Article

THE IMPORTANCE OF WILD BEE COMMUNITIES AS URBAN POLLINATORS AND THE INFLUENCE OF HONEYBEE HIVE DENSITY ON WILD BEE CROP VISITATION RATES

Julie A. Weissmann, Iris R. M. Walldorf, Hanno Schaefer

Technical University of Munich, Plant Biodiversity, Emil-Ramann-Str. 2, D-85354 Freising, Germany

Journal of Pollination Ecology, 29(16), 2021, pp 204-230

DOI: 10.26786/1920-7603(2021)641

Received 8 March 2021, accepted 5 August 2021

*Corresponding author: Julie.Weissmann@tum.de

Abstract—While urban beekeeping is on the rise, data on the role of wild bee communities as crop pollinators in cities is still scarce. We analysed wild bee visitation rates on apple, plum, cherry, pear, blackberry, raspberry, and strawberry in a Bavarian city with a very high honeybee density of c. 19 hives/km^2. During 137.5 hours of observation time, we observed 52 wild bee species on the studied crop plants. During more than 50 h of observation time on fruit trees in flower, we found that wild bees provided 41% of the total bee visits, honeybees the remaining 59%. Honeybee hive density had a significantly negative effect on wild bee abundance. Bumblebees appeared more tolerant to poor weather conditions than all other bee groups. Wild bee species richness on apple flowers was not significantly impacted by flower diversity in the surroundings of the trees. Together, our results suggest that species-rich wild bee communities in urban areas are important for pollination success in common fruit crops, especially under unstable spring weather conditions. Bee-friendly management of urban spaces should be prioritised to support wild bee communities as well as the increasing number of honeybees in cities. In order to reduce competition with endangered wild bees, the bee keepers should always consider the available floral resources in their surroundings from early spring to late autumn and adapt their number of hives accordingly.

Keywords—Biodiversity, urban beekeeping, agroecology, apple pollination, wild bees, bee pollination

INTRODUCTION

Recent studies highlight the importance of urban agriculture for food security (Edmondson et al. 2020), positive effects of urban agriculture on biodiversity in general (Lin et al. 2015), and on bee species diversity in particular (Normandin et al. 2017; Baldock et al. 2019; Lanner et al. 2020). At the same time, a large share of crops – including many of the species popular in urban gardens like pumpkin, raspberry and apple – depend on biotic pollination. Studies quantifying the relevance of animal pollination at the global scale showed that 85% of all flowering plants, c. 76% of the leading global food crops and 35% of global food production depend on animal pollination (Ollerton et al. 2011; Klein et al. 2007).

Numerous studies on a variety of crops in rural settings provide evidence that diverse pollinator communities increase crop yield e.g., in pumpkin (*Cucurbita moschata*) (Hoehn et al. 2008); highbush blueberry (*Vaccinium corymbosum*) (Rogers et al. 2014); sweet cherry (*Prunus avium*) (Eeraerts, Smagghe, et al. 2019); apple (*Malus domestica*) (Földesi et al. 2016; Mallinger & Gratton 2015; Martins et al. 2015); and coffee (*Coffea arabica*) (Klein et al. 2003). In particular, bee diversity has been shown to be important to assure continuous pollination in variable weather conditions (Rogers et al. 2014) and under phenological shifts (Bartomeus et al. 2013) accelerated by climate change.

Despite increasing interest in bee diversity and conservation potential of urban habitats (Hernandez et al. 2009; Baldock et al. 2015; Hall et al. 2017; Baldock 2020; Krahner & Greil 2020) much less attention has been directed towards pollination services in urban environments. This is somewhat worrying since e.g., a survey of community gardens in New York City found that 92% of the crops require bee pollination to some degree to set fruit or seed (Matteson & Langellotto 2009). Studies comparing pollination efficiency in urban, natural and agricultural habitats found that fruit and seed set of herbaceous plants (Cussans et al. 2010; Theodorou et al. 2020) and wild bee flower visitation rates and foraging activity (Leong et al. 2014; Theodorou et al. 2020; Kaluza et al. 2016) were highest in urban environments. Spatial modelling approaches assessing pollinator supply and demand across Iowa City found that pollinator supply meets demand only in 72% of the city (Zhao et al. 2019). In one of the rare studies on urban food crop pollinators, Lowenstein et al. (2015) found cucumber (*Cucumis sativus*), eggplant (*Solanum melongena*) and purple coneflower (*Echinacea purpurea*) in gardens in Chicago to be visited by different groups of pollinators with honeybees constituting less than 7% of visits, and fruit and seed set to increase with pollinator visitation and taxonomic richness.

Extensive research has been investigating potential drivers of species richness and abundance of flower visiting communities in agricultural and natural systems and found that local plant diversity and (semi-)natural habitat support species richness and abundance of crop flower visitors (Ricketts et al. 2008; Kremen et al. 2004; Martins et al. 2015; Nayak et al. 2015; Kammerer et al. 2016; Joshi et al. 2016; Motzke et al. 2016; Fisher et al. 2017; Alomar et al. 2018; Ganser et al. 2018; Saunders & Luck 2018; Eeraerts, Smagghe, et al. 2019; Fijen et al. 2019). Fewer studies focus on urban drivers of plant-pollinator interactions (Harrison & Winfree 2015) and their results indicate some divergences from non-urban settings: while visitation rates on flowering plants in Toledo (USA) declined with increasing impervious surface and increased with floral resource availability (Burdine & McCluney 2019a), a negative correlation to the amount of green area and a positive correlation to human population density have been identified in studies in Leuven (Verboven et al. 2014) and Chicago (Lowenstein et al. 2014), respectively.

Studies assessing the impact of honeybees on wild bees in agricultural and natural settings found evidence for negative effects of rising honeybee hive densities on wild bee communities and visitation rates through competition for food resources (Torné-Noguera et al. 2016; Dupont et al. 2004; Lindström et al. 2016; Mallinger et al. 2017; Geldmann & González-Varo 2018; Geslin et al. 2017). With urban beekeeping being on the rise, competition from increased numbers of honey bee hives has been identified as one of the main threats for urban pollinator conservation (Baldock 2020). While no significant effects of honeybee hive density on wild bee species richness were detected on study sites in Montréal with densities below 0.5 hives/km^2 (McCune et al. 2020), the only urban-based studies to our knowledge specifically investigating the impact of honeybee colony density on plant-pollinator interactions identified negative effects on wild pollinator visitation rates at average hive densities of 6.5 hives/km^2 in Paris (Ropars et al. 2019) and 16 to 22 hives/km^2 in Munich (Renner et al. 2021). In their attempt to disentangle the "modern gordian knot of urban beekeeping", Egerer & Kowarik (2020) identify challenges in balancing potential risks of urban beekeeping (e.g. floral resource competition, parasite and pathogen transmission, and changes in wild flora community composition due to changing plant-pollinator mutualisms) with the benefits of its contribution to pro-environmental behaviour, and call for scientific research on the matter oriented towards science-city partnerships for pollinator-friendly cities.

Our study focuses on five common fruit crops of the rose family in meadow orchards and gardens in an urban setting in Southern Bavaria. We analysed the flower visitor community composition of different crop species to determine the importance of wild bee pollinators, especially in comparison to honey bees. We tried to account for confounding factors like abundance of flowering plants in the surroundings and the impact of weather conditions.

We hypothesized that 1) a large proportion of the flower visits is performed by wild bees; 2) urban environments have a negative effect on wild bee abundance; 3) honeybee-hive density has a negative effect on wild bee abundance; 4) wild bees with bigger body sizes are less sensitive to low temperatures, higher humidity and wind.

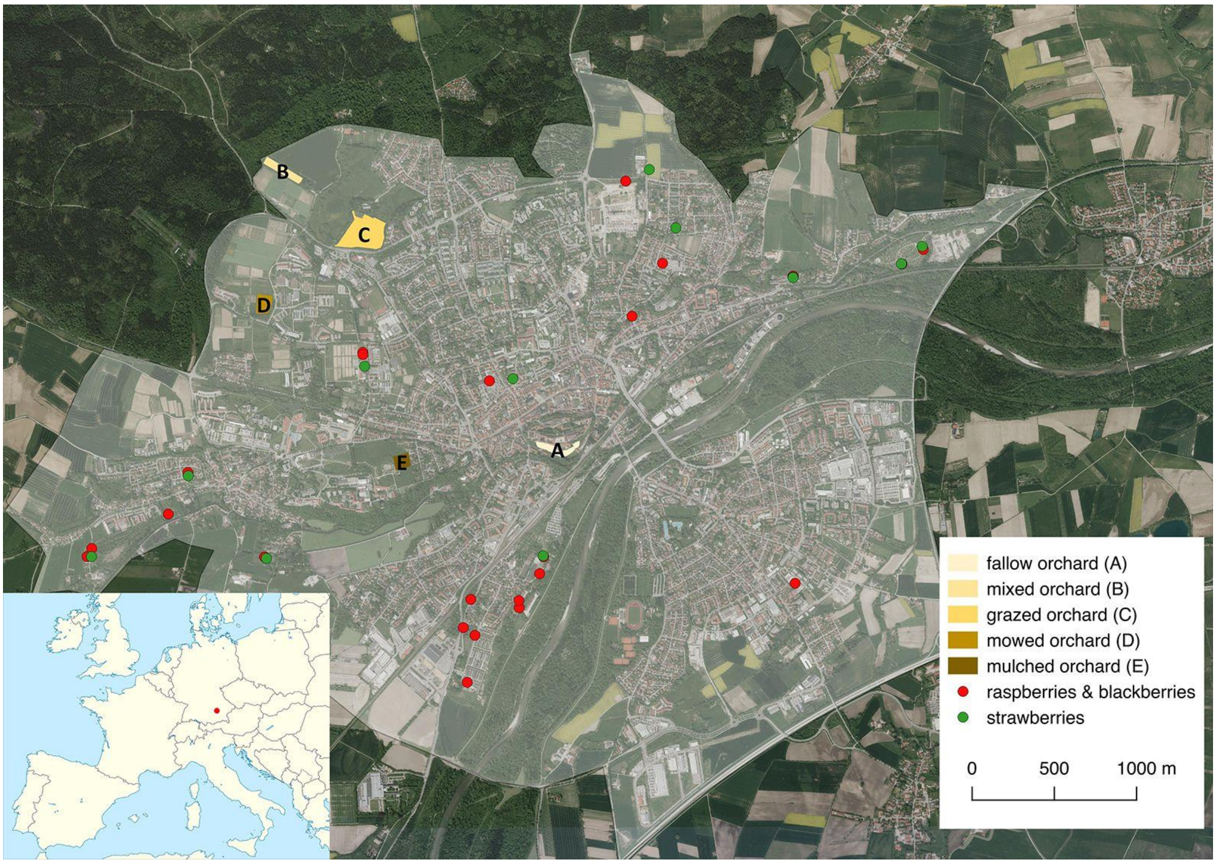

Figure 1. Study sites and management types (basemaps: Landesamt für Digitalisierung, Breitband und Vermessung (CC BY) & Wikimedia (CC BY-SA 3.0).

MATERIALS AND METHODS

STUDY SITES

The study was carried out in the city of Freising in southern Bavaria, Germany, which has a population of about 50,000 inhabitants and a total area of c. 89 km^2 (www.kreis-freising.de). Freising is situated in the lower Isar valley at an altitude of c. 460 m asl. The climate is temperate with annual rainfall of 807.32 mm and temperatures ranging from -15.2 to +33.7 (long-term average based on the values of the years 2010 to 2019, www.wetter-by.de). A total of 517 wild bee species have been recorded in Bavaria, and c. 300 species are estimated to exist in the administrative district of Freising (Scheuchl et al. 2018; Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen 2001). Pollinator surveys on fruit trees were performed in five fruit orchards distributed all over the city (Figure 1, sites A-E; A-C).

The surface area of the orchards varies between 0.8 – 4.25 ha, the number of fruit trees per orchard ranges between 50 – 216 trees of ten different species, the age of the trees ranges from 10 to more than 50 years (Table 1). The minimum distance between two orchards is 350 m, the maximum distance 2,500 m. The orchards have been subject to different management types and intensity ranging from fallow to grazing, mowing, and multiple mulching per season (Table 1, A-C). Additional observations on berry patches (*Rubus*, *Fragaria*) were performed in 23 private gardens, community gardens and fallow land sites throughout the city (Figure 1, red and green dots; D-H).

STUDY SPECIES

We selected nine species from the rose family: plum (*Prunus domestica* L.), cherry plum (*Prunus cerasifera* Ehrh.), sweet cherry (*Prunus avium* L.), sour cherry (*Prunus cerasus* L.), pear (*Pyrus communis* L.), apple (*Malus domestica* Borkh.), strawberry (*Fragaria* x *ananassa* Duchesne), raspberry (*Rubus idaeus* L.) and blackberry (*Rubus sect. Rubus,* mostly *Rubus armeniacus* Focke). These fruit crops are common and widespread for food production in urban environments and their simple flower morphology makes pollen and

Figure 2. Examples of study sites: A) grazed orchard; B) mulched orchard; C) mowed orchard; D) fallow land; E-H) urban gardens (A-C © I.W., D-H © J.W.).

nectar available to a broad range of insects. In our study orchards, this selection covered all present fruit trees except for three rare Rosaceae (*Cydonia oblonga* Mill., *Sorbus domestica* L. and *Mespilus germanica* L.), and the wind-pollinated walnut, *Juglans regia* L. (Table 1). From early spring (cherry and plum) to late summer (blackberry), our study species spanned the entire flowering season. The selected crops vary in different cultivars from self-incompatible to self-compatible, but fruit-set and fruit quality of all these species are increased through insect-pollination (Abrol 2015).

POLLINATOR SURVEY

Our systematic observation periods sum up to a total observation time of 137 hours and 30 minutes, with 101 h and 40 min dedicated to the trees, the remaining time spent on the berry patches (Table 2).

Pollinator surveys were performed between 9 AM and 6 PM during sunny weather with temperatures over 12°C on 19 days between April 16 and May 4, 2018, during full bloom of the fruit trees. Flower visitors were photographically recorded within an area of approximatively 4 m^2 during a standardized observation period of 10 minutes with the aim to at least differentiate between the four categories honeybee, bumblebee, large solitary bee (body size > 9 mm, which means larger than honeybee workers), and small solitary bee (body size up to 9 mm) and enable identification to genus or species level whenever possible. Only flower visitors touching stamen or

Table 1. Characteristics of the studied meadow orchards (A-E).

classification management	A fallow	B mixed	C grazed	D mowed	E mulched
size	0.98 ha	1.12 ha	4.25 ha	0.98 ha	0.80 ha
orientation	SE-SW	SW	SE-SW	E	N
altitude (m a.s.l.)	460-470	460-470	460-480	470-480	460-470
number of fruit trees	216	71	194	59	60
fruit tree species	*Malus domestica* (124, 39 varieties), *Pyrus communis* (21, 5 var.), *Prunus domestica/P. cerasifera* (64, 5 var.), *Prunus avium/P. cerasus* (5), *Juglans regia* (2)	*Malus domestica* (45, 12 var.), *Pyrus communis* (6, 2 var.), *Prunus domestica/P. cerasifera* (4), *Prunus avium* (6), *Juglans regia* (5), *Sorbus domestica* (5)	*Malus domestica* (99, 27 var.), *Pyrus communis* (50, 4 var.), *Prunus domestica/P. cerasifera* (8, 5 var.), *Prunus avium / P. cerasus* (17, 8 var.), *Cydonia oblonga* (5, 3 var.), *Sorbus domestica* (13), *Mespilus germanica* (2)	*Malus domestica* (58, 15 var.), *Pyrus communis* (1)	*Malus domestica* (60)
tree age in years	>15 to >50	> 30	>10 to >40	>50	>40
management of the trees	irregular pruning, replanting, shrub clearance	irregular pruning	irregular pruning, additional plantings	pruning, additional plantings	regular pruning
long-term management of the herb layer	introduction of hay from species-rich grasslands, 12 years of grazing by sheep, fallow since 2 years	extensification for 20 years, since 4 years ¼ hand-mown, ¾ grazed by sheep	mulched for many years, since 5 years partially mown, since 2 years extensive grazing by sheep and Shetland ponies	first mowing in June, second cut mid-July, mulched in late autumn, sometimes second mulching before apple harvest	6-7x mulching per year
management of the herb layer in 2018	fallow (partial mowing of pathways in end July)	¼ hand mown, ¾ grazing by horses from end July	extensive grazing by sheep, one-time mowing end July	first cut end of May, second cut mid-August	repeated mulching from mid-July

stigma were taken into account. To avoid double counts, flower visitor abundance was defined as the maximum of individuals of the same species and sex appearing simultaneously in one observation period. In total, 520 observation periods were accumulated over the season, 305 on the trees and 215 in berry patches. Directly after each 10 min observation period, an additional 10 min were dedicated to catch flower visitors to either identify them in the field or cool them down on a cold pack and take high-resolution pictures for later identification. Abundance records were based on 86 h 40 min of systematic observation periods. Species richness records were based on the total observation time of 137 h 30 min, which includes the additional 10 min of collection.

Pollinator surveys of berries were performed on 32 days between May 3rd and August 6, 2018. Citizen scientists, who had been trained on guided walks and through personal visits, contributed observations for 24 standardised observation periods of 10 minutes. Because of the lower number of flowers per site in the berry patches

Table 2. Observation time per study site and crop species.

Site	Crop species	No. of observed trees	No. of days of observation	No. of observation periods	Observation time	Total observation time (10 min frequency counts + 10 min additional observation time)
fallow	apple	24	5	34	12 h	24 h
	pear	5	5	13		
	cherry	4	4	12		
	plum	7	5	13		
mixed	apple	20	5	40	12 h 50 min	25 h 40 min
	pear	5	4	13		
	cherry	3	4	12		
	plum	3	4	12		
grazed	apple	30	6	43	13 h 50 min	27 h 40 min
	pear	9	4	12		
	cherry	7	3	16		
	plum	4	3	12		
mowed	apple	20	5	40	6 h 40 min	13 h 20 min
mulched	apple	15	4	33	5 h 30 min	11 h
sum for all sites	apple	109	14	190	31 h 40 min	63 h 20 min
	pear	19	8	38	6 h 20 min	12 h 40 min
	cherry	14	8	40	6 h 40 min	13 h 20 min
	plum	14	8	37	6 h 10 min	12 h 20 min
	strawberry	–	25	107	17 h 50 min	
	rasp- & blackberry	–	24	108	18 h	
sum orchards	tree crops	156	19	305	50 h 50 min	101 h 40 min
sum gardens	berries	–	32	215	35 h 50 min	
sum all sites	all crops		47	520	86 h 40 min	137 h 30 min

compared to the orchard trees, it was not possible to stick to a standardized area of 4 m². Therefore, each bee individual of the same species and sex was only counted once per observation period.

Bees were identified as far as possible to species level based on our field identification guide (Weissmann & Schaefer 2020). Species that are not distinguishable in the field (e.g., *Andrena minutula, A. minutuloides, A. falsifica, A. strohmella* and the very rare *A. subopaca, A. alfkenella, A. nana, A. semilaevis, A. rugulosa, A. floricola, A. niveata, A. pusilla, A. nanula, A. saxonica, A. anthrisci*) were treated as species groups with reference to the most common species (e.g., *Andrena* cf. *minutula).* For each species, information on body size and nesting ecology was compiled from Amiet et al. (1999), Amiet et al. (2001), Amiet et al. (2004), Amiet et al. (2007), Amiet et al. (2010) and Westrich (2018). We differentiated between ground nesting solitary bees (nesting in self-dug cavities in the soil), cavity nesting solitary bees (nesting in self-dug or pre-existing holes in dead wood, plant stems, walls, crevices, snail shells), and bumblebees (nesting predominantly in pre-existing holes like old rodent nests in the ground or under moss and turfs in the herb layer, some also in pre-existing holes aboveground e.g. behind walls, in piles of stones, in bird nests, in dead wood). Cuckoo bees were categorised according to the nesting preference of their host.

FLORAL RESOURCES IN THE HERB LAYER

In each of the studied tree patches, we mapped all insect-pollinated flowering plant species in the herb- and shrub layer of each orchard. The surveys took place over the entire spring and early summer season between April 30 and July 29, 2018, when most of the meadows had been mown.

LANDSCAPE METRICS

We quantified the proportion of urban habitat, agricultural habitat, lawns, flower-rich green spaces and woody habitat in 100 m, 300 m and 600 m zones surrounding the orchards based on aerial photographs (QGIS Development Team 2016).

Due to the close proximities of the study sites, there is considerable overlap in these zones at the 600 m distance but much less at the 300 m scale and none at the 100 m scale (Figure 2).

QUANTIFICATION OF HONEYBEE HIVES

The number of honeybee hives on the study sites and in zones of 300 m and 1,000 m diameter around each orchard was estimated based on data from the local veterinary office and personal observations on site. In total, c. 580 hives are registered at the regional veterinary office for the city of Freising and c. 900 hives for the entire municipal area, which represents a honey bee hive density of c. 19 hives/km^2 in the city (an area of c. 30 km^2) and 10 hives/km^2 for the whole municipal area of c. 88.6 km^2.

METEOROLOGICAL DATA

Meteorological data was obtained from the agrometeorological weather station of the Bavarian State Research Center for Agriculture (LfL) in Freising. For each observation period, we used the reference data of the previous full hour, e.g., we attributed weather data of 2 PM to all observation slots between 2-3 PM (Appendix I). The following weather parameters were obtained: temperature at 2 m elevation in °C, relative humidity in %, wind speed in m/s, and global radiation in Wh/m^2.

STATISTICAL ANALYSES

Importance of wild bees

All statistical analyses were performed using R version 4.0.3 (R Core Team 2020) and the packages ggplot2 (Wickham et al. 2019), dunn.test (Dinno 2017), MASS (Ripley et al. 2016), lme4 (Bates et al. 2020), car (Fox et al. 2020) and rich (Rossi 2016).´

Species richness

For each crop species, the cumulative wild bee species richness was summarized from all observation periods (137 h 30 min of total observation time). For each observation period on the fruit trees, we added the species recorded during the 10 minutes of systematic observation to those recorded in the 10 additional minutes dedicated to catch flower visitors. Values for *Prunus domestica*, *Prunus cerasifera*, *Prunus avium* and *Prunus cerasus* were pooled due to the low number of the available data for two of the tree species. We calculated the Sörensen index I_A to account for similarity between wild bee communities of each crop according to the following formula $I_A = (2g / (a+b)) * 100$ with g = total number of bee species occurring both on plant

Table 3. Land use types and potential resources for bees

land use type	structures	potential resources for bees
urban	residential areas, industrial areas, sport infrastructures, schools, parking lots, roads, small gardens, water	flowering plants in small gardens and ruderal areas as pollen source; bare soil, excavations e.g. in old walls as nesting site
lawns	intensively managed lawns with high proportion of grass	bare soil as nesting site
flower-rich green spaces	extensively managed meadows and gardens with high proportion of flowering plants	flowering plants as pollen source, bare soil as nesting site
woody	hedgerows, treelines, shrub, forest	dead wood, cavities and trees and woody stems as nest sites, shrubs as pollen source, hedgerows as mating places
agricultural	agricultural fields	crops like rapeseed and legumes as pollen and nectar source

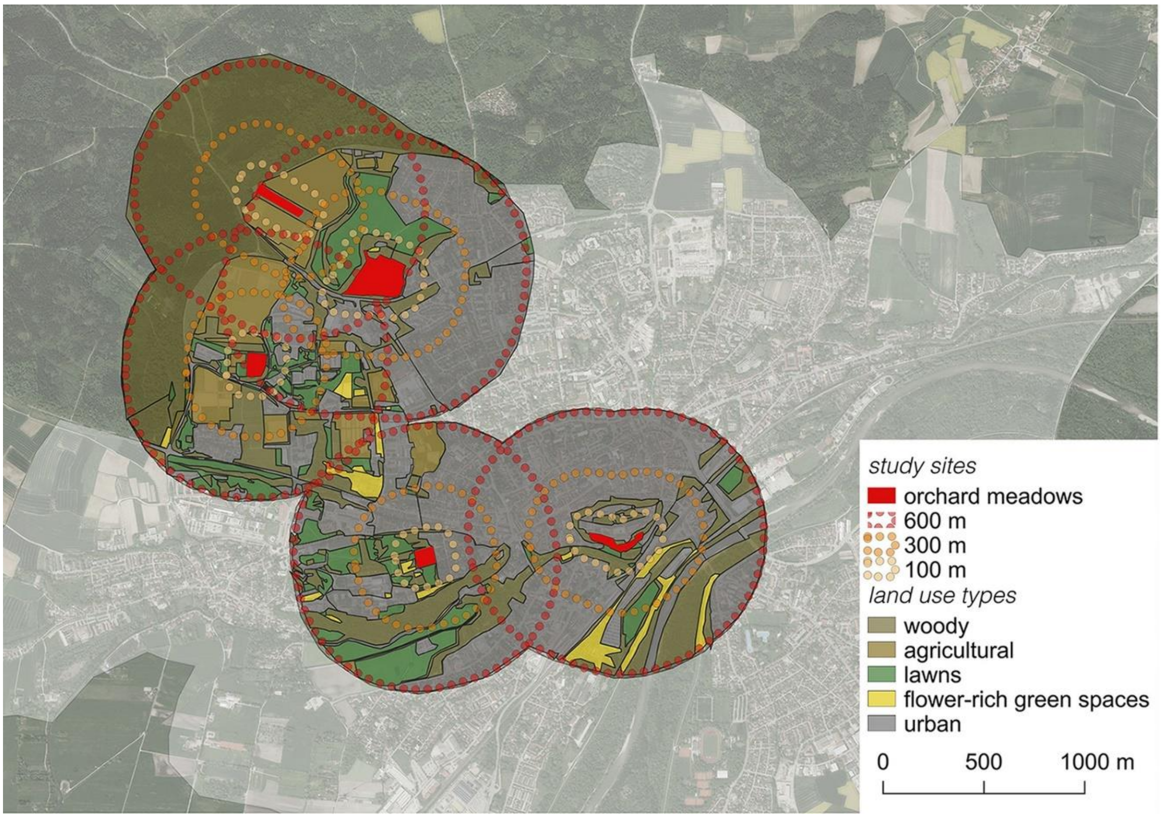

Figure 2. Land use surrounding the studied orchards (basemap: Landesamt für Digitalisierung, Breitband und Vermessung (CC BY)).

species A and on plant species B; a = total number of bee species occurring on plant species A; b = total number of bee species occurring on plant species B. We analysed the correlation of wild bee species richness to crop species based on all crop species on all sites. Species-time relationships were calculated as the mean number of wild bee taxa per 10 min. As the total number of observation periods per species varied from 37 on plum to 190 on apple, we calculated mean rarefied species richness for 35 sampling units with rarefaction curves (function rarc).

Abundance

Flower visitor abundance on fruit trees was summarized using the maximum values of individuals per species during each of the 305 systematic observation periods. In the comparison of bee abundance on trees and berries, each individual of the same species and sex was counted only once per 10 min observation period. We analysed the correlation of abundance of different functional groups of bees (based on bee size, genus and nesting type) to crop type (orchard trees vs. garden crops) based on all crop species on all sites.

To test whether honeybee and wild bee abundance on orchard trees are significantly different, we used an unpaired two-samples Wilcoxon test (function wilcox.test) for each tree species separately because the data is metric but not normally distributed. An unpaired two-sample t-test (function t.test) and a poisson regression (function glm) gave similar results. To test significant differences in abundance of different insect groups, we performed a Kruskal-Wallis rank sum test (function kruskal.test) for each tree species because the assumptions for an ANOVA were not met. As significant differences were detected by this global test for each of the tree species, we applied post-hoc tests for pairwise multiple comparisons (function dunn.test with bonferroni correction for p-values) to see which groups differ significantly.

To test whether the number of bee species per category is similarly distributed across all crop species, we performed Pearson's Chi-squared test (function chisq.test). Because some of the counts were less than 5, we confirmed that Fisher's Exact Test for Count Data (function fisher.test) gave similar results. As significant differences were detected by these global tests, we performed the same tests on the orchard trees and garden crops separately. As no significant differences were detected within these groups, we summed the number of bee species per category for the orchard trees and garden crops respectively and tested for differences between these two crop groups, where significant differences were detected.

Landscape effects

Using the data from the most common tree species, apple, we tested for a correlation of flower visitor abundance to the proportion of urban habitat at a 100 m, 300 m, and 1,000 m scale around each site using a Poisson regression model (function glm). Each bee type and each landscape scale represented a separate model.

To study the effects of local characteristics on wild bee diversity and abundance, we first pooled data of the pollinator surveys on apple blossoms for each orchard to obtain total wild bee species richness per orchard and then performed a correlation test (function cor.test) and a Poisson regression model (function glm) to investigate whether wild bee species diversity and abundance on apple flowers, respectively, are related to species diversity of flowering plants in the meadows.

To study the impact of honeybee-hive density at different scales on honeybee and wild bee abundance on apple flowers, we fitted a Poisson regression model (function glm). Wild bees and honeybees and each landscape scale (on site, 300 m radius, 1,000 m radius) represented a separate model.

Weather effects

To study the impact of weather conditions on bee abundance on all studied tree species per bee category, we fitted a Poisson regression model (function glm). As response variable, we used honeybee, bumblebee, large solitary bee, and small solitary bee abundance on all fruit tree flowers. As continuous predictor variables, we used temperature at 2 m elevation, relative humidity, wind, and global radiation. Each bee category represented a separate model. We used a stepwise automated model selection program to construct all possible models based on the set of explanatory variables and then rank these models based on their AIC (Package MASS, function stepAIC, mode of stepwise search: "both").

Joint models explaining the abundance of different bee groups on apple flowers

Finally, we included all explanatory variables in a single model to specify which of the above-mentioned predictor variables best explain bee abundances on apple flowers. Three of the explanatory variables are site-bound (honeybee hive abundance, proportion of urban habitat, floral diversity on site), but all 190 observations are time dependent regarding date and time of day and have individual values per sampling unit for all weather parameters. We did not include the variable "site" as a random effect as its influence was already included in the model through the three site-dependent explanatory variables. As the changes in the predictor variables honeybee hive abundance, floral diversity and proportion of urban habitat correspond to changes in study site, confounding factors like pollution or pesticide use might have an impact that is not accounted for in the model. For weather related variables, we only kept the parameter "global radiation", because this variable had been selected in all the models analysing the effect of different weather parameters on bee abundances. To test whether the remaining predictor variables are correlated, we performed linear models with small solitary bee, large solitary bee, bumblebee, total wild bee and honeybee abundance as response variables and computed the variance inflation factors (function vif). As all values were between 0 and 6, we left all predictor variables in the models and fitted a Poisson regression model (function glm) with small solitary bee, large solitary bee, bumblebee, total wild bee and honeybee abundance as response variables and proportion of urban habitat, species diversity of flowering plants, honeybee hive abundance and global radiation as predictor variables. Each landscape scale (honeybee hive abundance on site with proportion of urban habitat at the 100 m scale, honeybee hive abundance with proportion of urban habitat at the 300 m scales, honeybee hive abundance at the 1000 m scale with proportion of urban habitat at the 600 m scale) and each bee type constituted a separate model.

Table 4. Wild bee species observed on orchard trees, strawberries and rasp- & blackberries. Total wild bee species richness = 52 species, total observation time = 137 h 30 min. "x" indicates that the species was observed on the crop after the systematic observation periods.

bee species	orchard trees	strawberries	rasp- & blackberries
Andrena agilissima	0	1	1
Andrena cf. *bicolor*	1	0	0
Andrena cineraria	1	0	0
Andrena cf. *dorsata*	1	0	1
Andrena cf. *flavipes*	1	0	0
Andrena fulva	1	0	0
Andrena haemorrhoa	1	0	1
Andrena cf. *helvola*	1	0	0
Andrena cf. *minutula*	1	1	1
Andrena nitida	1	0	x
Andrena cf. *scotica*	1	0	1
Andrena cf. *tibialis*	0	0	1
Anthophora furcata	0	0	1
Anthophora plumipes	1	0	0
Bombus cf. *barbutellus*	0	0	1
Bombus hortorum	1	0	0
Bombus humilis	0	0	1
Bombus hypnorum	1	0	1
Bombus cf. *lapidarius*	1	0	1
Bombus pascuorum	1	0	1
Bombus pratorum	1	1	1
Bombus cf. *rupestris*	1	0	0
Bombus sylvarum	x	0	1
Bombus cf. *sylvestris*	x	0	0
Bombus terrestris agg.	1	0	1
Bombus cf. *vestalis*	1	0	0
Ceratina cyanea	0	1	1
Coelioxys cf. *aurolimbata*	0	0	1
Halictus rubicundus	1	0	0
Halictus subauratus	0	1	1
Halictus cf. *tumulorum*	0	0	1
Heriades truncorum	0	0	1
Hylaeus cf. *communis*	0	0	1
Hylaeus cf. *confusus*	0	1	1
Hylaeus cf. *difformis*	0	0	1
Hylaeus cf. *hyalinaeus*	0	1	1
Lasioglossum cf. *calceatum*	0	1	1
Lasioglossum cf. *morio*	1	1	1
Lasioglossum cf. *politum*	x	1	1
Lasioglossum cf. *zonulum*	0	0	1
Macropis fulvipes / M. europaea	0	1	0
Megachile cf. *centuncularis*	0	1	1
Nomada cf. *bifasciata*	1	0	1
Nomada cf. *flava*	1	0	0
Nomada cf. *flavoguttata*	1	1	0
Nomada cf. *succincta*	1	0	0
Osmia bicolor	1	0	0
Osmia bicornis	1	1	1
Osmia cf. *caerulescens*	1	1	0
Osmia cornuta	1	0	0
Osmia leucomelana	0	1	1
Stelis ornatula	0	1	1

RESULTS

WILD BEE COMMUNITIES

The wild bee flower visitor community of the study crops comprised a total of 52 taxa observed in 137 h 30 min (Table 4, Figure 3).

The total bee species diversity ranged from 14 (plum) to 34 species (rasp- and blackberries). The bee communities of the different plant species were most similar across the fruit trees and differed most between strawberries and the fruit trees and rasp- & blackberries and the fruit trees, respectively (Table 5).

The species-time relationship (the mean number of wild bee taxa per observation period), ranged from 0.08 for apple flowers to 0.31 on raspberry and blackberry flowers. Mean rarefied species richness for 35 observation periods ranged from 9 on strawberry to 23 on raspberry and blackberry flowers (Table 6).

Figure 3. Some of the bee species observed on the target crops: *Osmia bicornis* (A), *Andrena* cf. *flavipes* (B) and *Bombus terrestris* agg. (C) on plum; *Andrena fulva* (D) and *Andrena nitida* (E) on cherry; *Osmia cornuta* (F), *Bombus hypnorum* (G), *Andrena cineraria* (H) and *Andrena cf. minutula* (I) on apple; *Andrena haemorrhoa* (J) on pear; *Andrena agilissima* (K), *Megachile* cf. *centuncularis* (L), *Andrena* cf. *minutula* (M), *Halictus subauratus* (N), *Osmia leucomelana* (O), *Ceratina cyanea* (P), *Stelis* cf. *ornatula* (Q) and *Nomada* cf. *flavoguttata* (R) on strawberry; *Bombus sylvarum* (S), *Anthophora furcata* (T) and *Lasioglossum politum* (U) on raspberry; *Coelioxys* cf. *aurolimbata* (V), *Lasioglossum* cf. *calceatum* (W), *Hylaeus* cf. *hyalinatus* (X), *Apis mellifera* and *Hylaeus* cf. *confusus* (Y) on blackberry (slightly different scales; A-C, K-Y © J. W., D-J © I. W.).

Table 5. Sörensen index accounting for the similarity between wild bee communities of each crop. Darkening shades of grey indicate increasing similarity between plant species.

	plum	pear	apple	strawberry	rasp- & blackberry
cherry	60	74,3	66,7	18,2	32
plum	-	60,6	60,5	12,9	33,3
pear	-	-	70,8	16,7	33,9
apple	-	-	-	30,4	44,4
strawberry	-	-	-	-	54,9

Table 6. Cumulative species richness, species-time relationship and mean rarefied species richness of wild bees per plant species. Total wild bee species richness = 52 species, total observation time = 137 h 30 min.

	cherry	plum	pear	apple	strawberry	rasp- & blackberry
cumulative species richness	17	14	20	29	17	34
species-time relationship	0.21	0.19	0.26	0.08	0.16	0.31
mean rarefied species richness	12	11	16	19	9	23

The number of small solitary bees was highest on berry flowers, the number of bumblebees and large solitary bee species was highest on apple flowers (Figure 4). The number of bee species per bee category was not similarly distributed across the study plants (Pearson's Chi-squared test: *X*-squared = 25.636, df = 10, *P*-value = 0.004262; Fisher's Exact Test for Count Data: *P*-value = 0.006635). It was, however, similarly distributed within the tree species (Pearson's Chi-squared tests: X-squared = 0.80446, df = 6, *P*-value = 0.992) and the berries (*X*-squared = 3.3976, df = 2, *P*-value = 0.1829) and not similarly distributed between the orchard trees and garden crops (*X*-squared = 21.223, df = 2, *P*-value = 2.463e-05). The results of Fisher's Exact Tests for Count Data are similar (*P*-values = 0.9957; 0.1838; 3.101e-05, respectively).

The wild bee community of the orchard trees included 32 species of seven genera: *Andrena, Bombus, Osmia, Lasioglossum, Nomada, Anthophora,* and *Halictus* (sorted from most to least abundant). The wild bee community on strawberries included 17 species of 11 genera: *Lasioglossum, Hylaeus, Andrena, Halictus, Osmia, Megachile, Nomada, Bombus, Ceratina, Macropis,* and *Stelis*. The wild bee community on rasp- and blackberries included 34 species of 13 genera: *Bombus, Lasioglossum, Hylaeus, Andrena, Halictus, Osmia, Coelioxys, Heriades, Megachile, Nomada, Anthophora, Ceratina,* and *Stelis*. Overall, the wild bee community on the berry crops (straw-, rasp- and blackberries) included 37 species of 14 genera (Figure 5).

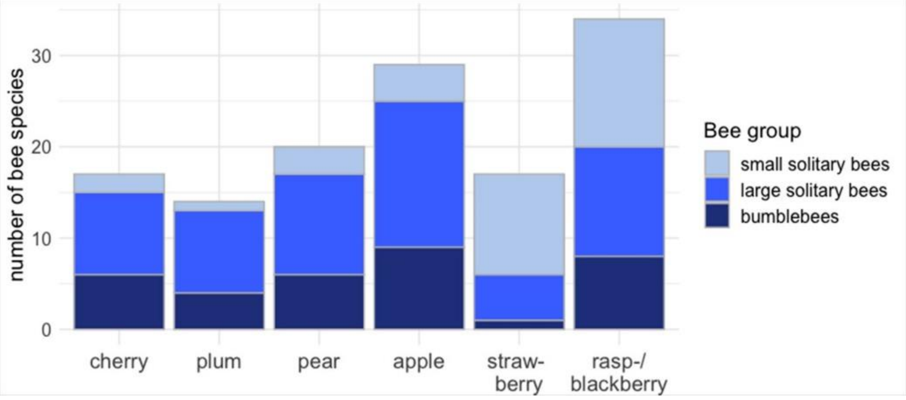

Figure 4. Number of wild bee species per group on the flowers of cherry, plum, pear, apple, strawberry and rasp- & blackberry. Total wild bee species richness = 52 species, total observation time = 137 h 30 min.

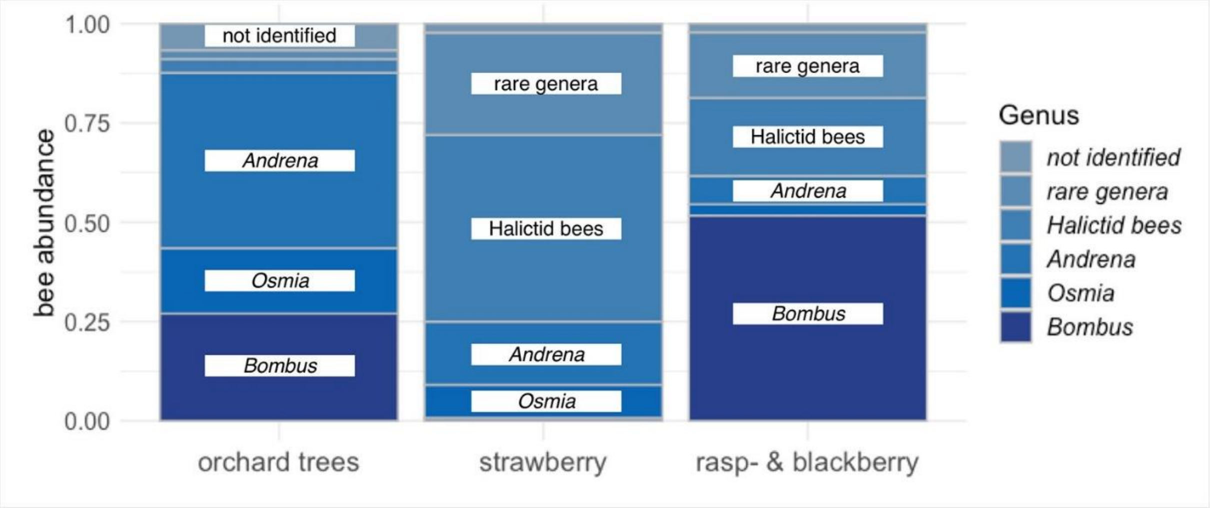

Figure 5. Relative abundance of wild bee genera on cherry, plum, pear, apple, strawberry and rasp- and blackberry. N.I.: flower visiting bees that could not be identified to genus level. Total bee abundance N = 768, total observation time = 86 h 40 min.

Among the group of non-bee flower visitors on orchard trees, 75% of all visits were by flies (Diptera), mainly bee flies (*Bombylius* spec.) and hoverflies (Syrphidae), 13% by Coleoptera (9% of all visits by the rose chafer, *Cetonia aurata*), 8% by non-bee Hymenoptera (7% of all visits by Vespidae, 1% by Symphyta) and 4% by Lepidoptera (c. 50% Pieridae, and 50% Nymphalidae).

Ground nesting solitary bees performed 43% of flower visits on all crops and were the most abundant flower visitors both on orchard trees and berry patches. All ground nesters combined (ground nesting solitary bees, ground nesting bumblebees and bumblebees which are flexible in their nesting behaviour) comprised 76% of all bee visits on orchard trees and 74% on berries. Cavity nesting solitary bees constituted 17% of flower visits on orchard trees and 22% of visits on berries (Figure 6).

VISITATION RATES OF HONEYBEES AND WILD BEES ON ORCHARD TREES

In total, we recorded 822 bee visits on the fruit trees in 50 h 50 min observation time. More than half of the visits were by honeybees, 41% by wild

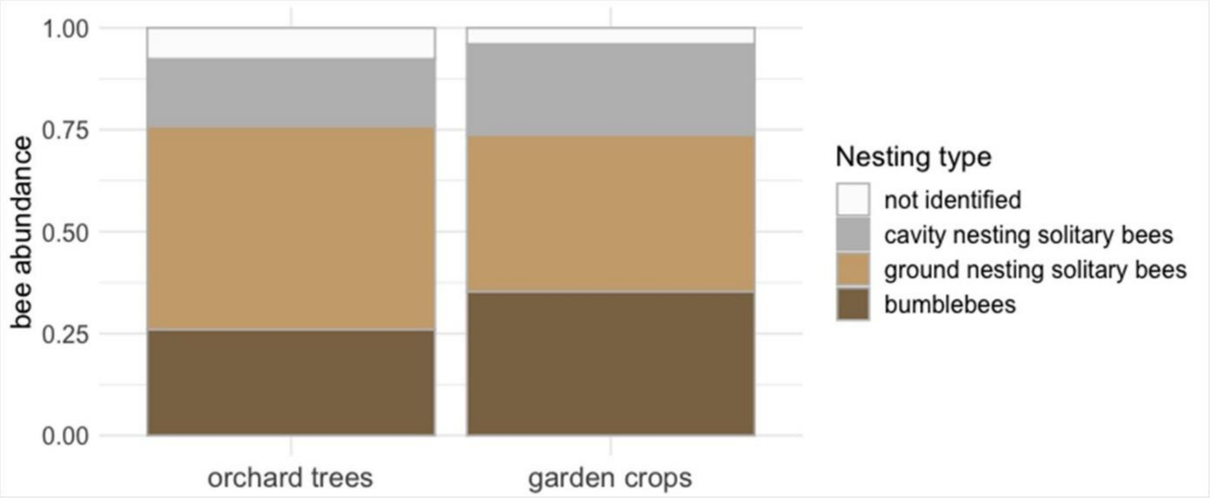

Figure 6. Relative abundance of wild bees visiting the study plants according to their nesting type. Total bee abundance N= 768, total observation time = 86 h 40 min.

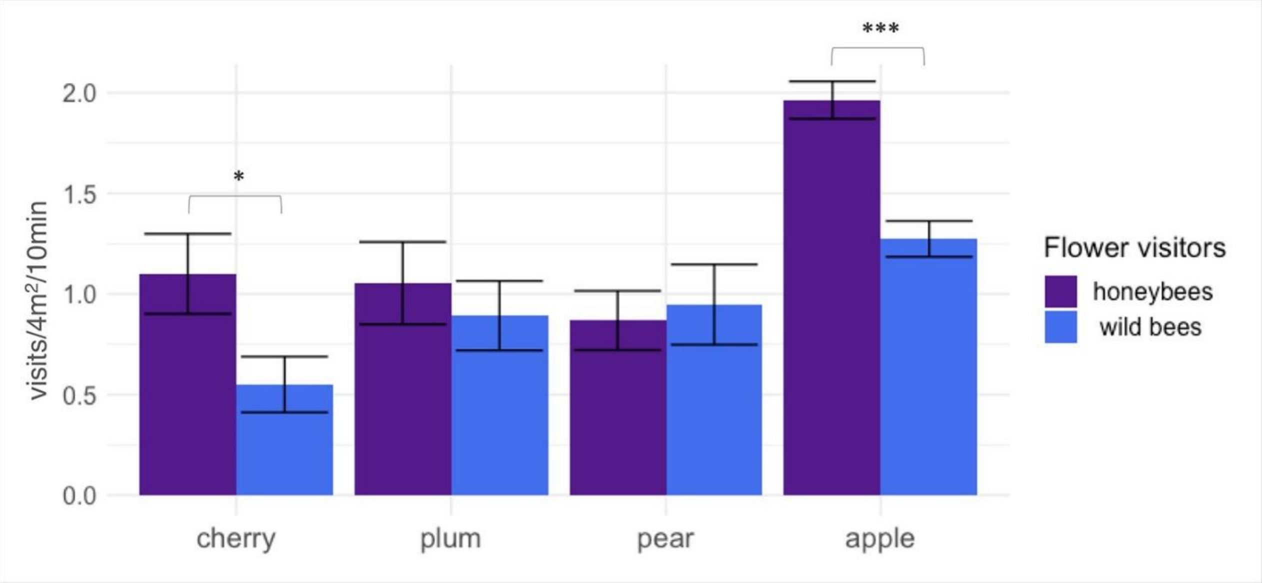

Figure 7. Abundance of honeybees and wild bees on cherry, plum, pear and apple flowers per 10 min observation period within a standardised 4 m^2 frame. Whiskers display the mean ± standard error. Bars with * are significantly different according to an unpaired two samples Wilcoxon test. Significance is marked with * at $P \leq 0.05$, ** at $P \leq 0.01$ and * at $P \leq 0.001$. Total bee abundance N = 822, total observation time = 50 h 50 min.**

bees. On plum and pear, wild bee and honeybee abundance were similar with about one bee individual of each category per 10 min per 4 m^2 (Figure 7). On cherry and apple, honeybee abundance was significantly higher than wild bee abundance: for cherry, on average 1.1 honeybees and 0.5 wild bees per 10 min and for apple 2 honeybees and 1.3 wild bees per 10 min.

Among the wild bee categories, large solitary bees were the most abundant flower visitors on all fruit trees, followed by bumblebees on cherry and apple, and by small solitary bees on plum and pear (Figure 8). All other flying insects performed 18% of all recorded flower visits.

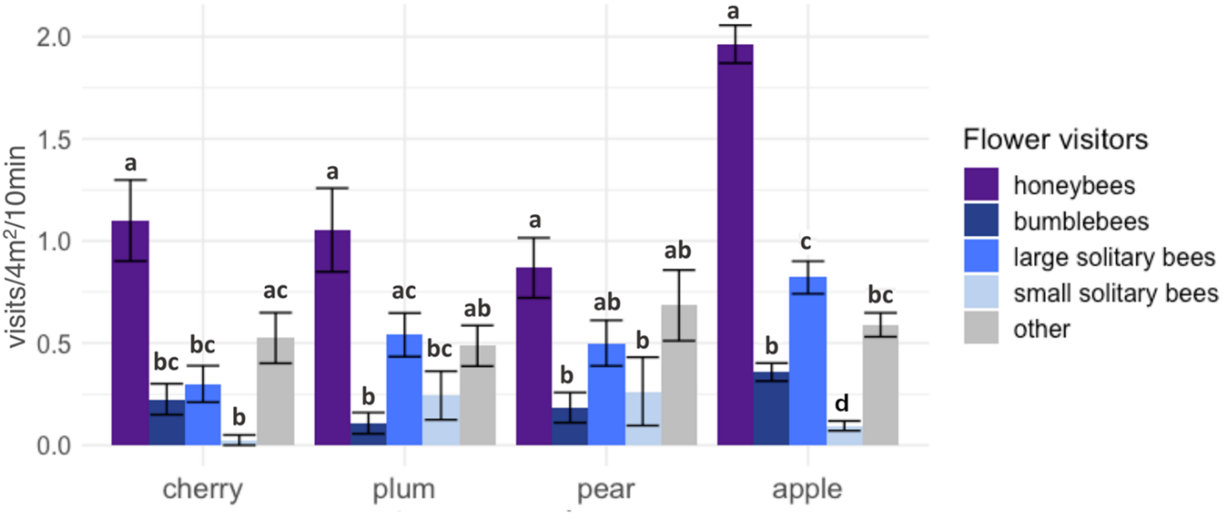

Figure 8. Abundance of honeybees, bumblebees, large solitary bees, small solitary bees and other insects on cherry, plum, pear and apple flowers per 10 min observation period within a standardised 4 m^2 frame. Whiskers display the mean ± standard error. Bars with different letters are significantly different according to pairwise comparisons using Dunn's test at $P \leq 0.025$. Total insect abundance N = 999, total observation time = 50h50.

FLORAL RESOURCES SURROUNDING THE TREES

In the herb- and shrub-layer of the meadow orchards, we recorded a total of 144 insect-pollinated flowering plant species of 34 families (Appendix II). Flowering plant species diversity ranged from 22 species on the mulched orchard to 79 species on the fallow orchard. The number of flowering plant species on site had a slightly positive impact on wild bee abundance on apple flowers (poisson model: estimate = 0.006459, std-error = 0.003008, *Z*-value = 2.147, *P*-value = 0.0318*), but the effect was not significant in the joint models. Species richness of wild bees on apple flowers is not significantly positively affected, probably due to the low number of study sites (correlation test: *T*-value = 1.8535, *P*-value = 0.1638, *N* = 5).

LANDSCAPE METRICS

When considered as sole variable, the proportion of urban habitat had a positive effect on total wild bee abundance at all scales. The positive effect was higher for small solitary bee abundance than for large solitary bee abundance. Bumblebee abundance was negatively affected by the proportion of urban habitat (Table 7).

In the joint models, the proportion of urban habitat positively affected small and large solitary bee abundance and negatively affected bumblebee and honeybee abundance: when the proportion of urban habitat increases by 10%, the mean number of small solitary bees visits on apple flowers per observation period more than doubles at the 100 m scale, the mean number of large solitary bees increases by 20% at all scales, the mean number of bumblebees is reduced by 20% at the 100 m and 600 m scales, and the mean number of honeybees is reduced by 10% at all scales (Table 11).

HONEYBEE-HIVE DENSITY

The number of honeybee-hives on site ranged between zero and ten. In the 300 m radius, values ranged from nine to 37 and in a 1 km radius from 90 to 147. When considered as sole variable, hive number had a slightly positive impact on honeybee abundance and a slightly negative impact on total wild bee abundance on apple flowers. The effect decreased with increasing distance of the hives from the site. The negative effect was higher for small solitary bees than for large solitary bees. For bumblebees, it was positive

Table 7. Results of poisson regression models assessing the effect of the proportion of urban habitat around each site on wild bee and honeybee abundance on apple flowers. Each landscape scale and bee type represent a separate model. Estimated parameters, standard errors, z-values and p-values are given. Significance is marked with * at P ≤ 0.05, ** at P ≤ 0.01 and * at P ≤ 0.001.**

landscape scale	response	estimate	std. error	z value	p-value
100 m	small solitary bee abundance	0.06139	0.01751	3.505	0.000456 ***
	large solitary bee abundance	0.024225	0.004948	4.896	9.80e-07 ***
	bumblebee abundance	-0.025734	0.007522	-3.421	0.000623 ***
	total wild bee abundance	0.012230	0.003866	3.163	0.00156 **
	honeybee abundance	-0.006057	0.003091	-1.959	0.0501
300 m	small solitary bee abundance	0.04619	0.01448	3.190	0.00142 **
	large solitary bee abundance	0.019643	0.003842	5.113	3.17e-07 ***
	bumblebee abundance	-0.018531	0.005157	-3.593	0.000327 ***
	total wild bee abundance	0.009058	0.002867	3.159	0.00158 **
	honeybee abundance	-0.004454	0.002189	-2.034	0.0419 *
600 m	small solitary bee abundance	0.04521	0.01489	3.036	0.00239 **
	large solitary bee abundance	0.020580	0.003964	5.191	2.09e-07 ***
	bumblebee abundance	-0.017809	0.005671	-3.141	0.00169 **
	total wild bee abundance	0.010341	0.002986	3.463	0.000534 ***
	honeybee abundance	-0.005660	0.002331	-2.428	0.0152 *

Table 8. Results of poisson regression models describing the effect of the number of honeybee hives at different landscape scales on wild bee and honeybee abundance on apple flowers. Each landscape scale and bee type represent a separate model. Estimated parameters, standard errors, z-values and p-values are given. Significance is marked with * at P ≤ 0.05, ** at P ≤ 0.01 and * at P ≤ 0.001.**

landscape scale	response	estimate	std. error	z value	p-value
on site	small solitary bee abundance	-0.07577	0.07500	-1.010	0.312
	large solitary bee abundance	-0.04850	0.02300	-2.109	0.035 *
	bumblebee abundance	-0.04361	0.03424	-1.274	0.203
	total wild bee abundance	-0.04894	0.01850	-2.646	0.00815 **
	honeybee abundance	0.03175	0.01169	2.716	0.00661 **
300 m	small solitary bee abundance	-0.07848	0.02281	-3.441	0.000579 ***
	large solitary bee abundance	-0.022011	0.005899	-3.731	0.000191 ***
	bumblebee abundance	0.026762	0.009614	2.784	0.00537 **
	total wild bee abundance	-0.012097	0.004683	-2.583	0.00979 **
	honeybee abundance	0.006609	0.003831	1.725	0.0845
1000 m	small solitary bee abundance	-0.04411	0.01209	-3.648	0.000265 ***
	large solitary bee abundance	-0.012802	0.003501	-3.657	0.000255 ***
	bumblebee abundance	0.010172	0.006127	1.660	0.09690
	total wild bee abundance	-0.009098	0.002835	-3.209	0.00133 **
	honeybee abundance	0.006206	0.002516	2.467	0.0136 *

at the 300 m scale (p-values are significant at $p \leq 0.05$ except for the impact of the number of honeybees on site on small solitary bee and bumblebee abundance, of the number of honeybee hives at the 300 m radius on honeybee abundance, and of the number of honeybee hives at the 1000 m radius on bumblebee abundance) (Table 8).

In the joint models, honeybee hive density had a negative effect on small solitary bee abundance at the 300 m and 1000 m scales (the mean number of small solitary bee visits per observation period is reduced by 72% and 50% when the number of bee hives increases by ten hives at the 300 m and the 1000 m scale, respectively) and a positive effect on honeybee abundance at the local scale (the mean number of honeybee visits per observation period increases by 56% when the number of bee hives on site is raised by ten hives) (Table 11).

WEATHER CONDITIONS

In 2018, when the fieldwork was performed, the flowering period of fruit trees in the orchards was earlier and shorter than usual. The year 2018 was the warmest year in Germany since the beginning of records in 1881 (deviation of 2+3 Kelvin from the period of reference 1961-1990). After low temperatures in February and March (Germany: -2.3 K and -1.1 K, Freising: -1.8 and -0.1), April and May 2018 were particularly warm (Germany: + 4.9 K and + 3.9 K, Freising: + 5.8 and + 4.4). While the beginning of the flowering period of sweet cherry in mid-April was average, the start of apple flowering on April 20th was c. 5 days earlier than the average of the period of reference (Imbery et al. 2018), (Agrarmeteorologie Bayern 2020). These particular weather conditions led to a shortened overall flowering period with a strong overlap between the studied fruit tree species.

When all parameters represented separate models, increases in temperature and radiation and decrease in humidity had a positive effect on honeybee, large solitary bee and small solitary bee abundance ($p < 0.05$ for all models except the one correlating temperature and large solitary bee abundance). The same weather conditions had the opposite effect on bumblebee abundance. Wind only had a significant (positive) effect on small solitary bee abundance (Table 9).

In the models selected by stepAIC, abundance of honeybees, large solitary bees and small solitary bees were best explained by humidity (negative impact) and radiation (positive impact). For large solitary bee abundance, temperature was included in the best model as a third parameter (with a positive impact). Abundance of bumblebees was

Table 9. Results of poisson regression models assessing the effect of temperature at 2 m elevation, relative humidity, wind, and global radiation on wild bee and honeybee abundance on fruit tree flowers. Each predictor and bee type represents a separate model. Estimated parameters, standard errors, z-values and p-values are given. Significance is marked with * at P ≤ 0.05, ** at P ≤ 0.01 and * at P ≤ 0.001.**

predictor	response	estimate	std. error	z value	p-value
temperature	small solitary bee abundance	0.15881	0.04404	3.606	0.000311 ***
	large solitary bee abundance	0.02028	0.01721	1.178	0.2388
	bumblebee abundance	-0.07067	0.02642	-2.675	0.00748 **
	honeybee abundance	0.03227	0.01124	2.871	0.00409 **
humidity	small solitary bee abundance	-0.05846	0.01391	-4.203	2.63e-05 ***
	large solitary bee abundance	-0.016854	0.004878	-3.455	0.000549 ***
	bumblebee abundance	0.018024	0.006304	2.859	0.00425 **
	honeybee abundance	-0.011526	0.003096	-3.723	0.000197 ***
wind	small solitary bee abundance	0.5260	0.1897	2.773	0.00556 **
	large solitary bee abundance	0.03703	0.09392	0.394	0.6934
	bumblebee abundance	-0.2393	0.1545	-1.549	0.1214
	honeybee abundance	0.03636	0.06112	0.595	0.5520
radiation	small solitary bee abundance	0.005449	0.001222	4.461	8.17e-06 ***
	large solitary bee abundance	0.0007566	0.0003345	2.262	0.0237 *
	bumblebee abundance	-0.001457	0.000478	-3.049	0.0023 **
	honeybee abundance	0.0006408	0.0002161	2.965	0.303

Table 10. Results of poisson regression models assessing the effect of temperature at 2 m elevation, relative humidity, and global radiation on the abundance of different bee groups on fruit trees. Models were selected using the stepAIC function (selection in both directions). Only best models are reported and model estimates, p-value and model selection statistics are given. Significance is marked with * at P ≤ 0.05, ** at P ≤ 0.01 and * at P ≤ 0.001.**

response	best model	factor	estimate	p-value	model selection statistics
small solitary bee abundance	relative humidity + global radiation	relative humidity	-0.077945	3.28e-05 ***	AIC= 212.13
		global radiation	0.006266	6.05e-06 ***	
large solitary bee abundance	temperature + relative humidity + global radiation	temperature	-0.0808387	0.00510 **	AIC= 685.09
		relative humidity	-0.0345199	8.87e-05 ***	
		global radiation	0.0005205	0.13628	
bumblebee abundance	temperature + global radiation	temperature	-0.0511215	0.0582	AIC= 408.14
		global radiation	-0.0011795	0.0176 *	
honeybee abundance	relative humidity + global radiation	relative humidity	-0.0100167	0.00202 **	AIC= 971.15
		global radiation	0.0004631	0.04007 *	

best explained by temperature and radiation (both with a negative impact) (Table 10).

In the joint models only considering flower visitors on apple flowers, global radiation had a significant and positive effect on the abundance of all bee groups except bumblebees (Table 11).

DISCUSSION

HOW DIVERSE IS THE FLOWER VISITOR COMMUNITY?

Overall, the observed wild bee community in Freising comprised a large number of species and genera characterized by a variety of functional traits. With 32 species on orchard trees, 17 on strawberries and 34 on raspberries, our results are

Table 11. Results of poisson regression models describing the effect of the number of honeybee hives at different landscape scales, of floral diversity on site, of the proportion of urban habitat at different landscape scales, and of global radiation on bee abundances on apple flowers. Each landscape scale and bee type represent a separate model. Estimated parameters, standard errors, z-values, p-values and model selection statistics are given. Significance is marked with * at P ≤ 0.1, * at P ≤ 0.05, ** at P ≤ 0.01 and * at P ≤ 0.001.**

landscape scale	response	predictor	estimate	std. error	z value	p-value	model selection statistics
honeybee hive abundance on site, urban habitat at the 100 m scale	small solitary bee abundance	honeybee hive abundance	0.085199	0.093175	0.914	0.36051	106.95
		floral diversity	0.006666	0.011261	0.592	0.55386	
		urban habitat	0.080696	0.025083	3.217	0.00129 **	
		global radiation	0.004634	0.001583	2.928	0.00341 **	
	large solitary bee abundance	honeybee hive abundance	-0.0165651	0.0255074	-0.649	0.51607	460.73
		floral diversity	0.0030187	0.0037510	0.805	0.42096	
		urban habitat	0.0225658	0.0053715	4.201	2.66e-05 ***	
		global radiation	0.0011849	0.0004014	2.952	0.00316 **	
	bumblebee abundance	honeybee hive abundance	-0.0423856	0.0380668	-1.113	0.26551	285.97
		floral diversity	0.0013902	0.0073971	0.188	0.85092	
		urban habitat	-0.0221494	0.0074159	-2.987	0.00282 **	
		global radiation	-0.0009650	0.0005559	-1.736	0.08257	
	total wild bee abundance	honeybee hive abundance	-0.0352123	0.0201002	-1.752	0.0798	556.79
		floral diversity	0.0023367	0.0031170	0.750	0.4534	
		urban habitat	0.0096354	0.0039527	2.438	0.0148 *	
		global radiation	0.0005361	0.0003067	1.748	0.0805	
	honeybee abundance	honeybee hive abundance	0.0444917	0.0137576	3.234	0.001221 **	607.52
		floral diversity	0.0059241	0.0029893	1.982	0.047509 *	
		urban habitat	-0.0079947	0.0034054	-2.348	0.018892 *	
		global radiation	0.0008497	0.0002562	3.317	0.000911 ***	
honeybee hive abundance and proportion of urban habitat at the 300 m scale	small solitary bee abundance	honeybee hive abundance	-0.127637	0.054575	-2.339	0.01935 *	103.8
		floral diversity	0.021343	0.012885	1.656	0.09764	
		urban habitat	-0.036181	0.035343	-1.024	0.30597	
		global radiation	0.005185	0.001630	3.181	0.00147 **	
	large solitary bee abundance	honeybee hive abundance	0.0046094	0.0128440	0.359	0.719690	459.69
		floral diversity	0.0017413	0.0043755	0.398	0.690651	
		urban habitat	0.0215644	0.0091757	2.350	0.018765 *	
		global radiation	0.0010197	0.0004319	2.361	0.018217 *	
	bumblebee abundance	honeybee hive abundance	-0.0166337	0.0231490	-0.719	0.4724	285.86
		floral diversity	0.0122167	0.0094594	1.291	0.1965	
		urban habitat	-0.0271224	0.0138821	-1.954	0.0507	
		global radiation	-0.0007272	0.0006060	-1.200	0.2302	
	total wild bee abundance	honeybee hive abundance	-0.0136379	0.0104684	-1.303	0.1927	559.21
		floral diversity	0.0070290	0.0037792	1.860	0.0629	
		urban habitat	-0.0007947	0.0069153	-0.115	0.9085	
		global radiation	0.0007078	0.0003391	2.087	0.0369 *	
	honeybee abundance	honeybee hive abundance	-0.0149470	0.0089362	-1.673	0.094398	613.31
		floral diversity	0.0059066	0.0033457	1.765	0.077492	
		urban habitat	-0.0146386	0.0054323	-2.695	0.007044 **	
		global radiation	0.0010078	0.0002726	3.697	0.000218 ***	

Table 11. continued

landscape scale	response	predictor	estimate	std. error	z value	p-value	model selection statistics
honeybee hive abundance at the 1000 m scale, proportion of urban habitat at the 600 m scale	small solitary bee abundance	honeybee hive abundance	-0.069583	0.028654	-2.428	0.01516 *	103.77
		floral diversity	0.017609	0.011736	1.500	0.13351	
		urban habitat	-0.032821	0.030642	-1.071	0.28412	
		global radiation	0.005081	0.001611	3.154	0.00161 **	
	large solitary bee abundance	honeybee hive abundance	-3.052e-05	6.083e-03	-0.005	0.9960	460.09
		floral diversity	1.594e-03	4.131e-03	0.386	0.6995	
		urban habitat	1.955e-02	7.775e-03	2.515	0.0119 *	
		global radiation	1.015e-03	4.298e-04	2.362	0.0182 *	
	bumblebee abundance	honeybee hive abundance	-0.0124229	0.0108631	-1.144	0.25280	286.75
		floral diversity	0.0144274	0.0085877	1.680	0.09296	
		urban habitat	-0.0292980	0.0110157	-2.660	0.00782 **	
		global radiation	-0.0006657	0.0006132	-1.086	0.27762	
	total wild bee abundance	honeybee hive abundance	-0.0097490	0.0050039	-1.948	0.0514	556.03
		floral diversity	0.0064453	0.0035081	1.837	0.0662	
		urban habitat	-0.0008473	0.0057810	-0.147	0.8835	
		global radiation	0.0007621	0.0003376	2.257	0.0240 *	
	honeybee abundance	honeybee hive abundance	-0.0025463	0.0042622	-0.597	0.550240	612.2
		floral diversity	0.0046628	0.0031613	1.475	0.140221	
		urban habitat	-0.0107740	0.0043973	-2.450	0.014280 *	
		global radiation	0.0009482	0.0002732	3.471	0.000519 ***	

comparable to findings in agricultural study sites. For example, 47 bee species have been identified in mixed meadow orchards in Baden-Württemberg (Schwenninger & Wolf-Schwenninger 2012), 22 bee species on sweet cherry orchards in Flanders (Eeraerts, Smagghe, et al. 2019), 27 bee species on apple orchards in Hungary (Földesi et al. 2016), 18 bee species on strawberry fields in Lower Saxony (Ahrenfeldt et al. 2015), and 47 bee species on raspberry in forests in Maine (Hansen & Osgood 1983). Since our species identification approach based on high resolution photographs instead of collected bees leads most likely to an under-estimation of total species numbers in difficult genera like *Lasioglossum* and *Nomada*, the real diversity in our study sites can be expected to be even higher.

The high proportion of bumblebee visitation in our study plants is in line with previous studies on these crops (Pardo & Borges 2020; Quinet et al. 2016; Ellis et al. 2017; Lye et al. 2011). Large wild bees were predominant on fruit trees in meadow orchards and small wild bees were more abundant on straw-, rasp- and blackberries in gardens. Considering that many small bodied wild bee species are more restricted in their flight range (Zurbuchen et al. 2010; Gathmann & Tscharntke 2002; Greenleaf et al. 2007; Hofmann et al. 2020), their higher share in garden crop visitation might be related to the fact that these sites provide a larger variety of microstructures at a small scale. Similarly, Bennett & Lovell (2019) found abundances of small-bodied and larger-bodied bee species in urban agricultural sites to respond most strongly to local site and landscape variables, respectively. The late flowering period of straw-, rasp- and blackberries might have an additional impact, as many small bees (e.g. *Hylaeus* spp., *Hoplitis* spp.) are active later in the season than larger-bodied species (e.g. *Andrena* spp., *Osmia* spp., and *Anthophora* spp.) (Westrich 2018).

The overall large share of ground-nesters reflects their predominance in the German wild bee fauna since c. 74% of all non-parasitic bee species known from Germany nest in self-dug or pre-existing cavities in the ground (Westrich 2018). The slightly higher share of hypogeic cavity-nesters on garden crops compared to orchard trees might be related to higher heterogeneity and abundance of aboveground-microstructures within these sites (Fortel et al. 2014; Matteson et al. 2008). In particular, species of three of the genera forming the group of small bodied bees – *Hylaeus*, *Ceratina*, *Osmia* (*Hoplitis*) – nest in stems of rasp- and blackberries (Westrich 2018).

WHAT IS THE ROLE OF WILD BEES IN POLLINATION OF TREES AND BERRIES FROM THE ROSE FAMILY?

More than half of the flower visits on apple in the urban meadow orchards were performed by honeybees. The large proportion of honeybees can be explained by the high density of honeybee hives within the city with a minimum of 90 honeybee hives in a 1 km radius around each site (containing in late spring up to 4.5 Mio worker bees), and by the large flight range of honeybees as they routinely forage in distances of 1.5 km, and can travel more than 10 km in search of floral rewards (Beekman & Ratnieks 2000; Waddington & Visscher 1994; Visscher & Seeley 1982; Zurbuchen et al. 2010). At the same time, our study shows that wild bees provide an important share of total bee flower visits. The wild bee proportions of 33% of total bee visits on cherry, 39% on apple, 46% on plum, and 52% on pear is comparable or higher than rates recorded in orchards outside urban areas. In a study on mixed orchards in Baden-Württemberg, 16% of bee visits on apple, 38% on *Prunus* spp. and 40% on pear were performed by wild bees (Schwenninger & Wolf-Schwenninger 2012), in a study on orchards in northern Hesse, about one third of the bee visits on sweet cherry were from wild bees (Holzschuh et al. 2012).

The relevance of wild bees for urban food crop production might exceed their mere share in flower visitation rate because of pollination effectiveness, interspecific facilitation and complementary pollination behaviour. In a study on 41 crop systems worldwide, Garibaldi et al. (2013) found fruit set to increase twice as strongly with increased visitation by wild insects as with an equivalent increase in visitation by honeybees. Studies investigating the pollination behaviour of different insect groups have shown that many hairy large solitary bees like *Andrena* and *Osmia* ssp. outperform honeybees in pollination effectiveness because the dry-collected pollen in dense brushes on the hind legs or beneath the abdomen is more likely to be transferred from flower to flower and because of their flower visitation rate and behaviour (Stavert et al. 2016; Eeraerts, Vanderhaegen, et al. 2019; Pardo & Borges 2020; Mallinger & Gratton 2015; Russo et al. 2017). Pollination observations on raspberries and apple blossoms showed that bumblebees outperform honeybees in pollen deposition on stigmata and forage over longer periods of the day and during poorer weather conditions (Thomson & Goodell 2002; Willmer et al. 1994). Research on interspecies facilitation in almond and sweet cherry orchards provided evidence that interspecies interactions between wild bees and honeybees increase the pollination effectiveness of honeybees (Brittain et al. 2013; Eeraerts et al. 2020). Studies on strawberry fields identified the relevance of complementary pollination behaviour of wild and honeybees for fruit quality (Chagnon et al. 1993). All this points to an important role of wild bees as urban pollinators.

WHAT IS THE IMPACT OF LAND USE TYPES SURROUNDING THE CROP SPECIES?

While honeybee and bumblebee abundance on apple flowers were negatively affected by the proportion of urban habitat, small and large solitary bee and total wild bee abundance were positively affected. It is likely that the high proportion of small private gardens and green balconies in these areas made them more attractive to wild bee species than would have been expected. In previous studies, some urban environments have been shown to support wild bee visitation of some bee clades in adjacent crops (Carré et al. 2009; Langellotto et al. 2018; Martins et al. 2018). In particular, urbanised habitats have been found to filter for small solitary bee species, possibly because their lower quantitative requirements in pollen and nectar and smaller flight ranges make them well adapted to urban environments which often provide structurally diverse habitats at a small scale (Banaszak-Cibicka & Żmihorski 2012; Wilson & Jamieson 2019; Buchholz & Egerer 2020). The negative effect on bumblebee abundance in turn might be related to the scarcity of potential nesting sites in largely sealed urban areas. Overall, the partially positive effect of urban habitats on wild bee abundance in

Freising indicates that some urban environments like private gardens can support crop visiting wild bee communities.

We find no significant effect of flowering plant cover in the herb layer on abundance and species richness of wild bees visiting apple flowers. Other studies suggested that additional floral resources in the herb layer of orchards are necessary to support wild bees because the flowering period of fruit trees is shorter than the life cycle of wild bees (Bertrand et al. 2019; Eeraerts et al. 2019; Alomar et al. 2018; Saunders & Luck 2018). In our mixed orchards, however, the combined flowering period of plum, cherry, apple, and pear spanned several weeks and this might be the reason why even the orchards with intense mowing regime had a diverse wild bee community.

WHAT IS THE IMPACT OF HONEYBEE HIVE DENSITY AT THE LANDSCAPE SCALE ON WILD BEE ABUNDANCE?

Honey bee density in Freising is incredibly high with an absolute number of hives almost as high as in the entire city of Paris and a hive density 2-3 times as high as in Berlin, Hamburg (Beckedorf 2015) and Paris, where negative effects on wild bee communities have been demonstrated (Ropars et al. 2019). We also show that wild bee visitation rate on orchard crops was negatively correlated to honey bee hive densities, which is in line with previous studies in natural habitats, agroecosystems and urban environments (Torné-Noguera et al. 2016; Alomar et al. 2018; Ropars et al. 2019; Renner et al. 2021). In Paris, Ropars et al. (2019) found a significant negative effect of honeybee hive densities on large solitary bees and bumblebees but not on small solitary bees, and hypothesised that the latter might be less sensitive to increases of honeybee hive densities because of resource complementarity, smaller species often preferring shallow flowers while larger pollinators prefer deep flowers. Interestingly, in our study focusing exclusively on plants with shallow flowers, the negative effect of honey bee hive density was significant and strongest for small solitary bee species, which indicates that they might be particularly sensitive to direct competition.

These results support the theory that honey bees outcompete other pollinators especially when resources are limited (Cane & Tepedino 2017; Mallinger et al. 2017). In light of social and conservation benefits of beekeeping, calls for inclusive solutions to preserve both biodiversity and beekeeping activities have been articulated (Aebi et al. 2012; Kleijn et al. 2018; Egerer & Kowarik 2020) to promote beekeeping *for* vs. beekeeping *of* the city (Sponsler & Bratman 2020). Specific measures should combine adapting hive densities to local floral supply (taking into account floral abundance, species composition and phenology) e.g. through the definition of precautionary zones (Stange et al. 2017; Cane & Tepedino 2017; Henry & Rodet 2020) with the coupling of beekeeping and floral resource enhancement adapted to the specific requirements of diverse wild bee communities e.g. regarding plant species composition and provenience (Baldock 2020; Nichols et al. 2019; Bucharowa et al. 2021).

WHAT IS THE IMPACT OF WEATHER CONDITIONS ON DIFFERENT BEE GROUPS?

The observation that the abundance of honeybees, large and small solitary bees increased with lower humidity and higher temperature and radiation levels while bumblebee abundance decreased under the same weather conditions corresponds to findings that bee species differ in sensitivity to climatic conditions (Burdine & McCluney 2019b). Bumblebees in particular are more tolerant to poor weather (Nielsen et al. 2017; Tuell & Isaacs 2010) and this suggests that they are especially valuable pollinators in early spring and during bad weather periods. Unfortunately, this makes them also more vulnerable to climate change, where the increasing number of very hot days seems to affect the long-term survival of bumblebee populations around the world (Soroye et al. 2020). In cities, where the urban heat effect contributes often to an even higher number of hot days, bumblebees will suffer even faster declines (Hamblin et al. 2017) unless sufficient cooler green space is provided as a refugium.

CONCLUSIONS

Our results demonstrate the importance of diverse wild bee communities for fruit crop pollination in the urban environment. The broad variety of wild bee species differing in size, flight range, nesting behaviour, seasonality and tolerance to weather conditions can guarantee efficient pollination. Honeybees alone are unlikely to reach such a level. Bee-friendly management of green spaces in cities, including private gardens and orchards is a cheap and easy way to support wild bees as well as urban honeybees. Appropriate measures to improve resource availability and connectivity should consider the specific needs of diverse wild bee communities regarding nesting habitat, nesting materials and flowering plant species composition and provenience. This could also reduce potential conflict due to increasing density of honey bee hives in cities and make urban insect communities and fruit crop production more resilient to changing climates.

ACKNOWLEDGEMENTS

We thank the Regierung von Oberbayern for permission to collect wild bees in the city of Freising (permit numbers 55.1-8646-4-2018 and ROB-55.1-8646.NAT_02-8-23-5). The following individuals granted permission to perform pollinator observations on their orchards or those of their institution: E. Hobelsberger, M. Maino and F. Eichhorn, R. Lackermaier, P. Jungbeck, S. Kilian, I. Ghasemi, and S. Grünwald. We are especially grateful to all citizen scientists in Freising who participated in the project, to D. Rzehaczek for pollinator observations on *Rubus*, and to S. Haug (TUM|Stat), D. Ankerst and M. Mühlbauer for Statistics advice.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Meteorological data

Appendix II. Flowering plant species in the herb- and shrub-layer of the meadow orchards

REFERENCES

Abrol DP (2015) Pollination Biology, Vol.1. Springer International Publishing, Cham.

Aebi A, Vaissière BE, vanEngelsdorp D, Delaplane KS, Roubik DW, Neumann P (2012) Back to the future: Apis versus non-Apis pollination—a response to Ollerton et al. Trends in Ecology & Evolution 27:142–143.

Agrarmeteorologie Bayern (2020) Wetterstation Freising. [online] URL: https://www.am.rlp.de/Internet/AM/NotesBAM.nsf/bamweb/89952241408487f9c12573920045299b?OpenDocument&TableRow=3.1.2,3.5 (accessed 16 December 2020).

Ahrenfeldt EJ, Klatt BK, Arildsen J, Trandem N, Andersson GKS, Tscharntke T, Smith HG, Sigsgaard L (2015) Pollinator communities in strawberry crops – variation at multiple spatial scales. Bulletin of Entomological Research 105:497–506.

Alomar D, González-Estévez MA, Traveset A, Lázaro A (2018) The intertwined effects of natural vegetation, local flower community, and pollinator diversity on the production of almond trees. Agriculture, Ecosystems & Environment 264:34–43.

Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Apidae 3 - Halictus, Lasioglossum. - Fauna Helvetica 6. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Apidae 4 - Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis. - Fauna Helvetica 9. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Apidae 5 - Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa. - Fauna Helvetica 20. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Amiet F, Herrmann M, Müller A, Neumeyer R (2010) Apidae 6 - Andrena, Melitturga, Panurginus, Panurgus. - Fauna Helvetica 26. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Amiet F, Müller A, Neumeyer R (1999) Apidae 2 - Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha. - Fauna Helvetica 4. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Baldock KC (2020) Opportunities and threats for pollinator conservation in global towns and cities. Current Opinion in Insect Science 38:63–71.

Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Morse H, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Staniczenko PPA, Stone GN, Vaughan IP, Memmott J (2019) A systems approach reveals urban pollinator hotspots and conservation opportunities. Nature Ecology & Evolution:363–373.

Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Stone GN, Vaughan IP, Memmott J (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proceedings of the Royal Society B: Biological Sciences 282:20142849–20142849.

Banaszak-Cibicka W, Żmihorski M (2012) Wild bees along an urban gradient: winners and losers. Journal of Insect Conservation 16:331–343.

Bartomeus I, Park MG, Gibbs J, Danforth BN, Lakso AN, Winfree R (2013) Biodiversity ensures plant-pollinator phenological synchrony against climate change. Ecology Letters 16:1331–1338.

Bates D, Maechler M, Bolker B, Walker S (2020) Package "lme4." [online] URL: https://cran.r-project.org/web/packages/lme4/lme4.pdf (accessed 1 February 2021).

Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen (Ed) (2001) Arten- und Biotopschutzprogramm Bayern. Landkreis Freising, aktualisierter Textband. [online] URL: https://www.lfu.bayern.de/natur/absp_lkr_stadt/index.htm (accessed 2 January 2021).

Beckedorf S (2015) Der Boom hält an. Deutsches Bienen-Journal 23:6–7.

Beekman M, Ratnieks FLW (2000) Long-range foraging by the honey-bee, *Apis mellifera* L.: *Honey-bee foraging*. Functional Ecology 14:490–496.

Bennett AB, Lovell S (2019) Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. PLOS ONE 14:e0212034.

Bertrand C, Eckerter PW, Ammann L, Entling MH, Gobet E, Herzog F, Mestre L, Tinner W, Albrecht M (2019) Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. Journal of Applied Ecology 56:2431–2442.

Brittain C, Williams N, Kremen C, Klein A-M (2013) Synergistic effects of non-Apis bees and honey bees for pollination services. Proceedings of the Royal Society B: Biological Sciences 280:20122767–20122767.

Bucharowa A, Lampei C, Conrady M, May E, Matheja J, Meyer M, Ott D (2021) Plant provenance affects pollinator network: Implications for ecological restoration. Journal of Applied Ecology 00:11-11.

Buchholz S, Egerer MH (2020) Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. Biodiversity and Conservation 29:2779–2801.

Burdine JD, McCluney KE (2019a) Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. Oecologia 190:715–723.

Burdine JD, McCluney KE (2019b) Differential sensitivity of bees to urbanization-driven changes in body temperature and water content. Scientific Reports 9:1643.

Cane JH, Tepedino VJ (2017) Gauging the Effect of Honey Bee Pollen Collection on Native Bee Communities: Apis pollen depletion and native bees. Conservation Letters 10:205–210.

Carré G, Roche P, Chifflet R, Morison N, Bommarco R, Harrison-Cripps J, Krewenka K, Potts SG, Roberts SPM, Rodet G, Settele J, Steffan-Dewenter I, Szentgyörgyi H, Tscheulin T, Westphal C, Woyciechowski M, Vaissière BE (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. Agriculture, Ecosystems & Environment 133:40–47.

Chagnon M, Gingras J, DeOliveira D (1993) Complementary Aspects of Strawberry Pollination by Honey and IndigenQus Bees (Hymenoptera). Journal of Economic Entomology 86:416–420.

Cussans J, Goulson D, Sanderson R, Goffe L, Darvill B, Osborne JL (2010) Two Bee-Pollinated Plant Species Show Higher Seed Production when Grown in Gardens Compared to Arable Farmland. PLoS ONE 5:e11753.

Dinno A (2017) dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.5. [online] URL: https://cran.r-project.org/package=dunn.test (accessed 2 January 2021).

Dupont YL, Hansen DM, Valido A, Olesen JM (2004) Impact of introduced honey bees on native pollination interactions of the endemic Echium wildpretii (Boraginaceae) on Tenerife, Canary Islands. Biological Conservation 118:301–311.

Edmondson JL, Childs DZ, Dobson MC, Gaston KJ, Warren PH, Leake JR (2020) Feeding a city – Leicester as a case study of the importance of allotments for horticultural production in the UK. Science of The Total Environment 705:135930.

Eeraerts M, Smagghe G, Meeus I (2019) Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. Agriculture, Ecosystems & Environment 284:106586.

Eeraerts M, Smagghe G, Meeus I (2020) Bumble bee abundance and richness improves honey bee pollination behaviour in sweet cherry. Basic and Applied Ecology 43:27–33.

Eeraerts M, Vanderhaegen R, Smagghe G, Meeus I (2019) Pollination efficiency and foraging behaviour of honey bees and non- *Apis* bees to sweet cherry. Agricultural and Forest Entomology:afe.12363.

Egerer M, Kowarik I (2020) Confronting the Modern Gordian Knot of Urban Beekeeping. Trends in Ecology & Evolution 35:956–959.

Ellis CR, Feltham H, Park K, Hanley N, Goulson D (2017) Seasonal complementary in pollinators of soft-fruit crops. Basic and Applied Ecology 19:45–55.

Fijen TPM, Scheper JA, Boekelo B, Raemakers I, Kleijn D (2019) Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. Proceedings of the Royal Society B: Biological Sciences 286:20190387.

Fisher K, Gonthier DJ, Ennis KK, Perfecto I (2017) Floral resource availability from groundcover promotes bee abundance in coffee agroecosystems. Ecological Applications 27:1815–1826.

Földesi R, Kovács-Hostyánszki A, Kőrösi Á, Somay L, Elek Z, Markó V, Sárospataki M, Bakos R, Varga Á, Nyisztor K, Báldi A (2016) Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts: Importance of wild pollinators in apple orchards. Agricultural and Forest Entomology 18:68–75.

Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, Rollin O, Vaissière BE (2014) Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. PLoS ONE 9:e104679.

Fox J, Weisberg S, Price B (2020) Package "car." [online] URL: https://cran.r-project.org/web/packages/car/car.pdf (accessed 1 February 2021).

Ganser D, Mayr B, Albrecht M, Knop E (2018) Wildflower strips enhance pollination in adjacent strawberry crops at the small scale. Ecology and Evolution 8:11775–11784.

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhoffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipolito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlof M, Seymour CL, Schuepp C, Szentgyorgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339:1608–1611.

Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71:757–764.

Geldmann J, González-Varo JP (2018) Conserving honey bees does not help wildlife. Science 359:392–393.

Geslin B, Gauzens B, Baude M, Dajoz I, Fontaine C, Henry M, Ropars L, Rollin O, Thébault E, Vereecken NJ (2017) Massively Introduced Managed Species and Their Consequences for Plant–Pollinator Interactions. In: Advances in Ecological Research. Elsevier, pp 147–199. [online] URL: https://linkinghub.elsevier.com/retrieve/pii/S0065250416300563 (accessed 8 December 2020).

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KCR, Fowler R, Frankie G, Goulson D, Gunnarsson B, Hanley ME, Jackson JI, Langellotto G, Lowenstein D, Minor ES, Philpott SM, Potts SG, Sirohi MH, Spevak EM, Stone GN, Threlfall CG (2017) The city as a refuge for insect pollinators: Insect Pollinators. Conservation Biology 31:24–29.

Hamblin AL, Youngsteadt E, López-Uribe MM, Frank SD (2017) Physiological thermal limits predict differential responses of bees to urban heat-island effects. Biology Letters 13:20170125.

Hansen RW, Osgood EA (1983) Insects visiting flowers of wild red raspberry in spruce-fir forested areas of eastern Maine. 94:147–151.

Harrison T, Winfree R (2015) Urban drivers of plant-pollinator interactions Evans K (ed). Functional Ecology 29:879–888.

Henry M, Rodet G (2020) The apiary influence range: A new paradigm for managing the cohabitation of honey bees and wild bee communities. Acta Oecologica 105:103555.

Hernandez JL, Frankie GW, Thorp RW (2009) Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. Cities and the Environment 2:1–15.

Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society B: Biological Sciences 275:2283–2291.

Hofmann MM, Fleischmann A, Renner SS (2020) Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. Journal of Hymenoptera Research 77:105–117.

Holzschuh A, Dudenhöffer J-H, Tscharntke T (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biological Conservation 153:101–107.

Imbery F, Friedrich K, Fleckenstein R, Bissolli P, Engels A, Koppe C (2018) Wärmster April seit 1881 mit sommerlichen Temperaturen in Deutschland. [online] URL: https://www.dwd.de/DE/leistungen/besondereereignisse/temperatur/20180502_bericht_april2018.pdf?__blob=publicationFile&v=2 (accessed 1 July 2020).

Joshi NK, Otieno M, Rajotte EG, Fleischer SJ, Biddinger DJ (2016) Proximity to Woodland and Landscape Structure Drives Pollinator Visitation in Apple Orchard Ecosystem. Frontiers in Ecology and Evolution 4:1–9.

Kaluza BF, Wallace H, Heard TA, Klein A-M, Leonhardt SD (2016) Urban gardens promote bee foraging over natural habitats and plantations. Ecology and Evolution 6:1304–1316.

Kammerer MA, Biddinger DJ, Rajotte EG, Mortensen DA (2016) Local Plant Diversity Across Multiple

Habitats Supports a Diverse Wild Bee Community in Pennsylvania Apple Orchards. Environmental Entomology 45:32–38.

Kleijn D, Biesmeijer K, Dupont YL, Nielsen A, Potts SG, Settele J (2018) Bee conservation: Inclusive solutions. Science 360:389–390.

Klein A, Steffan–Dewenter I, Tscharntke T (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:955–961.

Klein A-M, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303–313.

Krahner A, Greil H (2020) Assessing the efficacy of bee promoting measures (Hymenoptera, Apiformes) along an urban-rural gradient. Journal of Cultivated Plants 72:173–184.

Kremen C, Williams NM, Bugg RL, Fay JP, Thorp RW (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California: Area requirements for pollination services to crops. Ecology Letters 7:1109–1119.

Langellotto G, Melathopoulos A, Messer I, Anderson A, McClintock N, Costner L (2018) Garden Pollinators and the Potential for Ecosystem Service Flow to Urban and Peri-Urban Agriculture. Sustainability 10:2047.

Lanner J, Kratschmer S, Petrović B, Gaulhofer F, Meimberg H, Pachinger B (2020) City dwelling wild bees: how communal gardens promote species richness. Urban Ecosystems 23:271–288.

Leong M, Kremen C, Roderick GK (2014) Pollinator Interactions with Yellow Starthistle (Centaurea solstitialis) across Urban, Agricultural, and Natural Landscapes. PLoS ONE 9:e86357.

Lin BB, Philpott SM, Jha S (2015) The future of urban agriculture and biodiversity-ecosystem services: Challenges and next steps. Basic and Applied Ecology 16:189–201.

Lindström SAM, Herbertsson L, Rundlöf M, Bommarco R, Smith HG (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proceedings of the Royal Society B: Biological Sciences 283:20161641.

Lowenstein DM, Matteson KC, Minor ES (2015) Diversity of wild bees supports pollination services in an urbanized landscape. Oecologia 179:811–821.

Lowenstein DM, Matteson KC, Xiao I, Silva AM, Minor ES (2014) Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). Biodiversity and Conservation 23:2857–2874.

Lye GC, Jennings SN, Osborne JL, Goulson D (2011) Impacts of the Use of Nonnative Commercial Bumble Bees for Pollinator Supplementation in Raspberry. Journal of Economic Entomology 104:107–114.

Mallinger RE, Gaines-Day HR, Gratton C (2017) Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLOS ONE 12:e0189268.

Mallinger RE, Gratton C (2015) Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop Tim (ed). Journal of Applied Ecology:323–330.

Martins KT, Albert CH, Lechowicz MJ, Gonzalez A (2018) Complementary crops and landscape features sustain wild bee communities. Ecological Applications 28:1093–1105.

Martins KT, Gonzalez A, Lechowicz MJ (2015) Pollination services are mediated by bee functional diversity and landscape context. Agriculture, Ecosystems & Environment 200:12–20.

Matteson KC, Ascher JS, Langellotto GA (2008) Bee Richness and Abundance in New York City Urban Gardens. Annals of the Entomological Society of America 101:140–150.

Matteson KC, Langellotto GA (2009) Bumble Bee Abundance in New York City Community Gardens: Implications for Urban Agriculture. Cities and the Environment 2:1–12.

McCune F, Normandin É, Mazerolle MJ, Fournier V (2020) Response of wild bee communities to beekeeping, urbanization, and flower availability. Urban Ecosystems 23:39–54.

Motzke I, Klein A-M, Saleh S, Wanger TC, Tscharntke T (2016) Habitat management on multiple spatial scales can enhance bee pollination and crop yield in tropical homegardens. Agriculture, Ecosystems & Environment 223:144–151.

Nayak GK, Roberts SPM, Garratt M, Breeze TD, Tscheulin T, Harrison-Cripps J, Vogiatzakis IN, Stirpe MT, Potts SG (2015) Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). Agriculture, Ecosystems & Environment 199:58–66.

Nichols RN, Goulson D, Holland JM (2019) The best wildflowers for wild bees. Journal of Insect Conservation 23:819-830.

Nielsen A, Reitan T, Rinvoll AW, Brysting AK (2017) Effects of competition and climate on a crop pollinator community. Agriculture, Ecosystems & Environment 246:253–260.

Normandin É, Vereecken NJ, Buddle CM, Fournier V (2017) Taxonomic and functional trait diversity of wild bees in different urban settings. PeerJ 5:e3051.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321–326.

Pardo A, Borges PAV (2020) Worldwide importance of insect pollination in apple orchards: A review. Agriculture, Ecosystems & Environment 293:106839.

QGIS Development Team (2016) QGIS Geographic Information System. Open Source Geospatial Foundation Project. [online] URL: https://qgis.org

Quinet M, Warzée M, Vanderplanck M, Michez D, Lognay G, Jacquemart A-L (2016) Do floral resources influence pollination rates and subsequent fruit set in pear (*Pyrus communis* L.) and apple (*Malus x domestica* Borkh) cultivars? European Journal of Agronomy 77:59–69.

R Core Team (2020) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. [online] URL: https://www.r-project.org (accessed 2 January 2021).

Renner SS, Graf MS, Hentschel Z, Krause H, Fleischmann A (2021) High honeybee abundances reduce wild bee abundances on flowers in the city of Munich. Oecologia 195: 825–831.

Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng' A, Viana BF (2008) Landscape effects on crop pollination services: are there general patterns? Ecology Letters 11:499–515.

Ripley B, Venables B, Bates D, Hornik K, Gebhardt A, Firth D (2016) MASS: Support Functions and Datasets for Venables and Ripley's MASS. R Package Version 7.3.45. [online] URL: https://cran.r-project.org/web/packages/MASS/ (accessed 2 January 2021).

Rogers SR, Tarpy DR, Burrack HJ (2014) Bee Species Diversity Enhances Productivity and Stability in a Perennial Crop. PLoS ONE 9:e97307.

Ropars L, Dajoz I, Fontaine C, Muratet A, Geslin B (2019) Wild pollinator activity negatively related to honey bee colony densities in urban context. PLOS ONE 14:e0222316.

Rossi J-P (2016) Introduction to the R package rich. [online] URL: https://cran.r-project.org/web/packages/rich/vignettes/rich_introduction.pdf (accessed 27 January 2021).

Russo L, Park MG, Blitzer EJ, Danforth BN (2017) Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards. Agriculture, Ecosystems & Environment 246:102–108.

Saunders ME, Luck GW (2018) Interaction effects between local flower richness and distance to natural woodland on pest and beneficial insects in apple orchards: Local and landscape interaction effect on insects. Agricultural and Forest Entomology 20:279–287.

Scheuchl E, Schwenninger HR, Kuhlmann M (2018) Aktualisierung der Checkliste der Bienen Deutschlands. Kommission zur Taxonomie Wildbienen des Arbeitskreises Wildbienen-Kataster. [online] URL: http://www.wildbienen-kataster.de (accessed 15 February 2019).

Schwenninger HR, Wolf-Schwenninger K (2012) Ermittlung der Wildbienenarten als Bestäuberpotenzial von Streuobstwiesen und Entwicklung eines speziellen Maßnahmenkonzepts zu ihrer dauerhaften Förderung. [online] URL: https://pudi.lubw.de/detailseite/-/publication/10019 (accessed 3 January 2021).

Soroye P, Newbold T, Kerr J (2020) Climate change contributes to widespread declines among bumble bees across continents. Science 367:685–688.

Sponsler DB, Bratman EZ (2020) Beekeeping in, of, or for the city? A socioecological perspective on urban apiculture. EcoEvoRxiv. [online] URL: https://ecoevorxiv.org/5whu8/ (accessed 5 January 2012).

Stange E, Zulian G, Rusch G, Barton D, Nowell M (2017) Ecosystem services mapping for municipal policy: ESTIMAP and zoning for urban beekeeping. One Ecosystem 2:e14014.

Stavert JR, Liñán-Cembrano G, Beggs JR, Howlett BG, Pattemore DE, Bartomeus I (2016) Hairiness: the missing link between pollinators and pollination. PeerJ 4:e2779.

Theodorou P, Radzevičiūtė R, Lentendu G, Kahnt B, Husemann M, Bleidorn C, Settele J, Schweiger O, Grosse I, Wubet T, Murray TE, Paxton RJ (2020) Urban areas as hotspots for bees and pollination but not a panacea for all insects. Nature Communications 11:576.

Thomson JD, Goodell K (2002) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers: Comparative pollination of apples and almonds. Journal of Applied Ecology 38:1032–1044.

Torné-Noguera A, Rodrigo A, Osorio S, Bosch J (2016) Collateral effects of beekeeping: impacts on pollen-nectar resources and. Basic and Applied Ecology 17:199–209.

Tuell JK, Isaacs R (2010) Weather During Bloom Affects Pollination and Yield of Highbush Blueberry. Journal of Economic Entomology 103:557–562.

Verboven HAF, Aertsen W, Brys R, Hermy M (2014) Pollination and seed set of an obligatory outcrossing plant in an urban–peri-urban gradient. Perspectives in Plant Ecology, Evolution and Systematics 16:121–131.

Visscher PK, Seeley TD (1982) Foraging Strategy of Honeybee Colonies in a Temperate Deciduous Forest. Ecology 63:1790.

Waddington KD, Visscher RK (1994) Comparisons of forager distributions from matched honey bee colonies in suburban environments. Behavioral Ecology and Sociobiology 35:423–429.

Weissmann J, Schaefer H (2020) Feld-Bestimmungshilfe für die Wildbienen Bayerns. Nachrichtenblatt der Bayerischen Entomologen 69:1–64.

Westrich P (2018) Die Wildbienen Deutschlands. Eugen Ulmer KG, Stuttgart.

Wickham H, Chang W, Henry L, Pedersen T, Takahashi K, Wilke C, Woo K, Yutani H, Dunnington D (2019) ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R Package Version 3.2.1. [online] URL: https://cran.r-project.org/web/packages/ggplot2/ (accessed 2 January 2021).

Willmer PG, Bataw AAM, Hughes JP (1994) The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecological Entomology 19:271–284.

Wilson CJ, Jamieson MA (2019) The effects of urbanization on bee communities depends on floral resource availability and bee functional traits. PLOS ONE 14:e0225852.

Zhao C, Sander HA, Hendrix SD (2019) Wild bees and urban agriculture: assessing pollinator supply and demand across urban landscapes. Urban Ecosystems 22:455–470.

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669–676.