture negatively affects many bee species, causing direct mortality (Desneux et al. 2007; Goulson et al. 2015), reduced productivity (Whitehorn et al. 2012) or indirect effects such as changes in behaviour, e.g. the deterioration of cognition and memory (Siviter et al. 2018). The decline in wild bees has significant ecological and economic consequences (Corbet et al. 1991; Pywell et al. 2006; Gallai et al. 2009; Potts et al. 2010; Garibaldi et al. 2014), as they are important pollinators and play a crucial role in food webs and agricultural production. The decline of wild bees and possible mitigating measures have therefore attracted considerable attention among conservation biologists all over the world.

As extensively used semi-natural habitats are becoming rare in modern landscapes, alternative habitats have recently been considered as realistic alternatives to host a substantial proportion of pollinating insects (Berg et al. 2016). These

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include openings in forested landscapes, railway and road verges, and industrial areas. (Morón et al. 2014; Blixt et al. 2015; Pustkowiak et al. 2018). As a notable proportion of natural landscapes was converted into urbanised areas during the previous century (Antrop 2004; Giulio et al. 2009), cities are also considered to be important refuges for wild bees. Moreover, many recent studies suggest that cities may host diverse populations of wild pollinators, including bees, compared to non-urban areas (Saure 1996; Sirohi et al. 2015; Normandin et al. 2017; Banaszak-Cibicka et al. 2018), and they may act as refuges for them (Baldock et al. 2015; Hall et al. 2017; Choate et al. 2018). Expansive and diversified urban parks and gardens can provide adequate nesting sites for bees with different requirements, like bare soil, pithy or hollow plant stems, small rock cavities, abandoned insect or rodent burrows, or even snail shells. These areas may also provide food plants throughout the bees' flight period (Banaszak-Cibicka et al. 2016). Such areas can be attractive for many bee species and comparable to more natural environments outside the city (Banaszak-Cibicka et al. 2018). Moreover, cities can provide suitable habitats not only for common species but also for rare and declining ones with specific requirements, e.g. species with higher thermal requirements, which in cities have favorable conditions for development (Banaszak-Cibicka 2014). These findings are in contrast to the general belief that the development of urban areas leads to biotic homogenisation, as was shown for diverse taxa (McKinney 2006; Morelli et al. 2016).

However, most of the earlier studies which suggested that cities play an important role for wild bees referred to the local α -diversity of bee communities. For instance, they compared local species' richness or abundance in urbanised and non-urban areas (Baldock et al. 2015; Sirohi et al. 2015) or along an urbanisation gradient (Verboven et al. 2014). Biodiversity at local α -diversity is important but a substantial proportion of biodiversity loss is caused by reduced temporal and spatial variation among local communities (β -diversity), which leads to biotic homogenisation (Olden and Rooney 2006). Furthermore, the spatiotemporal patterns of α -diversity are not always consistent with those recorded for β -diversity, e.g. a local increase and a global decrease (Sax and Gaines 2003). Therefore, studies limited only to the local scale are likely to miss the relevant spatial scale of biodiversity and thus may lead to biased conclusions (Socolar et al. 2016; Roden et al. 2018). There have only been a few studies addressing β -diversity patterns in wild bees along the gradients of anthropogenic habitat disturbance (Quintero et al. 2010; Hendrickx et al. 2007; Tylianakis et al. 2005; Verboven et al. 2014; Hung et al. 2017). To the best of our knowledge, there have been no studies on β -diversity of bees in the urbanisation gradient.

In this study, we compared wild bee species composition and diversity patterns in urban, suburban and rural areas in West Poland. We conducted a three-year study on bee

community composition, abundance and diversity patterns in order to determine the importance of urban areas for sustaining bee diversity. The local α -diversity of bee assemblages and local bee abundance in the three city classes of urbanization was compared. As local diversity is usually affected by the local availability of preferred habitats (Kearns and Oliveras 2009), we therefore also expected to find high bee diversity at sites in the city. Secondly, the local species diversity was upscaled to investigate β - and γ -diversity patterns. Different ecological mechanisms might affect local and regional diversities (Socolar et al. 2016). Therefore, we hypothesised that regional patterns may be substantially different from local ones. Finally, we performed nestedness analysis and checked whether bee samples from the three city classes of urbanization are randomly distributed in the maximally packed matrix.

Materials and methods

Study area and sampling design

The research was conducted in Poznań (52° 25' N, 16° 58' E), a city with 560,000 residents, located in western Poland. Sampling sites were located in green areas along an urbanisation gradient covering three levels of urbanization: urban, suburban and rural. The plots were divided on the basis of the distance from the city center and the characteristics of the plots. The sites were located in green areas which were typical of each class of urbanization. In the urban areas, these were parks surrounded by concentrated settlements of tenement houses and green areas of sparse housing estates. In the suburban areas, these were backyard gardens in districts with detached houses and suburban parks, whereas in the rural areas these were meadows and forests. Detailed data on the research sites' characteristics and their distribution can be found in Table 1, in Fig. 1 and in Online Resource 1. In order to describe the degree of area modification resulting from human activity, the area with man-made structures (buildings, streets, parking lots etc.), percentage of green spaces cover, percentage of tree cover and the distance to the city centre was calculated at each research site based on satellite images. We intend to quantify habitat composition in a 500-metre. The area of these buffers is connected with the predicted foraging range of wild bee species. A close neighbourhood of nesting and foraging resources within few hundred meters is crucial to maintain populations of bees (Zurbuchen et al. 2010). Maximum bee foraging distances at the species level might be longer (1100–1400 m) but such long distances concern only single females (Zurbuchen et al. 2010). All the transects were located at least 1.5 km apart to avoid spatial autocorrelation. On the basis of the percentage of built up areas within a 500 m radius from the sites, percentage of tree cover within

Table 1 Characteristics of sampling sites

Class of urbanization	Habitat type	Site	Distance to the city centre (m)	% built up areas, r = 500 m	% green space, r = 500 m	% trees, r = 500 m
Urban	Housing estate	HE1	4256	40	60	20
	Housing estate	HE2	3600	40	60	15
	Housing estate	HE3	3700	45	55	10
	Urban Park	P1	520	70	30	10
	Urban Park	P2	600	75	25	10
	Urban Park	P3	530	60	35	5
Suburban	Suburban Park	GA1	5630	15	75	25
	Suburban Park	GA2	6670	15	65	50
	Suburban Park	GA3	5338	15	85	60
	Detached houses district	DH1	7000	35	65	20
	Detached houses district	DH2	5819	30	70	25
	Detached houses district	DH3	7300	35	65	25
Rural	Meadow	M1	23110	5	92	20
	Meadow	M2	22180	5	90	10
	Meadow	M3	30870	5	90	15
	Forest	F1	29550	5	95	70
	Forest	F2	24360	10	90	60
	Forest	F3	2646	5	95	75

500 m radius, percentage of green areas cover (including tree cover) within 500 m radius and distance from the city centre six sampling sites were designated in each class of urbanization (3 class of urbanization \times 6 research sites within each class = 18 sampling sites).

Bee sampling

For three years (2014–2016) bees were collected at all 18 sampling sites along transects. Each transect was 200 m long and 1 m wide. The sample collection lasted about 60 min (Banaszak 1980). During a passage, all bees were collected by means of an entomological net. Most bumblebees and other species that were easy to distinguish were identified alive during the field visits, but the specimens which could not be identified in the field were collected for species identification in a laboratory. The subgenus *Bombus sensu stricto* includes four species in Poland (*Bombus terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus*). Their classification is particularly complicated (Bertsch et al. 2004). As it was difficult to identify these species in the field, especially workers, they were classified as *Bombus* s. str.

Each site was visited 6–10 times (on average 8 times - the differences resulted from weather issues) each year, every 7–10 days from March to September. The high frequency of visits throughout the season is particularly important to record

rare species and those that are active for a short period of time (Magurran and McGill 2011; Banaszak et al. 2014). All visits took place between 10 a.m. and 4 p.m., on warm and sunny days with an air temperature during sampling above 16 °C (Krauss et al. 2009). The sites were visited in a random order to ensure that all of them would receive roughly equal morning and afternoon sampling. During the three years of the study, a total of 436 samples were collected (148 in the urban area, 140 in the suburban area and 148 in the rural area). One sample is a collection of insects caught during one day on a research site.

All individual bees that were not identified in the field were pinned in the laboratory, sorted and identified to the species level according to various keys (Banaszak 1993; Scheuchl 1995; Schmid-Egger and Scheuchl 1997; Banaszak et al. 2001; Pesenko et al. 2002; Pawlikowski and Celary 2003).

Statistical analysis

The species diversity (α -diversity) and the abundance of all individuals per single transect visit were compared across the three city classes of urbanization. Two generalised linear mixed models with Poisson (for species richness) and quasi-Poisson (for abundance) error distribution were built as formal statistical tests. The site ID and year were used as two random effects and the city class of urbanization was used as a fixed categorical factor in the models. Next, the local diversity patterns were upscaled by using rarefaction curves. This allowed

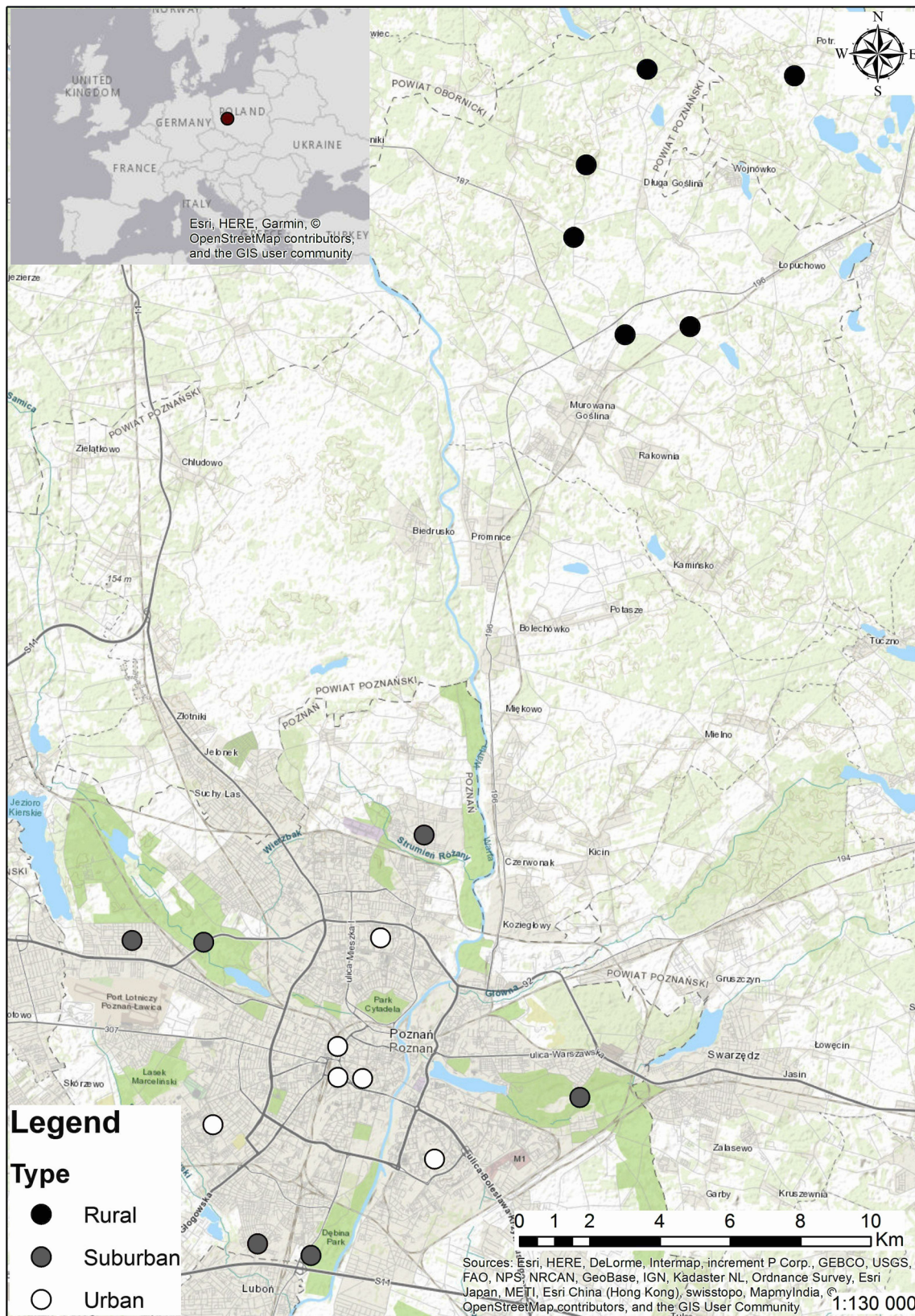


Fig. 1 Distribution of the studied sites: urban, suburban and rural in western Poland

for the estimation of β -diversity and pooled species diversity for each city class of urbanization, i.e. γ -diversity. Both

sample-based and individual-based rarefaction accompanied by unconditioned 95% confidence intervals were computed in

the ‘*iNEXT*’ package (Hsieh et al. 2016) in R (R Core Team 2018).

Finally, we checked for the nested pattern in bee communities found in the three city classes of urbanization. For this purpose we used a ‘*bipartite*’ package (Dormann et al. 2008) in R. We calculated the mean rank of the samples in a maximally packed matrix collected from the three city areas (urban, suburban, rural): nestedness means that species-poor sites (i.e. those with a high rank in the nested matrix) are subsets of species-rich sites (those with a low rank). We compared the rank of samples in the maximally packed matrix with the Kruskal-Wallis test.

Results

Community composition and similarity

In total 6,839 individuals of 176 species were recorded (Online Resource 2). The collection represented six families: Colletidae, Andrenidae, Halictidae, Melittidae, Megachilidae and Apidae. The most common species were: *Apis mellifera* (Linnaeus, 1758) (17% of total number of observed specimens), *Bombus pascuorum* (Scopoli, 1763) (13.3%), *Bombus lapidarius* (Linnaeus, 1758) (8.6%), *Bombus* s. str. (7.9%), *Dasypoda hirtipes* (Fabricius, 1793) (4.4%), *Andrena haemorrhoea* (Fabricius, 1781) (3.4%), *Anthophora plumipes* (Pallas, 1772) (3.4%), and *Evylaeus calceatus* (Scopoli, 1763) (2.2%).

Apart from common species, 24 species (13.6% of the total number of species recorded) that are on the Red List of Threatened Species in Poland were also recorded (Banaszak 2002). They are classified as vulnerable (VU) – 8 species: *Hylaeus rinki* (Gorski, 1852), *Andrena falsifica* Perkins, 1915, *Andrena florea* Fabricius, 1793, *Andrena limata* Smith, 1853, *Anthocopa papaveris* (Latreille, 1799), *Proanthidium oblongatum* Latreille, 1809, *Bombus jonellus* (Kirby, 1802), *Bombus veteranus* (Fabricius, 1793), data deficient (DD) – 13 species: *Colletes similis* Schenck, 1853, *Hylaeus bisinuatus* Förster, 1871, *Hylaeus cornutus* Curtis, 1831, *Hylaeus gracilicornis* (Morawitz, 1867), *Hylaeus gredleri* Förster, 1871, *Hylaeus pictipes* Nylander, 1852, *Hylaeus signatus* (Panzer, 1798), *Andrena bimaculata* (Kirby, 1802), *Dufourea minuta* Lepeletier, 1845, *Evylaeus brevicornis* (Schenck, 1863), *Seladonia semitecta* (Morawitz, 1874), *Coelioxys alata* (Förster, 1853), *Nomada bifasciata* Olivier, 1811, least concern (LC) – 3 species: *Megachile nigriventris* Schenck, 1868, *Nomada moeschleri* Alfken, 1913, *Nomada zonata* Panzer, 1798.

Many species were observed in all the three classes of urbanization, but there were 38 species found only in the rural area, 20 species found only in the suburban area, and 12 species found only in the urban area. There

were 10 species from the Red List of Threatened Species in Poland in the rural area (Banaszak 2002), 15 in the suburban area, and 10 in the urban area.

Local species diversity (α -diversity) and abundance

The average species diversity per sample, i.e. α -diversity, did not differ significantly between the city classes of urbanization (GLM, $p > 0.25$ in all cases). The average number of individuals per sample, i.e. the local abundance, also did not differ significantly between the city classes of urbanization (GLM, $p > 0.26$) (Fig. 2). The highest number of species per sample was observed in the suburban area, followed by the urban area (in both areas it exceeded 20 species per sample). There was a similar pattern observed in the local abundance: there were more than 50 bee individuals observed in only one sample in the rural area, while in the suburban and urban areas there were 10 and 9 such samples, respectively.

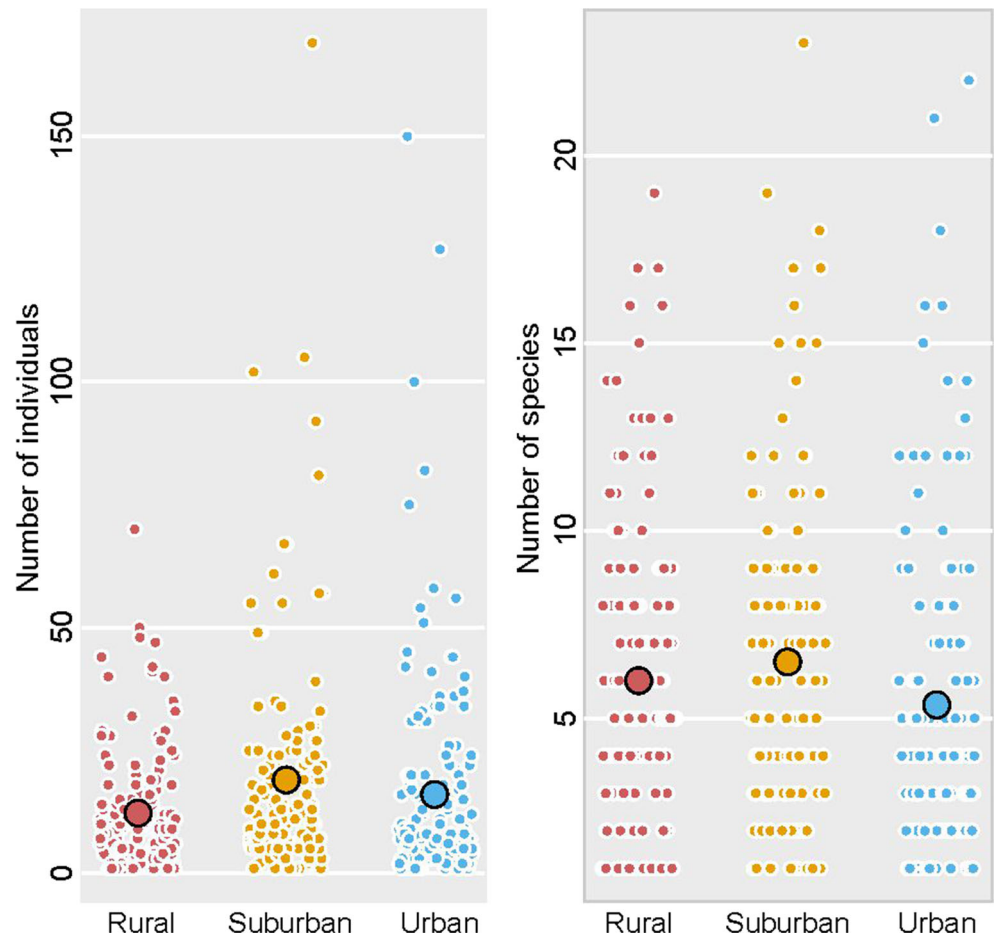
Species turnover and regional diversity (β - and γ -diversity)

Rarefaction analysis partly contradicted the results recorded on the local scale, as there were clear differences in rarefied species diversity among the city classes of urbanization. The highest dissimilarity in species composition between the samples was observed in the rural area, whereas the lowest was found in the urban area. This resulted in the highest γ -diversity (cumulative number of species) in the rural area and the lowest in the urban area. The differences were significant (95% CI did not overlap) and relatively large: among 3,000 randomly selected individuals one may expect about 150 wild bee species in the rural area and only slightly more than 100 in the urban area (Fig. 3, left-hand panel). Sample-based rarefaction (cumulative species diversity recalculated per one transect visit) showed a similar pattern, although the difference between the rural and suburban areas was less noticeable (Fig. 3, right-hand panel).

Nestedness

The bee community in the habitats studied was significantly nested, indicating that species-poor sites (sites with high rank) constituted subsets of species-rich sites (sites with low rank) and that this pattern was not random (Fig. 4). Samples collected in the urban area had a significantly higher nestedness rank compared to samples from the other two classes of urbanization (Kruskal-Wallis test, $\text{Chi} = 19.9$; $p < 0.0001$).

Fig. 2 The average number of individuals and bee species per sample in the three classes of urbanization in Poznań, Poland



Discussion

Our study showed that the pooled γ -diversity of wild bees was substantially larger in the rural landscape than in cities, while

nestedness analysis suggests that local urban bee communities constitute, to some extent, subsets of bee communities found in suburban and rural areas. Our results therefore seem to question numerous studies concluding that from the bees’

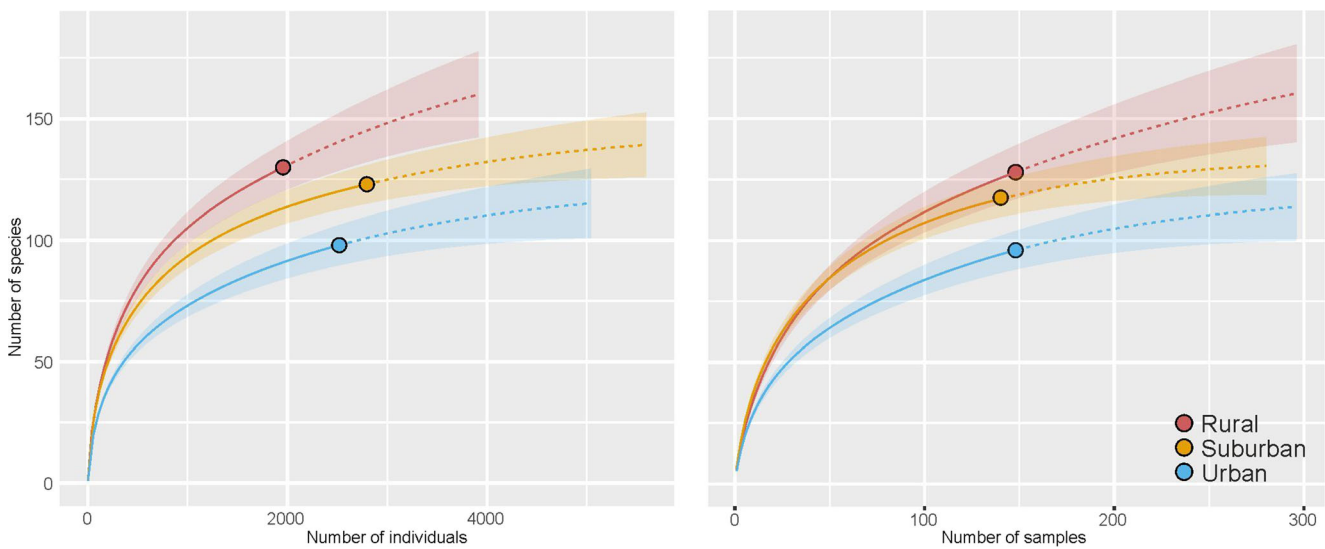
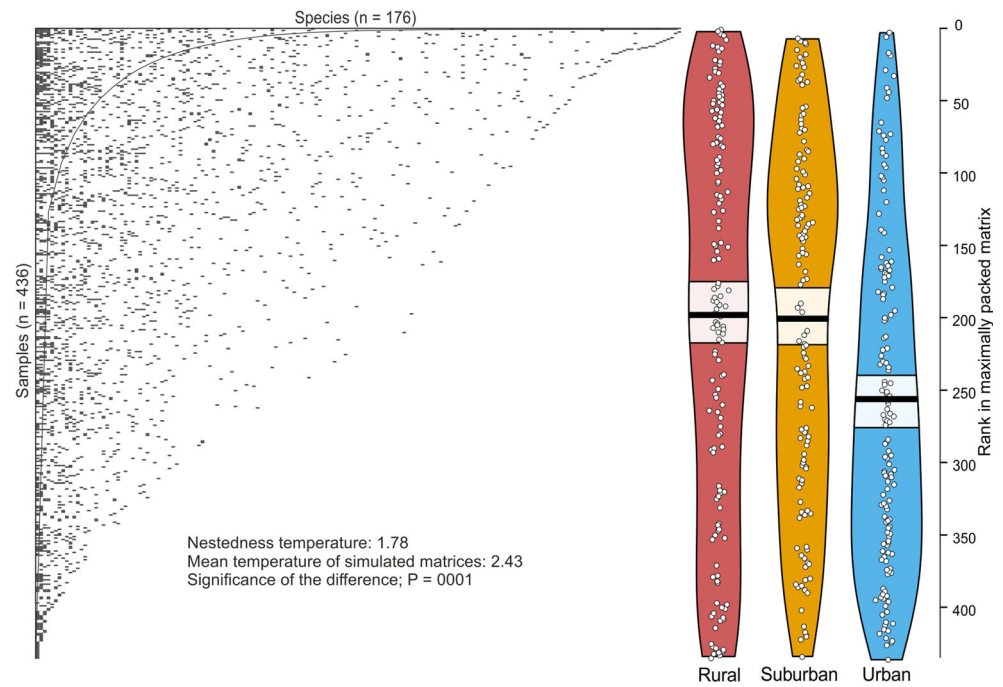


Fig. 3 Rarefaction curves showing the expected number of bee species as a function of sampling effort (expressed as the number of individuals or

samples) in the three classes of urbanization in Poznań, Poland. Solid curves show the empirical result, dashed curves show extrapolation

Fig. 4 Nestedness structure of bee community in the three classes of urbanization. Maximally packed matrix is presented on the left, violin plots on the right show single ranks (points), mean rank (horizontal line), and Bayesian Highest Density Intervals of the mean (white belt) for each city area separately



perspective urban greenery can be an alternative to natural areas outside the city (Baldock et al. 2015; Kaluza et al. 2016; Banaszak-Cibicka et al. 2018). Below we discuss the possible mechanisms driving the patterns that were observed and their consequences.

The bee community recorded in our study was relatively rich in species. There were 176 bee species, i.e. 37% of all bee species found in Poland (Banaszak 2000), and more than 55% of the bee species known in the Wielkopolska-Kujawy Lowland region (Banaszak 2010). This number is only slightly smaller than the richness of bee fauna in other habitats. For example, the entire Polish part of the Białowieża Primeval Forest supports 182 species (Banaszak 2009), whereas 244 species were found in the xerothermic swards in the lower Vistula valley (Banaszak et al. 2006). Furthermore, 34 species were represented by only one individual, i.e. singletons (Colwell and Coddington 1994), indicating that there are still undiscovered species in the urban-rural community (see also the dashed curves in Fig. 3). Singletons amounted to 19% of the total number of species collected, which is similar to the findings of other studies on bee communities (Fortel et al. 2014 with 20% of singletons Rollin et al. 2015 with 22% of singletons). It indicates that the sampling intensity in our study enabled the collection of a representative proportion of the bee community in the area.

The average species diversity (α -diversity) and the average number of specimens per sample (local abundance) were found to be similar in the three classes of urbanization. Diversified urban areas provide bees with nesting places and also a great diversity of forage plants (Hennig and Ghazoul 2012). Urban vegetation consists of plant species introduced

by humans, plants entering cities spontaneously, and remnant vegetation (Sudnik-Wójcikowska 1987). Some authors also claim that the negative effects of urban pressure influence bees less than other insects (Deguines et al. 2012; Baldock et al. 2015). That is why urban bee communities may be locally comparable to bee communities in rural areas (Baldock et al. 2015; Banaszak-Cibicka et al. 2018).

The rarefaction analysis, however, partly contradicted the results recorded on the local scale. The highest dissimilarity in the species composition among the samples (β -diversity) and the highest cumulative number of species (γ -diversity) were observed in the rural area, while the lowest was in the urban area. Furthermore, the bee community was nested and urban samples had a higher rank, thus suggesting that the urban bee community is a subset of the suburban and rural bee community. Even though α -diversity may be high in urban sites, habitat changes due to human activity may, in fact, decrease the total diversity within the pool of sites through homogenization of the bee fauna across the urban landscape.

Taxonomic homogenization - an increase in the similarity between communities - is caused by a successful invasion of the “winner” and a loss of the “loser” species (McKinney and Lockwood 1999). Reduced species turnover and homogenization of the bee fauna across the landscape may be associated with habitat disturbance (Quintero et al. 2010). Urban landscapes are designed mainly to meet the needs of city dwellers, who want attractive, aesthetic green areas for rest and recreation. Some practices related to the shaping and maintenance of green areas in cities (e.g. frequent mowing, cutting down trees, replacing plants with conifers) may negatively affect pollinating insects (Hülsmann et al. 2015; Lerman et al.

2018) and cause environmental filtering. Bee species requiring more natural habitats may avoid entering the urbanised landscape, while widespread, broadly tolerant species can spread and become dominant.

The species composition recorded in the urban area constituted a subset of the assemblages recorded in suburban and rural areas. Nestedness has been observed across many taxa and it is an important measurement with conservation implications, reflecting a non-random process of species loss (Slipinski et al. 2012; Sengupta et al. 2014). This result also emphasizes the biological importance of suburban areas with a lower management regime and a bigger percentage of green space cover in determining the diversity of species present in urban areas. Suburban areas may be more favorable than urban landscapes for many bee species (Winfree et al. 2007; Fretwell et al. 2008).

Despite the fact that rural areas seem to be better for bees, our results also indicate that an urban area can provide a suitable habitat for bee conservation, because it can harbour not only common but also rare species, and at the local level, bee communities can be even richer in species than communities found in more natural landscapes. Furthermore, some species were only found in the urban area, although further sampling could possibly change this pattern. Therefore, we suggest that bee-friendly management of urban greenery is worth considering as a pollinator conservation strategy. Leaving part of lawns unmown or promoting flowers used by bees might be appropriate courses of action (Hülsmann et al. 2015; Wastian et al. 2016).

Conclusions

The results based on α -diversity vs. β - and γ -diversity may lead to substantially different or even contradictory conclusions. Although urban habitats can locally host bee communities which are relatively rich in species, the species turnover between the sites within the urban area is reduced. Thus, the pooled number of city-dwelling bees is reduced, but it can only be detected when local patterns are upscaled to β - and γ -diversity. This is an important conclusion, which stresses that the full spectrum of biodiversity levels needs to be screened in order to identify the real biological consequences of urbanisation on bee communities. Local biodiversity indices may not be sufficient for reliable evaluation of biodiversity patterns across environmental gradients and only through an analysis of diversity across different spatial scales can reliable management recommendations be produced. Moreover, the nested structure of the bee community indicates that the species found in city centre can usually be found in suburban and rural areas as well. This clearly shows that in the long run, rural areas are of key significance for bee conservation. It would be hard to protect the regional bee species pool by

focusing solely on urbanised areas that host partly homogenized communities. Therefore, efforts should be concentrated outside urbanised landscapes, in more natural habitats. Subsidies promoting extensive agricultural management and bee-oriented agri-environment schemes are possible options.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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