



Keep trees for bees: Pollen collection by *Osmia bicornis* along the urbanization gradient

Aleksandra Splitt^{a,b,*}, Piotr Skórka^a, Aneta Strachecka^c, Mikołaj Borański^b, Dariusz Teper^b

^a Institute of Nature Conservation, Polish Academy of Sciences, Al. Mickiewicza 33, 31-120, Kraków, Poland

^b The National Institute of Horticultural Research, Apiculture Division in Puławy, ul. Konstytucji 3 Maja 1/3, 96-100 Skierniewice, Poland

^c Department of Zoology and Animal Ecology, Faculty of Environmental Biology, University of Life Sciences in Lublin, 20-950, Lublin, Poland

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ABSTRACT

Development of urban agglomerations and the intensification of agriculture profoundly affect bees' food resources, hence ecosystem services such as pollination. A solitary bee, *Osmia bicornis* (syn. *O. rufa*), is an effective springtime pollinator of crops, decorative and wild plants. However, it is largely unknown if this species is conservative or plastic in pollen collection in different environments. New breedings of *O. bicornis* were established in localizations qualified as urban (90 % of built-up infrastructure), suburban (55–65 %), and rural (up to 20 %). From each nest randomly chosen samples of unused pollen provisions were collected and analysed. Moreover, literature databases of food composition of *O. bicornis* was compiled to show overall tendencies in the choice of plant type, habitat, as well as pollen coating and size. Our field study showed that in the less human-modified environment *O. bicornis* collected higher diversity of pollen types to build its provision, compared to more urban areas (Simpson diversity index was 3.7 in rural, 2.8 in suburban and 2.2 in urban sites). Literature review showed that bees repeatedly collected pollen from commonly available trees like oaks, maples, horse chestnut and elms. Field data also revealed that the use of tree pollen was especially common in urban sites while bees from suburban and rural sites included pollen of herbaceous plants and shrubs. Neither the shape nor the size of the pollen mattered to bee foraging choices. However, bees frequently used pollen dispersed by wind in urban sites. The main conclusion is that polylectic bees opportunistically collect pollen of plants present in the environment and number of plant taxa may be limiting factor for studied bees. The welfare of *O. bicornis* requires planting trees such as oaks, willows, maples, and representatives from Rosaceae family, and it is especially advisable in urban sites where herbaceous flowering plants are less common than in urban and suburban areas. Hence, keeping even singular trees may complement the bee food base in urbanized areas.

1. Introduction

Many research, e.g. Belsky and Joshi (2019), report that there has been multitiered large-scale declines in bee abundance and species richness over the last decade. As one reason climatic alterations are mentioned, because they have disrupted synchronous bee emergence with flower blooming and reduced the availability of diverse floral resources. Also, urbanization, namely urban sprawl, often is pointed as having negative influence on insects' populations (Newman, 2016). All these phenomena may lead to impoverishing the diet of pollinating insects. Initially honeybees, because of their economic importance, appear to be of the greatest concerns, while it is wild bees that are more likely to

be adversely affected by shortages of food sources. Honeybees use a wide range of resources (pollen, nectar, resin) and also themselves produce e.g. royal jelly and store food in large quantities for the entire colony, whereas adult solitary bees use the flower resources on an ongoing basis and provide the offspring with food mainly in the form of pollen loads on which the larvae must feed themselves. While honeybees, as a managed species, might be fed by beekeepers when food is scarce, wild bees, which lead mostly solitary life and inhabit hollow plant stems or nest in the ground, are vulnerable to periods of starvation. It is particularly important as many solitary bees, such as *Osmia* in Europe are early-spring pollinators and their emerging period is just at the time when flower resources are scarce and only a limited number of

* Corresponding author at: Institute of Nature Conservation, Polish Academy of Sciences, Al. Mickiewicza 33, 31-120, Kraków, Poland.

E-mail addresses: los-aleksandra@o2.pl (A. Splitt), pskorka@iop.krakow.pl (P. Skórka), aneta.strachecka@up.lublin.pl (A. Strachecka), mikolaj.boranski@inhort.pl (M. Borański), dariusz.teper@inhort.pl (D. Teper).

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plants produce pollen. This takes on added significance if we consider that in temperate regions solitary bees are considered among the best pollinators for most plants and significantly outperform honeybees in pollination effectiveness (Willmer et al., 2017). However, filling gaps in knowledge regarding solitary bees' use of resources may help to indicate most effective plants to enrich environment, especially an anthropogenized one. Following Ayers and Rehan (2021) it can be stated that green spaces like parks and urban gardens may be potential refuges for pollinators. Also, Majewska and Altizer (2020) indicate that pollinators responded positively to high plant species diversity and woody vegetation in gardens. These may be supported also by Donkersley (2019) statement that woody habitat features like trees and hedgerows provide more efficient resources for pollinators in a number of ways. Tree and hedgerow are more efficient forage targets due to absolute resource density and also could provide more optimised foraging landscapes for pollinators. These measures might augment population of pollinators, especially solitary bees from the genus *Osmia* (Bosch and Kemp, 2002; Haider et al., 2013).

Currently, *Osmia bicornis* L. (Hymenoptera: Megachilidae) (syn. *O. rufa*) (species description is in Material and Methods) is known as being polylectic / polylege bee, which means that they are pollen generalists collecting food resources from the flowers of a variety of plants (e.g. Cripps and Rust, 1989; Haider et al., 2013; Krnić and Stanisavljević, 2006). However, it has been noted that *O. bicornis* might show a local specialization for either a genus or family of flowering plants. *Osmia bicornis* may prefer trees especially *Quercus* spp., *Salix* spp. and *Rosaceae*, and among herbaceous plant *Ranunculus* spp. (Raw, 1974; Radmacher and Strohm, 2010; Sedivy et al., 2011; Hansted et al., 2014; Coudrain et al., 2016). It is not known what affects these local preferences. One may suspect that difference in habitat composition e.g. along the urbanization gradient may be a major factor affecting pollen composition collected by these bees.

In this paper we tested if composition of pollen in nests of *O. bicornis* differ among sites varying with urbanization level. We predicted that number of collected pollen types is lower in urban sites than in suburban and rural because the latter have higher cover of green areas. We also checked pollen properties basing on the literature. Moreover, we compared our findings from field with the systematically searched literature. We implied that there are recurring patterns of bee' choices in the literature. Our goal was to search for all available, to our knowledge, pollen analyses of materials obtained from *O. bicornis* and to compare them in search of schemes, reoccurring information or environment influence on preferences.

2. Materials and methods

In our study we choose *O. bicornis* as research object. This species is good study object to address stated research questions. This bee gained interest among researchers due to practical usage as a pollinator of crops that resulted in numerous studies on its biology allowing effective literature search. Moreover, it has specific traits that make this species a good model. *Osmia bicornis* creates small collectivises composed of non-cooperating individuals which shows breeding-site fidelity (Steffan-Dewenter and Schiele, 2004) with flight range up to 200–500 m from the nesting place (Gathmann and Tschardt, 2002; Yoon et al., 2015; Zurbuchen et al., 2010). Adult individuals consume pollen and nectar resources (Howell and Alarcón, 2007). Females perform pollen-harvesting flights during which they use modified hairs on the abdomen (so called scopa) in order to provide pollinivory larvae with food supply (Haider et al., 2013; Seidelmann, 2018). Each fertile female builds separate compartment for a single egg with individual provision of pollen, wherein offspring is left unattended and has to feed and develop on the resources left by the mother (Seidelmann, 2018). According to Sedivy and Dorn (2014), one female produces approximately 30 descendants on average, and as Giejdasz et al. (2016) claimed, they are deposited into 5 nesting tubes. Moreover, according to Konrad et al.

(2008) and the publications cited therein, some results obtained for *O. bicornis* may be relevant as a model for approximately 700 other polylectic European solitary bees, especially foraging in an overlapping period.

Original population of *O. bicornis* came from The National Institute of Horticultural Research, Apiculture Division in Puławy (51°40'N, 21°96'E). The cocoons from this population were divided randomly into 500 pieces for each experimental breeding. To establish new breedings, composition of the chosen area was mapped to assign a built-up infrastructure (buildings, roads, sidewalks, etc.) and qualified as urban (90 % of built-up infrastructure), suburban (55–65 %), and rural (up to 20 %) category of an urbanization gradient. Categorization of the urbanization gradient followed Fortel et al. (2014), however, the range has been narrowed to the local conditions. We used QGIS software and satellite images freely available in Geoportal (<https://www.geoportal.gov.pl>). Moreover, we used distance to the city centre as the additional metric of urbanisation level. Nesting constructions of 45cm × 45cm × 45 cm dimensions on a wooden frame 0.5 m above ground level with 700 reed tubes of ±15 cm length and 7–12 mm inner diameter as nesting material and protected by a net in the front (mesh of 2 cm diameter) were settled in chosen locations: urban1, urban2, suburban1, suburban2, and rural (low-intensity cultured grasslands) in the Lubelskie region (Eastern Poland). Each localization was attended one month after bees' emergence to identify the presence of the 10 flowering plants with the highest cover level on designated round plots of 50 m radius from centralized nesting constructions (Table 1).

Beil et al. (2008) indicated pollen analysis as the method to provide valuable information about foraging on different spatial scales. We used the microscopic palynological analysis of the species composition of pollen samples to determine constitution of brood provisions. At the end of the season of bee activity in October reed tubes with *O. bicornis* nests were taken from the experimental localizations. Randomly chosen 50 sealed reeds with nesting chambers inside were cut open in order to inspect their contents. From these randomly chosen chambers found in different tubes in the mixed position in the tube (at least one from the end, one from the beginning and one from the middle of the tube) five samples of unused (not eaten by larvae) pollen provisions were collected from each localization into 2 mL Eppendorf type tubes. To state the relative frequency of pollen grains into each pollen package sample distilled water was added (5:1 by volume) and stirred for 1 h (until complete dispersion) in order to transfer 15 µl of homogeneous pollen solution to a microscope slide glass with further 30 µl of distilled water. The slide was dried and then protected with a cover slip and glycerol gelatine as a mounting medium. For each microscopic slide to achieve consistent results over 300 consecutive pollen grains were determined, when possible, into genus, species, family or type of build with the usage of pollen atlases, on-line databases (among others PalDat – a palynological database [2000 onwards, www.paldat.org]) and own collection of over 300 reference preparations using the classification by Zander (1935, 1937, 1941, 1949, 1951) in The National Institute of Horticultural Research, Apiculture Division in Puławy. The obtained numerical results (Suppl. 1) were summed up for particular types of environments in the urbanization gradient and a percentage table was made (Table 2). Additionally, originated plant traits, such as plant habit and vector of plant pollination along with the pollen coating and range of pollen sizes have been determined (Fig. 4A–D). It is supplemented with the traits of individual types of pollen (and origin plants) on a basis of PalDat – a palynological database (2000 onwards, www.paldat.org). Furthermore, an extensive literature search was performed using the Web of Science Core Collection™ bibliographical database section (<http://apps.webofknowledge.com/>). The TS function was used to define the search strings (i.e. the criteria key-words) in order to find articles in the topic of interest. All literature from 1900 until 2021 were searched. The complete search string was "[TS = *Osmia* AND TS = *rufo* OR TS = *bicornis* AND TS = pollen] AND [TS = *Osmia* AND TS = pollen]". This revealed 131 studies. Abstracts and full-texts of these 131 studies were

Table 1

Plant of high cover level on designated round plots of 50 m radius from centralized nesting constructions.

	Urban1	Urban2	Suburban1	Suburban2	Rural
Geographical coordinates	51°14'N, 22°32'E	51°14'N, 22°30'E	51°14'N, 22°29'E	51°17'N, 22°42'E	51°30'N, 22°55'E
Description	highly human-modified environment with local planting of decorative flowers and the presence of old trees		human-modified environment, without high buildings, plentiful lawns with decorative flowers and the presence of young trees		low-intensity cultured grasslands
Plant list	<i>Acer platanoides</i> <i>A. pseudoplatanus</i> <i>Aesculus hippocastanum</i> <i>Frangula alnus</i> <i>Juglans regia</i> <i>Magnolia loebneri</i> <i>Quercus petraea</i> <i>Q. robur</i> <i>Rhamnus cathartica</i> <i>Salix alba</i> <i>S. caprea</i>	<i>Acer platanoides</i> <i>A. pseudoplatanus</i> <i>Aesculus hippocastanum</i> <i>Euphorbia</i> spp. <i>Frangula alnus</i> <i>Iris reticulata</i> <i>Juglans regia</i> <i>Quercus petraea</i> <i>Q. robur</i> <i>Salix alba</i> <i>S. caprea</i>	<i>Brassica napus</i> <i>Aubrieta deltoidea</i> <i>Euphorbia</i> spp. <i>Juglans regia</i> <i>Malus</i> spp. <i>Ranunculus</i> spp. <i>Ranunculus acris</i> <i>Rosa</i> spp. <i>Ulmus laevis</i> <i>U. minor</i>	<i>Brassica napus</i> <i>Euphorbia</i> spp. <i>Juglans regia</i> <i>Ranunculoideae</i> spp. <i>Ranunculus acris</i> <i>Rhamnus</i> spp. <i>Rosa canina</i> <i>Rosa</i> spp. <i>Ulmus laevis</i> <i>U. minor</i>	<i>Acer platanoides</i> <i>A. pseudoplatanus</i> <i>Euphorbia</i> spp. <i>Juglans regia</i> <i>Papaver rhoeas</i> <i>Quercus petraea</i> <i>Q. robur</i> <i>Ranunculus</i> spp. <i>Rhamnus cathartica</i> <i>Rubus idaeus</i>

Table 2Proportions [%] of the identified pollens from pollen provisions sampled from the red mason bees (*Osmia bicornis*, syn. *O. rufa*) breedings conducted in environments of the urbanization gradient.

	Rural	Suburban 1	Suburban 2	Urban 1	Urban 2
<i>Acer</i>	25.73%		2.89%	20.73%	73.29%
<i>Aesculus</i>	1.98%	1.78%		6.32%	4.99%
<i>Betula</i>	0.21%				
Brassicaceae	0.78%	7.94%	3.49%		
Caryophyllaceae			1.68%		
Euphorbiaceae	4.03%	16.19%	3.13%	3.08%	4.63%
<i>Frangula</i>	1.89%		0.30%		
<i>Iris</i>					10.21%
<i>Juglans regia</i>	11.82%	28.32%	3.31%	5.17%	4.93%
Papaveraceae	9.47%			2.09%	
<i>Pinus</i>		0.70%	0.24%	0.22%	0.47%
<i>Plantago</i>		0.63%			
Poaceae			4.69%	0.33%	
<i>Quercus</i>	11.94%			33.86%	0.47%
Ranunculaceae	4.36%	0.89%	64.52%	6.93%	
Rhamnaceae	5.23%	3.68%		9.40%	
<i>Robinia</i>					1.01%
Rosaceae	1.61%	7.17%	7.04%		
Rosaceae - <i>Fragaria</i>	0.33%		0.66%		
Rosaceae - <i>Prunus</i> type	0.91%	0.57%		2.58%	
Rosaceae - <i>Rubus</i> type	14.66%		3.13%	0.44%	
<i>Salix</i>	1.07%	2.67%	1.14%	8.41%	
<i>Taraxacum</i> type	0.29%	0.25%	0.24%		
<i>Trifolium</i> type	0.62%			0.44%	
<i>Ulmus</i>		27.94%			
<i>Viscum</i>		1.27%			
other	3.09%	5.02%	3.55%	1.87%	1.42%

Pollen determination was made into genus, species, family or type of build – whichever possible, table cells with pollen find as main types (exceeding 5% of the package's volume) are shaded grey.

read for relevance, in order to select empirical studies that used original data and to exclude simulation-based studies. Also, additional studies, not found in the described systematic search, were included basing on expert knowledge of the authors. Analyses were complicated because, as it turned out, there are many not standardized methods in research especially as far as sampling method is concerned (pollen sampled from pollen provisions, faeces samples, pollen obtained from scopa hair or other parts of the body etc.). Finally, a total of 53 studies were selected for the review to show overall tendencies for choosing plant type, habit, way of pollination, as well as pollen coating and size by *O. bicornis* (Suppl. 2, 3). Simplified compilation of information from these studies can be found in Table 3.

All analyses were done in R environment (R Core Team 2019). We used canonical analysis of correspondence to find out if there are differences in plant taxa composition among sites along the urbanization

gradient. The analysis was performed in R package “vegan” (Oksanen et al., 2007). Also, co-correspondence analysis (Co-CA) (ter Braak and Schaffers, 2004) was used to reveal whether or not plant taxa abundance in pollen provisions can be explained by plant community composition in studied sites. In this analysis, performed in R package “cocorresp” (Simpson, 2009) data were averaged among samples per taxon for pollen provisions (dependent data) and the presence of plant taxa in each site (explanatory data).

We used linear model to test if diversity (Simpson reciprocal index) and number of plant taxa in pollen provision differ among sites along the urbanization gradient. We used robust regression, implemented in packages “MASS” (Venables and Ripley, 2002) and “sfsmisc” (Maechler et al., 2020) to correlate the number of plant taxa and number of pollen grains in the provision with the number of plant taxa present in a site.

Table 3*Osmia bicornis* main (exceeding 5% of the sample) pollen choices based on the literature data.

No.	Characteristics of breeding localization	Sample type	Main pollens		Refs.
			Plant	Average amount [%]	
1	Breedings next to winter oilseed rape	pollen provisions	<i>Brassica napus</i> <i>Quercus robur</i> <i>Salix</i> sp.	15.75 % 64.75 % 41.4 %	Ruddle et al. (2018)
2	<i>Prunus cerasus</i> orchards with <i>Salix</i> , <i>Acer</i> , <i>Betula</i> and <i>Quercus</i> trees within 100 m of the orchard, surrounded by cereal crops and pasture grassland [Taastrup, eastern Denmark]	pollen provisions	<i>Acer</i> spp. <i>Betula</i> <i>Prunus</i> -type <i>Quercus robur</i> <i>Acer</i> spp.	33.24 % 8.16 % 8.16 % ? ?	Hansted et al. (2014)
3	set-aside orchards (mainly apple trees and grassland), landscaped grounds (several tree species and lawn), and farmland (rape and cereal crops) [near the Biocenter of the University of Würzburg, Germany]	pollen provisions	<i>Papaver rhoeas</i> , <i>P. dubium</i> <i>Ranunculus</i> spp. <i>Ranunculus</i> and <i>Quercus</i>	? ? 38.8 %	Radmacher and Strohm (2010)
4	NON-APPLICABLE [museum specimens across Europe]	scopal pollen	<i>Ranunculus</i>	58.576 %	Haider et al. (2013)
5	low-intensity grasslands of Swiss Plateau between the cities of Bern, Solothurn and Fribourg	pollen provisions	<i>Quercus</i> sp. <i>Rosaceae</i>	23.402 % 32.18 %	Coudrain et al. (2016)
6	8 locations in orchards [the Wachtberger Ländchen south of Bonn]	pollen provisions	<i>Salix</i> sp.	27.59 %	Schindler and Peters (2011)
7	area adjacent to home gardens and rapeseed plantations	faeces	<i>Juglans</i> <i>Brassicaceae</i>	2003 2004 10.87 17.57 % % 10.33 16.22 % % %	Teper (2007)
			<i>Aesculus</i>	9.24 % 10.81 %	
			<i>Rubus</i> -type	5.43 % 6.76 %	
			<i>Ranunculus</i>	5.43 % 7.43 %	
			<i>Pinus</i>	6.52 % –	
			<i>Lonicera</i>	8.15 % –	
			<i>Brassica napus</i> <i>Rosaceae</i>	16.0 % 32.6 %	
8	Breedings next to oilseed rape	pollen provisions	<i>Ranunculaceae</i> <i>Prunus</i> -type <i>Juglans</i>	26.6 % 10.33 % 31.67 %	Peters et al. (2016)
9	Puławy, Poland	pollen provisions	<i>Populus</i> <i>Salix</i> sp.	15.67 % 16.67 %	Biliński and Teper (2004)
10	Plantation consisting of several hundred hectares of winter rape	pollen provisions	<i>Brassica napus</i>	29.8 %	Teper and Biliński (2009)
11	Scania, south Sweden	pollen provisions	<i>Asteraceae</i> <i>Taraxacum</i> -type <i>Brassica napus</i> <i>Quercus</i> sp.	47.1 % 42.9 % 10 % 45 %	Söderman et al. (2018)
12	Nidda catchment in Central Germany	pollen provisions	<i>Aesculus</i> <i>hippocastanum</i> <i>Ranunculaceae</i> <i>Rosaceae</i>	45 % 45 % 45 %	Jauker et al. (2012)
13	1) grasslands adjacent to oilseed rape 2) grasslands isolated from oilseed rap 3) oilseed rape fields adjacent to grasslands 4) oilseed rape fields isolated from grassland 5) Gottingen, Lower Saxony, Germany	pollen provisions	<i>Brassica napus</i>	to 20 %	Holzschuh et al. (2013)

3. Results

The experimental breeding locations were covered with typical vegetation for this region in a temperate climate. The list of plants with high cover level among locations largely overlapped (regardless of their urbanization level) (Table 1).

Osmia bicornis bees used limited number of main pollen types (exceeding 5% of volume) for storage as pollen provisions (Table 2). Diversity ($F = 2.571$, $df = 4$, 22 , $P = 0.06$) and number of plant taxa ($F = 4.252$, $df = 4$, 22 , $P = 0.011$) in pollen provisions increased from urban, through suburban to rural site (Fig. 1). Bees made use of commonly available trees like oaks, maples, horse chestnut, walnuts and elms. The composition of collected pollen differed among sites as indicated by CCA analysis (Fig. 2). This CCA was statistically significant ($F = 2.54$, $df = 4$, 22 , $P < 0.001$). First axis explained 38 % of variation and separated suburban habitats from other habitats. Second axis explained 31 % of

variation and separated suburban2 from other sites (Fig. 2). Nevertheless, the composition of plant species present in a site well explained taxa composition in pollen provisions as indicated by Co-CA (Fig. 3). In this analysis axis 1 and 4 were statistically significant as indicated by the permutation tests ($P < 0.01$). Moreover, we found positive relation between number of plant taxa present in a site and number of pollen grains in a provision (robust regression: $r = 0.864$, $F = 33.984$, $df = 2$, 3 , $P = 0.01$) but not with number of taxa in pollen provision (robust regression: $r = -0.307$, $F = 0.024$, $df = 2$, 3 , $P = 0.884$). Breedings from suburban localizations had pollen of decoratively planted *Ranunculaceae*, *Euphorbiaceae* and *Papaveraceae* plants families in prominent quantities (Table 2). When *Rosaceae* and *Brassicaceae* plants are available nearby the nests, the solitary bees collect a small amount of pollen from their flowers as well (Table 2, Suppl. 1, 2, 3). Literature data analysis showed repeatability of some bee' choices as oak, willow and *Rosaceae* pollen in provisions (Suppl. 2, 3). Results from our experiment as well as

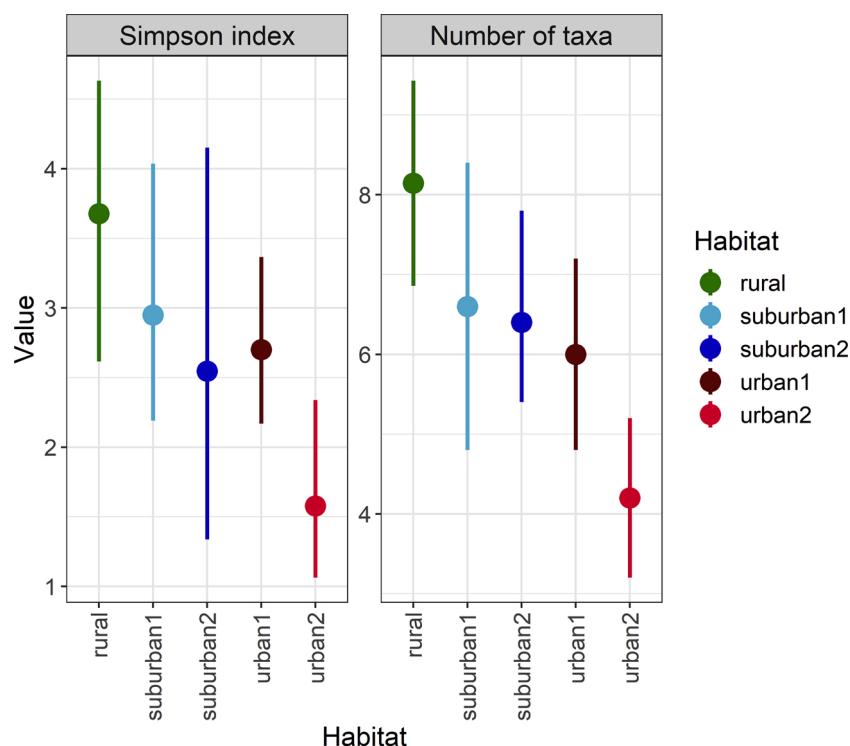


Fig. 1. Simpson diversity of plants (left) and number of plant taxa (species/families/types) in pollen collected by the red mason bees (*Osmia bicornis*, syn. *O. rufa*) in different sites and habitats along the urbanization gradient. Means with 95 % confidence intervals are presented (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

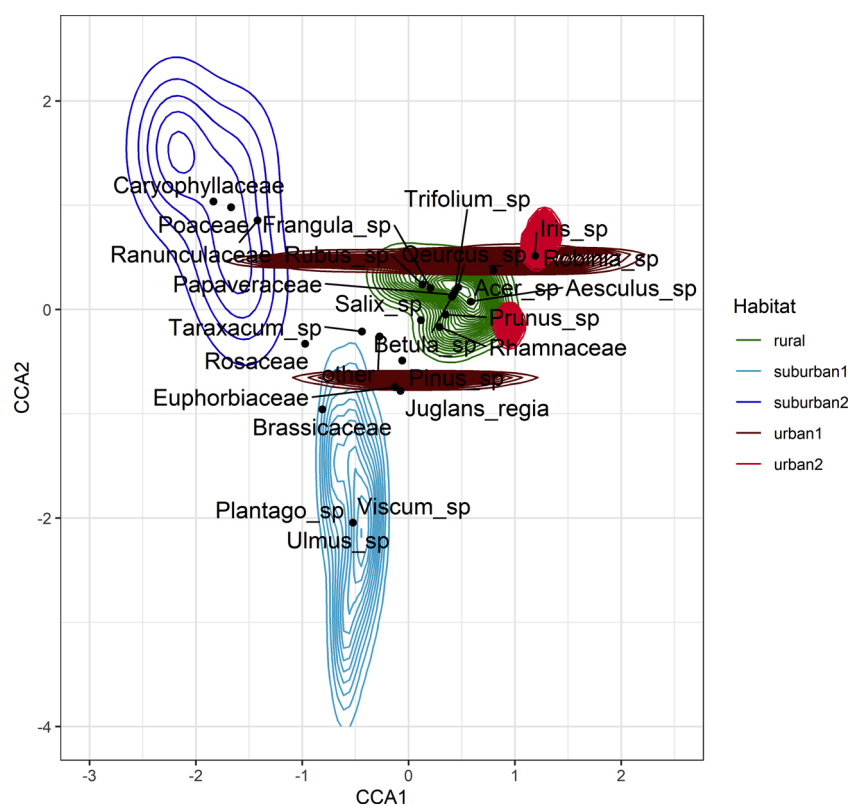


Fig. 2. The composition of plant species/families/types collected by the red mason bees (*Osmia bicornis*, syn. *O. rufa*) in different sites and habitats along the urbanization gradient. Results from the canonical correspondence analysis. For details see Table 1 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

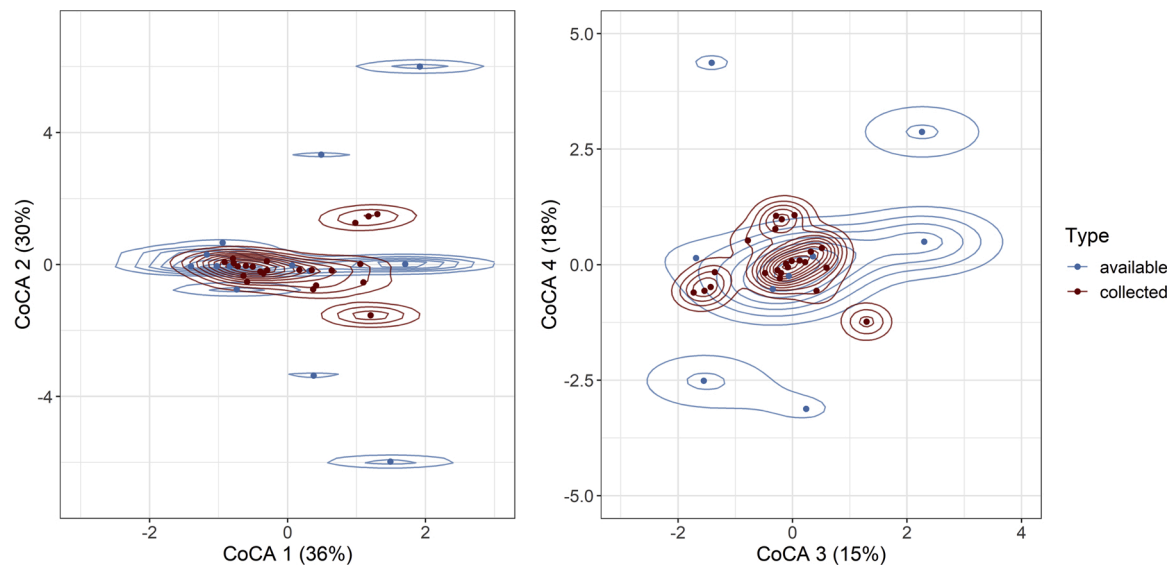


Fig. 3. Co-correspondence ordination of plant taxa found in pollen and plant taxa present in study sites. Kernel density estimator was used to show over.

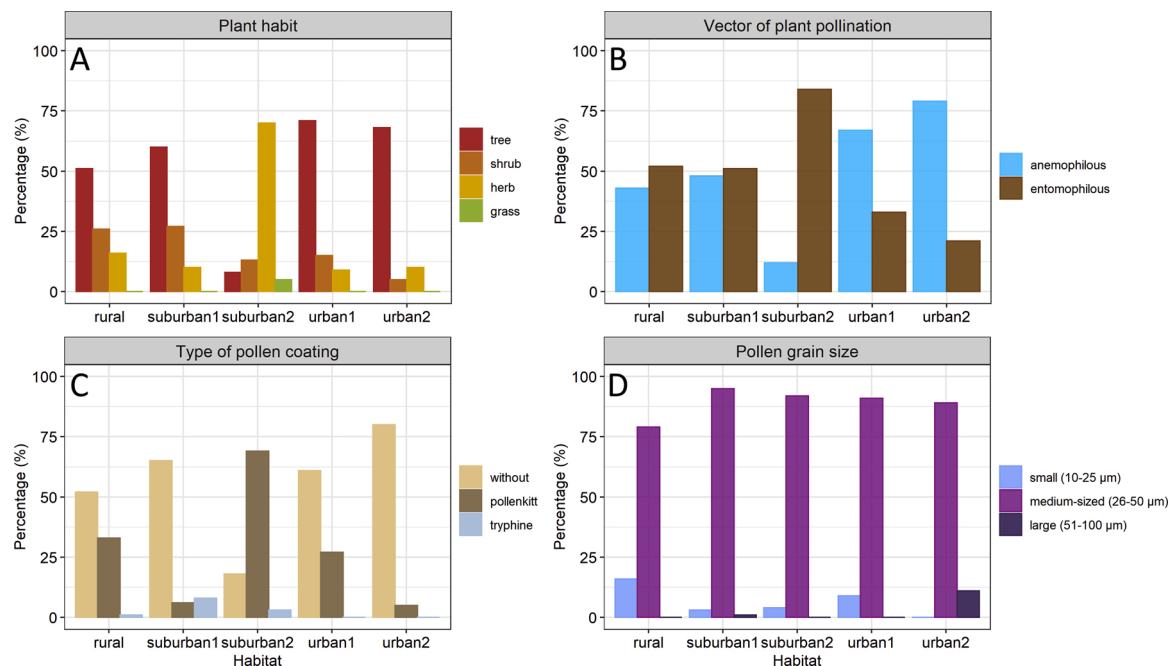


Fig. 4. Traits of pollens (and their origin plants) harvested by the red mason bees (*Osmia bicornis*, syn. *O. rufa*) to create pollen provisions in different environments of urbanization gradient: A – plant habit; B – vector of plant pollination; C – type of pollen coating; D – pollen size (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

from literature data analyses showed that *O. bicornis* tended to use pollen mostly from trees (Fig. 4A). In urban areas bees collected pollen from anemophilous plants, whereas in other areas (suburban allotments, rural meadows) *O. bicornis* seemed to visit mostly entomophilous flowers (Fig. 4B). Literature data suggested over 60 % share of pollen from entomophilous plants in provisions stored by *O. bicornis* (Suppl. 2, 3). Pollenkitt on the surface of pollen was (most often) present when insects were the pollination vector of plants – and our data allowed to link these results (Fig. 4C). Most pollen used by *O. bicornis* for storage were of a medium range of size (26–50 μm), and to a lesser extent, small grains (10–25 μm) regardless of the environment (Fig. 4D).

4. Discussion

Adult bees use flower resources to obtain required nutrients i.e., pollen and nectar, in order to maintain all metabolic functions (Ollerton, 2017, 2021). According to Vaudo et al. (2020) bees obtain their protein and lipid nutrient intake from pollen, which is essential for larval growth and development as well as adult health and reproduction. As Roswell et al. (2019) confirmed the diets of male and female bees of the same species are often dissimilar as the diets of different species of bees. Additionally, Filipiak et al. (2021) stated sex-specific requirements and further development differences connected with sexual dimorphism of *O. bicornis*. The sexes differed fundamentally in the assimilation and allocation of acquired atoms, elemental phenotypes, and stoichiometric niches. Therefore, it is important to highlight that studies of *Osmia* –

including our – are largely focused on females which are believed to be more efficient pollinators and are easier to trace thanks to nest-side fidelity. Howell and Alarcón (2007) observed that in laboratory conditions adult *Osmia* females preferred flowers filled with nectar. However, analyses of free flying adult *O. bicornis* females' faeces made by Teper (2007), clearly indicated that they consume also pollen from plant which do not produce nectar at all. Moreover, Cane (2016) experimentally verified that in order to develop the basal oocytes to full size adult females of *O. californica* require access to pollen – only this enables them to lay eggs in provided nesting tubes. Ahrenfeldt et al. (2019) claimed on the example of strawberry flowers, that *O. bicornis* – commonly called red mason bee – is capable of assessing nectar and pollen quality and prioritize accordingly. The observed pattern indicated foraging changes depending on whether sugary-nectar or proteinaceous-pollen was collected. Giejdasz et al. (2005) mentioned that red mason bees with lower body mass often re-visit the same flowers and repeat scheme of foraging which entails lower energy consumption. In the same time heavier bees select flowers in more random mode and are thus able to visit higher number of flowers. However, it is important to keep in mind that bee fitness is shaped by chemical element availability in larval food (Filipiak and Filipiak, 2020). During larval development phosphorus which was firstly supporting growth is allocated mainly (55–75 %) to the cocoon. Moreover, also other elements acquired from pollen load by larvae such as Mn, Ca, Mg and Zn are later allocated to the cocoon probably influencing bee fitness by conferring protection. Additionally, an importance of pollen loads quality is emphasized by the fact that pollen nutritional value through direct influence on larval and adults' development, has high effect on bee populations (Filipiak, 2019). Dobson et al. (2012) studied chemical imprinting of *O. bicornis* larvae and suggested that rearing bees on a single plant can both directly and indirectly affect flower selection made by adults. Our results indicated that along the urbanization gradient, bees adjusted their choices and collected pollen from plants available in the surrounding environment. This showed that it is purposeful to maintain and moderate plant species composition of greeneries – especially urban ones – to influence the composition of pollen provisions and pollinators' diet.

It is worth noting, however, that despite local differences in pollen composition, some bee' choices are often repeated and even in small quantities (regardless of the environment) pollen of oak or willow can be found in the brood provisions. In our opinion pollen of *Salix* and *Quercus* trees always seem to be chosen by spring emerging bees if they are within their flight range. Some authors (e.g. Coudrain et al., 2016) indicated that high proportion of non-nectar producing anemophilous pollen *Quercus* may be connected with its high protein content (about 40 %) completed by high amount of nectar from *Salix*. Hansted et al. (2014) stated that if in the proximity of orchards competitor plant such as *Salix* is present – breeding of *O. bicornis* bees may be even insufficient to provide pollination services for crops. Persson et al. (2018) noticed that presence of oaks in 100 m proximity of nests led to higher proportions of their pollen in brood provisions, as well caused increased pace of nest construction in the beginning of nesting season and lengthened foraging flights. Meanwhile, Kratschmer et al. (2019) observed that willow and oak enhance floral resources and are frequently collected as a material for pollen provision also by *O. cornuta* (closely related to *O. bicornis*), specifically in intensively farmed agricultural areas. Interestingly, as can be followed in the Table 3, *O. bicornis* found in the vicinity of crops often also uses other food sources for pollen loads. Therefore, our and other authors' results confirmed that there are recurring patterns of bees' choices observed regardless of the environment character. Such convergent observations may indicate that the selection of food sources by bees is not completely random – they seem to prefer high-protein pollen over the less valuable ones.

Pinilla-Gallego and Isaacs (2018) found out that a relative of the red mason bee – blue orchard bee (*O. lignaria*), employed as a pollinator of commercial blueberries (*Vaccinium corymbosum*), in fact is reaching for

food-resources of: black cherries (*Prunus serotina*), white clovers (*Trifolium repens*), and red clovers (*Trifolium pratense*). Such results might suggest low usefulness of solitary bees in pollination of crop plants. In turn, in our analysis *Brassica napus* seemed to be one of the important provision sources in rural population of *O. bicornis* (Tables 2 and 3). Yet, we believe that proportion of oilseed rape pollen in brood provisions is overstated due to the fact that many experiments were deliberately conducted in the proximity of those mass-flowering spring crops (see first column of Suppl. 3). Bees consumed *B. napus* pollen without having other alternative protein source available nearby. Nevertheless, bees from oilseed studies conducted in proximity of such trees as oaks, willows or walnuts collected and profited from their pollen (e.g. Ruddle et al., 2018; Teper, 2007).

Schenk et al. (2018) concluded that short temporal mismatches (among bee emerging / foraging and plant pollinating) can cause clear fitness losses in solitary bees. Although their results suggested that bees have evolved species-specific strategies to mitigate fitness losses after temporal mismatches. What is more, according to Persson et al. (2018) pattern of resources choice is changed during the season and later *O. bicornis* forage is dominated by buttercup (*Ranunculus* spp.). Also, Coudrain et al. (2016) verified that *O. bicornis* can nest in a variety of conditions by compensating scarcity of its main larval food by exploiting alternative food sources such as *Ranunculus* flowers. Our results confirmed that Ranunculaceae pollen in brood provisions, particularly in breedings located in the suburban sites. Sedivy et al. (2011) found that *O. bicornis* developed well on *Ranunculus* pollen, whereas provision made from *Ranunculus* pollen cause dwarfism of *O. cornuta*. Eckhardt et al. (2014) results also showed that pure *Ranunculus* pollen diet have a lethal effect on developing larvae of *O. cornuta*. However, they found that larval survival and development time as well as adults' body mass remained nearly unaffected by the admixture of up to 50 % of *Ranunculus* pollen diet to the larval food. Therefore, the ability of *O. bicornis* to use *Ranunculus* pollen resources can therefore be seen as its adaptation to exploit available resources or maybe to control other potential kleptoparasites for which this pollen may be lethal. Also pollen of the Asteraceae, according to Spear et al. (2016), is known to be a poor-quality food source that significantly reduces survival of parasites' larvae. As these authors claimed – the compensatory benefits of a pollinators' poor diet may include protection from natural enemies. Therefore, it seems reasonable to say that larvae of pollen generalists can benefit from the nutrient content of unfavourable pollen without being negatively affected by its adverse chemical properties and even use them as an advantage. Additionally, against the randomness of the bees' choices is suggestion of Bukovinsky et al. (2017) that resources collected from one plant species may influence the usefulness of pollen from another plant species. In the context of bees' choice, it is established that *Osmia* bees used limited number of main pollen types (exceeding 5% of volume) for storage as pollen provisions. Therefore, Eckhardt et al. (2014) claimed that pollen mixing is a common behaviour of these solitary bees. Our results showed that from 2 to 4 main pollen resources can be expected in one pollen provision of *O. bicornis* at the same time with scarce (less than 5% of volume) addition of other pollens. We observed that the number of major pollen types appears to be higher in more rural environments. Other authors also received similar results (see Suppl. 3), what is more solitary bees from the *Osmia* genus (even from other continents) also use about 3 major food resources to create storage for offspring (e.g. MacIvor et al., 2014). Widespread pollen mixing by females of pollen generalist should be considered as a possible strategy to exploit flowers with unfavourable pollen and to optimize larval food quality (Eckhardt et al., 2014).

The problem of insects vanishing, in particular those contributing as pollinators, is widely recognized and effective remedies have been sought for some time. As one of the conservation measures wildflower seed mixtures are popularly used in variety of environments (e.g. Gresty et al., 2018; Hicks et al., 2016). However, the extent to which key pollinator groups such as solitary bees exploit and benefit from these

resources remains unclear. Rollings and Goulson (2019) stated that we do not yet fully understand what factors drive insect pollen preferences. Leonhardt et al. (2020) on a basis of literature research claimed the need for more studies on the comparative sensory ecology, underlying nutritional quality assessment, cue perception and decision making to fully understand how insects adjust resource selection and exploitation in response to environmental heterogeneity and variability. Many authors i.a. Wood et al. (2016) or Gresty et al. (2018) suggested that plant species promoted currently by agri-environment schemes (AES) are not optimal for solitary bees' foraging and whether a diverse community of pollinators is to be supported additional flora species ought to be included in these mixtures. Moreover, AES are designed for agricultural landscape while more and more research indicates role of solitary bees in urban environment (Banaszak-Cibicka and Żmihorski, 2020; Buchholz and Egerer, 2020). Pamminer et al. (2019) pointed out that in future greater emphasis in the selection of plants should be placed on their quality and nutrient content of pollen and nectar. This is supported by the newest reports of Filipiak and Filipiak (2020) and Filipiak et al. (2021) who indicated that not all pollens are nutritionally balanced for bees and the information on the fitness effects of nutritional mismatches between bee demand and the supply of specific elements in food is still to be verified. Even though some solutions such as Belgian pollinator strips of flower-rich hay meadows seems to be effective resources, they still support pollination services mainly during summer. Therefore Ouvrard et al. (2018) stated that spring and autumn food-sources remain poor and could reduce the strips' effectiveness for supporting long-term insect diversity. Klaus et al. (2021) confirmed that bee reproduction increased due to plant diversity and additionally availability of complementary flower resources can offset negative effects of neonicotinoid-treated oilseed rape on wild bee reproduction. Compared to reduced bee larval to adult development by 69 % when exposed to monocultures. Thus, Gresty et al. (2018) stated *Rosa canina* as worth adding to the plant mixtures. Nichols et al. (2019) have come to similar conclusions indicating that including a range of Apiaceae, Asteraceae, and Geraniaceae in seed mixes would cater for a wide diversity of bee species. On the other hand, Jachula et al. (2018) suggested consideration of Lamiaceae species because of their abundant flowering and good pollen nutritional value which might improve food resources, especially for bees. An interesting argument for discussion was provided by Hicks et al. (2016) who verified that perennial meadows produced up to 20x more nectar and up to 6x more pollen than annual ones and earlier in season. Ergo, the design of seed mixes should be directed at perennial plants to ensure continuity in floral resources availability throughout the year, and to identify suitable species to fill food-supply gaps in established mixes (Hicks et al., 2016). To confirm that this is a global problem it can be pointed out that this is in line with the findings of Wilson et al. (2021) that bees (in their case Australian social bee *Tetragonula carbonaria*, Meliponini) use "many small" rather than a "few large" pollen sources. Therefore, pollinators should have access to a variety of floral resources year-round which may be achieved through targeted planting of key families of plants and / or maintaining weeds while they are flowering in the orchard. Land managers may consider planting in unproductive areas such as riparian zones, edges or between crop rows if space is limited.

Apart from promoting flowers being food resources and suitable early- and late-flowering forbs as basic measure to sustain food supply for wide range of pollinators some authors (Persson et al., 2018; Filipiak, 2019; Jachula et al., 2021) implicated that increasing habitat heterogeneity with trees and shrubs, flower strips and hedgerows or man-made non-cropped areas is more profitable for in wild bee conservation and may help to mitigate the largest pollinators' food gaps. By extension human-induced environmental heterogeneity interacts to shape plant-solitary bee networks. In the urban areas Hülsmann et al. (2015) emphasized the importance of flower-rich parks and gardens even as isolated patches in the city centre and Kratschmer et al. (2018) showed that green roofs as potentially valuable habitats in urban areas, because

wild bees' diversity and abundance is strongly positively affected by increasing foraging availability. However, as Kaluza et al. (2017) stated the decreasing diversity of available resources may impact consumers primarily by reduced resource abundance and secondly by reduced resource functionality. Thus, plant species richness should support pollinators by providing not only a continuous resource supply, but also floral resources of high nutritional quality (Trinkl et al., 2020). Eventually, according to Kaluza et al. (2018) available resource diversity and abundance are related to resource (quality and quantity) intake and bees' reproduction. This indicate that plant diversity is a key driver of bee fitness as they used more resources, increased food stores and their populations grew faster in more florally diverse environments.

Not only palynological studies of the composition of *O. bicornis* pollen provisions indicated that it is worth paying attention to trees in the conservation of insects. According to Ostaff et al. (2015) willows could be used to support the early vernal pollinators' community before the flowering period of commercially valuable crops. Moquet et al. (2015) verified that willows offered pollen with higher polypeptide and essential amino acid contents than blueberry (*Vaccinium myrtillus*, Ericaceae). They observed also that during the overlapping flowering period of these two-plant species, pollinators seemed to favour high quality and easily accessible pollen of *Salix*. Although, it is necessary to pay attention to the invasive nature of some tree species, such as walnuts (e.g. Lenda et al., 2018) or *Robinia* spp. (e.g. Poblador et al., 2019) because even though they are a good food-source for bees, they still pose a threat to the environment. Therefore, as advisable measure of insect conservation in European temperate climate planting such trees as native oaks, willows, maples, elms and even various species of Rosaceae should be considered as measure to complement environment, especially in cities and towns. Nevertheless, planting individual trees could adjunct the bees' forage base, because according to Kasprzyk et al. (2019) a solitary tree produces more pollen than a tree growing near other trees of the same species. This data encourages consideration of additional plantings of singular trees in an urban environment where space for plant maintenance is limited. Moreover, as Bastin et al. (2019) suggested the restoration of trees is the most effective strategy for climate change mitigation. Global tree restoration is even mentioned as one of the most effective carbon drawdown solutions to date and also has many other positive environmental effects. Additionally, according to Bodden et al. (2019) using anemophilous plants as source of food may be bees' defence mechanism, because they are most likely not platforms for transferring diseases among insects. Our analyses revealed that solitary, spring-occurring bees tend to harvest significant amount of pollen to create provisions for offspring from trees. We believe that supplementing the landscape (especially urban one) with trees is advisable, particularly willows and oaks planting might provide a sufficient food base.

Author statement

AS^{1,2}, PS, AS³: Conceptualization.
 AS^{1,2}, PS: Data Curation.
 AS^{1,2}, PS: Formal Analysis.
 AS^{1,2}: Funding Acquisition.
 AS^{1,2}, PS, DT, MB, AS³: Investigation.
 AS^{1,2}, PS: Methodology.
 AS^{1,2}: Project Administration.
 AS^{1,2}: Resources.
 AS^{1,2}, PS: Supervision.
 AS^{1,2}, PS: Visualization.
 AS^{1,2}: Writing – Original Draft Preparation.
 PS, AS^{1,2}: Writing – Review & Editing.

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Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

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