Acta Oecologica 96 (2019) 56–64

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

What features of sand quarries affect their attractiveness for bees?

Lucyna Twerd[a,*], Weronika Banaszak-Cibicka[b], Elżbieta Sandurska[c]

[a] Kazimierz Wielki University, Institute of Environmental Biology, Department of Ecology, Ossolińskich 12, 85-093, Bydgoszcz, Poland
[b] Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625, Poznań, Poland
[c] Kazimierz Wielki University, Institute of Experimental Biology, Department of Genetics, Powstańców Wielkopolskich 10, 85-090, Bydgoszcz, Poland

ARTICLE INFO

Keywords:
Apiformes
Anthropopressure
Municipal and household waste
Ruderalization
Sand quarries
Synanthropization

ABSTRACT

Conservation of organisms usually focuses on areas that are not significantly altered by human activity. However, many areas under the influence of human activity can be important for maintaining biodiversity. Sand quarries became important substitute habitats for many species of insects, including wild bees. However, their attractiveness as a potential place for oligolectic bees to forage is insufficiently known. We examined the species richness and abundance of wild bees, including species with a specialized diet, in 20 used and inactive sand quarries differing in area (0.64–7.40 ha), succession stage and location in the landscape. Some of the inactive quarries were littered with municipal and household waste, i.e. mainly plant biomass and soil from home gardens and construction debris. We recorded 156 species of wild bees (32% of the domestic Polish fauna). Polylectic species accounted for 57% of the bee community (66% of the total abundance), 17% of the community were oligolectic species (25% of the total abundance) and 26% of the community were cleptoparasitic species (9% of the total abundance). The total number of polylectic species and their abundance increased with the increasing area of sand quarries. At the same time, the richness and abundance of oligolectic species increased with the increasing number and abundance of food species. Among the recorded oligolectic bees, 55% were common in the studied habitats, 30% were frequently reported, and only 15% were rare species.

1. Introduction

Bees are considered the most important group of pollinators in the world (Banaszak, 1992; Aizen and Harder, 2009; Potts et al., 2010). However, despite the key role they play in angiosperm reproduction (Potts et al., 2003), our knowledge of how man-made environmental degradation affects their diversity (Quinterno et al., 2010) is still fragmentary. Agricultural areas and their impact on populations of pollinating insects are relatively well researched (Banaszak, 1992; Tscharntke et al., 2005; Carvell et al., 2007), but the interest in industrialized areas has increased only recently (e.g. Krauss et al., 2009; Lenda et al., 2012; Tropek et al., 2016; Twerd and Banaszak, 2017). Brownfields as well as other heavily transformed areas (e.g. quarries, heaps, motocross tracks, railway lines) are the least well-known. In recent years, however, there is increasing evidence that these areas may also be more important for bees and other Aculeata than previously thought (Tropek et al., 2010; Banaszak and Twerd, 2010; Moroń et al., 2014; Heneberg et al., 2016, 2017; Twerd et al., 2017).

Natural sand and gravel aggregates belong to the most common minerals in Poland and Europe, and are extracted on a massive scale. The recent increase in the prices of rock raw materials and the growing demand for sand and gravel aggregates have led to an increase in the number of sites in which these minerals are mined (Santoul et al., 2004; Walentek et al., 2016). Sand quarries belong to specific environments in the landscape with bare soil patches maintained by regular human disturbances and occupied mainly by synanthropic vegetation, including ruderal communities with a wide range of distribution. These plants often colonize unstable biotopes which are subject to continuous succession changes, and their amount in a given habitat is strongly correlated with its alteration degree (Kuzmič and Šilic, 2017). The plant cover includes both native and foreign species that appear spontaneously or are intentionally introduced (Řehounková and Prach, 2010). What is more overgrown quarries are sometimes treated as places for illegal waste disposal (construction debris, building ceramics or used car tires and painting accessories). Such excavations also function temporarily as dumps of composted plant residues and storage sites for soil from home gardens, until the waste is removed. For this reason, cultivated and garden species (so-called involuntary escapees) are often growing in sand excavations, e.g. *Solanum lycopersicum*, *Galanthus nivalis*, *Iris* sp., *Lilium* sp. or *Scilla* sp. After some time, they give place to other species, but undoubtedly they periodically increase food resources in a given environment. In addition, organic waste sometimes

* Corresponding author.
E-mail address: l.twerd@ukw.edu.pl (L. Twerd).

https://doi.org/10.1016/j.actao.2019.03.005
Received 8 October 2018; Received in revised form 21 February 2019; Accepted 18 March 2019

occurring in sand quarries, are conducive to plants associated with soils rich in mineral salts and nitrogen compounds. A number of them, e.g. *Ballota nigra*, *Lamium purpureum* or *Leonurus cardiaca,* belong to the group of species that produce pollen and nectar and for this reason are eagerly visited by Apiformes.

The decisive factor for the occurrence of bees in a given environment is the availability of food plants and appropriate nesting sites (Ricketts et al., 2008; Ritchie et al., 2016). According to the classic concepts of resource use, bees are categorized as specialists (oligolectic) and generalists (polylectic). While oligolectic bees depend on pollen resources from a single plant species, genus or family, polylectic bees use a broad spectrum of flowering plants (Cane and Sipes, 2006; Weiner et al., 2010). At the same time, intraspecific differences in foraging may depend on the type of land use, sex and the stage of phenological development of plants (Dupont et al., 2009; Ritchie et al., 2016). Nutritional specialization is a factor that influences the species' greater sensitivity to environmental changes. The disappearance of food plants causes simultaneous disappearance of bee species associated with them (Goulson, 2003; Biesmeijer et al., 2006). Therefore, oligolectic bees are often rare species (Weiner et al., 2014), especially those associated only with one plant genus (monolectic bees).

The importance of synanthropic plant species as a source of food and their impact on the diversity of pollinators was studied in agricultural and urban landscapes (Williams et al., 2011; Lubiarz and Trzaskowska, 2013; MacIvor et al., 2014). However, to our knowledge, little is known about the comprehensive evaluation of the significance of synanthropic plant species, including foreign species, for bees in sand quarries.

This work is an attempt to determine the importance of post-excavation sand areas for bees with various diet specializations, including highly specialized species.

In connection with the above, the paper attempts to answer the following questions: what factors influence the richness and abundance of Apiformes in sand quarries? **(2)** Does the synanthropization/ruderalization of habitats promote the occurrence of oligolectic bees? **(3)** Which species of oligolectic bees prefer sand quarries as a feeding place?

2. Material and methods

2.1. Study sites

The studies were carried out in 2008 and in the years 2015–2016 in the Podlasie region (north-eastern Poland, 52^0–53^0 N, 23^0 E), in the immediate vicinity of large forest complexes of the Białowieża Forest (Hajnówka group, sites 1–10) and the Knyszyńska Forest (Supraśl group, sites 11–20) (Table A1, Fig. 1).

Sand quarries were located in various types of landscape (mid-forest, field, forest and field). Their area ranged from 0.64 to 7.40 ha. The research in each sand quarry was carried out after obtaining the owner's oral consent. The analyzed sand quarries were in various stages of spontaneous succession. They were mainly covered with herbaceous, synanthropic vegetation. The list of synanthropic plant species used by bees as a food source is given in Table A2. *Poa pratensis*, *Calamagrostis epigejos*, *Elymus repens* were the dominant grass species in this area. The dominant tree species was *Pinus sylvestris*. All listed plant species are common in Poland.

Currently, the Polish register includes over 9300 documented sand and gravel deposits (PIG-PIB, 2014). Most of sand quarries in Poland are deposits of up to 2 ha, which is related to the Act of July 2, 2004 on the freedom of economic activity (consolidated text: Dz.U. [Journal of Laws], 2010, No. 220, item 1447, as amended). This bill gives district heads the right to approve (issue) a concession for the exploitation of gravel pits. At the same time, from January 1, 2012, a provision in the Geological and Mining Law allows each individual to extract sands and gravels in the amount of 10 m^3 per year from his own property and for his own needs (Dz.U. [Journal of Laws], 2011 No. 163, item 981, as amended) (Kozłowska et al., 2016). These changes in regulations contributed to the division of larger fields into plots of up to 2 ha, and thus the formation of small sand quarries with limited mining potential. At the same time, this way of extracting minerals does not cause drastic changes in the environment, but leads to a varied terrain, modifying the existing habitat conditions, and thus increases the availability of diversified microhabitats. These sand quarries, after cessation or temporary limitation of extraction, are recultivated or, in the case of small surface excavations, are subject to the process of spontaneous plant succession, which can determine the diversity of insects.

None of the sand quarries under study were reclaimed, 3 excavations were used intensively, 17 sites were overgrown with spontaneous vegetation and sand was extracted from them occasionally. Five sand quarries were littered with waste. These excavations were at an earlier or later stage of succession.

2.2. Analysis of flora and landscape

A floristic inventory was carried out for each sand quarry. The number of synanthropic species **(C1)**, the number of synanthropic food species **(C2)** and the number of ruderal food species **(C3)** were determined based on the lists made. The degree of habitat alteration was measured on the basis of the percentage of native and foreign species associated with human activity (flora synanthropization index, in %) (Jackowiak, 1990). Within each sand quarry, the percentage of the area without plants, the area of herbaceous vegetation, the forested area and the area occupied by the blooming plants was determined. In subsequent analyzes, the first three variables were combined using the PCA method into one, referred to as the succession stage **(C4)**. The area occupied by plants currently in bloom **(C5)** remained a separate variable.

In addition, the analysis of the landscape structure was performed, i.e. the percentage coverage of forests and open areas within a radius of 500 m from the boundaries of individual sand quarries was determined. Also in this case, the last two parameters were combined into one variable, defined as the location of the sand pit **(C6)**. The sand quarry area **(C7)** was measured and the level of littering with household and domestic waste **(C8)** was estimated.

The analysis of the landscape structure was carried out on the basis of aerial photographs taken in 1:2000 scale using the ArcGis program and direct field work. The plant species nomenclature was adopted after Flora Europaea (Rutkowski, 2004). Species affiliation to particular biocoenotic groups was taken from Sudnik-Wójcikowska (2015), their origin and the degree of invasiveness from Tokarska-Guzik et al. (2012). The characteristics of sand quarries are shown in Table A1–A2.

2.3. Insect sampling

The research was conducted in 2008 (sites 12 and 13), and in 2015 and 2016 in May (10 days) and July (20 days) under conditions favorable for bee flights, i.e. in the absence or low wind (< 3 Beaufort), with the visibility of a cloudless sky at around 70% and with air temperature during sampling above 16 °C (Krauss et al., 2009). Due to the fact that the phenological period in Eastern Poland is delayed in relation to the central part of the country by about two weeks, the research was conducted in May and July in order to obtain the fullest possible number of both spring and summer species. In each sand quarry, the insects were caught in a 200 × 1 m transect (Banaszak, 1980). Each transect walk took about 30 min to complete. The number of delimited transects was adjusted to the size of sand quarry: 0.5–1.0 ha area (no more than 4 transects), 1.0–3.0 ha area (no more than 8 transects), > 3.0 ha area (no more than 12 transects). In total, 160 samples (transects) were collected in the summer. However, in the spring time, due to the small contribution of food plants to the spring flora of the analyzed quarries, the sampling time was reduced by half (a total of 80 samples).

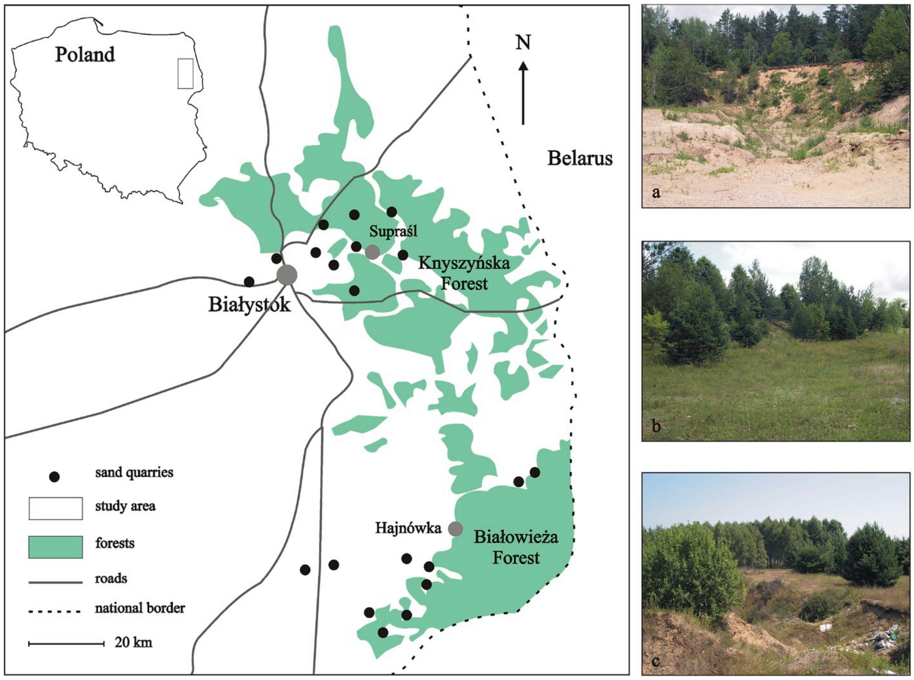

Fig. 1. Sand quarries: selected study sites: a = sand quarry during early succession; b = sand quarry during late succession; c = illegal landfill site.

To avoid self-replication, the sample sites were spaced more than 1.5 km apart. The collected specimens were pinned and identified to the species level. Bumblebees were identified *in situ*. Species nomenclature and information on their food source preferences (oligolectic vs. polylectic, cleptoparasitic) was taken after Michener (2007). Threat categories rated according to Red list of threatened animals in Poland (Banaszak, 2002) and Nomadini of Poland (Celary, 1995) (Table A3).

2.4. Statistical analysis

In order to determine the representativeness of collected material, the method of estimating the actual number of species, $chao_1$ and $chao_2$, was used. The computations were performed with EstimateS software (Colwell, 2006).

Frequency of a species was calculated as follows:

$$\text{Frequency of species}\ \ X = 100 * (N_X/N_F)$$

where N_X is the number of localities where species X was observed and N_F is the number of localities where any representative of a given family was found (see Sárospataki et al., 2005). Frequency indices were calculated separately for each family. The following categories of species frequency were used: rare ($\leq 5\%$), frequent (6%–15%), and common ($\geq 16\%$) (see also Sárospataki et al., 2005).

The numerical analysis of the collected data was carried out using the CANOCO v. 4 program (ter Braak and Šmilauer, 1998). A DCA indirect analysis was performed to detect the gradient in total variability of Apiformes data. The length of the analyzed set was less than 2.07 SD, so in further calculations linear methods were used (ter Braak and Šmilauer, 1998). Using the RDA method, we verified the hypothesis concerning the influence of the following factors on the occurrence of Apiformes: the number of synanthropic species (**C1**), the number of synanthropic food species (**C2**), the number of ruderal food species (**C3**), the succession stage (**C4**), the area occupied by plants currently in bloom (**C5**), the location in the landscape (**C6**), the sand quarry area (**C7**) and the level of littering (**C8**). The littering factor (**C8**) was treated as a nominal variable: 0 - quarries without waste, 1 - quarries with municipal and household waste. Data on species were transformed logarithmically [log(x)].

In order to determine which of the analyzed variables have the greatest impact on the richness and abundance of Apiformes, including oligolectic and polylectic species, a linear regression model with a qualitative variable representing the occurrence of waste was used. The significance of differences in the average number of synanthropic, synanthropic/ruderal plant species as well as the number and abundance of polylectic and oligolectic bees in uncluttered and littered habitats, was tested using the non-parametric Mann-Whitney *U* test. The Pearson's linear correlation coefficient was used to analyze the correlation of features. All statistical calculations were made using STATISTICA 12 software (StatSoft, 2014).

3. Results

3.1. Flora synanthropization index

The degree of transformation of the studied habitats was high, as evidenced by the large percentage of synanthropic plant species (75%). At the same time, synanthropic food species accounted for approximately 85% of the total plant species number. In this group, 58% were native species, 37% were foreign species permanently established in flora, while 5% were foreign invasive species: *Acer negundo, Conyza canadensis, Galinsoga parviflora, Solidago canadensis, Lupinus polyphyllus, Robinia pseudoacacia* (Table A2).

3.2. Oligolectic vs. polylectic and cleptoparasitic species

A total of 3752 specimens belonging to 156 species of wild bees (Hymenoptera: Apiformes) were found, which accounts for 32% of species known from Poland. The representativeness of collected material was very high and ranged from 93% ($chao_1$ method) to 90% ($chao_2$ method). In bee fauna studies, representativeness rarely exceeds 70% (Williams et al., 2001). In the collected material 27 species of oligolectic bees (17% of the community), and a total of 926 individuals (25% of the total abundance) were found (Table A3). Species associated only with one plant genus (monolectic bees) accounted for 2.96%.

The largest number of oligolectic species was found within the families of Megachilidae (8 species), Andrenidae (6 species), Melittidae (5 species), Apidae (4 species), Halictidae (3 species) and Colletidae (1

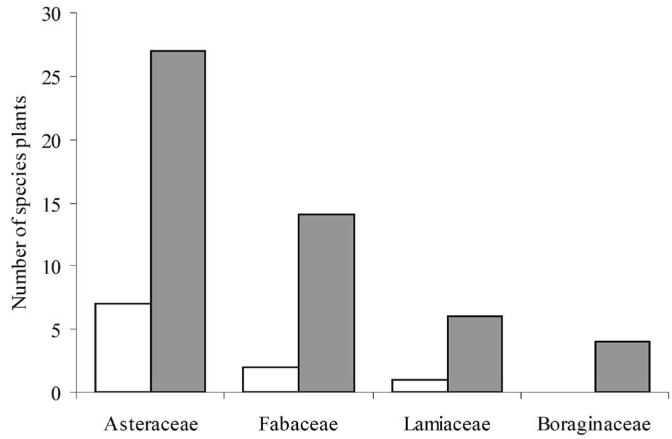

Fig. 2. Plant species of synanthropic habitats (gray) and other habitats (white) belonging to the main food families of oligolectic bees.

species). Five species (18.51%) were represented by $n > 50$ specimens, 14 species (51.87%) by $50 > n \geq 5$ individuals, and 8 species (29.62%) by $n < 5$ specimens (Table A3).

The most important food plants for oligolectic bees were species belonging to Asteraceae (9 oligolectic bees, 34 potential food species), Fabaceae (5 oligolectic bees, 16 potential food species), Lamiaceae (2 oligolectic bees, 7 potential food species), Boraginaceae (1 oligolectic species, 4 potential food species) (Fig. 2). Within the families of Campanulaceae, Dipsacaceae and Lythraceae, no synanthropic species were found.

In the group of polylectic and cleptoparasitic bees, 88 and 41 species were identified, and a total of 2472 and 354 individuals, respectively. In the group of polylectic bees, 11 species (12.50%) were represented by $n > 50$ individuals, 47 species (53.41%) by $50 > n \geq 5$ individuals, and 30 species (34.09%) by $n < 5$ specimens. Nineteen species of cleptoparasites (46.34%) were represented by $50 > n \geq 5$ individuals, 22 species (53.66%) by $n < 5$ individuals (Table A3).

Thirty species infrequently found in Poland were reported, of which 17 species (10.8%) were species in the Red List of Endangered and Threatened Animal Species in Poland (Banaszak, 2002). In the group of oligolectic bees there were four species in the Red List: *Andrena nasuta*, *Systropha curvicornis*, *Tetralonia malvae* and *Tetralonia salicariae* (Table A3).

3.3. Factors influencing occurrence of Apiformes

Using RDA analysis specified factors determining occurrence of Apiformes under the conditions of ongoing synanthropization of the habitat. The following variables had a significant impact: the level of littering (C8) ($p = 0.001$, $F = 2.912$), the number of synanthropic food species (C2) ($p = 0.001$, $F = 2.389$), area occupied by plants currently in bloom (C5) ($p = 0.001$, $F = 2.349$), the sand quarry area (C7) ($p = 0.002$, $F = 2.041$) and the number of ruderal food species (C3) ($p = 0.003$, $F = 1.964$) (Table 1) (Fig. 3).

3.4. Factors influencing the richness and abundance polylectic and oligolectic bees

The regression model was built carefully after the prior elimination of independent variables strongly correlated with each other, choosing the one that had the highest correlation coefficient with the dependent variable (Table 2).

The linear regression model showed that the area of sand quarries had the greatest impact on the richness and abundance of polylectic species ($p < 0.001$ in both cases) (C7) (Fig. 4 a,b). The obtained regression models can be presented in the following form:

$$\text{Richness} = 22.058 + 2.453{*}\text{C7}$$
$$\text{Abundance} = 71.672 + 21.611{*}\text{C7}$$

The regression model obtained for the richness of oligolectic species has shown that this variable is dependent significantly on the coverage of flowering plants ($p < 0.001$) (C5). Moreover, the addition of a variable representing the presence of waste on sand quarries (C8), although it was not statistically significant in the regression model, it definitely improved it - giving higher values of R^2 and lower values in standard estimation error and coefficient of random variation *w*. The model constructed in this way shows that the presence of waste gives even higher values of the richness of oligolectic species.

$$\text{Richness} = \begin{cases} 3.302 + 0.240{*}\text{C5};\ \text{waste}- \\ 4.880 + 0.240{*}\text{C5};\ \text{waste}+ \end{cases}$$

An interesting regression model was obtained for the abundance of oligolectic species. If there was a waste (C8) in a sand quarry, there was a strong dependence of the abundance of oligolectic bees on the number of synanthropic food species ($p < 0.001$) (C2) (Fig. 5b). When there was no waste in an excavation, the responsible factor was not found. The regression model adopted the following form:

$$\text{Abundance} = \begin{cases} 25.667;\ \text{waste}- \\ 280.342 - 3.549{*}\text{C2};\ \text{waste}+ \end{cases}$$

The parameters of each regression model are presented in Table 3.

3.5. Synanthropization/ruderalization of habitats vs. oligolectic bees

It was shown that the number and abundance of oligolectic species increased with the ongoing synanthropization and ruderalization of the habitat. In inactive sand quarries that were treated as illegal landfill sites (sites 8, 12, 14, 17, 18) (Table A1), the average number of synanthropic species ($p < 0.001$, $z = -5.428$), synanthropic food species ($p < 0.001$, $z = -6.900$) and ruderal food species ($p = 0.002$, $z = -3.011$) were significantly higher than in other quarries. At the same time, in the littered sand quarries, a significantly higher number of oligolectic species was observed ($p = 0.010$, $z = -2839$). In addition, oligolectic species exhibited a significantly higher abundance in these quarries ($p < 0.001$, $z = -9.862$). In sand quarries with waste, the number of oligolectic species ranged from 8 to 16 (average 13). In other sand quarries the number varied from 3 to 9 (average 6). The abundance of oligolectic bees ranged from 80 to 124 (mean 110.0), and from 6 to 59 (mean 25.66) in other sand quarries. Into each landfill site the waste was "dropped off" approximately 5 years ago, and their amount did not exceed 1% of the area. In these sand quarries the following species occurred abundantly: *Arctium lappa*, *Arctium tomentosum*, *Ballota nigra*, *Lamium purpureum*, *Malva neglecta*, *Sonchus arvensis*, *Sonchus oleraceus* and *Taraxacum officinale*. A high percentage of the above mentioned species and other ruderal plants indicated on high degree of ruderalization of selected sand quarries (Table A2). Richness ($p = 0.570$, $z = -0.567$) and abundance ($p = 0.176$, $z = -1.352$) of polylectic bees did not differ statistically between sand quarries littered with waste and those without waste.

3.6. Frequency of oligolectic species

It was shown that among 27 species of oligolectic bees, 15 were classified as species occurring commonly in the studied habitats (55.56%), 8 were frequently recorded (29.63%), and only 4 were rare (14.81%) (Table 4). *Melitta haemorrhoidalis* and *Chelostoma rapunculi* were rare species showing strong affiliation with the genus *Campanula*, while *Lasioglossum brevicorne* was associated with the Asteraceae.

In the group of common species, the highest frequency (> 50%) was obtained by *Dasypoda hirtipes*, *Melitta leporina*, *Anthidiellum strigatum*. In the case of species frequently listed, the highest frequency (> 10%) was observed for *Andrena denticulata*, *Andrena labialis*, *Macropis europaea* and *Hoplitis adunca* (Table 4).

Table 1
Results of stepwise selection of variables and a Monte Carlo Permutation Test – analysis of the significance of the effect of studied variables on the occurrence of all species Apiformes; variables were significant at $p < 0.05$.

Variables	RDA			
	Level of significance	Variation	% of explained variation	VIF
C8 – level of littering	**0.001**	0.14	2.912	4.200
C2 – number of synanthropic food species	**0.001**	0.12	2.389	7.223
C5 – area occupied by plants currently in bloom	**0.001**	0.12	2.349	5.441
C7 – area of sand quarry	**0.002**	0.10	2.041	1.387
C3 – number of ruderal food species	**0.003**	0.10	1.964	9.165
C4 – succession stage	0.109	0.07	1.345	1.522
C6 – location	0.207	0.06	1.202	1.791

Due to collinearity (VIF > 10), variable C1 was removed from the RDA analysis.

4. Discussion

Obtained results indicate that sand quarries are an important secondary habitat for wild bees, including oligolectic bees with specialized dietary requirements. Most oligolectic species were noted both in unlittered as well as littered sand quarries. *Andrena labialis*, *Anthocopa spinulosa* and *Chalicodoma ericetorum* were observed only in unlittered sand quarry. These species were associated with the Asteraceae and Fabiaceae families.

Many studies have pointed to the negative role of anthropopressure in maintaining the diversity of pollinators (Ricketts et al., 2008; Winfree et al., 2009). It is believed that one of the main reasons for this is the loss of flowering plant resources. However, there are studies showing that in some cases the increase in anthropopressure is not correlated with a decrease in the diversity of pollinators because it may leads to the creation of artificial biotopes characterized by specific

Table 2
Correlation between the features of sand quarries and richness and abundance of polylectic and oligolectic bees. M – average, SD – standard deviation.

Variables	M	SD	C1	C2	C3	C5	C7
Richness							
polylectic	27.90	6.21	0.188	0.256	0.208	0.287	**0.747**
oligolectic	7.90	3.65	**0.731**	**0.795**	**0.680**	**0.900**	0.108
Abundance							
polylectic	123.15	55.86	0.246	0.372	0.407	**0.423**	**0.733**
oligolectic	46.75	40.78	**0.764**	**0.808**	**0.748**	**0.731**	0.148

C1 – number of synanthropic species, C2 – number of synanthropic food species, C3 – number of ruderal food species, C5 – area occupied by plants currently in bloom, C7 – area of sand quarry. In the analyzes, statistically insignificant variables were omitted: C4 – succession stage and C6 – location. The data marked in bold are statistically significant at the level of significance $p < 0.001$.

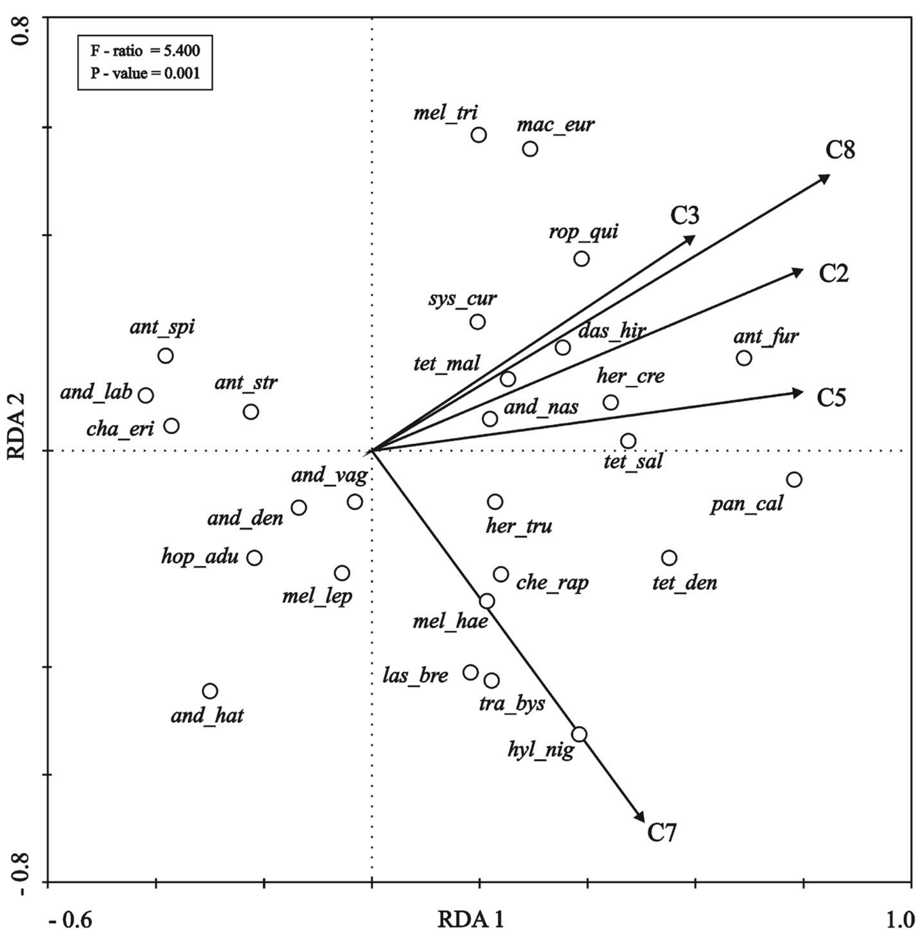

Fig. 3. Ordination diagram based on RDA method, presenting the distribution of 27 oligolectic species with respect to I and II axes, and vectors of the analyzed variables. The variables shown in the figure explained significantly 53.8% of the variation in all Apiformes species data (the sum of all canonical eigenvalues: 0.538, the sum of all eigenvalues: 1.000; 0.538/1.000 = 0.538 i. e. 53.8%).
Legend: **and_den** - *Andrena denticulata*, **and_hat** - *Andrena hattorfiana*, **and_lab** - *Andrena labialis*, **and_nas** - *Andrena nasuta*, **and_vag** - *Andrena vaga*, **ant_spi** - *Anthocopa spinulosa*, **ant_str** - *Anthidiellum strigatum*, **ant_fur** - *Anthophora furcata*, **cha_eri** - *Chalicodoma ericetorum*, **che_rap** - *Chelostoma rapunculi*, **das_hir** - *Dasypoda hirtipes*, **her_cre** - *Heriades crenulata*, **her_trun** - *Heriades truncorum*, **hop_adu** - *Hoplitis adunca*, **hyl_nig** - *Hylaeus nigritus*, **las_bre** - *Lasioglossum brevicorne*, **mac_eur** - *Macropis europaea*, **mel_hae** - *Melitta haemorrhoidalis*, **mel_lep** - *Melitta leporina*, **mel_tri** - *Melitta tricincta*, **pan_cal** - *Panurgus calcaratus*, **rop_qui** - *Rophites quinquespinosus*, **sys_cur** - *Systropha curvicornis*, **tra_bys** - *Trachusa byssina*, **tet_den** - *Tetraloniella dentata*, **tet_mal** - *Tetralonia malvae*, **tet_sal** - *Tetralonia salicariae*.

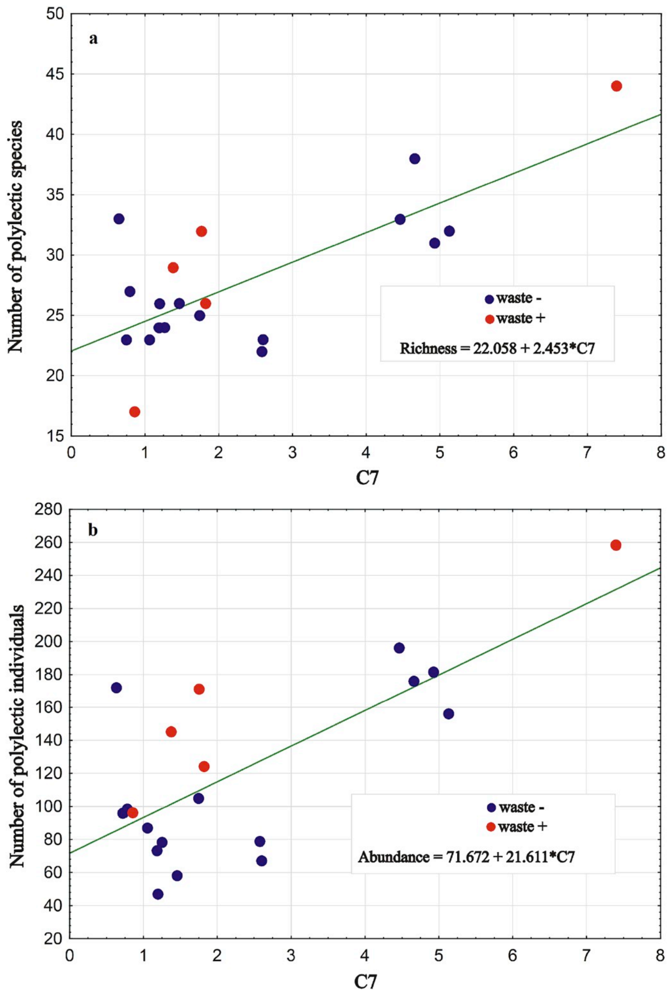

Fig. 4. a, b. Richness (a) and abundance (b) of polylectic bees depending on the size of the sand quarry (C7) for sites where waste was present (red) and those without waste (blue). Straight lines symbolize simple regression or lack of dependence for each group after multiple regression taking into account the presence of waste. Legend: - for sites without waste, + for sites littered with waste. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

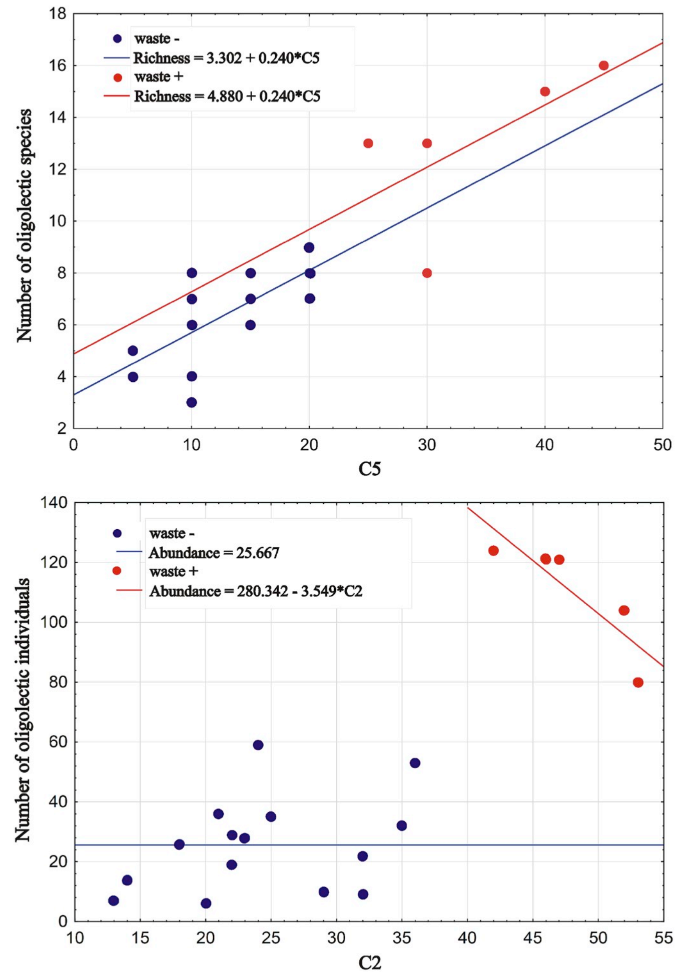

Fig. 5. a,b. Richness (a) and abundance (b) of oligolectic bees depending on the area occupied by plants currently in bloom (C5) and the number of synanthropic food species (C2) for sites where waste was present (red) and those without waste (blue). Straight lines symbolize simple regression or lack of dependence for each group after multiple regression taking into account the presence of waste. Legend: - for sites without waste, + for sites littered with waste. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Parameters of regression models for polylectic and oligolectic bees and the qualitative variable representing the occurrence of waste.

Model parameters	Polylectic		Oligolectic	
	Richness	Abundance	Richness	Abundance
R^2	0.559	0.537	0.819	0.877
Standard estimation error	4.238	39.040	1.663	15.151
Coefficient of random variation *w*	15.19%	31.7%	21.05%	32.41%

ecological features. For example, anthropogenic habitats occurring in a diversified agricultural landscape (Hoehn et al., 2008; Williams et al., 2011) or in an urbanized area (Baldock et al., 2015; Banaszak-Cibicka et al., 2018) can provide a high diversity of pollinating insects compared to natural areas. Also the positive role of sand quarries as new, important habitats for various groups of organisms, including pollinating insects is pointed out (Eversham et al., 1996; Heneberg et al., 2013; Heneberg and Řezáč, 2014; De Smedt and Van de Poel, 2017). These relationships can be modified by both the type of landscape and the type of habitat in which they occur as well as by the abundance of native and foreign plant species (Williams et al., 2011; Banaszak-Cibicka et al., 2016).

Plant species of foreign origin that penetrate into native ecosystems cause changes in the existing relationships and interfere with the stability of interactions in the system of plants and pollinating insects (Richardson et al., 2000). These new relationships, characterized at the level of individual interactions (Traveset and Richardson, 2006), as well as the entire pollination network (Montero-Castaño and Vilá, 2012) are still insufficiently known, especially in anthropogenically altered habitats. Still little research has been done so far to comprehensively evaluate the impact of all species of foreign plants on the diversity of pollinators, which may lead to a premature and even erroneous assessment of their significance in both natural and anthropogenic habitats (Williams et al., 2011). The key problem is to distinguish between the influence of species of foreign origin classified as invasive and that of foreign plants settled in a given area and not exhibiting invasive characteristics.

Anthropogenic environments are usually dominated by synanthropic plants, so their importance in these habitats for local bee fauna must be significant, especially when considering the fact that a large percentage of species are small, solitary bees, for which the feeding range is about 150–600 m from the nesting site (Gathmann and

Table 4
Frequency of oligolectic bees in sand quarries.

Family	Species	Frequency (%)	Frequency Category	Associated plants
Colletidae	*Hylaeus nigritus*	25.0	common	Asteraceae
Andrenidae	*Andrena denticulata*	15.0	frequent	Asteraceae
	Andrena hattorfiana	50.0	common	Dipsacaceae
	Andrena labialis	15.0	frequent	Fabaceae
	Andrena nasuta	10.0	frequent	Boraginaceae
	Andrena vaga	45.0	common	Salix
	Panurgus calcaratus	50.0	common	Asteraceae
Halictidae	*Lasioglossum brevicorne*	5.0	rare	Asteraceae
	Rophites quinquespinosus	10.0	frequent	Lamiaceae
	Systropha curvicornis	55.0	common	Convolvulus
Melittidae	*Dasypoda hirtipes*	90.0	common	Asteraceae
	Macropis europaea	15.0	frequent	Lysimachia
	Melitta haemorrhoidalis	5.0	rare	Campanula
	Melitta leporina	60.0	common	Fabaceae
	Melitta tricincta	20.0	common	Odontites
Megachilidae	*Anthidiellum strigatum*	60.0	common	Fabaceae
	Anthocopa spinulosa	10.0	frequent	Asteraceae
	Chalicodoma ericetorum	10.0	frequent	Fabaceae
	Chelostoma rapunculi	5.0	rare	Campanula
	Heriades crenulata	45.0	common	Asteraceae
	Heriades truncorum	20.0	common	Asteraceae
	Hoplitis adunca	15.0	frequent	Echium
	Trachusa byssina	40.0	common	Fabaceae
Apidae	*Anthophora furcata*	30.0	common	Lamiaceae
	Tetraloniella dentata	30.0	common	Asteraceae
	Tetralonia malvae	5.0	rare	Malvaceae
	Tetralonia salicariae	50.0	common	Lythrum

Tscharntke, 2002). In our studies, bees of small and medium size accounted for about 95% of species; species with a size of at least 8 mm accounted for 29% (Table A3). This confirms the importance of the local flora as a source of food for the analyzed bee species. Larger species can use habitat complex consisting of several partial habitats (Westrich, 1996). Recent research indicates that the interactions between pollinators and native plants or plants of foreign origin are highly dependent on the level of environmental disturbances and the alteration of the habitat in a given area (Williams et al., 2011). As shown, the degree of transformation of the studied habitats was high, as evidenced by the large percentage of synanthropic plant species.

The positive role of synanthropic plants in determining the diversity of pollinators was demonstrated amongst others in urban areas (Eremeeva and Sushchev, 2005; Lubiarz and Trzaskowska, 2013). The assumption adopted for this work that one of the factors influencning the diversity of Apiformes in the studied area might be the richness of local flora, mainly synanthropic species, was valid, especially for oligolectic bees. Their number and abundance significantly increased with the ongoing synanthropization and ruderalization of the habitat and with the increasing percentage of attractive food species An interesting regularity was also observed: in sand quarries where a small amount of waste had been "dropped off", the percentage of synanthropic/ruderal plants increased. In these excavations, the number and abundance of oligolectic bees were significantly higher than in others. At the stage of research, we are not able to precisely determine all factors that influence the differentiation of bees in the analyzed sand quarries. As we have shown, the share of the analyzed factors was low, and individual variables explained merely a small % of the total data variability. The suggests the existence of variables that we have not taken into account in our analysis, and which could have influenced the occurrence of Apiformes. Perhaps this was also caused by a small number of samples, i.e., sand quarries littered with waste. Most likely, the richness and abundance of oligolectic bees were modified by the time of waste storage. A longer waste storage time and a successive waste disposal could increase the probability of occurrence of bees associated with a given genus or family of flowering plants that prefer certain habitat conditions.

Regardless of what factors influence the occurrence of plants and what is the pollination pattern, it is determined mainly by the abundance of plants or by the preference of pollinators towards specific species (Williams et al., 2011). In typical habitats, the bee community structure is asymmetric, i.e. the community is dominated by polylectic species that use many plant species as a food source, while there are much fewer specialized bee species because they ecologically, physiologically and phenologically depend on limited floral resources (Ritchie et al., 2016). In the presented studies polylectic bees accounted for ca. 57%, while oligolectic species accounted for approximately 17% of all species. A similar percentage of oligolectic bees was also demonstrated in other anthropogenic habitats, e.g. 12% in the habitats of the gray dunes at the Baltic Sea coast (Banaszak, 2016) or 13% in Poznań (Banaszak-Cibicka and Żmihorski, 2012). A larger number of oligolectic species is observed in semi-natural communities (e.g. about 30% in the wet *Molinietum* (Poaceae)) meadows near Kraków and about 19% in xerothermic grassland habitats in the Vistula valley (Banaszak et al., 2006; Moroń et al., 2008). However, in contrast to the cited works, the majority of oligolectic bees observed in the quarry areas were commonly and often found there (about 85%). This may suggest a high attractiveness of the analyzed sand quarries for plants and oligolectic bees associated with them. Insufficient recognition of post-excavation sites in Poland and Europe, especially in the context of the interaction of plants and wild bees, does not allow for a wider comparative analysis of the results obtained.

It was demonstrated that while the occurrence of oligolectic species was conditioned mainly by the availability of food resources, the richness and abundance of bees, including polilectic species, were influenced primarily by the size of sand quarry. This is in line with the results of other studies on wild bees in limestone quarries (Krauss et al., 2009) or beetles in sand excavations (Lönnberg and Jonsell, 2012). A positive correlation between the habitat area and species richness is one of the basic laws in ecology derived from the theory of island biogeography (e.g. Rosenzweig, 1995). It is believed that certain species groups may react differently to habitat loss (Ewers and Didham, 2006; Hambäck et al., 2007). For example, specialized species, such as solitary, cleptoparasitic or oligolectic bees, are more vulnerable to adverse changes than the generalists (Krauss et al., 2009). However, in our studies we did not find such a relationship. Oligolectic bees did not show significant response to neither habitat loss nor its succession. The percentage share of cleptoparasitic species was also surprisingly high.

Cleptoparasitic species usually comprise 15–20% of all species in the community (Wcislo and Cane, 1996), while in transformed environments their richness and abundance decreases, which is why they are considered an indicator group (Sheffield et al., 2013). In our study, the parasitic bees accounted for 26% of all species and 9% in terms of species abundance. A high percentage of parasites in the community indicates the stability of the population of host species occurring in the analyzed sand quarries (Cierzniak, 2003). However, the lack of reaction of oligolectic bees on the loss of habitat was probably due to the fact that the negative changes were compensated by the abundance of plants attractive for pollinators which was associated with the littering of sand quarries. Plant biomass from home gardens and construction debris created a convenient habitat for ruderal plants that was an attractive source of food for bees. Undoubtedly, this factor significantly modified the existing dependencies in the pollination network. However, we believe that over the years, with the successive transformations of the habitat (changes in the abundance of plants and the loss of suitable places for nesting), these interactions will change again.

5. Conclusions

Undoubtedly, in disturbed landscapes, the abundance of plants associated with human activity is much higher than in natural habitats. In these habitats, synanthropic plants probably play a key role in maintaining bee resources. Importantly, the impact of landscapes heavily transformed by humans on native pollinators, as shown in these studies, is not always unambiguously negative. What's more, contrary to popular opinion, habitats altered by human activity, which until now have been largely neglected, may be important for the protection of fauna, including specialized species. Sand excavations modify the existing habitat conditions and lead to a more varied terrain, thus increasing the availability of diverse microhabitats and food plants. Such newly created, artificial places can become an important habitat for many species, including rare and threatened taxa (Heneberg et al., 2013). This is particularly important due to the observed and growing process of losing natural habitats. Therefore, research on the importance of sand quarries as places of life and protection of various groups of organisms should be continued. At the same time, the analysis of factors increasing biodiversity in post-industrial areas will enable the development of guidelines aimed at improving the quality of these areas for local fauna.

Authors' contributions

LT conceived the project, carried out field and lab research. All authors conducted the data analysis and drafted the manuscript.

Acknowledgements

We would like to thank Mrs. Renata Hoffmann for botanical consultations. The authors declare that they have no conflict of interest. This study was partly supported by the Polish Minister of Science and Higher Education, under the program "Regional Initiative of Excellence" in 2019-2022 (Grant No. 008/RID/2018/19).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2019.03.005.

References

Aizen, M.A., Harder, L.D., 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr. Biol. 19, 915–918. http://doi.org/10.1016/j.cub.2009.03.071.

Baldock, K.C.R., Goddard, M.A., Hicks, D.E., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scot, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proc. Roy. Soc. Lond. B 282, 2014–2849.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera, Apoidea). Pol. Ecol. Stud. 6 (2), 355–366.

Banaszak, J., 1992. Strategy for conservation of wild bees in an agricultural landscape. Agric. Ecosyst. Environ. 40, 179–192. http://doi.org/10.1016/0167-8809(92)90091-O.

Banaszak, J., 2002. Apoidea pszczoły. In: Głowaciński, Z. (Ed.), Red List of Threatened Animals in Poland. Instytut Ochrony Przyrody PAN, Kraków, pp. 69–75 (in Polish).

Banaszak, J., 2016. Distribution and ecology of bees on the polish Baltic coast (Hymenoptera, Apoidea, Apiformes). Pol. J. Entomol. 85, 269–309. http://doi.org/10.1515/pjen-2016-0016.

Banaszak, J., Twerd, L., 2010. High number of cuckoo wasps (Hymenoptera: Chrysididae) in areas directly affected by lime and sodium industry. Pol. J. Entomol. 79, 291–305.

Banaszak, J., Cierzniak, T., Kriger, R., Wendzonka, J., 2006. Bees of xerothermic swards in the lower Vistula valley: diversity and zoogeographic analyses (Hymenoptera: Apoidea: Apiformes). Pol. J. Entomol. 75, 511–537.

Banaszak-Cibicka, W., Żmihorski, M., 2012. Wild bees along an urban gradient: winners and losers. J. Insect Conserv. 16, 331–343 http//doi.org/10.1007/s10841-011-9419-2.

Banaszak-Cibicka, W., Ratyńska, H., Dylewski, Ł., 2016. Features of urban green space favourable for large and diverse bee populations (Hymenoptera: Apoidea: Apiformes). Urban For. Urban Gree 20C, 448–452. https://doi.org/10.1016/j.ufug.2016.10.015.

Banaszak-Cibicka, W., Twerd, L., Fliszkiewicz, M., Giejdasz, K., Langowska, A., 2018. City parks vs. natural areas - is it possible to preserve a natural level of bee richness and abundance in a city park? Urban Ecosyst. 21, 599–613. https://doi.org/10.1007/s11252-018-0756-8.

Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.F., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect pollinated plants in Britain and The Netherlands. Science 313, 351–354. http://doi.org/.10.1126/science. 1127863.

Cane, J.H., Sipes, S.D., 2006. Characterizing floral specialization by bees: Analytical methods and a revised lexicon for oligolecty. In: Waser, N.M., Ollerton, J. (Eds.), Specialization and Generalization in Plant-Pollinator Interactions. University of Chicago Press, Chicago, pp. 99–122.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee and diversity on arable field margins. J. Appl. Ecol. 44, 29–40. http://doi:10.1111/j.1365-2664.2006.01249.x.

Celary, W., 1995. Nomadini (Hymenoptera, Apoidea, Anthophoridae) of Poland. Polish Academy of Sciences, pp. 281.

Cierzniak, T., 2003. Ekologia pszczół w dynamicznym kręgu zbiorowisk grądowych. Wydawnictwo Akademii Bydgoskiej, Bydgoszcz (in Polish).

Colwell, R.K., 2006. EstimateS: statistical estimation of species richness and shared species from sample. Version 8.0.0. User's Guide and applications published at: http://purl.oclc.org/estimates.

De Smedt, P., Van de Poel, S., 2017. Succession in harvestman (Opiliones) communities within an abandoned sand quarry in Belgium. Belg. J. Zool. 147 (2), 155–169. http://doi.org/10.26496/bjz.2017.13.

Dupont, Y.L., Padrón, B., Olesen, J.M., Petanidou, T., 2009. Spatio-temporal variation in the structure of pollination networks. Oikos 118, 1261–1269. http://doi.org/10.1111/j.1600-0706.2009.17594.x.

Eremeeva, N.I., Sushchev, D.V., 2005. Structural changes in the fauna of pollinating insects in urban landscapes. Russ. J. Ecol. 36 (4), 259–265. https://doi.org/10.1007/s11184-005-0070-6.

Eversham, B.C., Roy, D.B., Telfer, M.G., 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Ann. Zool. Fenn. 149–156.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81, 117–142. https://doi.org/10.1017/S1464793105006949.

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71, 757–764. http://doi.org/10.1046/j.1365-2656.2002.00641.x.

Goulson, D., 2003. Conserving wild bees for crop pollination. J. Food Agric. Environ. 1, 142–144.

Hambäck, P.A., Summerville, K.S., Steffan-Dewenter, I., Krauss, J., Englund, G., Crist, T.O., 2007. Habitat specialisation, body-size and family identity explains Lepidopteran density-area relationships in a cross-continental comparison. Proc. Natl. Acad. Sci. U S A. 104, 8368–8373. https://doi.org/10.1073/pnas.0611462104.

Heneberg, P., Řezáč, M., 2014. Dry sandpits and gravel–sandpits serve as key refuges for endangered epigeic spiders (Araneae) and harvestmen (Opiliones) of Central European steppes aeolian sands. Ecol. Eng. 73, 659–670. http://doi.org/10.1016/j.ecoleng.2014.09.101.

Heneberg, P., Bogusch, P., Řehounek, J., 2013. Sandpits provide critical refuge for bees and wasps (Hymenoptera: Apocrita). J. Insect Conserv. 17, 473–490. http://doi.org/10.1007/s10841-012-9529-5.

Heneberg, P., Bogusch, P., Řezáč, M., 2016. Off-road motorcycle circuits support long-term persistence of bees and wasps (Hymenoptera: Aculeata) of open landscape at newly formed refugia within otherwise afforested temperate landscape. Ecol. Eng. 93, 187–198. https://doi.org/10.1016/j.ecoleng.2016.05.026.

Heneberg, P., Bogusch, P., Řezáč, M., 2017. Roadside verges can support spontaneous establishment of steppe-like habitats hosting diverse assemblages of bees and wasps (Hymenoptera: Aculeata) in an intensively cultivated central European landscape. Biodivers. Conserv. 26, 843–864. http://doi.org/10.1007/s10531-016-1275-7.

Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. Proc Biol Sci. B: Biol. Sci. 275, 2283–2291. https://doi.org/10.1098/rspb.2008.0405.

Jackowiak, B., 1990. Antropogeniczne przemiany flory roślin naczyniowych Poznania. Wyd. Nauk. UAM, B, 42, Poznań, pp. 232 (in Polish).
Kozłowska, O., Sołomacha, M., Walentek, I., 2016. Nowe dane o zasobach kruszyw piaskowo-żwirowych dla inwestycji drogowych i kubaturowych w Polsce. Mineral Resources Management 32 (1), 103–118 (in Polish).
Krauss, J., Alfert, T., Steffan-Dewenter, I., 2009. Habitat area but not habitat age determines wild bee richness in limestone quarries. J. Appl. Ecol. 46, 194–201. http://doi.org/10.1111/j.1365-2664.2008.01582.x.
Kuzmič, F., Šilic, U., 2017. Alien species in different habitats types of Slovenia: analysis of vegetation database. Period. Biol. 19 (3), 199–208. http://doi.org/10.18054/pb.v119i3.5183.
Lenda, M., Skórka, P., Moroń, D., Rosin, Z.M., Tryjanowski, P., 2012. The importance of the gravel excavation industry for the conservation of grassland butterflies. Biol. Conserv. 148 (1), 180–190.
Lönnberg, L., Jonsell, M., 2012. Sand pits as habitats for beetles (Coleoptera): does area affect species number and composition? Biodivers. Conserv. 21 (3), 853–874. https://doi.org/10.1007/s10531-012-0225-2.
Lubiarz, M., Trzaskowska, E., 2013. The potential importance of synanthropic vegetation to bumblebees in urban ecosystems on the example of Lublin. Acta Agrobot. 66 (4), 143–156. http://doi.org/10.5586/aa.2013.061.
MacIvor, J.S., Cabral, J.M., Packer, L., 2014. Pollen specialization by solitary bees in an urban landscape. Urban Ecosyst. 17, 139–147. http://doi.org/10.1007/s11252-013-0321-4.
Michener, ChD., 2007. The Bees of the World. The Johns Hopkins University Press, Baltimore.
Montero-Castańo, A., Vilá, M., 2012. Impact of landscape alteration and invasions on pollinators: a meta-analysis. J. Ecol. 100, 884–893. https://doi.org/10.1111/j.1365-2745.2012.01968.x.
Moroń, D., Szentgyörgyi, H., Wantuch, M., Celary, W., Westphal, C., Settele, J., Woyciechowski, M., 2008. Diversity of wild bees in wet meadows: implications for conservation. Wetlands 28 (4), 975–983. http://doi.org/10.1672/08-83.1.
Moroń, D., Skórka, P., Rożej-Pabijan, E., Wantuch, M., Kajzer-Bonk, J., Celary, W., Mielczarek, Ł.E., Tryjanowski, P., 2014. Railway embankments as new habitat for pollinators in an agricultural landscape. PLoS One 9 (7), e101297. http://doi.org/10.1371/journal.pone.0101297.
PIG-PIB, 2014. Balance of Resources for Mineral Deposits in Poland, by Condition on 31.12.2014 r.
Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'toole, C., Roberts, S., Willmer, P., 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. Oikos 101, 103–112. http://doi.org/10.1034/j.1600-0706.2003.12186.x.
Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. http://doi.org/10.1016/j.tree.2010.01.007.
Quinterno, C., Morales, C.L., Aizen, M.A., 2010. Effects of anthropogenic habitat disturbance on local pollinator diversity and species turnover across a precipitation gradient. Biodivers. Conserv. 19, 257–274. http://doi.org/10.1007/s10531-009-9720-5.
Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107.
Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11, 499–515. http://doi.org/10.1111/j.1461-0248.2008.01157.x.
Ritchie, A.D., Ruppel, R., Jha, S., 2016. Generalist behavior describes pollen foraging for perceived oligolectic and polylectic bees. Environ. Entomol. 45 (4), 900–919. http://doi.org/10.1093/ee/nvw032.
Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
Rutkowski, L., 2004. Klucz do oznaczania roślin Polski Niżowej. Wydawnictwo Naukowe PWN, Warszawa, pp. 814 (in Polish).
Santoul, F., Figuerola, J., Green, A.J., 2004. Importance of gravel pits for the conservation of waterbirds in the Garonne river floodplain (southwest France). Biodivers. Conserv. 13, 1231–1243. https://doi.org/10.1023/B:BIOC.0000018154.02096.4b.
Sárospataki, M., Novák, J., Molnár, V., 2005. Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe. Biodivers. Conserv. 14, 2437–2446. http://doi.org/10.1007/s10531-004-0152-y.
Sheffield, C.S., Pindarm, A., Packer, L., Kevan, P., 2013. The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. Apidologie 44 (5), 501–510. http://doi.org/10.1007/s13592-013-0200-2.
StatSoft, Inc, 2014. STATISTICA (data analysis software system), version 12. www.statsoft.com.
Sudnik-Wójcikowska, B., 2015. Rośliny synantropijne. Flora Polski. MULTICO Oficyna Wydawnicza, Warszawa, pp. 336 (in Polish).
ter Braak, C.J., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). Microcomputer Power, (Ithaca, NY, USA).
Tokarska-Guzik, B., Dajdok, Z., Zając, M., Zając, A., Urbisz, A., Danielewicz, W., Hołdyński, Cz, 2012. Rośliny obcego pochodzenia w Polsce ze szczególnym uwzględnieniem gatunków inwazyjnych. Generalna Dyrekcja Ochrony Środowiska, Warszawa, pp. 197 (in Polish).
Traveset, A., Richardson, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol. Evol. 21, 208–216. http://doi.org/10.1016/j.tree. 2006.01. 006.
Tropek, R., Kadlec, T., Karešová, P., Spitzer, L., Kočárek, P., Malenovský, I., Banar, P., Tuf, I.H., Hejda, M., Konvicka, M., 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. J. Appl. Ecol. 47, 139–147. http://doi.org/10.1111/j.1365-2664.2009.01746.x.
Tropek, R., Cerna, I., Straka, J., Kocarek, P., Malenovsky, I., Tichanek, F., Sebek, P., 2016. In search for a compromise between biodiversity conservation and human health protection in restoration of fly ash deposits: effect of anti-dust treatments on five groups of arthropods. Environ. Sci. Pollut. Res. 23 (14), 13653–13660. http://doi.org/10.1007/s11356-015-4382-1.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8 (8), 857–874. http://doi:10.1111/j.1461-0248.2005.00782.x.
Twerd, L., Banaszak, J., 2017. Monitoring of wild bees in postindustrial wastelands in the Kujawy region. Inżynieria Ekol. 18 (2), 180–188 (in Polish).
Twerd, L., Krzyżyński, M., Waldon-Rudzionek, B., Olszewski, P., 2017. Can soda ash dumping grounds provide replacement habitats for digger wasps (Hymenoptera, Apoidea, Spheciformes)? PLoS One 12 (4), e0175664. http://doi.org/10.1371/journal.pone.0175664.
Walentek, I., Sołomacha, M., Olejniczak, K., 2016. Problem of unlicensed aggregates exploitation in Poland. Mineral Resources Management 32 (1), 119–136. (in Polish). http://doi.org/10.1515/gospo-2016-0003.
Wcislo, W.T., Cane, J.H., 1996. Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. Annu. Rev. Entomol. 41 (1), 257–286.
Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.E., Bluthgen, N., 2010. Pollen amino acids and flower specialisation in solitary bees. Apidologie 41, 476–487. http://doi.org/10.1051/apido/2009083.
Weiner, C.N., Werner, M., Linsenmair, K.E., Blüthgen, N., 2014. Lands use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95 (2), 466–474. http://doi.org/10.3410/f.718325695.793501464.
Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats. Linn. Soc. Symp. Ser. 18, 1–16 (Academic Press Limited).
Williams, N.M., Minckley, R., Silviera, F., 2001. Variation in native bee faunas and its implications for detecting community changes. Conserv. Ecol. 5 (1), 7. https://www.jstor.org/stable/26271796.
Williams, N.M., Cariveau, D., Winfree, R., Kremen, C., 2011. Bees in disturbed habitats use, but do not prefer, alien plants. Basic Appl. Ecol. 12, 332–341. http://doi.org/10.1016/j.baae.2010.11.008.
Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. How do bees respond to anthropogenic disturbance? A synthesis and meta-analysis. Ecology 90, 2068–2076.
Řehounková, K., Prach, K., 2010. Life-history traits and habitat preferences of colonizing plant species in long-term spontaneous succession in abandoned gravel–sand pits. Basic Appl. Ecol. 11 (1), 45–53. http://doi.org/10.1016/j.baae.2009.06.007.