ARTICLE

ECOLOGICAL
APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Vegetation complexity and nesting resource availability predict bee diversity and functional traits in community gardens

Julia Felderhoff[1] | Anika K. Gathof[2,3] | Sascha Buchholz[2,3,4] | Monika Egerer[2,5]

[1]Freie Universität Berlin, Berlin, Germany

[2]Department of Ecology, Technische Universität Berlin, Berlin, Germany

[3]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

[4]Institute of Landscape Ecology, University of Münster, Münster, Germany

[5]Urban Productive Ecosystems, Department of Life Science Systems, School of Life Sciences, Technical University of Munich, Freising, Germany

Correspondence
Monika Egerer
Email: monika.egerer@tum.de

Abstract

Urban gardens can support diverse bee communities through resource provision in resource poor environments. Yet the effects of local habitat and landscape factors on wild bee communities in cities is still insufficiently understood, nor is how this information could be applied to urban wildlife conservation. Here we investigate how taxonomic and functional diversity of wild bees and their traits in urban community gardens are related to garden factors and surrounding landscape factors (e.g., plant diversity, amount of bare ground, amount of nesting resources, amount of landscape imperviousness). Using active and passive methods in 18 community gardens in Berlin, Germany, we documented 26 genera and 102 species of bees. We found that higher plant species richness and plant diversity as well as higher amounts of deadwood in gardens leads to higher numbers of wild bee species and bee (functional) diversity. Furthermore, higher landscape imperviousness surrounding gardens correlates with more cavity nesting bees, whereas a higher amount of bare ground correlates with more ground-nesting bees. Pollen specialization was positively associated with plant diversity, but no factors strongly predicted the proportion of endangered bees. Our results suggest that, aside from foraging resources, nesting resources should be implemented in management for more pollinator-friendly gardens. If designed and managed using such evidence-based strategies, urban gardens can create valuable foraging and nesting habitats for taxonomically and functionally diverse bee communities in cities.

KEYWORDS
conservation, habitat management; Berlin, pollinators, urban ecosystems, urbanization

INTRODUCTION

Biodiversity and ecosystem function are essential for maintaining ecosystem services (Mace et al., 2012). In terrestrial ecosystems, the dispersal of pollen by animal vectors plays a key role in plant pollination (Ollerton et al., 2011; Pellmyr, 2002). Wild bees (Hymenoptera) in particular contribute an essential share to the pollination of wild and cultivated plants. Fruit and seed production of many agricultural crops requires or benefits from

cross-pollination by bees, with about 75% of the world's major crops having higher yields with animal pollination than without (Klein et al., 2007). This species interaction generates hundreds of billions of dollars in annual pollination services (Gallai et al., 2009; Lautenbach et al., 2012; Porto et al., 2020).

Declines in pollinator species richness and abundance as a part of global biodiversity loss from, for example, land-use change can have major negative ecological impacts (Brondizio et al., 2019). In particular, urban environments can be understood as a mosaic of seminatural land use, with the proportion of green space decreasing as the proportion of impervious land (i.e., paved surface, buildings) increases, and high amounts of compacted soil (Swan et al., 2021); these environmental changes through human land use can affect the plant and animal biodiversity of these landscapes and their associated functions (Piano et al., 2017, 2020). Although environmental change in urban landscapes often has a negative effect on insect distribution and abundance (Fenoglio et al., 2020), studies show high numbers of wild bee species can occur in cities (Baldock et al., 2015, 2019; Rahimi et al., 2022). For example, 262 bee species were recorded over a 5-year period in green spaces in Berlin (Saure, 1996), 113 bee species were recorded in community gardens in Vienna (Lanner et al., 2020), 59 bee species were recorded in 18 community gardens in the California Central Coast, and 110 species were recorded in 21 domestic gardens in New York (Fetridge et al., 2008). High species diversity of bees in urban areas compared to rural areas may be because of declining quality of habitat in surrounding rural landscapes due to agricultural intensification that leads to species loss, whereas urban areas still maintain habitat for many species (Hall et al., 2017; Lin et al., 2015; Wenzel et al., 2020). In addition, the warmer microclimate of cities could mean that urban habitats may be among the first places where southern species that are expanding their range will be found (Dew et al., 2019).

The functional diversity of wild bee populations in cities is increasingly important to understand because a study of taxonomic diversity alone is insufficient to determine which ecosystem functions are lost with species loss (Buchholz & Egerer, 2020). It is the characteristics, or "traits," not the individual taxonomic identity, that form the functional basis of ecosystems and ensure the provision of ecosystem services, such as pollination (Cadotte et al., 2015). Functional diversity combines morphological, ecological, and life-cycle characteristics to describe differences and similarities among species (Tilman, 2001). Different wild bee species have different life history strategies that consist of different constellations of functional traits. Pollen specialization, nesting mode, social behavior,

voltinism (i.e., generations per year), and phenology are among such bee functional traits (Buchholz & Egerer, 2020).

For urban habitats to support wild bees, the habitat must meet the criteria for reproduction, including food resources and suitable nesting habitat (Buchholz et al., 2020; Normandin et al., 2017). Bees are highly dependent on floral resources that provide food, nesting sites, and shelter (Smith et al., 2006). Furthermore, nesting resources like deadwood, open soil and sand areas, dry stone walls, and cavities are also necessary for many solitary species that build nests in these structures, with many species additionally requiring building materials for the brood cells (Westrich, 1996). At the local habitat scale, parks and gardens can provide a continuous supply of flowering vegetation (Hülsmann et al., 2015), so local factors such as plant species richness and flower density or cover can promote bee taxonomic diversity and functional trait diversity (Buchholz et al., 2020; Lanner et al., 2020). At the landscape scale, moderately urbanized areas, such as those at the peri-urban fringe (e.g., 20%–50% landscape imperviousness), show a positive impact on pollinator diversity, whereas if the proportion of compacted area increases in the inner-city center (>50% landscape imperviousness), pollinator diversity decreases (Wenzel et al., 2020), potentially due to limited nesting resources for some aboveground-nesting bees (Everaars et al., 2011; Fortel et al., 2016).

Urban agroecosystems are habitats that contribute to the quality of the city landscape for biodiversity and ecosystem services. For example, community gardens are urban agroecosystems that are collectively organized and managed by residents at the individual garden plot level as well as entire garden level (Holland, 2004). The focus is not only on growing one's own fruits and vegetables but also on the joint design of inner-city open spaces and the promotion of civic engagement (Kingsley et al., 2020). Community gardens improve the physical and mental health of users (Wolch et al., 2014), provide educational opportunities (Graham et al., 2005), and support community nutrition through food production (Alaimo et al., 2008). Furthermore, they can be highly productive and contribute to the approximately 15%–20% of the global diet derived from urban agriculture (Armar-Klemesu, 2000; Lin et al., 2015).

To better understand how urban landscapes—and specifically agroecosystems like community gardens within them—can support diverse wild bee communities, we must determine which habitat factors, including vegetation resources (e.g., floral diversity) and nesting resources (e.g., ground cover composition, woody structures, stone structures), can have a positive impact on wild bees. Here we examined the diversity of wild bee

species in community gardens in Berlin, Germany, to analyze the influence of local garden habitat factors on wild bees and to determine which factors may be beneficial for specific wild bee traits. We asked: (Q1) What local garden factors, including vegetation resources (plant species number, diversity, and floral availability) and nesting resources (ground cover, deadwood, drywall), affect wild bee abundance, species number, and diversity (taxonomic and functional)? (Q2) What urban landscape factors (landscape imperviousness) surrounding gardens affect wild bee abundance, species number, and diversity (taxonomically and functionally)? And (Q3) How do bee traits associate with garden factors and landscape factors? We proposed the following hypotheses: (H1) Higher plant species numbers and diversity, as well as increased vegetation and nesting resource availability, will positively affect wild bee abundance, species numbers, and diversity. (H2) Higher amounts of landscape imperviousness will decrease wild bee species diversity and ground-nesting species. (H3) Certain wild bee functional traits will strongly associate with garden factors and more impervious landscapes, where, for example, aboveground-nesting species with generalist pollen feeding will positively associate with lower vegetation diversity and higher landscape imperviousness.

MATERIALS AND METHODS

Study sites

We studied 18 community gardens throughout the city of Berlin ($52°31'27''$ N, $13°24'37''$ E, 43 m above sea level), Germany (Figure 1; Appendix S1: Table S1). Berlin spans 891 km^2 and has a population of 3.66 million (Statistisches Bundesamt, 2021). The climate is temperate, humid, and characterized by warm summers (Kottek et al., 2006). In 2020, when this research took place, Berlin was the warmest and driest German state, with an average annual temperature of 11°C and a mean precipitation of 492 L/m^2 (Senatsverwaltung für Stadtentwicklung und Umwelt, 2020a). Berlin has 158 km^2 of forest land (18.1% total land area), 107 km^2 of public green space (12% total land area) (Senatsverwaltung für Stadtentwicklung und Umwelt, 2016), and over 200 community gardens (Senatsverwaltung für Stadtentwicklung und Umwelt, 2020b). The gardens in this study are approximately >2 km apart and range in size (mean 3345 m^2; range = 265–11,961 m^2) (Appendix S1: Table S1).

The landscape surrounding the gardens ranged from highly sealed impervious areas (e.g., concrete slab next to an old brewery) to less impervious areas (e.g., grassland on Tempelhofer Feld). The amount of landscape impervious surface area surrounding the gardens (i.e., amount of sealed surface) was determined using land-cover data (2×2 m resolution) from the Berlin Environmental Atlas (Senatsverwaltung für Stadtentwicklung und Umwelt, 2016) and the Zonal statistical tool in QGIS software version 2.18.0 (QGIS Development Team, 2018) within radii of 500, 1000, and 2000 m. Of the 18 gardens surveyed, data were recorded in 14 gardens monthly at three survey time points during June to August 2020. In four gardens, data were collected at two study time points (June and August) due to logistical constraints. At the center of the garden, we set an area of 20×20 m (400 m^2) as our study plot (henceforth referred to as the plot); in three gardens this encompassed the entire garden. Where the shape of the garden did not allow for this layout (one garden), we established a plot with dimensions of 10×40 m. Data collection was conducted under warm (>15°C), dry weather conditions between 8:00 A.M. and 6:00 P.M.

Bees

We used active and passive sampling methods to survey bees in the gardens. For observations, all bees within the 20×20-m plot were recorded for a total observation time of 60 min. The plots were divided into four parallel transects of 5×20 m each, along which two observers walked the transects slowly, pausing regularly to survey flowers and flowering areas for bees. All bees on flowers and in flight were counted and identified as accurately as possible at the order, family, or genus level. Individuals that could not be identified to the species level in the field were netted, transferred to plastic containers previously covered with formalin-soaked absorbent cotton, and taken to the laboratory for species identification. The observation time was paused during handling of individuals to maintain the 60-min observation, and we avoided double counting individuals. A total of 50 plot observations were made with 3000 min of observation.

Ultraviolet (UV)-color pan traps were placed in the gardens for 72 h three times, directly after field sampling (maximum 1 week later in good weather conditions) for the passive collection of bees. Pan traps consisted of a set of three plastic bowls with a 15-cm diameter, and the UV colors were painted light yellow, blue, and white (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany), as used in numerous studies (Hall, 2016), and cover a wide range of wavelengths. Pan traps were attached to wooden rods approximately 40 cm above the ground and filled with 300 ml of a 4% formaldehyde solution and a drop of detergent to reduce surface tension. Trapping was conducted in 14 of 18 gardens because it
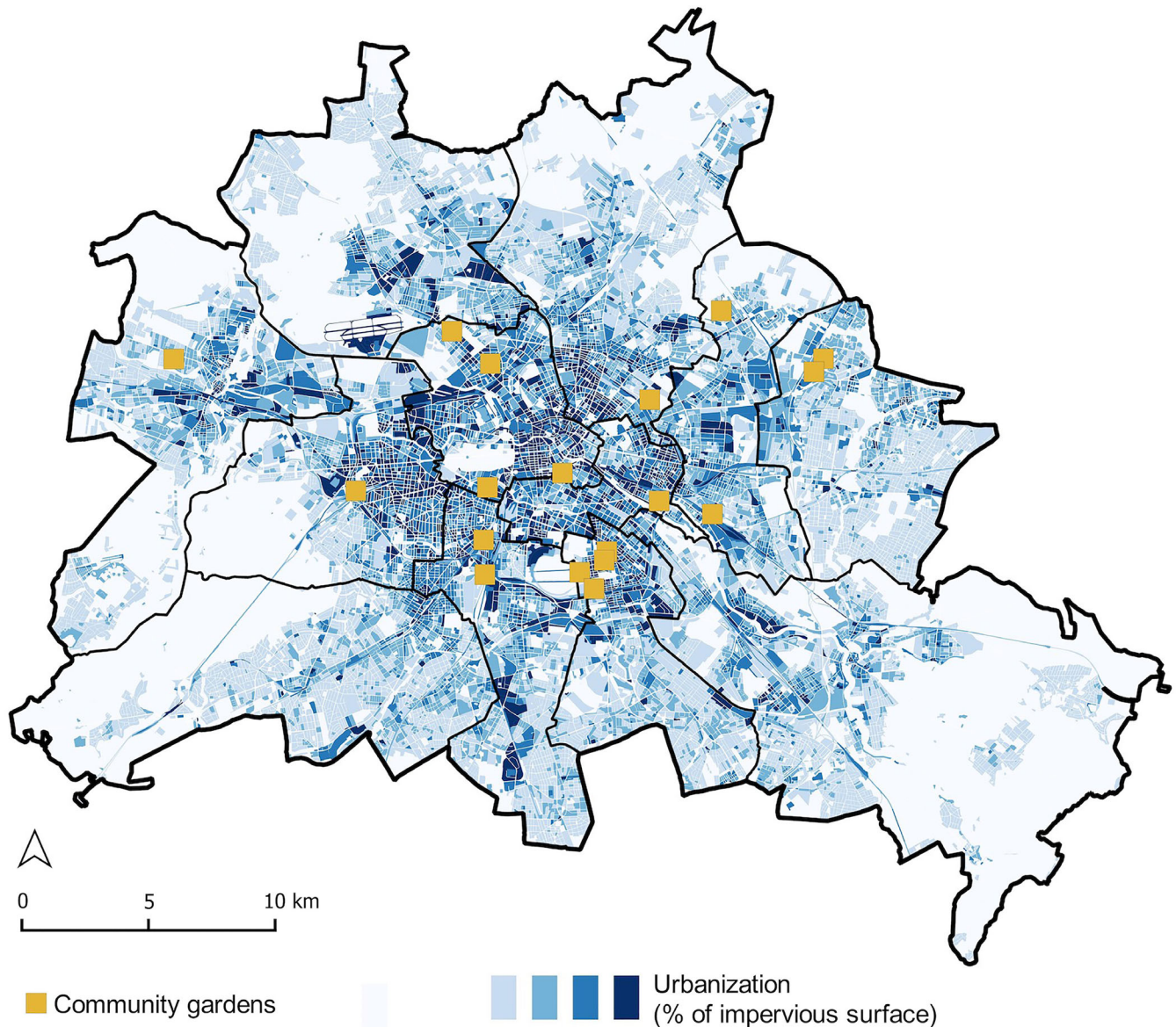
FIGURE 1 Investigated community gardens, Berlin, Germany (yellow squares), surrounded by different levels of landscape imperviousness (percentage of impervious surface), where dark blue represents higher amounts of imperviousness and white represents low to no amounts of imperviousness.

was not desired by gardeners in four gardens; thus, we used garden as a random factor in our analysis (see subsequent discussion). Samples were collected, transferred to plastic containers, and brought to the laboratory, and bees (Apidae) were sorted out for identification. Bees from both the active and passive sample collections were sorted by genus and then further identified to species level by F. Koch from the Museum für Naturkunde Berlin and critical species confirmed by C. Schmid-Egger.

The functional traits of bee species were identified according to Westrich (2018) and included social behavior, nesting mode, food, pollen transport, and voltinism (Table 1). Social behavior was categorized into social,

solitary, and parasitic. Nesting mode was categorized as subterranean (endogeic) and aboveground (hypergeic) or both and further categorized into ability to build and dig nests by themselves (self-digging), respectively. Pollen specialization refers to the pollen collected for raising offspring and is either polylectic (generalist from a variety of different plant species and families) or oligolectic (specialized in one to a few plant species or families). Voltinism refers to the number of generations per year and was classified as either univoltine (one generation) or bivoltine (two generations).

In addition, we assessed whether the species were of endangered status or of conservation concern in Berlin.

TABLE 1 Traits of wild bees, number of bee species, and number of individuals showing this behavior observed in study.

Trait	Trait classification	No. species	No. individuals	No. gardens	Percentage of individuals (%)	Percentage of species (%)
Social behavior	Social	17	794	18	49.97	16.67
	Solitary	69	666	18	41.91	67.65
	Parasitic	16	44	13	2.77	15.69
Nesting behavior	Endogeic	48	972	18	61.17	47.06
	Hypergeic	27	313	18	19.70	26.47
	Endo- or hypergeic	11	175	18	11.01	10.78
	Digging	49	869	18	54.69	48.04
	existing cavities	52	627	18	39.46	50.98
	Both	1	8	5	0.50	0.98
Voltinism	Univoltine	80	1324	18	83.32	78.43
	Uni- or bivoltine	15	130	18	8.18	14.71
	Bivoltine	7	50	11	3.15	6.86
Pollen specialization	Polylectic	69	1260	18	79.30	67.65
	Oligolectic	17	200	15	12.59	16.67
Pollen transport	Leg	54	1121	18	70.55	52.94
	Ventral hairs	18	135	13	8.50	17.65
	Crop	13	201	18	12.65	12.75
	Leg, crop	1	3	2	0.19	0.98
Hibernation	Larva	39	464	18	29.20	38.24
	Imago	22	93	14	5.85	21.57
	Female (mated)	35	921	18	57.96	34.31
	Unknown	6	26	10	1.64	5.88

Note: No. gardens where wild bees with this behavior were found and proportion of individuals and species showing this behavior.

Species were individually classified, and the proportions of endangered bee species under the categories 1, 2, 3, V according to the Red List of Berlin (Saure, 2005) were summed together for each garden.

Garden factors

To identify vegetation resources for bees, we simultaneously conducted monthly vegetation surveys in the 20 × 20-m plots to account for variation in vegetation across the sampling season (Seitz et al., 2022). In eight 1 × 1-m quadrats randomly placed in the 20 × 20-m plots along four parallel 5 × 20-m transects (two random plots per transect), all herbaceous plants (except grasses) were identified to species level using Jäger (Jäger et al., 2016) and the Pl@ntNet Handheld Application (https://plantnet.Org/en/). We counted the total number of all flowers (counting also all flowers in an inflorescence or floral unit, for example, counting all flowers in each capitula of Asteraceae, umbel of Apiaceae) within

each quadrat and estimated the percentage of ground cover of bare soil, grass, herbaceous plants, rocks, leaf litter, straw, and mulch wood chips.

To identify nesting resources for bees, we visually estimated nesting structure availability within the 20 × 20-m plot. Here we estimated amount of total lying and standing deadwood structures in square meters, measured total length of existing drystone walls in meters, and visually estimated the proportion of bare ground cover. Bare ground cover was determined by summing the amount of visually estimated sand and soil cover into a bare ground category (above).

Data analysis

We built generalized linear mixed models (GLMMs) to test how garden factors influenced the following response variables related to wild bee biodiversity: wild bee abundance, wild bee species number (richness), wild bee Shannon's diversity (H′), proportion of endangered wild

bees, Pielou's species equality, and functional dispersion (FDis) of wild bees. FDis was calculated using the FD package in R (Laliberté et al., 2014) and represents the mean of the distances in a multidimensional property space of each species to the centroid of all species (Laliberté & Legendre, 2010), where species abundance is captured by shifting the position of the centroid toward the abundant species, scoring individual species based on their abundance. FDis is less sensitive to outliers and is independent of the number of species, and it describes functional diversity by the breadth of functional roles performed by species under the hypothesis that a higher community FDis has a higher resilience (Schmitt et al., 2020). The managed honeybee *Apis mellifera* was excluded from the analysis in the response because we were interested in the effect of garden environmental factors on wild bees; yet, because honeybees may impact wild bees in natural and managed systems (Mallinger et al., 2017), we tested the direct effect of honeybees on wild bees in preliminary analyses. In addition, we tested the relationship between wild bee abundance and wild bee species richness since species richness may be sensitive to the number of individuals collected (Gotelli & Colwell, 2001).

A GLMM for each response variable consisted of five uncorrelated predictor variables related to the garden factors of vegetation, ground cover, nesting resource availability, floral availability, and landscape imperviousness. Garden was a random effect in all models, also to account for missing data from some gardens. Round was not included as a random effect because we do not focus on temporal dynamics here and due to limited number of levels within the variable (Bolker et al., 2009). To test which of the two nesting resource variables (drystone wall or deadwood), vegetation variables (number of species of plants or diversity of plants), and ground-cover variables (open soil or mulch) were used in the full models, they were tested individually against the respective dependent variable, with the garden as a random effect in a minimal model. The variable that had the lower value of the Akaike information criterion (AIC; Akaike, 1973) in each case was used. This resulted in the following variables in the model: flower cover as the floral-availability variable, deadwood or drystone structures as the nesting-habitat variable, bare ground as the ground-cover variable, and the percentage impervious surface within a radius of 1000 m of the center of the gardens as the landscape variable. Preliminary analyses included garden size as a predictor variable, but, due to worse model fit, it was removed from the final analysis to reduce the number of variables for the data set and thereby to prevent model overfitting (Bolker et al., 2009).

For count data (bee abundance, species number), the Poisson model (with log link) was used with Laplace approximation and tested for overdispersion using the *testDispersion* function from the DHARMa package in R (Hartig, 2021). We used Gaussian distributions for Shannon diversity and FDis and a binomial distribution for the proportion of endangered species. Models were selected based on the AIC, where the model with the lowest AIC was preferred. Then we removed covariates stepwise based on AIC until removing additional covariates no longer improved the AIC. To test for multicollinearities between the independent variables of the models, variance inflation factors (VIFs) were calculated using the *vif* function of the car package in R (Weisberg & Sanford, 2019). All VIFs were between 1 and 1.8. For the Poisson and Gaussian models, the residuals were tested for normal distribution using histograms and a Shapiro–Wilk test. The AIC values of the final models were compared with the AIC values of the null model. The null model consisted of the corresponding dependent variables, which were tested against the random effect (garden site). We used the *glmer* function in the lme4 package in R for GLMMs (Walker et al., 2015).

To evaluate covariation between garden factors and wild bee traits, we used a combination of RLQ and fourth-corner analysis. The RLQ method is an extension of correspondence analysis and provides an overview of multivariate associations by searching for combinations of traits (Table Q) and environmental factors (Table R) with a maximum covariance weighted by species abundance (Table L). RLQ is used to identify principal structures, where environmental gradients and trait effects are calculated. A permutation test tested the significant association between the R and Q matrix (Dray & Dufour, 2007). The fourth-corner analysis tested bivariate associations between each environmental factor and trait variable using the Pearson product–moment correlation coefficient (r), which indicates both the strength and direction (positive or negative) of the relationships between garden factors and bee traits (Legendre et al., 1997). Here we excluded rare species with less than three observations (Appendix S1: Table S3). We used a Permutation Model 6 with 9999 permutations to test whether species communities depend on garden factors (Permutation Model 2) or whether species traits depend on garden factors (Permutation Model 4) (Legendre et al., 1997). Both models were combined to obtain a corrected level of Type I error when applying an a priori significance level of 5% (Dray & Legendre, 2008).

RESULTS

Garden factors

A total of 413 plant species from 285 genera and 81 plant families were recorded in the gardens, ranging

from 42 to 128 recorded total plant species (mean = 89 species) per garden. The most abundant plant families were Asteraceae (22%), Lamiaceae (7%), Brassicaceae (7%), and Fabaceae (6%). Overall, the gardens had high plant taxonomic diversity (mean = 4.07, range = 3.39–4.42) and Pielou's species equality (mean = 0.91, range = 0.83–0.94). The gardens vary in their nesting resource availability, including the percentage of bare ground (mean = 21%, range = 4%–51%), percentage of mulch cover (mean = 4.5%, range = 0%–28%), availability of deadwood structures (mean = 6 m^2, range = 0–25.5 m^2), and availability of drystone walls (mean = 8 m, range = 0–65 m). The percentage of landscape imperviousness included the following parameters: within a 500-m buffer (mean = 60%, range = 31%–86%); within a 1000-m buffer (mean = 57%, range = 33%–73%); and within a 2000-m buffer (mean = 56%, range = 35%–73%).

Bee taxonomic diversity and functional traits

We sampled 1589 bee individuals from 26 genera and 102 species, excluding honeybees (*Apis mellifera* [L.] 210 individuals). On average, 29 wild bee species were found per garden over the study, with a maximum of 49 wild bee species and a minimum of 14 species. The most common wild bee species included *Lasioglossum morio* (N = 238 individuals; 15% of total), *Lasioglossum pauxillum* (N = 104; 6.5%), *Bombus terrestris* (N = 77; 5%), *Lasioglossum laticeps* (N = 68; 4%), and *Lasioglossum calceatum* (N = 55; 3%) (Appendix S1: Table S2). We documented 24 wild bee species that are on Berlin's Red List, including *Anthophora aestivalis* (Category 1) and the corresponding cuckoo (cleptoparasitic) bee *Melecta luctuosa* (Category 2). In addition, we documented a species previously undocumented in Berlin, *Lasioglossum limbellum*, that is usually found in southern Europe in sandy coastal habitats (Egerer, 2022a). The majority of species exhibited solitary behavior and endogeic nesting behavior, have one generation a year, and are polylectic pollen gatherers.

Predictors of taxonomic and functional diversity, and bee traits

We found associations between garden factors and bee diversity. Deadwood positively associated with the number of wild bee species ($p < 0.001$) and abundance ($p < 0.01$) (Table 2, Figure 2). Similarly, the number of plant species was positively associated with the number of wild bee species ($p < 0.05$), abundance ($p < 0.001$), and taxonomic diversity (Shannon diversity) ($p < 0.01$) (Table 2, Figure 2). Bee functional diversity (FDis) increased with higher vegetation taxonomic diversity (Shannon diversity) ($p < 0.05$) (Table 2, Figure 2). No model outperformed the null model for the proportion of endangered wild bee species. Of note, the abundance of wild bees sampled was related to wild bee species richness, whereas honeybee abundance did not significantly predict wild bee response variables (Appendix S1: Tables S4 and S5).

The RLQ and fourth-corner analysis found that the first two axes explained 93.5% (74.1% Axis 1 and 19.4% Axis 2) of the variation and associate with the species matrix (Table 3). Axis 1 associated with nesting behavior, the Axis 2 with social behavior and pollen specialization (Figures 3 and 4). Bare ground cover positively associated with Axis 1, whereas landscape imperviousness (1000 m) was negatively associated. Here, ground-nesting and self-building species positively associated with higher amounts of bare ground, and ground-nesting and cavity-nesting species positively associated with higher amounts of landscape imperviousness. Bee species associated with Axis 1 included *Halictus subauratus*, *Bombus sylvarum*, *Ceratina cyanea*, *Andrena subopaca*, *Hylaeus brevicornis*, and *Hylaeus communis*. Where *Ceratina cyanea*, *Hylaeus brevicornis*, and *Hylaeus communis* are particularly associated with high landscape imperviousness.

Bare ground cover positively associated with Axis 2, whereas plant species number and diversity negatively associated with Axis 2. Here, social and polylectic species positively associated with higher amounts of bare ground, whereas solitary, oligolectic, and bivoltine species positively associated with higher numbers and diversity of plant species. Bee species that particularly associated with plant diversity included *Anthidium oblongatum*, *Anthophora furcata*, *Megachile ericetorum*, and *Rhophitoides canus*.

In the combined fourth-corner and RLQ method, garden factors influenced trait occurrence (Model 2: $p < 0.05$); however, traits did not determine species distribution in gardens (Model 4: $p > 0.05$). We found a significant negative relationship between the proportion of bare ground on solitary social behavior ($p = 0.015$) and a positive relationship with social behavior ($p = 0.015$). The proportion of landscape imperviousness positively associated with aboveground nesting ($p = 0.013$) and pollen transport in the crop ($p = 0.04$). The fourth-corner analysis found 11 significant correlations between garden factors and bee traits (Figure 3). Axis R1 negatively correlated with aboveground nesting ($p = 0.001$) and nesting in available cavities (building: no) ($p = 0.01$). Axis R2 positively correlated with social behavior ($p = 0.014$) and polylectic pollen collection ($p = 0.01$). On the other hand,

TABLE 2　Results of generalized linear mixed models for (a) number of species, (b) abundance, (c) taxonomic diversity (Shannon diversity), and (d) functional diversity (functional dispersion) of wild bees.

Response variable	Predictor variable	Estimate	SE	z-value	t-value	p-value	AIC	χ²
(a) No. species	Intercept	2.75	0.10	26.93		<0.001	241.6	
	Deadwood structures	0.12	0.05	2.34		<0.05		5.49
	Mulch	4.03	2.31	1.75		0.08		3.05
	Flower coverage	−0.01	0.01	−1.15		0.25		1.33
	No. plant species	0.15	0.05	2.83		<0.01		8.01
(b) Abundance	Intercept	3.26	0.14	23.77		<0.001	364.3	
	Deadwood structures	0.20	0.11	1.82		0.07		3.31
	Mulch	2.80	2.95	0.95		0.34		0.90
	Flower coverage	<0.001	<0.005	0.12		0.90		0.02
	No. plant species	0.24	0.06	4.15		<0.001		17.25
(c) Taxonomic diversity	Intercept	1.81	0.24		7.59	<0.001	41.90	
	Drystone wall	<−0.003	0.02		−0.13	0.90		0.02
	Mulch	3.31	2.47		1.34	0.19		1.79
	No. plant species	0.01	<0.005		2.65	<0.05		7.04
(d) Functional diversity	Intercept	−0.01	0.11		−0.08	0.94	−130.90	
	Drystone wall	<0.002	<0.001		1.44	0.17		2.09
	Plant diversity	0.06	0.03		2.37	<0.05		5.62
	Landscape imperviousness	0.11	0.07		1.67	0.12		2.78

Note: Models represent the best-fit model as determined through stepwise removal analysis of predictor variables and evaluated for best fit using Akaike information criterion (AIC). Significance taken at alpha = 0.05. SE, standard error.

Axis R1 positively correlated with endogeic nesting behavior ($p = 0.006$) and self-building nesting behavior (building: yes) ($p = 0.015$), whereas Axis R2 negatively correlated with oligolectic pollen collection ($p = 0.02$). Finally, Axis Q1 negatively correlated with bare ground ($p = 0.04$) and negatively correlated with landscape imperviousness at all spatial scales investigated: 500 m ($p = 0.01$), 1000 m ($p = 0.02$), and 2000 m ($p = 0.03$).

DISCUSSION

Local garden management factors as well as landscape-scale urbanization factors influence the taxonomic diversity and functional traits of wild bees in community gardens. Specifically, an increase in the species number and diversity of plants promotes increases in the abundance, species number, and diversity of wild bees. Increasing urbanization measured as the proportion of landscape imperviousness promotes aboveground-nesting species, bare ground favors belowground-nesting and self-burrowing species, higher plant diversity associates with pollen-specialized species, and an increase in the amount of deadwood overall promotes a higher number of wild bee species. Our results suggest that, given

land-use intensification causing bee declines (Sánchez-Bayo & Wyckhuys, 2019), urban community gardens may be "biodiversity hotspots" for wild bees (Baldock et al., 2019; Lanner et al., 2020; Rahimi et al., 2022), largely through the provision and management of diverse vegetation and nesting resources that drive species and trait diversity.

Wild bee species and their traits in urban gardens

Urban gardens can harbor a diversity of wild bee species, as has been documented in other city contexts (Baldock et al., 2015; Hall et al., 2017). In Berlin, the >100 wild bee species we observed represent approximately 40% of the city's species (Saure, 1996). Furthermore, urban gardens can support particular wild bee species with different functional traits—including a diversity of pollen collection (and transport) behaviors, nesting behavior, and sociality. These biological characteristics of bee species are highly relevant to efficient pollination services in these gardens, which host a high diversity of food plants and wild plants (Seitz et al., 2022).
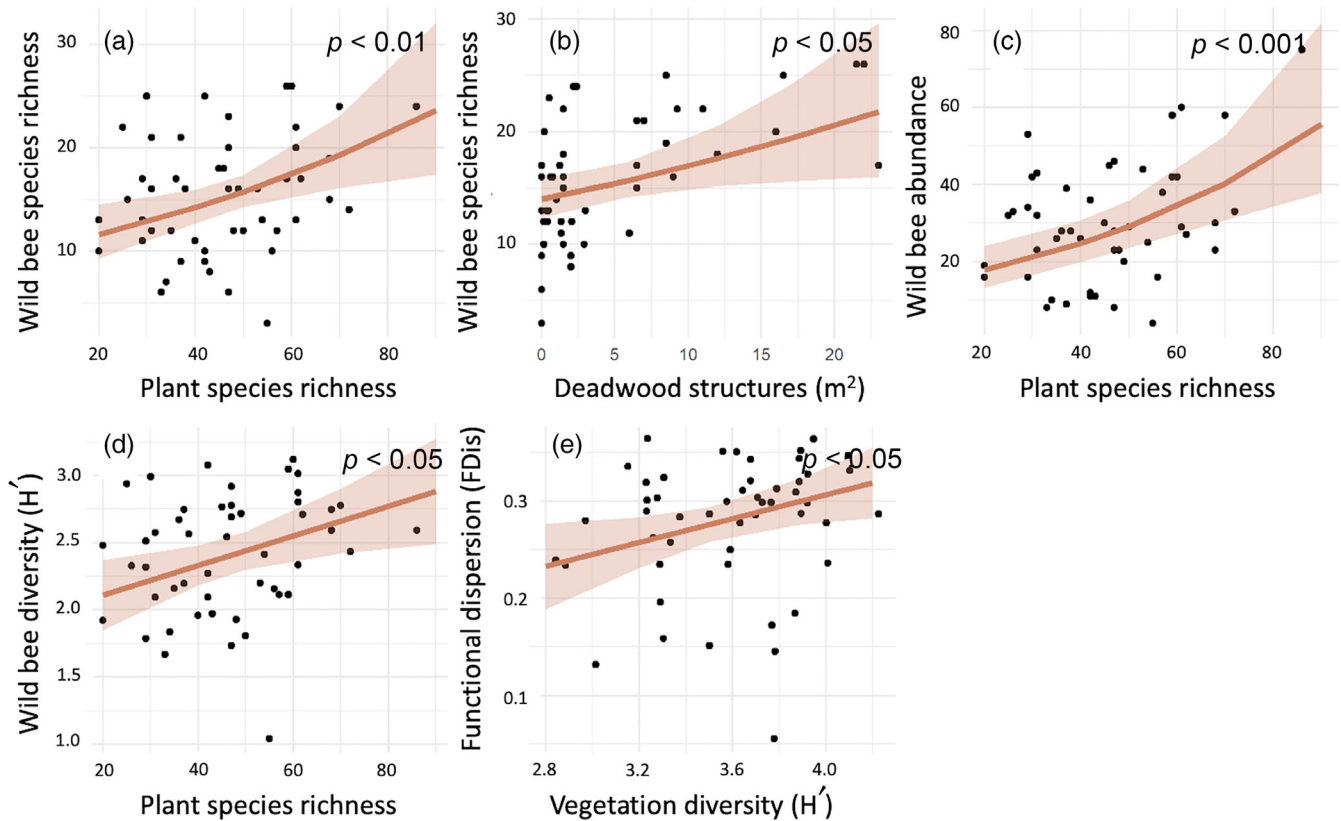
FIGURE 2 (a, b) Number of species, (c) abundance, (d) taxonomic diversity (Shannon index), and (e) functional diversity (functional dispersion) of wild bees in relation to (a,c,d) plant species richness, (d) deadwood structures (total m^2), and (e) vegetation diversity (Shannon diversity). Each point represents one sampling event, red line represents best-fit generalized linear mixed model, and shading represents a $\pm$95% confidence interval. Significance value provided as p-value.

TABLE 3 Summary of RLQ statistics from combined RLQ and fourth-corner analysis.

RLQ statistics	Axis 1	Axis 2
Eigenvalue	0.04	0.01
Inertia (%)	74.11	19.40
Covariance	0.21	0.11
Correlation with L matrix	0.23	0.21

The wild bee species present in our system lend insight into how gardens may function as small hotspots for both common and rare bee species. Species of *Lasioglossum*, *Bombus*, and *Hylaeus* were dominant in our sample. Within *Lasioglossum*, the common *L. morio* is a social, polylectic, endogeic bee species, and its frequency may be explained by its generalist pollen-collecting behavior and nesting behavior. The species nests in a variety of substrates, including mortar joints of walls, in weathered debris, or on flat or steeply sloping surfaces (Scheuchl & Willner, 2015). Its habitat generality and its eusociality could also be advantageous traits in

urban areas (Buchholz & Egerer, 2020). Furthermore, *Hylaeus* also mainly shows generalist pollen-collecting behavior and aboveground cavity-nesting behavior, which could be positive traits that facilitate species adaptation to urban habitats. Indeed, species of this genus (e.g., *H. leptocephalus* and *H. punctatus*) have associated with increasing amounts of impervious surface in a cityscape (Bennett & Lovell, 2019).

Yet we also discovered rarer or surprising species in our sample. This included *Lasioglossum limbellum*, documented here for the first time in Berlin in a garden created on concrete slabs of raised beds with annual and perennial plants. As a cavity-nesting species that nests in soft rock cliffs (Scheuchl & Willner, 2015)—a natural habitat usually functionally nonexistent in urban areas—the traits of this species make this discovery relevant to the role of urban gardens as hotspots for common, rare, and specialized species (Egerer, 2022a). Furthermore, the documentation of *Anthophora furcata* is noteworthy because it is the only digger bee that is oligolectic on Lamiaceae with a strong preference for *Stachys* species—planted in gardens for diverse medicinal qualities—which it exploits using a special
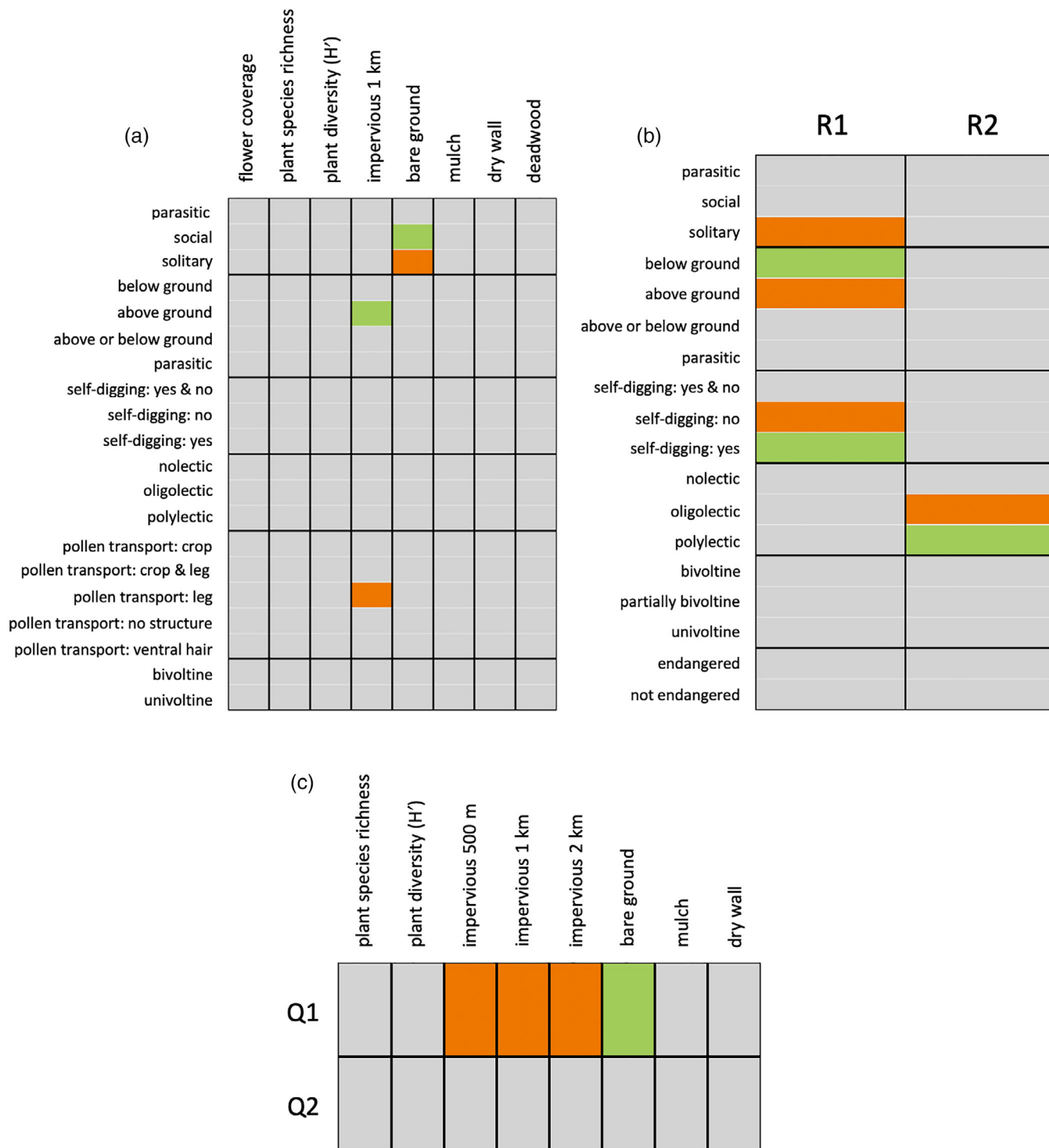
FIGURE 3   (a) Biplot fourth-corner analysis of wild bee traits in relation to environmental factors. (b) Biplot of fourth-corner test between wild bee traits and first two RLQ axes for environmental factors (AxcR1 and AxcR2). (c) Biplot of fourth-corner test between environmental factors and first two RLQ axes for wild bee traits (AxcQ1 and AxcQ2). Orange indicates negative correlations between factors and green indicate positive correlations between factors. Black lines separate different variables, white lines separate levels of categorical variables.

vibrating mechanism on its hairy forehead. This species is also one of few that can excavate their brood cells in rotting wood. We also found interesting species with pollen specializations: those oligolectic on Fabaceae (*Rophitoides canus*, *Megachile ericetorum* and *Melitta leporina*), on Brassicaceae (*Osmia brevicornis*), and
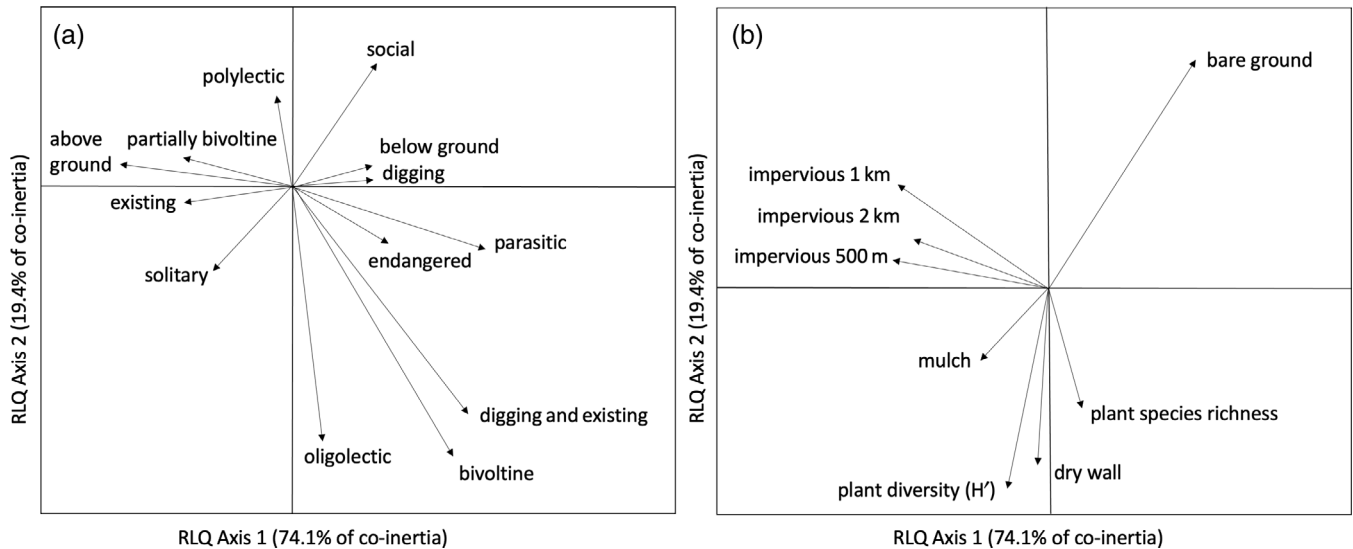
FIGURE 4 Correspondence analysis of environmental variables and wild bee species traits. Figures show coefficients for (a) wild bee traits and (b) environmental variables in gardens.

Asteraceae (*Osmia leaiana*). The life histories of such bees found in the gardens illuminate why garden factors such as plant diversity and deadwood availability are so important, particularly for specialists (Scheuchl & Willner, 2015).

Garden factors and bee taxonomic diversity

Vegetation is one of the main drivers of wild bee diversity in these gardens, supporting our first hypothesis. We found that bee species number, abundance, and taxonomic diversity increase with increasing plant species numbers. Furthermore, as the taxonomic diversity of vegetation increases, the functional dispersion of wild bees also increases; the more taxonomically diverse the composition of a garden's flora, the more functionally diverse its wild bee fauna becomes (Erickson et al., 2021; Theodorou et al., 2020). In theory and in practice, diverse plant communities should provide a diverse availability of nectar and pollen. Choice of pollen resources is species specific, with wild bees having different preferences and specializations (Blüthgen & Klein, 2011; Westrich, 2018). Physical characteristics such as bee tongue length and body size also determine which flowers or flower forms can be used by bees (Greenleaf et al., 2007; Westrich, 2018). Therefore, the diversity of (flowering) plants can also promote diverse wild bee traits. Floral availability in the form of floral density or abundance is an important factor for bees and bee traits in urban habitats (Blackmore & Goulson, 2014; Buchholz et al., 2020; Hennig & Ghazoul, 2012; Hülsmann et al., 2015); for example, high floral diversity and density in community

gardens in Montreal, Canada, promotes wild bee abundance (Normandin et al., 2017).

In support of our second hypothesis, we found that the number of wild bee species increased in gardens with a higher amount of deadwood and that bare ground availability positively influenced ground-nesting bee species. The majority of native species (>50%) nest endogeously, which likely explains why bare ground is so important in these gardens. Thus, unsealed and nonovergrown areas found in urban gardens can provide important niches in urbanized areas for ground-nesting bees. Wild bees require diverse nesting materials (e.g., resin, leaf or flower petals, clay) and nesting substrates such as soil, deadwood, or pithy plant stems to complete their life cycle (Roulston & Goodell, 2011). In anthropogenically managed landscapes, dead trees are often cut down, deadwood removed, and small structures (e.g., dry plant material such as mullein [*Verbascum thapsus*]) eliminated, thereby contributing to bee declines (McFrederick & LeBuhn, 2006; Westrich et al., 2011). Deadwood as a potential nesting site and component of structural complexity represents an important local factor that influences bee abundance and species diversity (da Encarnacao Coutinho et al., 2018; Fortuin & Gandhi, 2021; Garibaldi et al., 2018). Indeed, in forest ecosystems, experimentally increasing deadwood structures has been shown to increase the abundance of aboveground-nesting solitary bees and parasitic bees (Eckerter et al., 2021). In urban gardens, deadwood may be a novel resource in the urban context that promotes bees where natural nesting resources are lost. Deadwood is home to many beetles and other insects that create burrows (Gossner et al., 2013); these

beetle feeding tunnels are then, in turn, also sought out as nesting sites by bee species that nest in cavities. The amount of deadwood may be in effect a proxy for garden "wildness," with wildness creating more habitat niches and resources, which may be why deadwood overall promotes wild bee richness.

Bare ground availability and deadwood structures were significant factors for bees and bees of particular functional traits, which opens the door to further ask about the mechanisms driving this relationship. Although many studies show an influence of vegetation on urban bees (Cohen et al., 2021; Hennig & Ghazoul, 2012; Hülsmann et al., 2015; Normandin et al., 2017; Quistberg et al., 2016), studies that focus on nesting substrates (e.g., deadwood and drystone walls for aboveground-nesting species and bare ground for ground-nesting species) are limited in urban areas. Future researchers could observe these structures to determine whether and which bee species nest in which structures and investigate which structures are accepted as substitutes to determine how species may adapt to new "unnatural" structures and colonize secondary biotopes. Further research could also investigate how slope or gradient and solar radiation, temperature and moisture content, compaction and sediment type for soil, wood type, and availability of cavities of species-specific size and diameter for wood structures (Harmon-Threatt, 2020; Morato & Martins, 2006; Potts & Willmer, 1997) influence bee use.

We found no influences of landscape imperviousness (impervious surface at various spatial scales) on wild bee abundance, species numbers, or diversity. Landscape imperviousness can have a negative impact on wild bee abundance and species numbers (Bennett & Lovell, 2019; Frankie et al., 2009; Zanette et al., 2005) or have no clear relationship with bee species numbers (Hall et al., 2017; Wenzel et al., 2020). The lack of a relationship here may be related to the high structural heterogeneity and adequate supply of potential pollen sources in these gardens, despite high local to landscape imperviousness. Alternatively, the relationship may be nonlinear, with the highest diversity of bees at intermediate amounts of landscape imperviousness and with an increase in the ratio of aboveground versus belowground nesters (see subsequent discussion; Wenzel et al., 2020). In many community gardens, it is common practice to creatively repurpose different materials and assemble them in structurally diverse ways to create raised beds and flower pots that optimize space use for cultivation and subsequent plant availability. These resources may be able to mitigate negative urbanization effects if an array of wild bee species are supported.

Garden factors and bee traits

In support of our third hypothesis, certain wild bee functional traits associated with local garden factors and with landscape imperviousness, namely nesting traits and feeding traits. Landscape imperviousness was positively associated with the abundance of aboveground-nesting wild bee species, confirming that urbanization can select for specific bee traits. This may be due to the high availability of potential aboveground nesting sites associated with urban structures such as buildings and walls, but also insect hotels (Cane et al., 2006; Frankie et al., 2009; Wenzel et al., 2020). Our results are in line with work showing that nesting traits are a good indicator of wild bee response to habitat change due to increasing urbanization, where these traits can limit bee diversity (Cane et al., 2006; Cohen et al., 2021; Potts et al., 2005). Increasing amounts of sealed land implies decreases in suitable nesting opportunities for ground-nesting species (Xie et al., 2013), whereas more bare ground and sandy to clayey soils can provide colonization opportunities for wild bees (Frankie et al., 2009). An abundance of ground-nesting wild bees correlates with the amount of bare ground in a habitat (Harmon-Threatt, 2020; Potts et al., 2005), and open habitats created by clearcutting in forests support a variety of species, most of which exhibit ground-nesting and social behavior (Fortuin & Gandhi, 2021).

A generalist (polylectic) mode of pollen collection dominated in our samples (80%) and positively associated with landscape imperviousness. These findings join a growing body of literature linking higher numbers of polylectic species with increasing landscape-level urbanization (Buchholz et al., 2020; Hausmann et al., 2016). For example, 93% of sampled bees in residential gardens in New York were polylectic (Fetridge et al., 2008), 89% of sampled bees along railways in Chicago were polylectic (Gruver & Caradonna, 2021), as were 74% of sampled bees in green spaces in Poznan (Banaszak-Cibicka & Żmihorski, 2012). On the other hand, specialist (oligolectic) species were positively associated with garden plant diversity. Specialized bees depend on the availability of their forage plant, so promoting higher plant diversity can increase the availability of suitable food sources. More oligolectic species have been found in urban gardens and parks compared with seminatural sites, likely due to high plant diversity in these managed habitats that can provide food for a wide range of bee species (Baldock et al., 2015; Banaszak-Cibicka et al., 2018; Martins et al., 2017).

Finally, we found social behavior to be a common bee trait that associated negatively with landscape imperviousness and positively with the amount of bare

ground. This parallels findings that showed social behavior to be dominant in urban wild bee communities (Banaszak-Cibicka et al., 2018; Harrison et al., 2018). Social bees show ecological and ethological plasticity and high tolerance to environmental change and are more adaptable to unfavorable conditions than solitary species in urban environments (Chapman & Bourke, 2001). Urban habitats may offer a wide range of suitable nesting habitats for social wild bees, or social species may make better use of common structures in cities (Cane et al., 2006). Though not explored here, solitary wild bees may be negatively affected by high honeybee densities in cities because they have less access to food resources (Ropars et al., 2019). Current knowledge on wild bees, however, shows unclear trends in the association between social behavior and urban landscapes (Guenat et al., 2019); some have found solitary species dominant in particular ecosystems like green roofs (Kratschmer et al., 2018).

ECOLOGICAL APPLICATIONS

Community gardens can host a diversity of wild bee species and bee life-history traits including endangered and specialist species, but habitat factors of these gardens influence the functional composition of these bee communities. Our research demonstrates that vegetation as well as nesting resources are of particular importance, where an increase in the number of species and diversity of vegetation, as well as increases in deadwood, leads to an increase in the number of species and diversity of wild bees. Furthermore, higher amounts of bare ground cover favor ground-nesting, self-burrowing species, whereas a high degree of landscape imperviousness promotes the occurrence of aboveground-nesting species. The fact that garden factors are important drivers in terms of abundance, species numbers, and taxonomic and functional diversity of bees means that gardeners can promote and protect wild bees through their management and, thus, arguably maintain pollination services in the city. Gardeners can increase vegetation diversity to provision floral resources, but should also consider and provide suitable nesting resources in the form of open bare soil and sand ground cover and deadwood structures, which are often missing in city landscapes. These nesting factors represent natural elements and create wild nooks and niches for biodiversity to thrive. Nesting resources are often overlooked in both research and practice, largely due to the aesthetic qualities and norms around, for example, deadwood. Urban green space management must rethink "aesthetic requirements" to add more "wild edges" to urban ecosystems to achieve urban conservation goals.

CONCLUSION

The importance of local garden management on wild bees suggests that the city is a permeable space for wild bees given the right mix of necessary resources in habitats like gardens. Yet, due to changes in land use, privatization, and investment, many of Berlin's community gardens are at acute risk of displacement—a concern in turn for the biodiversity of the wild bees they support. Sealing gardens means a disturbance not only to urban biodiversity but also to potential synergies between people and ecological systems. Urban community gardens are often inclusive public places of environmental and agricultural education that offer opportunities for nature conservation in practical, interactive, and creative ways alongside urban food production. Gardens create awareness that biodiversity exists and can be preserved and promoted. In conclusion, if managed with biodiversity in mind, urban gardens can deliver positive effects for people and animals and function to solve dual crises around sustainable land management and biodiversity conservation in the city.

DATA AVAILABILITY STATEMENT

Data (Egerer, 2022b) are available in Dryad at https://doi.org/10.7291/D1NH46.

ORCID

Monika Egerer https://orcid.org/0000-0002-3304-0725

REFERENCES

Akaike, H. 1973. "Information Theory and an Extension of the Maximum Likelihood Principle." In *Proceedings of the 2nd International Symposium on Information, Bn Petrow, f. Czaki.* Budapest: Akademiai Kiado.

Alaimo, K., E. Packnett, R. A. Miles, and D. J. Kruger. 2008. "Fruit and Vegetable Intake among Urban Community Gardeners." *Journal of Nutrition Education and Behaviorutrition Education and Behavior* 40: 94–101.

Armar-Klemesu, M. 2000. "Urban Agriculture and Food Security Nutrition and Health. Thematic Paper 4." In *Growing Cities, Growing Food: Urban Agriculture on the Policy Agenda*, edited by N. Bakker, M. Dubbeling, S. Gündel, U. Sabel-Koschella, and H. de Zeeuw, 99–118. Fefdafing, Germany: DSE.

Baldock, K. C. R., M. A. Goddard, D. M. Hicks, E. Kunin, N. Mitschunas, L. M. Osgathorpe, S. G. Potts, et al. 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: 1–10.

Baldock, K. C. R., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, H. Morse, L. M. Osgathorpe, et al. 2019. "A Systems Approach Reveals Urban Pollinator Hotspots and Conservation Opportunities." *Nature Ecology & Evolution* 3: 363–73.

Banaszak-Cibicka, W., L. Twerd, M. Fliszkiewicz, K. Giejdasz, and A. Langowska. 2018. "City Parks vs. Natural Areas—Is It Possible to Preserve a Natural Level of Bee Richness and Abundance in a City Park?" *Urban Ecosystems* 21: 599–613.

Banaszak-Cibicka, W., and M. Żmihorski. 2012. "Wild Bees along an Urban Gradient: Winners and Losers." *Journal of Insect Conservation* 16: 331–43.

Bennett, A. B., and S. Lovell. 2019. "Landscape and Local Site Variables Differentially Influence Pollinators and Pollination Services in Urban Agricultural Sites." *PLoS One* 14: e0212034.

Blackmore, L. M., and D. Goulson. 2014. "Evaluating the Effectiveness of Wildflower Seed Mixes for Boosting Floral Diversity and Bumblebee and Hoverfly Abundance in Urban Areas." *Insect Conservation and Diversity* 7: 480–4.

Blüthgen, N., and A.-M. Klein. 2011. "Functional Complementarity and Specialisation: The Role of Biodiversity in Plant–Pollinator Interactions." *Basic and Applied Ecology* 12: 282–91.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. "Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution." *Trends in Ecology and Evolution* 24: 127–35.

Brondizio, E. S., J. Settele, S. Díaz, and H. T. Ngo, eds. 2019. *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn: IPBES Secretariat.

Buchholz, S., and M. H. Egerer. 2020. "Functional Ecology of Wild Bees in Cities: Towards a Better Understanding of Trait-Urbanization Relationships." *Biodiversity and Conservation* 29: 2779–801.

Buchholz, S., A. K. Gathof, A. J. Grossmann, I. Kowarik, and L. K. Fischer. 2020. "Wild Bees in Urban Grasslands: Urbanisation, Functional Diversity and Species Traits." *Landscape and Urban Planning* 196: 103731.

Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S.-L. E. Yasui. 2015. "Predicting Communities from Functional Traits." *Trends in Ecology & Evolution* 30: 510–1.

Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams. 2006. "Complex Responses within a Desert Bee Guild (Hymenoptera: Apiformes) to Urban Habitat Fragmentation." *Ecological Applications* 16: 632–44.

Chapman, R. E., and A. F. G. Bourke. 2001. "The Influence of Sociality on the Conservation Biology of Social Insects." *Ecology Letters* 4: 650–62.

Cohen, H., M. Egerer, S.-S. Thomas, and S. M. Philpott. 2021. "Local and Landscape Features Constrain the Trait and Taxonomic Diversity of Urban Bees." *Landscape Ecology* 37: 583–99.

da Encarnacao Coutinho, J. G., L. A. Garibaldi, and B. F. Viana. 2018. "The Influence of Local and Landscape Scale on Single Response Traits in Bees: A Meta-Analysis." *Agriculture, Ecosystems & Environment* 256: 61–73.

Dew, R. M., D. P. Silva, and S. M. Rehan. 2019. "Range Expansion of an Already Widespread Bee under Climate Change." *Global Ecology and Conservation* 17: e00584.

Dray, S., and A.-B. Dufour. 2007. "The ade4 Package: Implementing the Duality Diagram for Ecologists." *Journal of Statistical Software* 22: 1–20.

Dray, S., and P. Legendre. 2008. "Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited." *Ecology* 89: 3400–12.

Eckerter, T., J. Buse, J. Bauhus, M. I. Förschler, and A. M. Klein. 2021. "Wild Bees Benefit from Structural Complexity Enhancement in a Forest Restoration Experiment." *Forest Ecology and Management* 496: 119412.

Egerer, M. 2022a. "Bee Discovery Suggests the Importance of Urban Gardens in a Changing World." *Renewable Agriculture and Food Systems* 37: 371–4.

Egerer, M. 2022b. "Vegetation Complexity and Nesting Resource Availability Predict Bee Diversity and Functional Traits in Community Gardens." Dryad, dataset. https://doi.org/10.7291/D1NH46.

Erickson, E., H. M. Patch, and C. M. Grozinger. 2021. "Herbaceous Perennial Ornamental Plants Can Support Complex Pollinator Communities." *Scientific Reports* 11: 17352.

Everaars, J., M. W. Strohbach, B. Gruber, and C. F. Dormann. 2011. "Microsite Conditions Dominate Habitat Selection of the Red Mason Bee (Osmia Bicornis, Hymenoptera: Megachilidae) in an Urban Environment: A Case Study from Leipzig, Germany." *Landscape and Urban Planning* 103: 15–23.

Fenoglio, M. S., M. R. Rossetti, and M. Videla. 2020. "Negative Effects of Urbanization on Terrestrial Arthropod Communities: A Meta-Analysis." *Global Ecology and Biogeography* 29: 1412–29.

Fetridge, E. D., J. S. Ascher, and G. A. Langellotto. 2008. "The Bee Fauna of Residential Gardens in a Suburb of new York City (Hymenoptera: Apoidea)." *Annals of the Entomological Society of America* 101: 1067–77.

Fortel, L., M. Henry, L. Guilbaud, H. Mouret, and B. E. Vaissiere. 2016. "Use of Human-Made Nesting Structures by Wild Bees in an Urban Environment." *Journal of Insect Conservation* 20: 239–53.

Fortuin, C. C., and K. J. K. Gandhi. 2021. "Functional Traits and Nesting Habitats Distinguish the Structure of Bee Communities in Clearcut and Managed Hardwood & Pine Forests in Southeastern USA." *Forest Ecology and Management* 496: 119351.

Frankie, G., R. Thorp, J. Hernandez, M. Rizzardi, B. Ertter, J. Pawelek, S. Witt, M. Schindler, R. Coville, and V. Wojcik. 2009. "Native Bees Are a Rich Natural Resource in Urban California Gardens." *California Agriculture* 63: 113–20.

Gallai, N., J.-M. Salles, J. Settele, and B. E. Vaissière. 2009. "Economic Valuation of the Vulnerability of World Agriculture Confronted with Pollinator Decline." *Ecological Economics* 68: 810–21.

Garibaldi, L. A., G. K. S. Andersson, F. Requier, T. P. M. Fijen, J. Hipólito, D. Kleijn, N. Pérez-Méndez, and O. Rollin. 2018. "Complementarity and Synergisms among Ecosystem Services Supporting Crop Yield." *Global Food Security* 17: 38–47.

Gossner, M. M., A. Floren, W. W. Weisser, and K. E. Linsenmair. 2013. "Effect of Dead Wood Enrichment in the Canopy and on the Forest Floor on Beetle Guild Composition." *Forest Ecology and Management* 302: 404–13.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness." *Ecology Letters* 4: 379–91.

Graham, H., D. L. Beall, M. Lussier, P. McLaughlin, and S. Zidenberg-Cherr. 2005. "Use of School Gardens in Academic Instruction." *Journal of Nutrition Education and Behavior* 37: 147–51.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. "Bee Foraging Ranges and their Relationship to Body Size." *Oecologia* 153: 589–96.

Gruver, A., and P. Caradonna. 2021. "Chicago Bees: Urban Areas Support Diverse Bee Communities but with More Non-Native Bee Species Compared to Suburban Areas." *Environmental Entomology* 50: 982–94.

Guenat, S., W. E. Kunin, A. J. Dougill, and M. Dallimer. 2019. "Effects of Urbanisation and Management Practices on Pollinators in Tropical Africa." *Journal of Applied Ecology* 56: 214–24.

Hall, D. M., G. R. Camilo, R. K. Tonietto, J. Ollerton, K. Ahrné, M. Arduser, J. S. Ascher, et al. 2017. "The City as a Refuge for Insect Pollinators." *Conservation Biology* 31: 24–9.

Hall, H. G. 2016. "Color Preferences of Bees Captured in Pan Traps." *Journal of the Kansas Entomological Society* 89: 273–6.

Harmon-Threatt, A. 2020. "Influence of Nesting Characteristics on Health of Wild Bee Communities." *Annual Review of Entomology* 65: 39–56.

Harrison, T., J. Gibbs, and R. Winfree. 2018. "Forest Bees Are Replaced in Agricultural and Urban Landscapes by Native Species with Different Phenologies and Life-History Traits." *Global Change Biology* 24: 287–96.

Hartig, F. 2021. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R Package Version 0.4.4. https://CRAN.R-project.org/package=DHARMa.

Hausmann, S. L., J. S. Petermann, and J. Rolff. 2016. "Wild Bees as Pollinators of City Trees." *Insect Conservation and Diversity* 9: 97–107.

Hennig, E. I., and J. Ghazoul. 2012. "Pollinating Animals in the Urban Environment." *Urban Ecosystem* 15: 149–66.

Holland, L. 2004. "Diversity and Connections in Community Gardens: A Contribution to Local Sustainability." *Local Environment* 9: 285–305.

Hülsmann, M., H. von Wehrden, A.-M. Klein, and S. D. Leonhardt. 2015. "Plant Diversity and Composition Compensate for Negative Effects of Urbanization on Foraging Bumble Bees." *Apidologie* 46: 760–70.

Jäger, E. J., F. Ebel, P. Hanelt, and G. K. Müller. 2016. *Rothmaler-Exkursionsflora von Deutschland: Krautige Zier-und Nutzpflanzen*. Berlin: Springer-Verlag.

Kingsley, J., E. Foenander, and A. Bailey. 2020. "'It's about Community': Exploring Social Capital in Community Gardens across Melbourne, Australia." *Urban Forestry & Urban Greening* 49: 126640.

Klein, A.-M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. "Importance of Pollinators in Changing Landscapes for World Crops." *Proceedings of the Royal Society B: Biological Sciences* 274: 303–13.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. "World Map of the Köppen-Geiger Climate Classification Updated." *Meteorologische Zeitschrift* 15: 259–63.

Kratschmer, S., M. Kriechbaum, and B. Pachinger. 2018. "Buzzing on Top: Linking Wild Bee Diversity, Abundance and Traits with Green Roof Qualities." *Urban Ecosystem* 21: 429–46.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.

Laliberté, E., P. Legendre, and B. Shipley. 2014. "FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." R Package Version 1.0-12. https://www.imsbio.co.jp/RGM/R_rdfile?f=FD/man/FD-package.Rd&d=R_CC.

Lanner, J., S. Kratschmer, B. Petrović, F. Gaulhofer, H. Meimberg, and B. Pachinger. 2020. "City Dwelling Wild Bees: How Communal Gardens Promote Species Richness." *Urban Ecosystem* 23: 271–88.

Lautenbach, S., R. Seppelt, J. Liebscher, and C. F. Dormann. 2012. "Spatial and Temporal Trends of Global Pollination Benefit." *PLoS One* 7: e35954.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. "Relating Behavior to Habitat: Solutions to Thefourth-Corner Problem." *Ecology* 78: 547–62.

Lin, B. B., S. M. Philpott, and S. Jha. 2015. "The Future of Urban Agriculture and Biodiversity-Ecosystem Services: Challenges and Next Steps." *Basic and Applied Ecology* 16: 189–201.

Mace, G. M., K. Norris, and A. H. Fitter. 2012. "Biodiversity and Ecosystem Services: A Multilayered Relationship." *Trends in Ecology and Evolution* 27: 19–26.

Mallinger, R. E., H. R. Gaines-Day, and C. Gratton. 2017. "Do Managed Bees Have Negative Effects on Wild Bees?: A Systematic Review of the Literature." *PLoS One* 12: 1–32.

Martins, K. T., A. Gonzalez, and M. J. Lechowicz. 2017. "Patterns of Pollinator Turnover and Increasing Diversity Associated with Urban Habitats." *Urban Ecosystem* 20: 1359–71.

McFrederick, Q. S., and G. LeBuhn. 2006. "Are Urban Parks Refuges for Bumble Bees Bombus Spp. (Hymenoptera: Apidae)?" *Biological Conservation* 129: 372–82.

Morato, E. F., and R. P. Martins. 2006. "An Overview of Proximate Factors Affecting the Nesting Behavior of Solitary Wasps and Bees (Hymenoptera: Aculeata) in Preexisting Cavities in Wood." *Neotropical Entomology* 35: 285–98.

Normandin, É., N. J. Vereecken, C. M. Buddle, and V. Fournier. 2017. "Taxonomic and Functional Trait Diversity of Wild Bees in Different Urban Settings." *PeerJ* 2050: 1–35.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120: 321–6.

Pellmyr, O. 2002. "Pollination by Animals." In *Plant–Animal Interactions, An Evolutionary Approach*, edited by C. M. Herrera and O. Pellmyr, 157–84. Hoboken: Wiley-Blackwell.

Piano, E., D. Giuliano, and M. Isaia. 2020. "Islands in Cities: Urbanization and Fragmentation Drive Taxonomic and Functional Variation in Ground Arthropods." *Basic and Applied Ecology* 43: 86–98.

Piano, E., K. De Wolf, F. Bona, D. Bonte, D. E. Bowler, M. Isaia, L. Lens, et al. 2017. "Urbanization Drives Community Shifts towards Thermophilic and Dispersive Species at Local and Landscape Scales." *Global Change Biology* 23: 2554–64.

Porto, R. G., R. F. de Almeida, O. Cruz-Neto, M. Tabarelli, B. F. Viana, C. A. Peres, and A. V. Lopes. 2020. "Pollination Ecosystem Services: A Comprehensive Review of Economic Values, Research Funding and Policy Actions." *Food Security* 12: 1425–42.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. "Role of Nesting Resources in Organising Diverse Bee Communities in a Mediterranean Landscape." *Ecological Entomology* 30: 78–85.

Potts, S., and P. Willmer. 1997. "Abiotic and Biotic Factors Influencing Nest-Site Selection by Halictus Rubicundus, a Ground-Nesting Halictine Bee." *Ecological Entomology* 22: 319–28.

QGIS Development Team. 2018. "QGIS Geographic Information System: Open Source Geospatial Foundation." http://qgis.osgeo.org.

Quistberg, R. D., P. Bichier, and S. M. Philpott. 2016. "Landscape and Local Correlates of Bee Abundance and Species Richness in Urban Gardens." *Environmental Entomology* 45: 592–601.

Rahimi, E., S. Barghjelveh, and P. Dong. 2022. "A Review of Diversity of Bees, the Attractiveness of Host Plants and the Effects of Landscape Variables on Bees in Urban Gardens." *Agriculture and Food Security* 11: 1–11.

Ropars, L., I. Dajoz, C. Fontaine, A. Muratet, and B. Geslin. 2019. "Wild Pollinator Activity Negatively Related to Honey Bee Colony Densities in Urban Context." *PLoS One* 14: 1–16.

Roulston, T. H., and K. Goodell. 2011. "The Role of Resources and Risks in Regulating Wild Bee Populations." *Annual Review of Entomology* 56: 293–312.

Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. "Worldwide Decline of the Entomofauna: A Review of its Drivers." *Biological Conservation* 232: 8–27.

Saure, C. 1996. "Urban Habitats for Bees: The Example of City of Berlin." In *The Conservation of Bees*, edited by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. Williams, 47–54. London: Academic Press.

Saure, C. 2005. *Rote Liste und Gesamtartenliste der Bienen und Wespen (Hymenoptera part.) von Berlin mit Angaben zu den Ameisen*. Berlin: Rote Liste der gefährdeten Pflanzen und Tiere von Berlin.

Scheuchl, E., and W. Willner. 2015. *Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt*. Wiebelsheim: Quelle & Meyer Verlag.

Schmitt, S., I. Maréchaux, J. Chave, F. J. Fischer, C. Piponiot, S. Traissac, and B. Hérault. 2020. "Functional Diversity Improves Tropical Forest Resilience: Insights from a Long-Term Virtual Experiment." *Journal of Ecology* 108: 831–43.

Seitz, B., S. Buchholz, I. Kowarik, J. Herrmann, L. Neuerburg, J. Wendler, L. Winker, and M. Egerer. 2022. "Land Sharing between Cultivated and Wild Plants: Urban Gardens as Hotspots for Plant Diversity in Cities." *Urban Ecosystems* 25: 927–39.

Senatsverwaltung für Stadtentwicklung und Umwelt. 2016. "Versorgung mit öffentlichen, wohnungsnahen Grünanlagen." https://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/index.shtml.

Senatsverwaltung für Stadtentwicklung und Umwelt. 2020a. "Auswirkungen des Klimawandels." https://www.berlin.de/sen/uvk/klimaschutz/anpassung-an-den-klimawandel/auswirkungen-des-klimawandels/.

Senatsverwaltung für Stadtentwicklung und Umwelt. 2020b. "Gemeinschaftsgärten in Berlin." https://www.berlin.de/gemeinschaftsgaertnern/gemeinschaftsgaerten/gemeinschaftsgaerten-in-berlin/artikel.879232.php.

Smith, R. M., K. Thompson, J. G. Hodgson, P. H. Warren, and K. J. Gaston. 2006. "Urban Domestic Gardens (IX): Composition and Richness of the Vascular Plant Flora, and Implications for Native Biodiversity." *Biological Conservation* 129: 312–22.

Statistisches Bundesamt, D. 2021. "Bevölkerung am 31.12.2020 nach Nationalitäten und Bundesländern:01.08.2021." https://www.destatis.de/DE/Home/_inhalt.html.

Swan, C. M., B. Brown, D. Borowy, J. Cavender-Bares, A. Jeliazkov, S. Knapp, Z. Lososová, et al. 2021. "A Framework for Understanding how Biodiversity Patterns Unfold across

Multiple Spatial Scales in Urban Ecosystems." *Ecosphere* 12: e03650.

Theodorou, P., S. C. Herbst, B. Kahnt, P. L. González, L. M. Baltz, J. Osterman, and R. J. Paxton. 2020. "Urban Fragmentation Leads to Lower Floral Diversity, with Knock-on Impacts on Bee Biodiversity." *Scientific Reports* 10: 21756–11.

Tilman, D. 2001. "Functional Diversity." *Encyclopedia of biodiversity* 3: 109–20.

Walker, D. B., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Weisberg, J. F., and W. Sanford. 2019. *An R Companion to Applied Regression*. Thousand Oaks, CA: Sage.

Wenzel, A., I. Grass, V. V. Belavadi, and T. Tscharntke. 2020. "How Urbanization Is Driving Pollinator Diversity and Pollination – A Systematic Review." *Biological Conservation* 241: 108321.

Westrich, P. 1996. *Habitat Requirements of Central European Bees and the Problems of Partial Habitats*. Linnean Society Symposium Series, 1–16. Washington, DC: Academic Press Limited.

Westrich, P. 2018. *Die Wildbienen Deutschlands*. Stuttgart: Verlag Eugen Ulmer.

Westrich, P., U. Frommer, K. Mandery, H. Riemann, H. Ruhnke, C. Saure, and J. Voith. 2011. "Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands." *Fassung* 5: 373–416.

Wolch, J. R., J. Byrne, and J. P. Newell. 2014. "Urban Green Space, Public Health, and Environmental Justice: The Challenge of Making Cities "Just Green Enough."." *Landscape and Urban Planning* 125: 234–44.

Xie, Z., J. Qiu, and X. Chen. 2013. "Decline of Nest Site Availability and Nest Density of Underground Bees along a Distance Gradient from Human Settlements." *Entomological Science* 16: 170–8.

Zanette, L. R. S., R. P. Martins, and S. P. Ribeiro. 2005. "Effects of Urbanization on Neotropical Wasp and Bee Assemblages in a Brazilian Metropolis." *Landscape and Urban Planning* 71: 105–21.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Felderhoff, Julia, Anika K. Gathof, Sascha Buchholz, and Monika Egerer. 2023. "Vegetation Complexity and Nesting Resource Availability Predict Bee Diversity and Functional Traits in Community Gardens." *Ecological Applications* 33(2): e2759. https://doi.org/10.1002/eap.2759