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City dwelling wild bees: how communal gardens promote species richness

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Abstract

Urban areas consist of wide expanses of impervious surfaces which are known to negatively affect insect biodiversity in general, but green spaces within cities have the potential to provide necessary habitat and foraging resources. Although, communal gardens were primarily intended to provide fresh, regional food to denizens, these green islands also host a surprisingly high number of wild bee species.

The gardens were characterized based on structural elements such as flower frequency, the relative percentage of lawn, trees, shrubs, planted crops and infrastructure (e.g. seating possibilities or garden houses). Further, the effects of different landscape structures surrounding the gardens and distance to the city center were analyzed on the total wild bee species richness and functional traits. Focusing on these putative influencing factors, statistical analyses calculating random decision forests along with generalized linear mixed models were applied. With 113 observed wild bee species, communal gardens provide habitat for a quarter of all known species in Vienna. In conclusion, results revealed that only elements within the gardens had an effect on species richness, with flower frequency as the major positive driver. The examined communal gardens promote and conserve wild bees independent from the location within the city or garden size. Furthermore, these green patches are important sanctuaries, hosting rare and threatened species as well as remarkably special wild bee communities.

Keywords Urban agriculture · Pollinator · Flower frequency · Life history traits · Apiformes

Introduction

Cities have grown steadily since 1950 and more than half of the world's population along with 74% of all Europeans live in urban areas (United Nations 2018). Increasing urbanization and associated changes in the surrounding environment lead to habitat loss or degradation, which is an actual threat for the local wild bee biodiversity (Biesmeijer 2006). Besides fewer foraging and nesting possibilities for wild bees resulting from soil-sealing, expanding urban areas bring with them increased anthropogenic pressures. Additionally, exotic plants often planted as ornamental flowers in parks and flowerbeds influence the native insect community in cities. For these reasons urbanization is negatively associated with wild bee species richness (Hernandez et al. 2009; Ahrné et al. 2009; Banaszak-Cibicka and Żmihorski 2012).

Conversely, urban areas also provide special and diverse microclimates for several species. Green spaces in cities have the potential to provide habitats for insects and maintain corridors between green patches for movement (Smith et al. 2006). Moreover, a long-term study evaluating intrinsic and extrinsic extinction traits of local bee communities has shown that bees, which occur in urban areas, have a lower extinction risk in contrast to wild bees preferring other habitats, like forests or wastelands (Hofmann et al. 2019). In general, cities are warmer and drier due to infrastructure and heat generated by human activity. Some species have adapted to these conditions and can be considered urbanophilic. This is why, wild bee communities within these urban heat islands (UHIs) differ in comparison to surrounding landscapes. Urban habitats enable wild bees to emerge earlier and thermophilic species are able to settle within cities (Banaszak-Cibicka 2014; Fortel et al. 2014). But also, plants can benefit from the microclimatic conditions found in urban habitats. UHIs lead to an earlier ripeness of crops, an affect which is utilized by the increasingly more popular urban agriculture movement. Urban

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agriculture has the potential to provide environmental, economic and social values, through its ability to reduce the ecological footprint of a city, while increasing quality of life and allowing inhabitants to experience nature (Potter and LeBuhn 2015). Green urban areas have important ecological impacts such as cooling effects or absorbing water from rainfalls (Bowler et al. 2010; Norton et al. 2015). Additionally, in rapidly growing cities, urban gardening is one possible answer to the growing demand for regional, sustainable and safe food production (Gunnarsson and Federsel 2014). Whereas, the most common motivating factors are being in contact with nature and the ability to consume fresh food (Matteson and Langellotto 2010; Guitart et al. 2012). Urban gardens also have the potential to conserve the local biodiversity as some crops act as important foraging resources for flower-visiting wild bees, as a variety of plants provide pollen, nectar or both (Matteson and Langellotto 2010). Intensification of agriculture is one of the major drivers causing insects decline globally (Sánchez-Bayo and Wyckhuys 2019). On the contrary, a recently published study revealed that communal gardens in four UK cities have the potential to counteract this trend as these gardens were shown to be diversity hotspots for wild bees (Baldock et al. 2019).

Communal gardens are defined as open space designed gardens, where the local community cultivates flowers and crops (Holland 2004; Kingsley et al. 2009). The production of crops like apples, cherries and pears, which are important crops in Austria, is highly dependent on insect pollination (Leonhardt et al. 2013). City beekeeping is gaining more and more popularity (Lorenz and Stark 2015; Stange et al. 2017). In Vienna 5000 honey bee hives are situated in the city center (Magistrat der Stadt Wien 2019). But within this study, the focus is on wild bees as one of the most important pollinator group for crops planted in urban areas. These important ecosystem service providers pollinate multiple plant species enhancing the fruit yield as well as the seed set of entomophilous plants (Lowenstein et al. 2015). Wild bees can be considered key species in urban areas. They are not just simply pollinators but are also members of trophic webs and represent important prey for different organisms, such as birds or wasps. Additionally, wild bees have the potential to raise awareness of urban biodiversity to city inhabitants and sensitize to conservation actions (Banaszak-Cibicka and Żmihorski 2012; Fortel et al. 2014).

Wild bees in urban habitats have been a research topic in several projects investigating cities like Gothenburg, Poznan, Lyon, Vancouver and San Francisco (Tommasi et al. 2004; Banaszak-Cibicka and Żmihorski 2012; Fortel et al. 2014; Gunnarsson and Federsel 2014; Potter and LeBuhn 2015). Furthermore, communal gardens have been well studied by social sciences, but not so much by the natural sciences (Alaimo et al. 2010; Firth et al. 2011; Guitart et al. 2012). Most biological research of community gardens has been performed in the UK, New York City and Sydney, but information about Central European communal gardens is lacking completely (Matteson and Langellotto 2010; Makinson et al. 2017; Baldock et al. 2019). The capital city of Austria is an exceptionally species-rich city due to its special climate conditions and extensive natural sites surrounding the city. With 465 reported Apiformes, Vienna has the highest number of species among cities in Central Europe (Zettel et al. 2015, 2016).

Many ecological studies have been carried out along urban-to-rural gradients, although these gradients do not often reflect the importance of (semi-) natural structures within urban areas. Green patches within cities are of great significance for projects concerning urban biodiversity (Ramalho and Hobbs 2012). To gain knowledge of the local wild bee biodiversity in urban agriculture, twelve communal gardens in Vienna were investigated. As flight distance is a function of body length, especially for small bee species it is crucial that nesting and foraging resources are only a few hundred meters apart (Gathmann and Tscharntke 2002; Zurbuchen et al. 2010). In close proximity to the city center, the proportion of impervious surface increases, while the amount of green areas decreases. This is why, the effect of the distance to the city center on species richness was tested. However, species diversity data alone is not always sufficient evaluating the habitat quality for bees (Sheffield et al. 2013), this is why we determined species-specific life history traits (LHTs) such as nesting and foraging types for the gardens' bee communities. The aim of this study was to answer the following research questions: (1) Which wild bee communities are attracted to communal gardens? (2) How does the flower frequency and certain bee-attracting plants within communal gardens influence the bee community? (3) How are different garden structures and surrounding landscape structures affecting wild bee species richness?

Material and methods

Study location

Vienna, the capital city of Austria, counts 1,888,776 inhabitants in 2018, which is an increase of 13% in comparison to the year 2008 (Himpele 2018). With a unique geographical location underlined by influences of the Atlantic and the continental climates, the average annual temperature was 12.7 °C with a maximum of 38.9 °C and a minimum of −10.4 °C in the year 2017, whereas the average annual precipitation was approximately 563 mm (ZAMG 2017). Vienna is characterized by spacious natural habitats surrounding the city, such as the Lobau as part of the Danube Floodplains National Park and the biosphere reserve Wienerwald. Therefore, the city includes 49.6% green areas at 41,487 ha and presents an exceptional interesting region for investigations into wild bee biodiversity (Himpele 2018).

Wild bees were studied in twelve communal gardens (Fig. 1) during seven periods between the end of June through the end of August 2016 and from early March until June 2017 in three weeks intervals. All community gardens were part of the "Gartenpolylog" club, which manages 69 gardens in Vienna (Madlener 2007). The twelve gardens are located throughout Vienna and were selected according to the amount of interest from the gardeners in supporting the present project. Nevertheless, as every examined garden cultivated crop in Vienna, in this study community gardens are synonymously exchangeable as urban agriculture.

Species sampling

Wild bees were collected by hand-netting specimens. The average sampling duration was 64 min per garden, but was adjusted to the respective garden size. The study focused on species richness and did not consider species abundance, thus only a few individuals per species were collected.

Sampling took place between 10 am and 4 pm in dry weather conditions, moderate wind and an average temperature of 24 °C (minimum of 16 °C in March and a maximum of 30 °C in June). Wild bees were stored in a snap cap with ethyl acetate and later prepared and identified at species level using appropriate literature (ScheuchI 1995; Amiet 1996, 2001; Scheuchl 1996; Schmid-Egger and Scheuchl 1997; Amiet et al. 2004; Gokcezade et al. 2010). Sampled specimens are stored in the wild bee collection at the Institute for Integrative Nature Conservation Research (University of Natural Resources and Life Sciences, Vienna). The majority of individuals of the genus *Bombus* were identified in the field alive and released afterwards. Counts of *Apis mellifera* L., 1758 were not included, as it is a domesticated species and two gardens hosted bee hives which would likely lead to bias in the results. Additionally, each garden was examined for nesting activities of wild bees. Species-specific ecological information (LHTs) the nesting type, sociality and floral specificity were compiled from primary literature (Westrich 1989, 2018; Michener 2007; Amiet and Krebs 2014; Scheuchl and Willner 2016) and described in Table 1.

Garden and landscape characters

The garden sizes ranged from 120 m^2 to 4000 m^2. On each sampling date, the communal gardens were characterized by the flower frequency as a proxy for foraging resources of wild bees. Studies have shown that a visual estimate of the floral cover is an acceptable and widely used method in ecology projects (Gallegos Torell and Glimskär 2009). Therefore, the relative flower frequency was estimated according to a previous project (Gunnarsson and Federsel 2014). All blooming plants were estimated with regard to each garden in four categories: "none" (<11%), "low" (11–25%), "moderate" (26–50%) to "high" (>51%). Additionally, the cover of the four major garden structures (i.e. crop plants; trees & shrubs; lawn; infrastructure) in each communal garden was estimated. On one hand, crops, trees and shrubs constitute an important foraging resource for these pollinators. On the other hand, a well-tended lawn and garden infrastructure, such as garden houses or seating accommodations can hardly be utilized by wild bees (Grimm et al. 2008; Wastian et al. 2016; Fischer et al. 2016; Zhao et al. 2019). Plants, where wild bees were observed feeding on pollen and/or nectar, were identified immediately or photos were taken for a later identification at least at the genus level. A detailed list including site coordinates, size and structure is attached in appendix Table 5.

The urban structures were mapped in ArcGis 10.4 (Environmental Systems Research Institute 2016) within a 500 m radius around each community garden. The data was extracted from the geodata viewer of the city of Vienna (Stadt Wien 2015). The urban structure data sets were summarized into 8 categories (Table 2). The percentages of urban structures within each circle were used for statistical analyses. Further entities (landscape types) such as agricultural lands, vineyards, wood and water areas were not included in the analyses as they occurred infrequently and therefore, would have led to biased statistical results.

Data analysis

Data analyses were carried out using the program R (R Core Development Team 2016). A detailed data exploration was carried out prior to the analyses (Zuur et al. 2010), whereas models including garden size and sampling time were calculated to evaluate possible biases in further calculations.

We tested the effect of a set of variables on wild bee species richness, calculating generalized linear mixed models (GLMM) with a Poisson error distribution and sampling interval as a random structure to account for temporal dependence of sampling with the R package "lme4" (Bates et al. 2014). Therefore, a model set of 21 GLMMs were calculated. For these model sets either one predictor (i.e. flower frequency, garden structures, landscape structures) or a combination were included. The entity "distance to the city center" and species richness of important crops were modeled without the flower frequency as they appeared to be collinear. In regard to GLMMs including the flower frequency, the category "none" was defined as baseline for parameter estimation. Model selection was performed using the second order Akaike Information Criterion (AICc), which is suitable for small sample sizes (Motulsky and Christopoulos) with the R package "AICcmodavg" (Mazerolle 2017). A cut-off ΔAICc $\geq$2 was defined previously and all models with an AICc

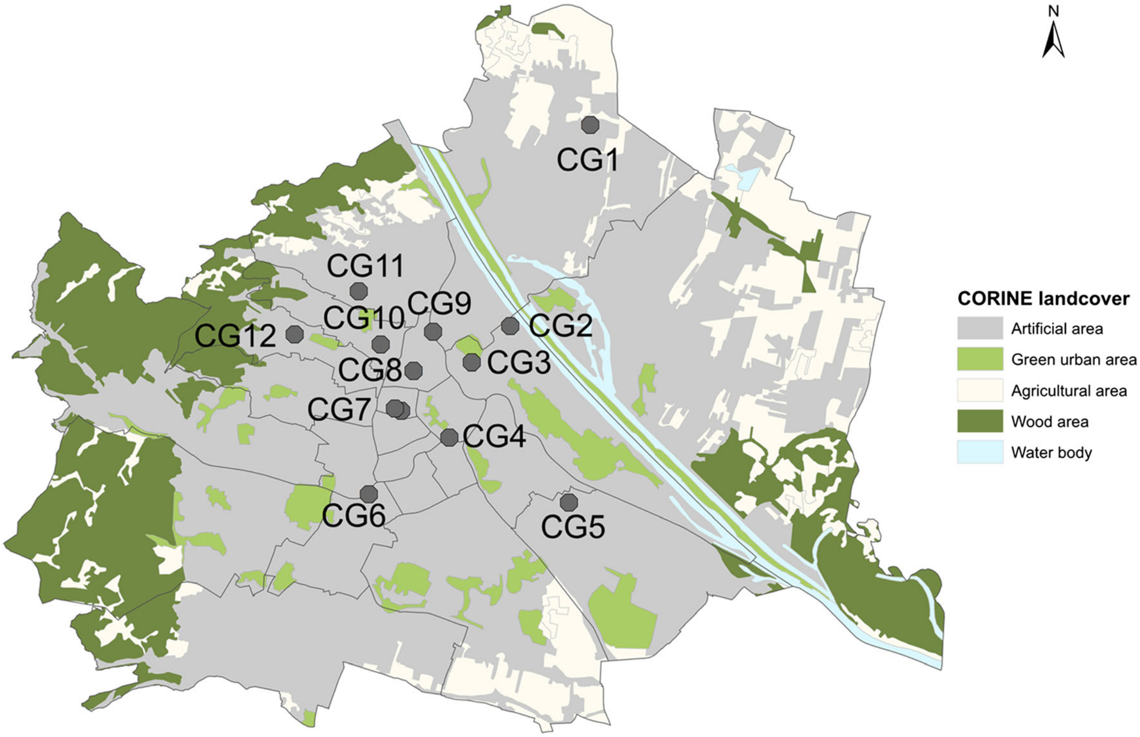


Fig. 1 Location of the twelve communal gardens examined during this project. The communal garden 7 (CG7) constitutes a combination of two gardens due to the short distance of 200 m and a collaborative organization (basic map of Vienna, GIS 2016)

difference > 2 from the most parsimonious model were not considered further to determine the reliability of the data.

To analyze the effect of the predictors on the species richness of LHTs a two-step approach was applied. First, for each trait a Random Forest (RF) with 500 trees was calculated using the R package “party” (Hothorn et al. 2018). The “Variable Importance” (VI) for each RF was based on a conditional permutation scheme (Strobl et al. 2008, 2009) and

Table 1 Life history traits (LHTs) of examined wild bee communities as well a definition and percentage of wild bees species known from Central Europe after Zurbuchen and Müller (2012), Wiesbauer (2017) and Westrich (2018)

LHTs	categories	definition	% of species in Central Europe
foraging type	polylectic (pl)	Bees are pollen generalists collecting and feeding on a variety of different plant species.	pl 60%
	oligolectic (ol)	These species collect pollen exclusively or with a high prevalence at a single plant family or genus.	ol 30%
		For 10% foraging preferences are unknown yet.	
sociality	solitary (so)	Single females take care of their brood without any cooperation, division of work or food reserves.	so 90%
	eusocial (eu)	Bee colonies include two generations (mother and their daughters), which are working togheter caring for the offspring. Eusociality can be found in wild bees within the genus *Bombus* Latreille, 1802 and *Lasioglussum* Curtis, 1833.	eu 10%
	parasitic (pa)	Females of parasitic bee species do not build nests nor collect pollen for their brood, rather they lay their eggs in nests of the hosts often destroying their brood, where the cuckoo larvae feed on the collected pollen (Bogusch et al. 2006; Bogusch and Straka 2012).	pa 25%
nesting type	below-ground (bg)	Bees are nesting in mined holes in the soil.	bg 50%
	above-ground (ab)	Possible nesting sites for over-ground nesting species are cavities (ca), plant stems (st), deadwood (dw) and free-building structures (fb).	ca 19%; st and dw 3%; fb 1%;
	parasitic (pa)	see explanation above	pa 25%

Table 2 Urban structures according to the City of Vienna (Stadt Wien - ViennaGIS 2015) used for landscape analysis

category	urban structures (city of Vienna)	mean area (%) ± SD
green areas	meadows, other green spaces, green areas, storage sites, construction sites, cemeteries	26.3 ± 14.4
buildings	monuments, fountains, roofs, buildings, glass buildings, kiosks, walls, porch, fences, other buildings,	35.3 ± 14
roads	crosswalks, traffic islands, telephone booths, street furniture, stairs, station equipment, various traffic areas, parking spaces, pavements, cycle paths, pedestrian areas, speed ramps, roads, railway tracks, railway sectors, bridge piers	27.2 ± 7.7
artificial and constructed entities	paved areas, courtyards, swimming pools, sports fields	6.5 ± 2

applied to assess which predictors were most important for the LHTs. In the second step GLMMs were formulated to assess the effect of these most important predictors on the species richness of the LHTs. Again, the sampling event was set as random structure, a Poisson error distribution was applied, and model selection was based on AICc.

Plants and crops found in communal gardens were compared with the primary literature (Pawelek et al. 2009; Zurbuchen and Müller 2012; Westrich 2018) and examined according to their attractiveness as pollen and / or nectar resources for wild bees. A detailed list of the crops can be found in appendix Table 6.

Results

In total, 113 wild bee species belonging to 22 genera were collected in twelve communal gardens in Vienna. A detailed list of all collected species including their LHTs “lecty”, “sociality” and “nesting type” is listed in appendix Table 7. The genus containing the highest number of species counted was *Lasioglossum* Curtis, 1833 with 23 species followed by *Andrena* Fabricius, 1775 and *Hylaeus* Fabricius, 1793 with 12 species. The species richest garden (CG8) hosted 48 wild bee species in comparison to a garden with only 17 (CG9).

Wild bee communities

When considering foraging preferences, the majority of all species were generalists (95 species), as opposed to oligolectic bees (18 sp.). The wild bee community was composed of mainly solitary species (76 sp.). Nesting types were separated into parasitic bees and two main groups of above- (34 sp.) and below-ground (54 sp.) nesting bees (Fig. 2, Tab. 2). In addition to the 59% (54 sp.), which were below-ground nesting species, 22% (25 sp.) cavity nesting wild bees were found in Vienna’s communal gardens. Nesting-activity of wild bees within the gardens were observed for *Osmia cornuta* (Latreille, 1805) at an artificial bee home as well as for *Hylaeus moricei* (Friese, 1898) in a reed fence. Honey bees were observed in every communal garden and two gardens hosted bee hives (CG4 & CG5) (Table 3).

Flower frequency and wild bee attracting crops

The effect of flower frequency was strongly positive from none to moderate level, but wild bee species richness decreased from the moderate to high level of flower frequency (Fig. 3).

Thirty-seven wild bee-attracting crops and wild flowers were identified in communal gardens. These plants were used by wild bees as resources for nectar, pollen or both. Furthermore, these plant species are known to attract many wild bee generalists and also some foraging specialists. Among these wild bee attracting plants were 12 Asteraceae, 10 Lamiaceae, 3 Rosaceae and Boraginaceae, 2 Malvaceae, one species each of Ranunculaceae, Campanulaceae, Cucurbitaceae, Fabaceae, Apiaceae, Araliaceae and Amaryllidaceae.

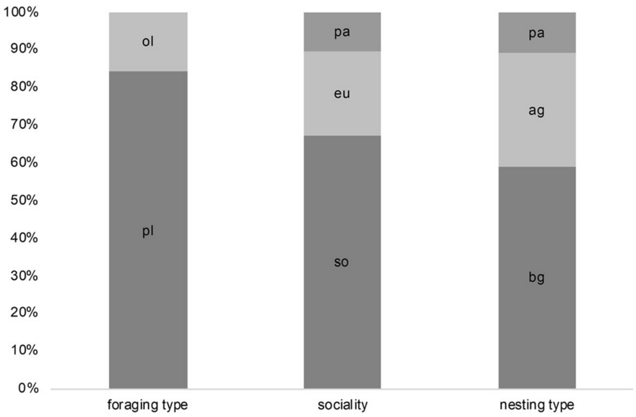


Fig. 2 Percentage of life history traits (LTHs) of the sampled wild bee species. Abbreviations: pl = polylectic, ol = oligolectic; so = solitary, eu = eusocial, pa = parasitic; ag = above-ground nesting, bg = below-ground nesting

Table 3 Percentage of bee species belonging to six families as well as a specified list of above-ground nesting wild bees

family	% species ($n = 113$)	above-ground nesting type	% species (n = 113)
Andrenidae	11%	cavity nesting	22%
Apidae	17%	stem nesting	6%
Colletidae	12%	deadwood nesting	1%
Halictidae	34%	free-building structure nesting	1%
Megachilidae	25%		
Melittidae	2%		

In 6 out of 12 communal gardens most wild bee species were found from the end of June to the beginning of July, followed by the sampling period at the end of July (4 gardens). The lowest number of species was found in March (4 gardens) and in April (3 gardens). On average, wild bee species richness in all communal gardens was lowest in March, increasing until the end of June and dropping again until August. Species richness of wild bee-attracting crops and plants showed a similar result, although numbers dropped at the end of June and increased again in July (Fig. 4).

Garden structures and surrounding entities

Another three models including flower frequency and all four observed garden structures “crop”, “trees & shrubs”, “infrastructure” and “lawn” were equaly parsimonious (Fig. 5). The effect of flower frequency did not change (Appendix Table 8). The percentage of “crops”, infrastructure and “trees & shrubs” in the gardens increased wild bee species richness (Fig. 5a-c), while an increasing proportion of lawn had a negative effect on wild bee species richness. Models including flower frequency and landscape structures around the gardens (e.g. buildings, traffic, green areas surrounding the garden, artificial elements) had ΔAIC values higher than 2 and were therefore not considered as influencing variables on wild bee species richness (Table 4).

When considering LHTs and structural elements, the calculated RFs of VI for the traits: “sociality” and “nesting type” presented a clear outcome for flower frequency as the most important predictor. The VI values differed from graph to graph, but it is possible to compare them only for the same response variable. Flower frequency was the most important predictor of species richness for each trait and its effect was the same as in fig. 3 with the largest influence at moderate scales. Other elements within and outside of the communal gardens were of minor importance in contrast to flower frequency (Fig. 6). The proportion of crops as well as trees and shrubs within the gardens were of importance to eusocial bee populations and had a positive effect on the diversity of solitary wild bees. For solitary bee communities the proportion of crops was of greatest significance (Appendix Fig. 7). When examining nesting types, again flower frequency affected both above- and below-ground nesters, but also crops and buildings influenced the species richness of below-ground nesters (Appendix Fig.8). For ground-nesting Apiformes, crops and flower frequency had a positive effect and the increasing proportion of buildings surrounding the communal garden had a negative effect. When analyzing above-ground nesting species only flower frequency had a conclusive VI.

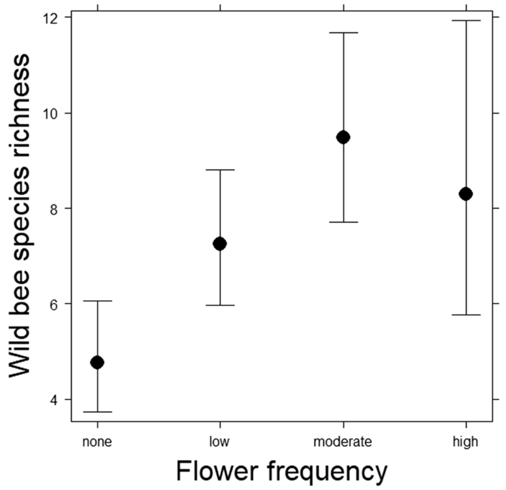
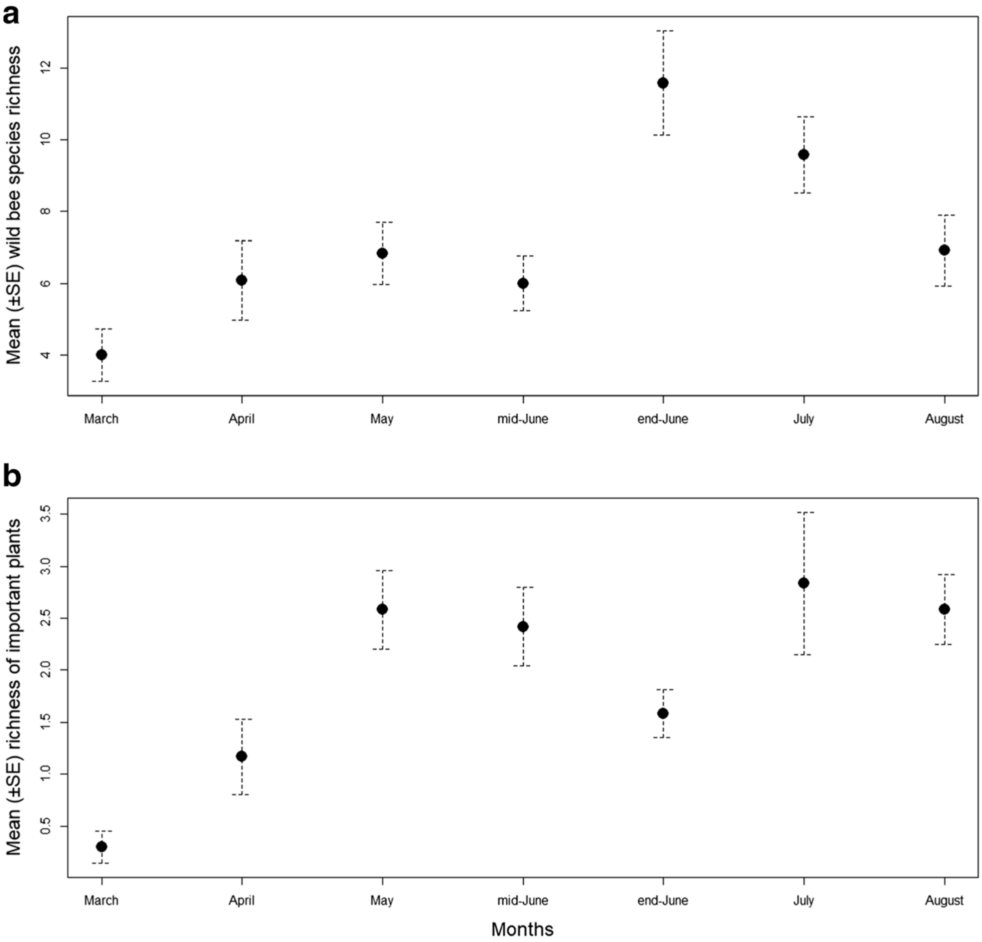


Fig. 3 Effect of flower frequency on wild bee species richness. Error bars = 0.95 confidence intervals

Discussion

Within this study, 113 wild bee species were found in twelve communal gardens, which constitutes 25% of all known species in Vienna. Therefore, communal gardens host similar species numbers as Vienna’s roof tops (90 sp.), cemeteries (96 sp.) or the extensive area of the Danube Island (144 sp.) (Pachinger and Hölzler 2006; Pachinger et al. 2014; Kratschmer et al. 2018). Green islands within urban areas have the potential to conserve the local wild bee biodiversity by acting as sanctuaries (Sirohi et al. 2015), as very uncommon or threatened species were found in the investigated gardens. In particular *Halictus tectus* Radoszkoswki 1876, a species assumed to be locally extinct in Austria was documented in garden CG1. This very uncommon furrow bee as well as the

Fig. 4 Mean (±SE) species richness of (**a**) wild bees and (**b**) important plants during the vegetation period



flower bee *Anthophora aestivalis* (Panzer, 1801) are typically residents of dry habitats such as sand or gravel pits (Wiesbauer 2017), which communal gardens in Vienna can provide through their diverse microhabitats.

Comparison of different studies with previously generated results from literature focusing on species richness may be problematic due to differences in sampling methods and primary study focus. Additionally, every city has different developmental histories and geographic settings resulting in different species assemblages (Sirohi et al. 2015). Thus, studies focusing on communities or guilds specified by their LHTs instead of taxonomy-based groups have the potential to solve these issues and make conclusive comparisons between the same landscape type possible (Sheffield et al. 2013).

Wild bee communities in communal gardens

The majority of all wild bees found were pollen generalists (84%), soil nesting (48%) and solitary (67%), which is comparable to another study in Poland investigating urban public

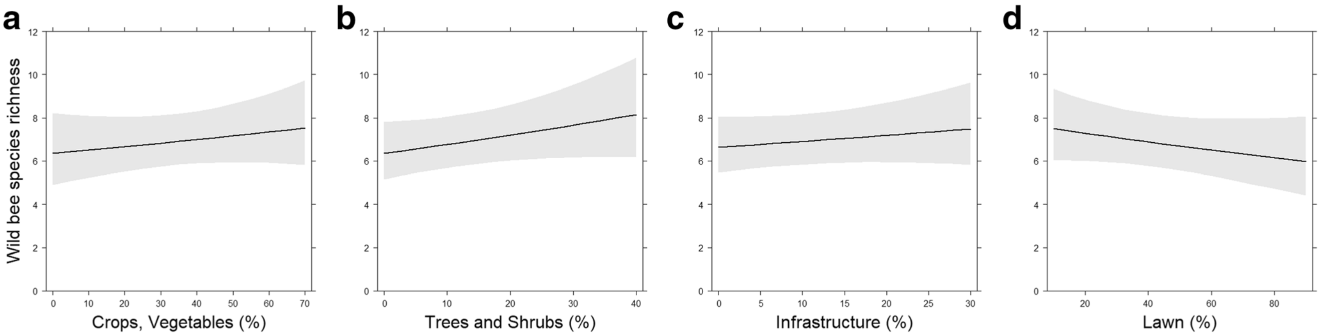


Fig. 5 Effects of the proportion of (**a**) crops & vegetables, (**b**) trees & shrubs, (**c**) infrastructures and (**d**) lawn on wild bee species richness in communal gardens. Grey shading = 0.95 confidence intervals

gardens (Banaszak-Cibicka and Żmihorski 2012). In Austria more than 30% are oligolectic species (Zurbuchen and Müller 2012; Amiet and Krebs 2014) in comparison to the low numbers of pollen specialists (16%) found in communal gardens. Outside of this study, other projects also reported a lack of oligolectic species in urban habitats (Matteson and Langellotto 2010; Banaszak-Cibicka et al. 2016; Makinson et al. 2017). In Vienna's communal gardens mostly crops and a few wild flowers were cultivated. Here, specialized wild bees obtain few if any foraging resources, thus explaining the low species richness of oligolectic species found. Gardens designed with diverse flower compositions, support high species numbers and special communities such as oligolectic bees (Biesmeijer 2006; Goulson et al. 2008; Pawelek et al. 2009). Nevertheless, rare oligolectic representatives observed in communal gardens, were discovered: e.g. the uncommon sand bee *Andrena agilissima* (Scopoli, 1770), which prefers different cabbage species as foraging resources or *Rophites quinquespinosus* Spinola, 1808, which forages on Lamiaceae (Falk 2015; Westrich 2018). Species of the families Lamiaceae and Fabaceae are considered especially attractive for bumble and other wild bees (Ahrné et al. 2009). Labiates were often found in every communal garden due to the popularity of herbs like mint, sage or oregano.

When discussing nesting sites, the results revealed that above-ground nesters find appropriate habitat in communal gardens. The proportion of above-ground nesting wild bees is comparable to other studies focusing on green patches in urban areas (Banaszak-Cibicka and Żmihorski 2012; Sirohi et al. 2015). Such an example of an above-ground nesting bee, which benefits from communal gardens, is *Ceratina chalybea* Chevrier, 1872, which prefers blackberry or rose stems as nesting sites (Wiesbauer 2017).

An unusual discovery was *Hylaeus moricei*, as it is assumed that it depends on reed galls in wetlands for nesting (Amiet and Krebs 2014; Scheuchl and Willner 2016). Here, *H. moricei* was captured exiting a reed fence. Therefore, this provides another example where artificial garden structures are able to enhance species richness. Besides this uncommon mask bee, the gardens generally hosted a relatively high proportion of Colletidae with 12% of all species collected. On the contrary, from all known wild bee species in Vienna Colletidae accounted for 41 species (9%) (Gusenleitner et al. 2012; Zettel et al. 2015). The two collected species of the genus *Colletes* Latreille, 1802 are oligolectic specialists for Asteraceae (Müller and Kuhlmann 2008). *Colletes daviesanus* Smith, 1846 prefers foraging on Asteraceae like chamomile species (Falk 2015), which are a popular plant in communal gardens. Furthermore, the 12 sampled mask bee species were with the exception of *Hylaeus signatus* (Panzer, 1789), which feeds exclusively on *Reseda* (Michener 2007), all generalists. *Hylaeus* species prefer carrots and diverse allium plants as pollen resources (Gosek et al. 1995; Müller et al. 2006). These tendencies might have led to the high occurrence of Colletidae in communal gardens.

As cavity nesters are not reliant on sparsely vegetated ground patches, they are considered "moderately urbanophilic" wild bees (Fortel et al. 2014). Beside cracks in walls as nesting possibilities, appropriate artificial bee homes are able to host cavity nesting species, such as *O. cornuta* and *Osmia bicornis* (Linnaeus, 1758) (Wilkaniec and Giejdasz 2003; Sedivy and Dorn 2014). Therefore, the sampling sites hosted a remarkably high species richness of mason bees (7 species) or leafcutter bees (8 species). Beside the artificial bee home inhabitants, another mason bee, *Osmia niveata* (Fabricius, 1804), is worth mentioning along with its cleptoparasitic counterpart *Stelis punctulatissima* (Kirby, 1802), both found in Vienna's communal gardens.

Within this study, parasitic wild bees composed 11% (12 sp.) of all species found. In comparison, a study on the Danube Island revealed that 19% of the sampled bees were parasitic (Pachinger and Hölzler 2006). Studies have shown that cleptoparasites can act as indicator taxa for the stability of wild bee communities (Sheffield et al. 2013), because cuckoo bees respond quickly to disturbances and thus reflect the high quality and diversity of habitats (Fortel et al. 2014). Therefore, cities can be considered as a disturbing factor resulting in low numbers of parasitic species, as their species richness and abundancy depends on their hosts.

Foraging resources within communal gardens

With the communal garden season starting in March, most flower beds were empty and hardly any crop or wild flower was blooming in early spring. Therefore, foraging resources were probably the major limiting factor in low species numbers found in March and April. Additionally, with the main phenology in June or July, early spring species are generally rare in urban areas (Banaszak-Cibicka and Żmihorski 2012). This is why, not only in Vienna but also other cities (Tommasi et al. 2004), most wild bee species were reported from late spring and early summer.

When considering foraging resources, flower frequency had clearly the strongest effect on wild bee species richness. This means that the availability of pollen or nectar resources was the main factor enhancing wild bee richness in communal gardens. This result conforms with previous studies, which demonstrated that increased flower frequencies enhanced the species richness and abundance of wild bees in parks, ornamental flower

Table 4 GLMMs for species richness and structure elements within and outside communal gardens

response	structure element	k	AICc	ΔAIC	ω_i	LL
wild bee species richness	flower frequency	5	421.22	**0.00**	0.24	250.20
	flower frequency + trees & shrubs	6	422.40	**1.18**	0.13	204.62
	flower frequency + infrastructure	6	423.32	**1.65**	0.09	204.89
	flower frequency + crop	6	422.90	**1.69**	0.10	204.87
	flower frequency + lawn	6	422.94	**1.72**	0.10	205.08
	flower frequency + traffic	6	423.26	423.26	0.09	205.05
	flower frequency + buildings	6	423.33	423.33	0.08	205.08
	flower frequency + green area	6	423.47	423.47	0.08	205.15
	flower frequency + artificial elements	6	423.51	423.51	0.08	205.17
	sampling duration	3	438.60	438.60	0.00	216.14
	garden size	3	459.93	24.24	0.00	226.81

The first four predictors (marked in bold) counted ΔAIC values lower than 2 and therefore, were considered as influencing variables. Abbreviations: K = Number of estimated parameters, AICc = Second order Akaike Information Criterion, Δ AICc = Difference between AICc to the next most parsimonious model, ω_i = Akaike's weight

beds, green strips along roads and roof tops (Werrell et al. 2009; Hennig and Ghazoul 2012; Gunnarsson and Federsel 2014; Makinson et al. 2017; Kratschmer et al. 2018). The effect of flower frequency on species richness peaked at the moderate level and dropped off at the level "high". This may be an artifact, due to high flower frequencies being measured only four times in the gardens. Another possible explanation might be that the mass-flowering of a few plant species provided foraging resources to a restricted number of wild bee species. This pattern was also observed in other studies, where the mass-flowering of single crops influenced the abundance of some wild bee taxa and certain functional traits like cavity-nesters positively (Holzschuh et al. 2013; Kovács-Hostyánszki et al. 2013).

However, gardeners have the power to design the green area to attract wild bees and in return yield more harvest (Werrell et al. 2009). By beginning the garden season with early blooming crops (e.g. fruit trees or *Allium* species like onions or garlic) and extending the flowering period in autumn, a wide range of wild bees will be attracted (Gunnarsson and Federsel 2014). Consequently, special wild bee communities can be enhanced, such as some species of the genera *Anthophora* Latreille, 1803 and *Andrena,* these are considered spring species which emerge in late March and

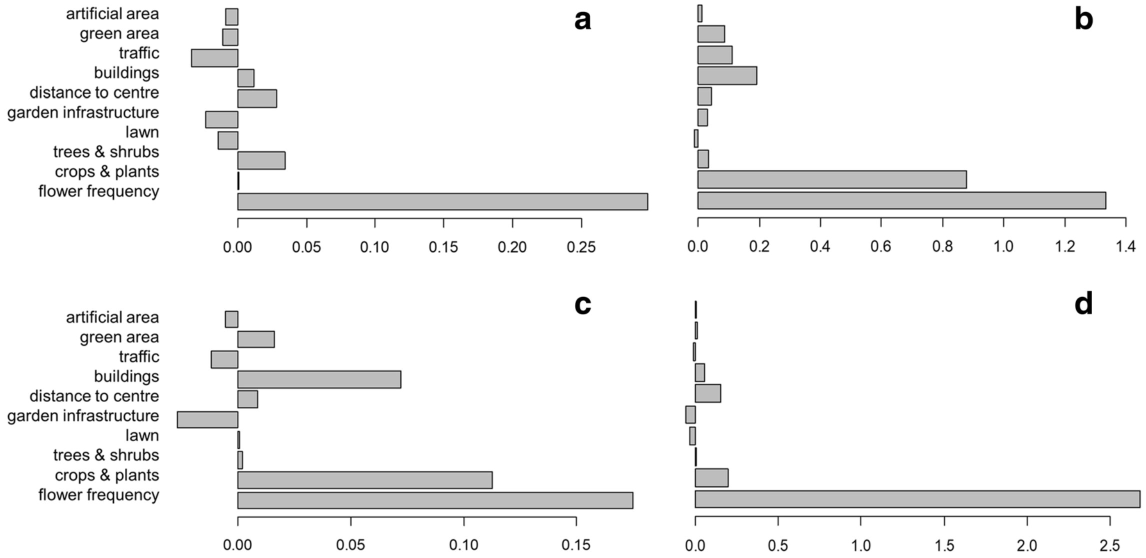


Fig. 6 Calculated Random Forests (RF) for structure elements influence on species richness of A: eusocial and B: solitary; C: below-ground nesters, D: above-ground nesting wild bee communities. On the y-axis the structure elements were presented, while on the x-axis the Variable Importance (VI) was applied. In all four graphs A to D flower frequency had an informative VI

April, whereas bumble bees are active until September (Amiet and Krebs 2014; Westrich 2018). Further, wild flowers attract wild bees and with higher abundancies and species numbers, the pollination service increases resulting in a rich harvest (Potter and LeBuhn 2015; Lowenstein et al. 2015). This positive feedback loop can also be exploited by deliberately planting wild bee attracting plants (Appendix Table 6). Referring to high species numbers and observed structure elements, two gardens (CG1 and CG8) were in accordance with this scheme.

Garden elements and landscape structures

Several landscape structures were modeled in statistical calculations to test the effect on species richness. Neither buildings, traffic nor artificial elements like courtyards surrounding the studied communal gardens influenced the wild bee species richness. As the distance to the city center had no effect on species richness, it appeared that urban areas of Vienna include adequate green spaces to act as corridors or habitats for wild bees. Also, garden size and sampling duration did not influence the number of wild bees found.

Furthermore, in contrast to projects in Sydney and Stockholm (Andersson et al. 2007; Makinson et al. 2017), green areas nearby did not influence the total number of observed species. Although, it can not be concluded that green areas nearby were not affecting the existing wild bee diversity at all, the areas included into the statistical models might have been too small for an observable effect. Only buildings surrounding the communal gardens had a negative effect on soil nesting bee communities as extensive areas of impervious surfaces in building developments within cities are the primary reason for a limitation of suitable habitats for below-ground nesters (Matteson et al. 2008).

Nevertheless, several studies have shown that landscape heterogeneity and green corridors promote wild bee species and abundance (Tommasi et al. 2004; Jauker et al. 2009). Conservation corridors can shelter diverse insect groups by providing feeding resources and nesting possibilities, but are also very important for migration (Samways 2018). By connecting habitats, individuals have the opportunity to move from one population to another group (Forman 1995; Hong et al. 2017), thus geneflow can be maintained between isolated populations minimizing the risk of an inbreeding depression. In an urban setting, patches and green corridors that increase habitat connectivity are likewise flower beds, parks, botanical gardens, green roofs, backyards (Kadas 2006; Pinheiro et al. 2006; Smith et al. 2006; Hunter and Hunter 2008; Braaker et al. 2014) or designated wild corners like the “Stadtwäldchen” opposite the communal garden CG8.

Our results show that elements in the communal gardens were affecting wild bees. As garden size was no influencing factor, which has also been supported by previous studies (Gunnarsson and Federsel 2014; Potter and LeBuhn 2015), even small green islands like communal gardens within an urban landscape have the potential to support the local wild bee community. With regard to structural elements within the gardens, species numbers are significantly higher when the garden contained more crops, trees and shrubs. The positive effect of crops was also observed for soil nesting and solitary wild bee communities.

On the other hand, a higher percentage of lawn areas negatively affected species richness. Therefore, tidy gardens with a perfect lawn may be aesthetically pleasing for some humans but cannot be considered bee friendly. Whereas, wild or unmanaged corners have a huge positive effect on insects (Matteson and Langellotto 2010). One of the communal gardens (CG8) with the highest number of observed species offered several unmanaged areas creating different microhabitats. These wild areas contained wild flowers or a mound of loose soil. Furthermore, a brick wall with countless small holes hosted cavity nesters.

Conclusion

The examined communal gardens host a quarter of all described species in Vienna. These green islands within the city are able to provide feeding and nesting resources for diverse wild bee communities as well as for rare specimens. Although, the gardens host a surprisingly high number of species, there was lack of oligolectic wild bees. Also, the city is a disturbing factor resulting in fewer cuckoo bee species. The more diverse the garden was designed, the more attractive it was for wild bees. As the flowering frequency on moderate scales proved itself a major driver for species richness, diverse crops mixed with wild flowers extending the flowering season from March to October are recommended to promote these pollinators. Also, microhabitats such as sparsely vegetated ground patches, walls, a reed fence or unmanaged areas within communal gardens provide nesting sites for rare species. Therefore, diverse communal gardens within urban areas are important spaces for conserving the local wild bee biodiversity. In cooperation with architects, city planners and biologists environmental damage can be minimized by taking green areas, such as communal gardens, into account when planning landscapes that enhance biodiversity.

According to the presented results, it is simple to create a communal garden, which is wild bee friendly by following these suggestions:

- The design of structurally diverse communal gardens should be a primary aim during the planning process.
- Woody plants like shrubs and trees as well as wild corner with extensive maintenance should be prioritized to increase the structural diversity of communal gardens.
- Microhabitats such as sparsely vegetated ground patches, walls, dead-wood elements or a bamboo fence provide nesting sites for a variety of species.
- Establishing a mix of different insect pollinated crops and native wild flowers attract both, oligo- and polylectic species.
- In order to promote species richness, extending the flowering season from March to October is recommended.
- The extend of frequently mown lawn should be reduced to a minimum.

Acknowledgements First of all, we want to thank the gardeners for their support and interest in this project. Furthermore, we wish to thank Andreas Werner Ebmer for the confirmation of the determination of *Halictus tectus*, Sabine Schoder for assisting with the identification of difficult *Hylaeus* species, Monika Kriechbaum with the determination of certain plant species and David Horner for proof reading.

Author contribution JL wrote the manuscript and along with BäPa conceived the original idea and identified the specimens on species level. Field work was conducted by JL and FG in the context of FG's Bachelor thesis. SK performed the statistical computations with R. BoPe contributed the GIS results. All authors discussed the results and contributed to the final version of the manuscript.

Compliance with ethical standards

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

Appendix 1

Table 5 Detailed list of the studied communal gardens specifying the observed entities

communual garden	coordinates	garden size (m^2)	crop plants (%)	trees & shrubs (%)	lawn (%)	infrastructure (%)	total species	distance to city centre (m)
CG1	N48°17′18.06″/E16°25′ 39.40”	4000	30	30	30	10	42	9680
CG2	N48°13′54.24″/E16°23′ 37.81”	400	40	20	10	30	40	3090
CG3	N48°13′17.54″/E16°22′ 39.44”	2000	50	10	40	0	44	1510
CG4	N48°12′1.40″/E16°22′5.29”	2000	30	20	30	20	25	900
CG5	N48°10′55.35″/ E16°25′6.58”	1700	40	5	50	5	34	4740
CG6	N48°11′3.83″/ E16°20′3.35”	1000	50	10	35	5	36	3890
CG7	N48°12′30.91″/E16°20′ 42.89”	520	20	10	40	5	23	2060
CG8	N48°13′8.97″/E16°21′11.14”	300	35	10	40	15	48	2060
CG9	N48°13′48.54″/E16°21′ 40.70”	400	20	5	70	5	18	2570
CG10	N48°13′35.62″/E16°20′ 21.31”	150	60	0	10	20	31	3280
CG11	N48°14′29.63″/E16°19′ 47.97”	120	20	10	70	0	28	5180
CG12	N48°13′45.77″/E16°18′ 10.94”	1500	20	30	40	10	34	5720

Appendix 2

Table 6 List of plants found in Vienna's communal gardens, where wild bees were observed feeding

plant family	taxon name	foraging resource	plant family	taxon name	foraging resource
Adoxaceae	*Viburnum plicatum var. tomentosum*		Campanulaceae	*Campanula sp.*	NP
Adoxaceae	*Viburnum sp.*		Caryophyllaceae	*Agrostemma githago*	
Amaranthaceae	*Amaranthus sp.*		Caryophyllaceae	*Gypsophila elegans sp.*	
Amaranthaceae	*Beta vulgaris*		Crassulaceae	*Sedum floriferum*	
Amaryllidaceae	*Allium schoenoprasum*	NP	Crassulaceae	*Sedum sp.*	
Amaryllidaceae	*Allium tuberosum*		Cucurbitaceae	*Cucurbita sp.*	NP
Apiaceae	*Anethum graveolens*		Ericaceae	*Rhododendron sp.*	
Apiaceae	*Apium graveolens*		Fabaceae	*Lupinus sp.*	
Apiaceae	*Coriandrum sativum*		Fabaceae	*Phaseolus vulgaris*	
Apiaceae	*Daucus carota*	NP	Fabaceae	*Robinia sp.*	
Apiaceae	*Pastinaca sativa*		Fabaceae	*Trifolium pratense*	NP
Apiaceae	*Petroselinum crispum*		Geraniaceae	*Geranium sanguineum*	
Araliaceae	*Hedera helix*	NP	Hypericaceae	*Hypericum sp.*	
Asteraceae	*Achillea sp.*	P	Lamiaceae	*Antirrhinum majus*	
Asteraceae	*Anthemis austriaca*		Lamiaceae	*Ballota nigra*	NP
Asteraceae	*Bellis perennis*	NP	Lamiaceae	*Dracocephalum sp.*	
Asteraceae	*Calendula officinalis*	NP	Lamiaceae	*Glechoma hederacea*	NP
Asteraceae	*Centaurea sp.*	NP	Lamiaceae	*Lamium sp*	NP
Asteraceae	*Coreopsis sp.*	NP	Lamiaceae	*Lavendula sp.*	NP
Asteraceae	*Cosmos bipinatus*	NP	Lamiaceae	*Melissa sp.*	
Asteraceae	*Cyanus segetum*		Lamiaceae	*Mentheae sp.*	N
Asteraceae	*Cynara cardunculus*		Lamiaceae	*Nepeta sp.*	
Asteraceae	*Doronicum sp.*		Lamiaceae	*Ocimum basilicum*	
Asteraceae	*Echinacea sp.*	NP	Lamiaceae	*Oreganum vulgare*	NP
Asteraceae	*Erigeron annuus*	NP	Lamiaceae	*Rosmarinus officinalis*	N
Asteraceae	*Gaillardia sp.*	NP	Lamiaceae	*Salvia nemorosa*	
Asteraceae	*Helenium sp.*	NP	Lamiaceae	*Salvia officinalis*	NP
Asteraceae	*Helianthus annuus*	NP	Lamiaceae	*Salvia pratensis*	NP
Asteraceae	*Leucanthemum sp.*	NP	Lamiaceae	*Salvia sclarea*	
Asteraceae	*Matricaria chamomilla*		Lamiaceae	*Salvia sp.*	
Asteraceae	*Matricaria sp.*		Lamiaceae	*Thymus sp.*	NP
Asteraceae	*Scorzonera hispanica*		Malvaceae	*Alcea rosea*	N
Asteraceae	*Tagestes sp.*		Malvaceae	*Malva sylvestris*	NP
Asteraceae	*Tanacetum parthenium*		Oleaceae	*Syringa sp.*	
Asteraceae	*Taraxacum ruderalia*		Papaveraceae	*Chelidonium majus*	
Asteraceae	*Zinnia elegans*		Papaveraceae	*Papaver rhoeas*	
Begoniaceae	*Begonia × semperflorens-cultorum*		Phytolaccaceae	*Phytolacca esculenta*	
Boraginaceae	*Borago officinalis*	NP	Polygonaceae	*Fagopyron cymosum* cf.	
Boraginaceae	*Echium vulgare*	NP	Ranunculaceae	*Aconitum napellus*	NP
Boraginaceae	*Myosotis arvensis*		Ranunculaceae	*Aquilegia sp.*	
Boraginaceae	*Myosotis sp.*		Ranunculaceae	*Clematis vitalba*	
Boraginaceae	*Phacelia sp.*	NP	Ranunculaceae	*Consolida ajacis*	
Brassicaceae	*Alliaria petiolata*		Rosaceae	*Duchesnea indica*	
Brassicaceae	*Armoracia sp.* Cf..		Rosaceae	*Fragaria sp.*	NP
Brassicaceae	*Aurinia saxatilis*		Rosaceae	*Kerria japonica*	
Brassicaceae	*Brassica sp.*		Rosaceae	*Malus sp.*	

Table 6 (continued)

plant family	taxon name	foraging resource	plant family	taxon name	foraging resource
Brassicaceae	*Lunaria annua*		Rosaceae	*Potentilla sp.*	
Brassicaceae	*Raphanus sativus*		Rosaceae	*Prunus sp.*	NP
Brassicaceae	*Sinapis alba*		Rosaceae	*Rosa sp.*	
Brassicaceae	*Sinapis sp.*		Rosaceae	*Rubus idaeus*	NP
Brassicaceae	*Sisymbrium sp.*		Rosaceae	*Spirea sp.*	
			Rubiaceae	*Pentas lanceolata* cf.	
			Solanaceae	*Solanum sp.*	
			Tropaeolaceae	*Tropaeolum sp.*	

37 plants are known to be especially attractive as foraging resource for wild bees (Pawelek et al. 2009; Zurbuchen and Müller 2012; Westrich 2018). Those crops and wild plants are either used for collecting nectar and pollen = NP, pollen = P or nectar = N

Appendix 3

Table 7 List of 113 collected wild bee species along with their life history traits

taxon name	nesting typ	foraging preference	sociality	taxon name	nesting typ	foraging preference	sociality
Andrena agilissima (Scopoli, 1770)	bg	ol	solitary	*Hylaeus moricei (Friese, 1898)*	st	pl	solitary
Andrena bicolor Fabricius, 1775	bg	pl	solitary	*Hylaeus pictipes Nylander, 1852*	c, st	pl	solitary
Andrena danuvia E. Stoeckert, 1950	bg	pl	solitary	*Hylaeus punctatus (Brullé, 1832)*	c	pl	solitary
Andrena dorsata (Kirby, 1802)	bg	pl	solitary	*Hylaeus signatus (Panzer, 1798)*	c, d	ol	solitary
Andrena flavipes Panzer, 1799	bg	pl	solitary	*Hylaeus sinuatus (Schenck, 1853)*	c, st	pl	solitary
Andrena gravida Imhoff, 1832	bg	pl	solitary	*Lasioglossum calceatum (Scopoli, 1763)*	bg	pl	eusocial
Andrena haemorrhoa (Fabricius, 1781)	bg	pl	solitary	*Lasioglossum glabriusculum (Morawitz, 1853)*	bg	pl	eusocial
Andrena minutula (Kirby, 1802)	bg	pl	solitary	*Lasioglossum interruptum (Panzer, 1798)*	bg	pl	eusocial
Andrena minutuloides Perkins, 1914	bg	pl	solitary	*Lasioglossum laticeps (Schenck, 1870)*	bg	pl	eusocial
Andrena nigroaenaea (Kirby, 1802)	bg	pl	solitary	*Lasioglossum lativentre (Schenck, 1853)*	bg	pl	solitary
Andrena nitida (Muller, 1776)	bg	pl	solitary	*Lasioglossum leucopus (Kirby, 1802)*	bg	pl	solitary
Andrena taraxaci Giraud, 1861	bg	ol	solitary	*Lasioglossum leucozonium (Schrank, 1781)*	bg	pl	solitary
Anthidium manicatum (Linnaeus, 1758)	c	pl	solitary	*Lasioglossum lineare (Schenck, 1869)*	bg	pl	solitary
Anthidium nanum Mocsary, 1881	st	ol	solitary	*Lasioglossum lucidulum (Schenck, 1861)*	bg	pl	solitary
Anthidium oblongatum (Illiger, 1806)	c	pl	solitary	*Lasioglossum majus (Nylander, 1852)*	bg	pl	solitary
Anthidium septemspinosum Lepeletier, 1841	c	pl	solitary	*Lasioglossum malachurum (Kirby, 1802)*	bg	pl	eusocial
Anthophora aestivalis (Panzer, 1801)	c	pl	solitary	*Lasioglossum marginatum (Brullé, 1832)*	bg	pl	eusocial
Anthophora plumipes (Pallas, 1772)	bg	pl	solitary	*Lasioglossum morio (Fabricius, 1793)*	bg	pl	eusocial
Anthophora quadrimaculata (Panzer, 1798)	bg	pl	solitary	*Lasioglossum nigripes (Lepeletier, 1841)*	bg	pl	eusocial
Bombus hortorum (Linnaeus, 1761)	c	pl	eusocial	*Lasioglossum nitidulum (Fabricius, 1804)*	bg	pl	solitary
Bombus humilis Illiger, 1806	c	pl	eusocial	*Lasioglossum parvulum (Schenck, 1853)*	bg	pl	solitary
Bombus hypnorum (Linnaeus, 1758)	c	pl	eusocial	*Lasioglossum pauxillum (Schenck, 1853)*	bg	pl	eusocial
Bombus lapidarius (Linnaeus, 1758)	c	pl	eusocial	*Lasioglossum politum (Schenck, 1853)*	bg	pl	eusocial
Bombus lucorum (Linnaeus, 1761)	c	pl	eusocial	*Lasioglossum pygmaeum (Schenck, 1853)*	bg	pl	solitary
Bombus pascuorum (Scopoli, 1763)	c	pl	eusocial	*Lasioglossum semilucens (Alfken, 1914)*	bg	pl	solitary
Bombus pratorum (Linnaeus, 1761)	c	pl	eusocial	*Lasioglossum trichopygum (Bluethgen, 1923)*	bg	ol	solitary
Bombus terrestris (Linnaeus, 1758)	c	pl	eusocial	*Lasioglossum villosulum (Kirby, 1802)*	bg	pl	solitary
Ceratina chalybea Chevrier, 1872	st	pl	solitary	*Lasioglossum xanthopus (Kirby, 1802)*	bg	pl	solitary
Ceratina cyanea (Kirby, 1802)	st	pl	solitary	*Macropis fulvipes (Fabricius, 1804)*	bg	pl	solitary
Chelostoma campanularum (Kirby, 1802)	c, st, d	ol	solitary	*Megachile centuncularis (Linnaeus, 1758)*	c	pl	solitary
Chelostoma rapunculi (Lepeletier, 1841)	c	ol	solitary	*Megachile circumcincta Kirby, 1802*	c	pl	solitary
Coelioxys conoidea (Illiger, 1806)	par	pl	parasitic	*Megachile ericetorum Lepeletier, 1841*	c	pl	solitary
Coelioxys echinata Foerster, 1853	par	pl	parasitic	*Megachile pilicrus Morawitz, 1877*	st	ol	solitary
Coelioxys elongata Lepeletier, 1841	par	pl	parasitic	*Megachile pilidens Alfken, 1924*	c	pl	solitary
Colletes cunicularius (Linnaeus, 1761)	bg	ol	solitary	*Megachile rotundata (Fabricius, 1787)*	c	pl	solitary

Table 7 (continued)

taxon name	nesting typ	foraging preference	sociality	taxon name	nesting typ	foraging preference	sociality
Colletes daviesanus Smith, 1846	bg	ol	solitary	*Megachile versicolor Smith, 1844*	c, st	pl	solitary
Eucera chrysopyga Perez, 1879	bg	pl	solitary	*Megachile willughbiella (Kirby, 1802)*	c, d	pl	solitary
Eucera nigrescens Perez, 1879	bg	ol	solitary	*Melitta leporina (Panzer, 1799)*	bg	ol	solitary
Halictus maculatus Smith, 1848	bg	pl	eusocial	*Nomada fabriciana (Linnaeus, 1767)*	par	pl	parasitic
Halictus rubicundus (Christ, 1791)	bg	pl	eusocial	*Nomada fucata Panzer, 1798*	par	pl	parasitic
Halictus seladonius (Fabricius, 1794)	bg	pl	eusocial	*Nomada integra Brullé, 1832*	par	pl	parasitic
Halictus sexcinctus Fabricius, 1775	bg	pl	solitary	*Osmia adunca (Panzer, 1798)*	c	ol	solitary
Halictus simplex Bluethgen, 1923	bg	pl	solitary	*Osmia aurulenta Panzer, 1799*	c	pl	solitary
Halictus smaragdulus Vachal, 1895	bg	pl	eusocial	*Osmia bicornis (Linnaeus, 1758)*	c	pl	solitary
Halictus subauratus (Rossi, 1792)	bg	pl	eusocial	*Osmia caerulescens (Linnaeus, 1758)*	c	pl	solitary
Halictus tectus Radoszkowski, 1875	bg	pl	eusocial	*Osmia cornuta (Latreille, 1805)*	c	pl	solitary
Halictus tumulorum (Linnaeus, 1758)	bg	pl	eusocial	*Osmia leucomelana (Kirby, 1802)*	st	pl	solitary
Heriades crenulatus Nylander, 1856	c, st, d	ol	solitary	*Osmia niveata Fabricius, 1804*	d	ol	solitary
Heriades rubicola Perez, 1890	st	pl	solitary	*Rophites quinquespinosus Spinola, 1808*	bg	ol	solitary
Heriades truncorum (Linnaeus, 1758)	c, st, d	ol	solitary	*Sphecodes albilabris (Fabricius, 1793)*	par	pl	parasitic
Hylaeus brevicornis Nylander, 1852	c, st	pl	solitary	*Sphecodes ephippius (Linnaeus, 1767)*	par	pl	parasitic
Hylaeus communis Nylander, 1852	c, st	pl	solitary	*Sphecodes gibbus (Linnaeus, 1758)*	par	pl	parasitic
Hylaeus gibbus Saunders, 1850	c, st, d	pl	solitary	*Sphecodes monilicornis (Kirby, 1802)*	par	pl	parasitic
Hylaeus gredleri Foerster, 1871	c, st	pl	solitary	*Sphecodes sp.(rubicundus von Hagens, 1875 c.f.)*	par	pl	parasitic
Hylaeus hyalinatus Smith, 1842	c, st	pl	solitary	*Stelis punctulatissima (Kirby, 1802)*	par	pl	parasitic
Hylaeus intermedius Förster, 1871	fb	pl	solitary	*Systropha planidens Giraud, 1861*	bg	ol	solitary
Hylaeus leptocephalus (Morawitz, 1870)	c	pl	solitary				

Abbreviation bg = below-ground; above-ground nesting: c = cavity nesting, st = stem nesting, d = deadwood nesting, fb = free-building structure; par = parasitic; ol = oligolectic, pl = polylectic

Appendix 4

Table 8 GLMMs for garden factors with ΔAIC values above 2

response	structure element	k	AICc	ΔAIC	ω_i	LL
wild bee species richness	lawn	3	457.27	36.6	0.00	−225.48
	crops	3	457.66	36.45	0.00	−225.68
	trees & shrubs	3	460.04	38.82	0.00	−226.86
	buildings	3	460.53	39.32	0.00	−227.11
	garden infrastructure	3	461.47	40.25	0.00	−227.58
	green area	3	462.08	40.86	0.00	−227.89
	artificial elements	3	462.55	41.33	0.00	−228.12
	traffic	3	462.64	41.42	0.00	−228.16
	distance to center	3	462.83	41.61	0.00	−228.26
	month of sampling	2	460.82	39.60	0.00	−228.33

Abbreviations: K = Number of estimated parameters, AICc = Second order Akaike Information Criterion, Δ AICc = Difference between AICc to the next most parsimonious model, ω_i = Akaike's weight

Appendix 5

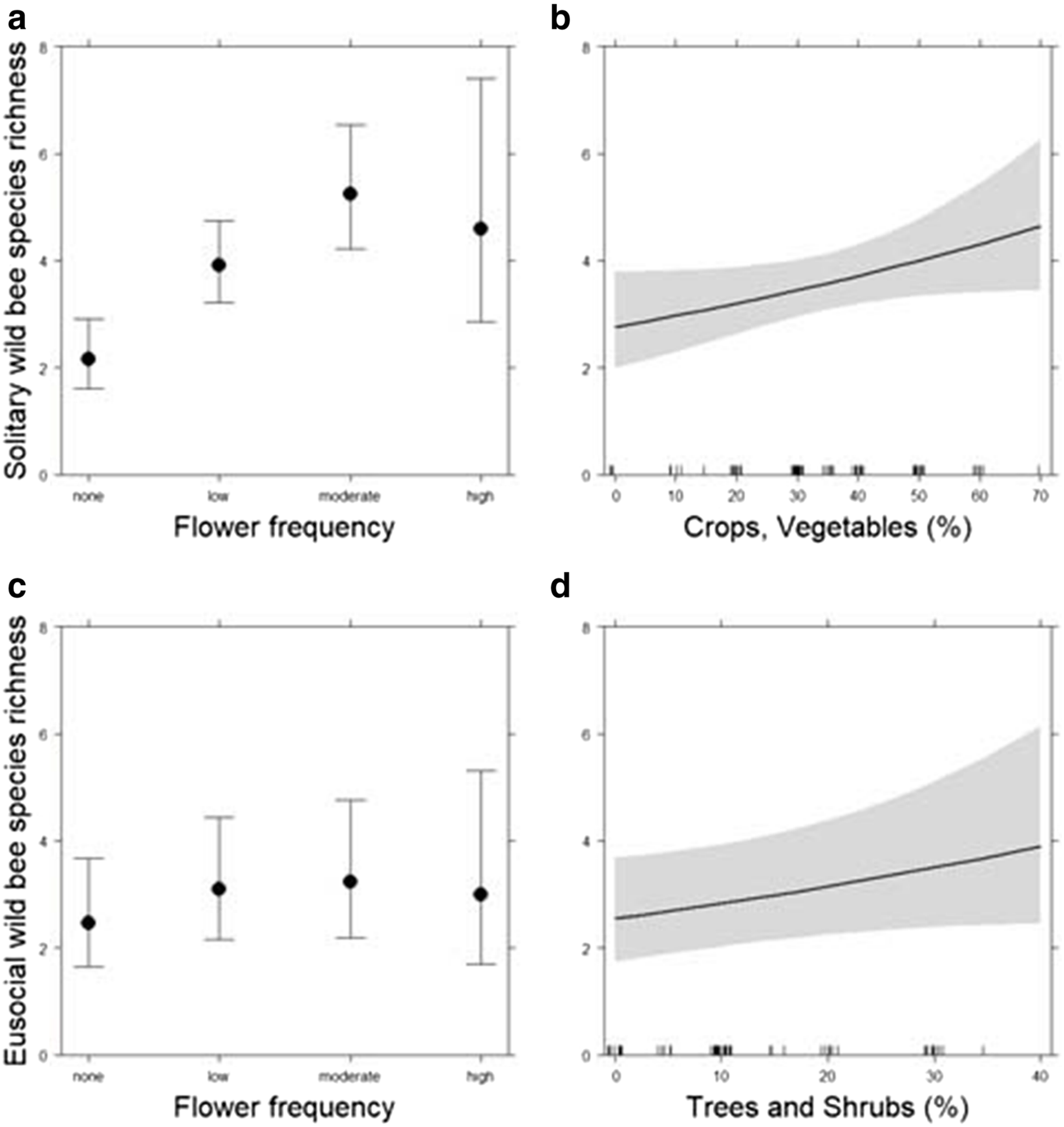


Fig. 7 Effect of most influential variables (according to Random Forests with a high Variable Importance) on (A, B) solitary and (C, D) eusocial species richness in communal. Grey shading = 0.95 confidence interval

Appendix 6

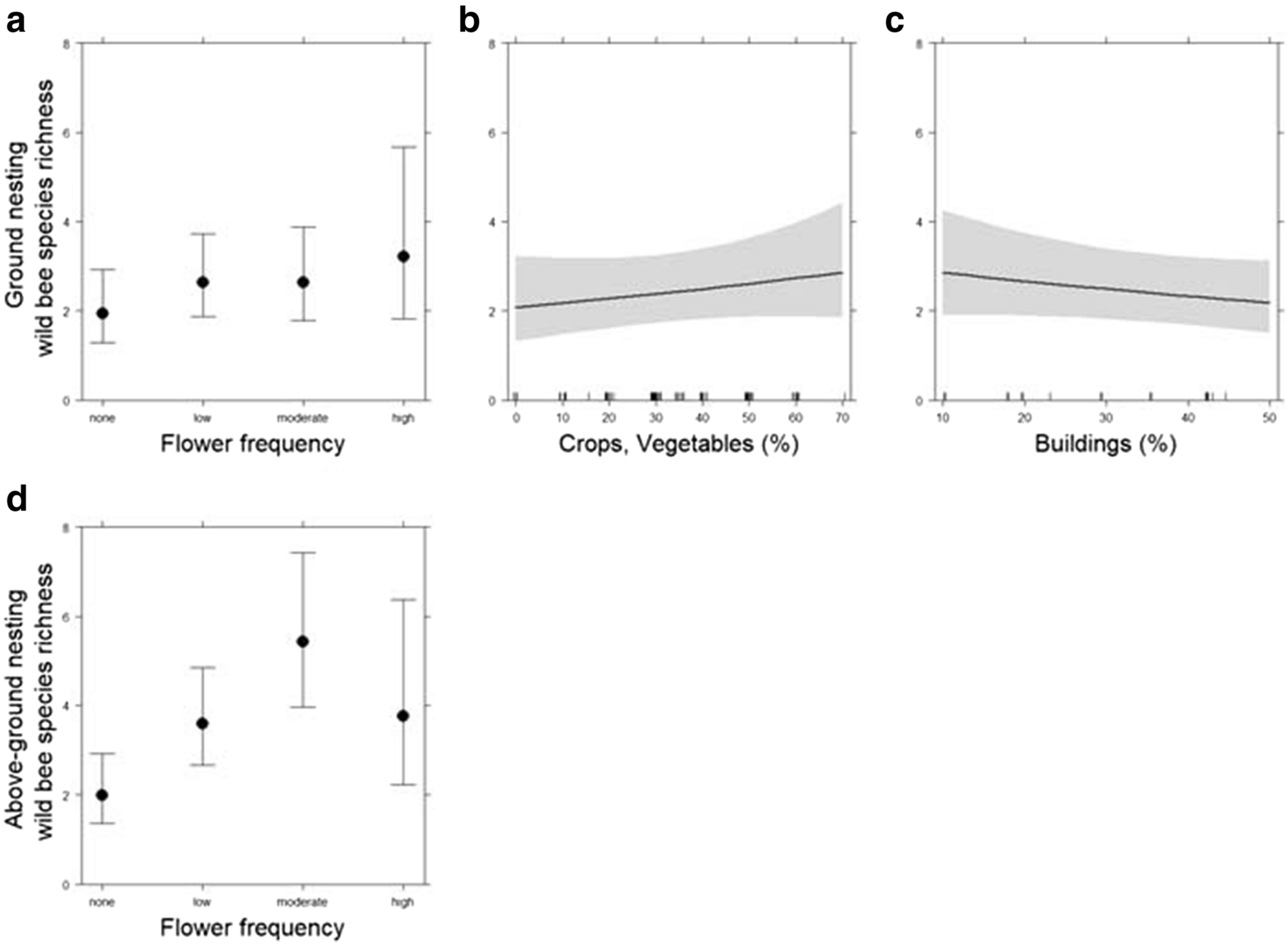


Fig. 8 Effects of most important variables (according to RFs with a high Variable Importance) on (A, B, C) below-ground nesting and (D) above-ground nesting species richness in communal. Grey shading = 0.95 confidence interval

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