



# Winners and losers at enhanced urban roadsides: Trait-based structuring of wild bee communities at local and landscape scale

Simon Dietzel <sup>a,\*</sup>, Sandra Rojas-Botero <sup>a</sup>, Anja Dichtl <sup>b</sup>, Johannes Kollmann <sup>a</sup>, Christina Fischer <sup>c</sup>

<sup>a</sup> Chair of Restoration Ecology, TUM School of Life Sciences, Technical University of Munich, Emil-Ramann-Straße 6, 85354 Freising, Germany

<sup>b</sup> District Government of Lower Bavaria, Department for Nature Conservation, Regierungsplatz 540, 84028 Landshut, Germany

<sup>c</sup> Faunistics and Wildlife Conservation, Department of Agriculture, Ecotrophology, and Landscape Development, Anhalt University of Applied Sciences, Strenzfelder Allee 28, 06406 Bernburg, Germany



## ARTICLE INFO

### Keywords:

Functional diversity  
Green space design  
Pollinators  
Road verges  
Urban ecology  
Urban filter

## ABSTRACT

Pervasive urbanization contributes to biodiversity declines globally, and with urbanization, road densities increase, amplifying habitat degradation and landscape homogenization. However, as a major part of urban green space, roadside vegetation permeates the urban fabric and, if enhanced, can be used to support insects, such as wild bees. To analyze local and landscape-scale effects of enhanced urban roadsides on wild bee communities and to identify bee traits affected by urban filtering, we established 78 wildflower patches with a native seed mixture along five major roads in Munich (S Germany). Species-poor roadsides with regular management were used as control. During a three-year experiment, we sampled wild bees with pan traps, monitored roadside vegetation, and analyzed landscape diversity and perimeter-area ratio of green space within a radius of 500 m. We gathered information on wild bee morphological, behavioral, phenological, and foraging traits and calculated their abundance, species richness and functional dispersion. Wild bee abundance, richness and functional dispersion increased with vegetation diversity. Functional dispersion was positively correlated with landscape diversity and distance from the city center, indicating trait-based urban filtering. A fourth corner analysis revealed that small, short-lived, and univoltine bees were disadvantaged at urban roadsides. While univoltine bees were discriminated in areas of high landscape diversity, large bees prevailed in the city outskirts, and solitary bees were associated with green space edges. We conclude that enhanced roadsides contribute to urban wild bee diversity and that identifying functional groups affected by urbanization can help to draw recommendations for effective conservation.

## 1. Introduction

During the past decades, biodiversity steeply declined due to land-use intensification and landscape homogenization, and insects significantly suffered from excessive habitat degradation, particularly in agricultural landscapes (Seibold et al., 2019). By contrast, insect populations in cities have been reported to be more diverse than in rural areas, as they contain structurally richer habitats and offer a more diverse range of floral resources throughout the year (Theodorou et al., 2020; Verboven et al., 2014). However, looking closer at the drivers that shape urban insect communities, the rural-urban narrative lacks precision. For example, pollinator diversity experiences an increase up to certain levels of urbanization, such as 60 % of impervious surface, but then sharply declines, even below the levels observed in their rural

counterparts (Wenzel et al., 2020). Thus, urban wild bees are threatened by increasing urban infill, triggering an urban filtering effect on species that do not fit the anthropogenic environment, such as food or nesting specialists, resulting in functionally simplified communities dominated by generalists (Ferrari and Polidori, 2022; Buchholz and Egerer, 2020).

Research on wild bee functional diversity has attracted considerable attention, leading to an improved mechanistic understanding of ecosystem functioning and niche filtering along urbanization gradients (Buchholz and Egerer, 2020; Gagic et al., 2015). Wild bees vary in morphological and phenological traits and life cycles; they have parasitic, solitary, or social behavior and often rely on specific nesting substrates and pollen resources. The surrounding urban landscape offers opportunities for foraging, resting, mating, and nesting and therefore determines the composition of local wild bee communities (Buchholz

\* Corresponding author.

E-mail address: [simon.dietzel@tum.de](mailto:simon.dietzel@tum.de) (S. Dietzel).

and Egerer, 2020). Thus, with increasing urban landscape homogenization, only some species can cope with excessive imperviousness and low-quality green space. Wild bee species that are low in their degree of ecological specialization, small in body sizes, socially organized or emerge late in the season most likely pass this urban filter (Buchholz and Egerer, 2020; Wong et al., 2019; but see Fauviau et al., 2022). On the other hand, larger bees, specialized on specific diet or nesting substrates, or are less competitive due to other morphological, phenological, or behavioral traits are discriminated. This leads to local clustering of species with similar traits and finally to functionally homogenous urban wild bee communities, leaving several ecological niches unoccupied (Williams et al., 2010). However, the mentioned trait-urbanization effects are reported ambiguously in several studies.

In times of globally increasing urbanization and habitat degradation, integrating biodiversity aspects into city planning can mitigate species losses (Kowarik et al., 2020). Still, contemporary design of urban green space focuses primarily on aesthetics and human needs (Knapp et al., 2021). Therefore, identifying urban areas of high ecological value and incorporating species requirements into urban green infrastructure can provide new opportunities for conservation (Parris et al., 2018; Dietzel et al., 2023). To support biodiversity, urban green space design must be adapted to meet the needs of vulnerable wildlife species, such as native plants and bees (Baldock, 2020). To offer concrete recommendations for conservation, it is essential to understand how species interact with their environment, and to identify the species traits affected by change due to excessive surface imperviousness (Winfrey, 2010).

In cities, roadsides can provide an overall high diversity of plants and pollinators, mitigating the negative effects of habitat fragmentation and degradation (Muñoz et al., 2015; Phillips et al., 2020). Roadsides form one of the major areal elements of urban green space cover and, therefore, offer a high potential to support biodiversity by providing a network-like green infrastructure (Marshall et al., 2019). However, little is known about the local and landscape-scale effects of urban roadsides on wild bee diversity and functional composition (Buchholz and Egerer, 2020). On the landscape scale, there is evidence that urban wild bee abundance and diversity are positively affected by the availability of green space and, more importantly, modulated by its extensive management (Herrmann et al., 2023; Anderson et al., 2023). Moreover, even small randomly vegetated patches contribute to urban wildflower diversity and thus provide bee forage (Vega and Küffer, 2021). This highlights the complex interplay of local habitat quality, connectivity, and resource availability. Therefore, predictions of wild bee community composition and diversity in relation to the surrounding urban landscape can lead to ambiguous results (Fauviau et al., 2022).

To evaluate the conservation value of enhanced urban roadsides for wild bees, it is necessary to understand how improved roadside vegetation influences their abundance, species richness, and functional composition. Additionally, identifying functional groups that are affected by urban filtering is necessary to develop solutions for their conservation. Especially for cities, more research is needed on the ecological functions of the so far overlooked roadsides, wild bee roadside communities, and how trait specific interactions shape their composition at local and landscape scale (Ricotta et al., 2015).

Thus, we designed a seed mixture of 26 wildflower species of regional provenance to study wild bee abundance, species richness and functional diversity at enhanced urban roadsides. During 2019–2021, 78 experimental wildflower patches were established along five main roads in Munich (S Germany), leading from the city's center to its boundaries. Covering a gradient of landscape diversity and green space cover, we investigated species co-occurrences and interactions of wild bee abundance, richness and functional composition, with the local vegetation and the urban landscape. Additionally, we analyzed how trait–environment interactions shape the local wild bee communities, i.e., which wild bee traits are filtered or favored by local and landscape factors. With our study, we addressed the following questions:

- i) Does wild bee abundance, species richness, and functional diversity increase with enhanced roadside vegetation in highly urbanized areas?
- ii) Which landscape-scale factors modify wild bee abundance, species richness and functional diversity?
- iii) How does urban filtering at urban roadsides affect wild bee functional groups?

## 2. Methods

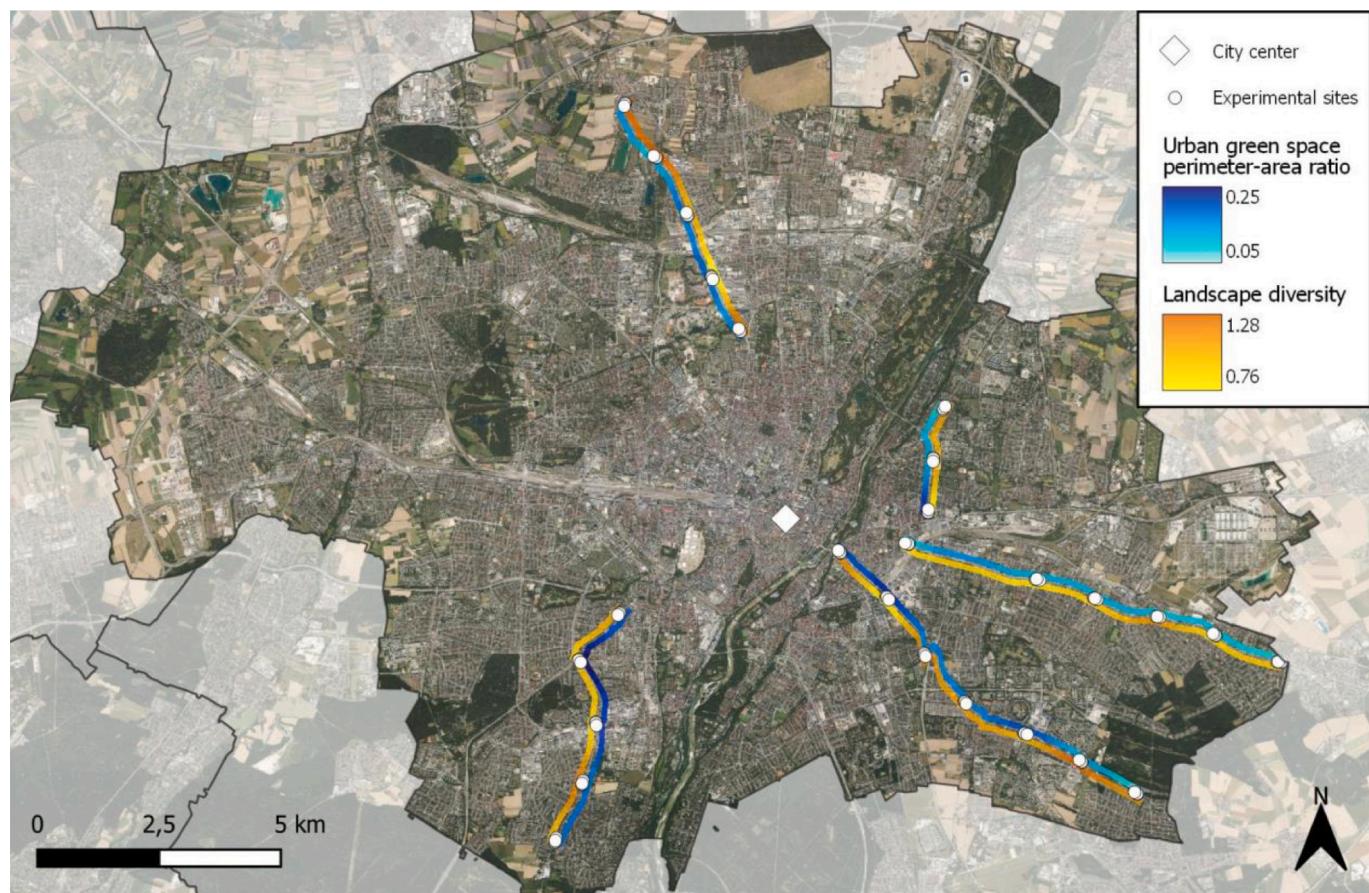
### 2.1. Study area and experimental design

Our study was conducted in Munich (48.13761, 11.57991; 515 m a.s.l.). With about 5100 inhabitants per km<sup>2</sup>, the city belongs to the most densely populated areas within the EU (Munich city administration, 2023; Eurostat, 2023). Five representative main roads were chosen, leading from the city center to its boundaries in different directions (Fig. 1). Roadside green covers around 20 % of Munich's total green space area (Bavarian State Statistics Office, 2020). Every 1.3 km, we established a triplet of experimental patches, using a customized wildflower seed mixture containing 26 annual and perennial native plant species from eleven families of regional origin, considering diverse flower morphologies and colors that are relevant for urban pollinators and can cope with the environmental conditions at urban roadsides (Table A.1). Starting in 2019, the first 23 wildflower patches were sown, and local control patches, without seeding, were established at 20 m and 75 m distance. In addition to the local control patches, we monitored the roadside vegetation of two independent roads, including ten distant control patches. However, local and distant controls were similar in plant and bee species richness. Thus, to avoid an unbalanced dataset, we excluded the distant control sites from the analysis, as they did not contribute any further variation, and chose only the triplets of plots for analysis (A.2). In 2020, the second set of 23 patches was seeded at the 20 m distance patches, and the last set at 75 m distance was established in 2021. This stepwise approach accounted for annual variation in wildflower establishment and plant compositional development (Rojas-Botero et al., 2023a) and thus produced more general results.

The wildflower patches covered 8 m<sup>2</sup> (2 m × 4 m). Before seeding, the turf grass was removed, and the underlying soil loosened. Afterward, a standardized nutrient-poor substrate was applied (8–10 cm thickness), and the seed mixture was sown with 4 g/m<sup>2</sup> density. The patches were mown once a year in fall and varied in plant composition and cover depending on their ages, i.e., planting year. Control patches, i.e., shortly trimmed roadside lawns, had the same dimensions as the wildflower patches. They received a mowing regime of more than five times a year, depending on weather and soil conditions. Vegetation height on these patches was <10 cm, though it could vary in species composition and flower abundance, depending on the individual management of the responsible district.

### 2.2. Wild bee sampling and identification

Wild bee sampling was conducted with pan traps colored with UV-luminescent paint (SPARVAR Leuchtfarbe, Spray-Color GmbH) in blue, white, and yellow. The pans were 15 cm in diameter and filled with 400 ml of water with a small quantity of odorless detergent. The traps were attached to a wooden pole and exposed at vegetation height in the center of the experimental patches for 48 h. Trapping took place three times a year in June–August, with a minimum of 27 days in between, when weather conditions were suitable for wild bee activity (Westphal et al., 2008). On control patches, the traps were placed at 40 cm height to avoid disturbance by dogs. Collected wild bees were counted and identified in the laboratory to species level using several identification keys (Amiet et al., 1999, 2001, 2004, 2007, 2010, 2017; Dathe et al., 2016; Scheuchl, 2000, 2006; Schmid-Egger and Scheuchl, 1997). Critical species were compared with reference material and later checked by



**Fig. 1.** Map of the study area and five major roads in Munich, leading from the center to the city boundaries. Three experimental patches were set up as 'site triplets' and sown sequentially between 2019 and 2021 with a customized native wildflower mixture. The perimeter-area-ratio of urban green space (blue gradient) and urban landscape diversity (orange gradient) were calculated as explanatory variables at a landscape scale within a radius of 500 m. For the map, the values of the experimental patches were interpolated (IDW interpolation) and determined for points at a distance of 1 m along the streets (geoprocessing and layout: QGIS 3.26.3). Background map: DOP80 © Bayerische Vermessungsverwaltung. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

the taxonomic specialist Klaus Mandery.

### 2.3. Trait selection and functional diversity

We selected five wild bee traits (Table 1), considering the review about trait–urbanization interactions by Buchholz and Egerer (2020). As sources of trait information, we used identification keys and literature on wild bee ecology (Table 1). To obtain consistent data, we adopted trait values from similar sources, and considered the protocol of Palacio et al. (2022). We took care to retain a balanced distribution of traits and tested for collinearity of traits with the hector function of the polycor R-package (version 0.8–1; Fox, 2022). We found a few cases of collinearity involving diet specialization with nesting locations and shorter life-spans. However, the use of a latent variable statistical approach was robust against collinearity; thus, the few existing correlations did not influence the results decisively.

With the trait data, we calculated Gower's distances with the R-package gawdis (version 0.1.4; deBello et al., 2021) and subsequently functional dispersion (FDis) using the FD-package (version 1.0–12.1; Laliberté and Legendre, 2010). Functional dispersion is the mean distance in multidimensional trait space of individual species to the centroid of all species, in which the centroid's position is shifted to the most abundant species, and distances to the centroid of individual species are weighed by their relative abundances. Therefore, functional dispersion is independent of species richness, and allows identifying functional filtering processes that shape the structure of wild bee

communities (Laliberté and Legendre, 2010). Species with similar traits will accumulate at sites where strong filtering occurs, resulting in low functional dispersion, whereas higher dispersion indicates an increased trait diversity and niche partitioning. The index has been successfully used in several wild bee studies (e.g., Martins et al., 2017; Buchholz et al., 2020).

### 2.4. Vegetation and landscape parameters

Vegetation was sampled once a year in summer (June–July) by recording all herbaceous plant species (seeded and non-seeded) and their cover. A 50 cm × 50 cm frame was systematically placed five times within the 4 m × 2 m wildflower patches to standardize vegetation sampling. Control patches were sampled entirely within the 4 m × 2 m plot, as herbaceous plants occurred only in limited numbers and cover. To account for the two sampling techniques, we calculated plant species cover per m<sup>2</sup> and, finally, the Shannon diversity index per patch and year using the R-package vegan (version 2.6–4; Oksanen et al., 2022). We decided to use Shannon diversity because it reflects the potential resource availability for bees over the three investigated vegetation periods. It was closely correlated with plant species richness and floral density (see also A.3). After planting, the wildflower patches changed in plant composition and cover, with annuals flowering in the first year and perennials taking over in the second and third years of sampling. As the patches were added on a yearly basis, floral composition varied between patches, according to their age, site, and weather conditions (A.4,

**Table 1**

Selected wild bee traits, their measure, and literature sources from which the trait information was obtained. Traits were classified as morphological, behavioral, phenological, and foraging types. Body size and lifespan were continuous data; the rest were categorical variables. Functional dispersion (FDis) was calculated using Gower's distance (R-packages FD and gawdis) from these traits.

Type	Trait	Measure	Source
Morphology	Body size [mm] ( <i>continuous</i> )	Body size of female bees as the mean value of the range in the identification keys	Amiet et al. (1999), Amiet et al. (2001), Amiet et al. (2004), Amiet et al. (2007), Amiet et al. (2010), Westrich (2019)
Behavior	Nesting location ( <i>categorical</i> )	Above- or belowground	Westrich (2019)
	Sociality ( <i>categorical</i> )	Parasitic, solitary, facultative social or social	Westrich (2019)
Phenology	Lifespan ( <i>continuous</i> )	Number of weeks of female nesting activity	Amiet et al. (1999), Amiet et al. (2001), Amiet et al. (2004), Amiet et al. (2007), Amiet et al. (2010), Amiet et al. (2017)
	Voltinism ( <i>categorical</i> )	Generations per year: Parasitic, univoltine, bivoltine or social	Westrich (2019)
Foraging	Diet specialization ( <i>categorical</i> )	Parasitic, oligoleptic, or polylectic	Westrich (2019)

A.4.1), resulting in a gradient of increasing vegetation cover and number of plant species.

The urban landscape was sampled within a radius of 500 m around every patch using ArcGIS (version 10.8.1, Esri Inc., 2020). Using data from the Open Street Map project (OSM), we obtained high-resolution information on areal dimensions of different types of urban green space cover, impervious surface cover, or areas of mixed-use development and categorized the found land-use types after the Corine Land Cover (CLC) classification (A.5; Open Street Map Contributors, 2020; EEA, 2018). With this data, we calculated Shannon landscape diversity. The study sites crossed a gradient of urban green space cover with 1.6–45.1 % (mean  $16.1 \pm 10.7\%$  SD). To analyze the relative importance of the configuration of urban green space areas, we calculated their perimeter-area ratios. Finally, as roads can act as barriers or corridors depending on the species of interest (Dániel-Ferreira et al., 2022; Krewenka et al., 2011), we used the distance to the city center as variable to detect possible community shifts or urban filtering along the roads (Gathof et al., 2022).

## 2.5. Statistical analysis

### 2.5.1. Analysis of wild bee abundance, species richness and functional dispersion

To analyze bee abundance, species richness, and functional dispersion, we applied generalized linear mixed effect models (glmm) using the R-package glmmTMB (version 1.1.4; Brooks et al., 2017). We used a negative binomial and a Poisson distribution formula to model bee abundance and species richness respectively, both with a single zero inflation parameter (*ziformula* = ~1). The data distribution of functional dispersion was Gaussian, except for an excess accumulation of zeros, originating from patches where no or just one bee species was found (Laliberté and Legendre, 2010). To address this data structure, we applied a Tweedie-glmm with zero inflation parameter (Stoklosa et al., 2022). As the single experimental patches were nested within the site triplets, we included them as random factor to control for spatial autocorrelation. Using a more differentiated random structure, e.g., by including the single roads, did not improve the models noticeably, so we left them out.

Explanatory variables were checked for collinearity by calculating Spearman correlation coefficients; none reached the limit of  $|r| > 0.7$  (Dormann et al., 2013). In both models, we integrated local and landscape variables of Shannon diversity of vegetation and landscape, distance to the city center, and green space perimeter-area ratio. We included the interaction of vegetation and landscape diversity to address possible changes in the effects of enhanced roadside vegetation in different urban landscape settings. In both models, the sampling year was integrated as a covariate to detect possible variation in bee sampling and vegetation due to the sowing of the seed mixture (Rojas-Botero et al., 2023a). In the bee species richness model, we included bee abundance as a covariate to avoid sampling effects.

After running a full model with all explanatory variables, we reduced the factors manually by considering AIC and *p*-values, and the results of the minimal models were presented. Model residuals (QQ, dispersion, outlier, quantiles, overdispersion, zero inflation) were checked using the R-package DHARMA (version 0.4.6; Hartig, 2021).

### 2.5.2. Fourth corner analysis

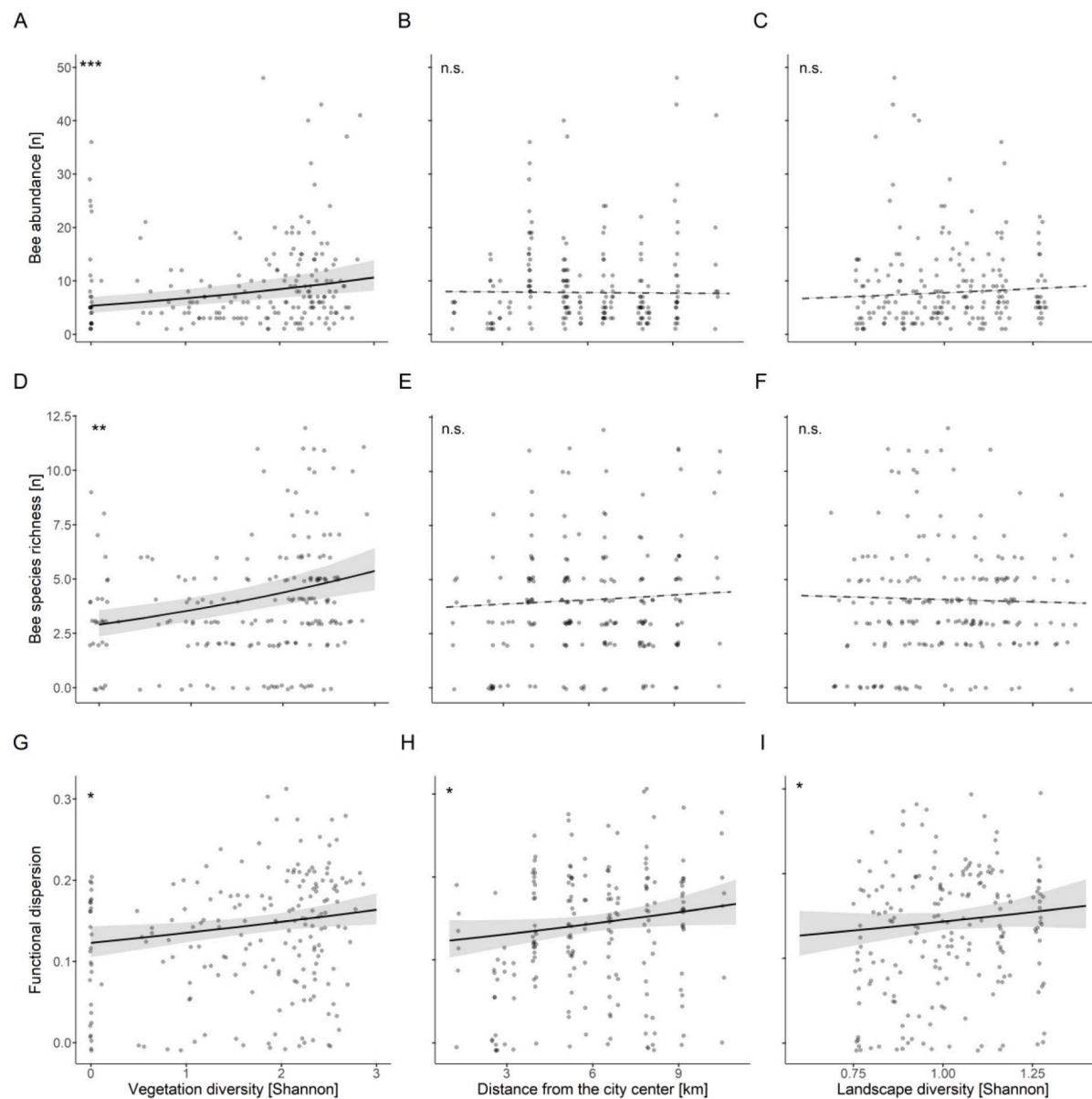
To analyze trait-specific interactions with the environment, we set up generalized linear latent variable models (gllvm) using the R-package gllvm (version 1.3.1; Niku et al., 2019b). This tool offers opportunities for ordination and analysis of multivariate species or trait responses to environmental gradients. Compared to methods with non-metric approaches, this model-based framework provides possibilities for quality checking and residual analysis as in standard linear modeling. We generated three matrices as overlapping layers containing information about species abundances, environmental conditions, and species-specific trait information (Table 1). We included the same environmental variables and the random effect term (site triplets), as in the glmmms. A Poisson model with two latent variables and fitted with the variational approximation method had the lowest AIC (Niku et al., 2019a). An interaction term was included with all environmental and trait variables, and a random slope effect was added to model excess heterogeneity of species responses to environmental factors (Niku et al., 2021). Species co-occurrence results of the gllvm were plotted as ordination with the ordiplot.gllvm-function. Model residuals were checked using the plot.gllvm-function of the gllvm package.

## 3. Results

Along the five major roads, we found 1632 wild bees, with  $9.0 \pm 8.3$  individuals per patch (means  $\pm$  SD; 1–48 individuals). The most abundant species were *Lasioglossum nitidulum* (25 %), *L. morio* (24 %), and *Hylaeus communis* (10 %). *Apis mellifera*, which was excluded from the analysis, amounted to 12 %. The wild bees belonged to 78 species out of 15 genera. We identified 11 oligoleptic and 67 polylectic species and 12 species that relied on specific nesting structures or substrates, whereas 66 were unspecialized nesters; 45 species were solitary, 23 were social, and six were parasitic. Most species had small body sizes, with  $7.3 \pm 2.3$  mm on average (range: 4.5–25.0 mm) and long lifespans with a mean of  $28.6 \pm 4.6$  weeks (range: 8.7–34.9 weeks).

### 3.1. Bee abundance, species richness, and functional dispersion

Bee abundance and species richness increased with the diversity of the roadside vegetation but were independent of the distance from the city center and the degree of landscape diversity (Fig. 2 A–C). Bee abundance and richness significantly increased with sampling years. Wild bee richness and abundance were positively correlated. Functional dispersion was positively correlated with vegetation diversity, distance from the city center, and landscape diversity (Fig. 2 D–F). The perimeter-area ratio of urban green space had no influence in all applied glmmms. Model result tables can be found in the Appendix (A.6).



**Fig. 2.** Results of three generalized linear mixed effect models (glmm). A–F Bee abundance and species richness increased with Shannon vegetation diversity ( $p < 0.001$ ;  $p < 0.01$ ), but were independent of any landscape variable; G–I Functional dispersion increased with vegetation diversity ( $p < 0.05$ ), distance from the city center ( $p = 0.05$ ), and landscape diversity ( $p < 0.05$ ). Solid lines represent model predictions, gray belts the 95 % confidence intervals, and dots the raw data. Asterisks indicate the level of significance ( $p < 0.05$  \*;  $p < 0.01$  \*\*;  $p < 0.001$  \*\*\*). Dashed gray lines indicate non-significant trends (n.s.).

### 3.2. Fourth-corner-analysis

Consistent with the findings from the linear models, vegetation diversity was the strongest predictor positively affecting wild bee communities. Nevertheless, univoltine bees and bees with smaller body sizes and shorter lifespans were negatively affected by increased vegetation diversity. Larger bees prevailed at the city boundaries, and univoltine bees were negatively associated with landscape diversity. Solitary bees were positively related to a higher perimeter-area ratio of urban green space, indicating the relative importance of green space edges for more than half of the species found (Fig. 3). We added a figure including all analyzed interactions to the appendix (A.7).

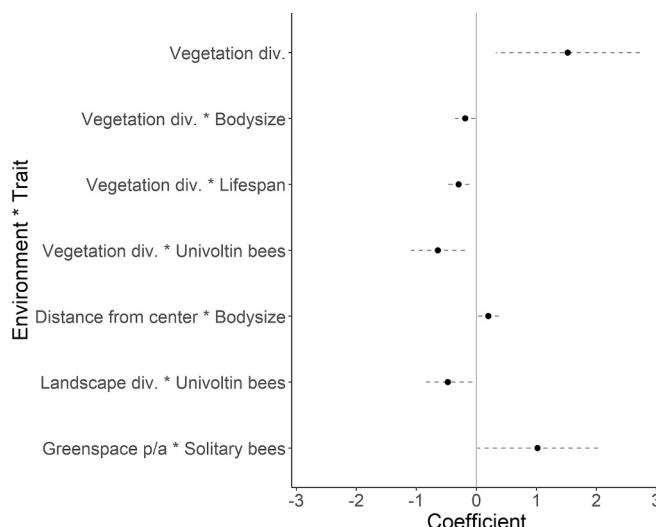
### 3.3. Case-analysis: species co-occurrence

An ordination of the two centered latent variables of the fourth

corner model revealed 15 indicator species (Fig. 4). Five species (*Hoplitis adunca*, *H. leucomelana*, *H. mitis*, *Bombus hypnorum*, *Halictus rubicundus*) had a strong association with the availability of green space edges, i.e., perimeter-area ratio (Table 2). The *Hoplitis* species were univoltine, solitary, aboveground nesting, short-lived bees, with *H. adunca* and *H. mitis* obligate pollen specialists, and nesting in cavities; *H. leucomelana* preferably foraging on *Lotus* plants and nesting in *Rubus* stems. Co-occurring *B. hypnorum* and *H. rubicundus* both were pollen generalists, with *B. hypnorum* creating its colonies above ground, favoring flowers of Rosaceae like *Rubus* spp.; and with *H. rubicundus*, a facultative social and relatively large species whose dispersal was limited to the city borders (Westrich, 2019).

## 4. Discussion

The three-year experiment showed that increasing the diversity of



**Fig. 3.** Results of the generalized linear latent variable model (gllvm), indicating single wild bee trait groups responded differently to environmental conditions. Only significant interactions are shown on the y-axis. Dots represent point estimates of coefficients of the fourth corner analysis, and dashed lines their 95 % confidence intervals. Positive coefficients indicate a favoring relationship between trait and predictor, whereas negative values suggest a filtering effect. Insignificant interactions include zero in their confidence intervals, as shown in the Appendix (A.7). Abbreviations: div.: diversity; p/a: perimeter-area ratio.

roadside vegetation had a positive impact on wild bee abundance, species richness, and functional dispersion. However, wild bee communities became functionally simplified by increasing landscape homogenization and proximity to the city center. Some species were disadvantaged at the relatively small experimental wildflower patches, such as bees with small body sizes, short lifespans, and only one generation per year. Univoltine bees were associated with the availability of green space edges, and large bees were found at the city boundaries. In analyzing functional diversity and trait–environment interactions, we aim to address community assembly and urban trait filtering of wild bees and

offer recommendations for urban conservation.

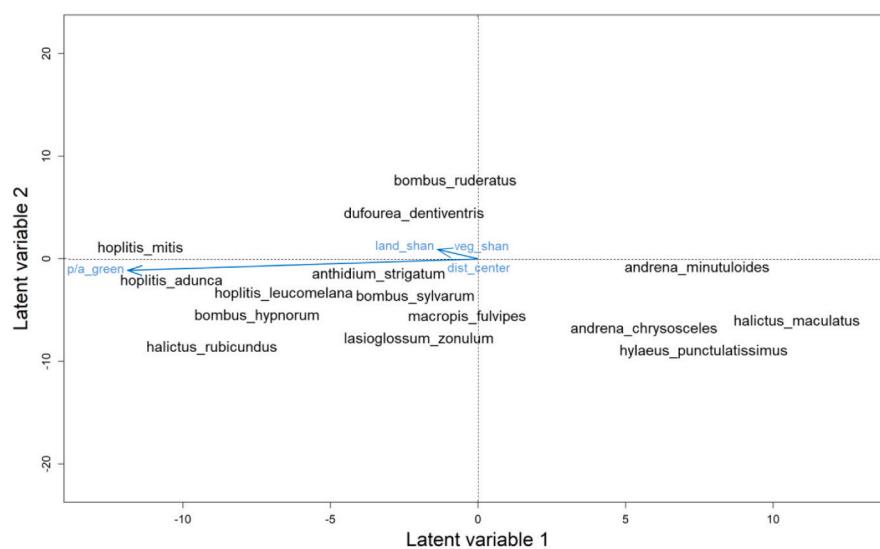
#### 4.1. Bee abundance and species richness

Increasing floral availability, measured as, e.g., flower cover, floral unit counts, or increasing  $\alpha$ -diversity of vegetation, generally causes an upswing in local wild bee abundance and richness and has already been verified for a range of urban habitats (Felderhoff et al., 2022; Fischer et al., 2016; Kratschmer et al., 2018; Schmack and Egerer, 2023). Both variables are commonly used as success indicators in restoration and conservation. However, focusing only on individual and species numbers hinders a deeper understanding of the underlying interactions between wild bees and their environment at network and community levels (Wong et al., 2019). Here, bee abundance and richness were not sensitive to any landscape factor, emphasizing the importance of local resources for wild bees. However, to conclude with relevant implications for the design and conservation of urban green space, analyzing these common variables could not sufficiently explain the ecological consequences of urbanization that shaped the urban roadside communities.

#### 4.2. Functional dispersion of wild bees

In our study, the functional dispersion of wild bee communities increased with vegetation diversity. Therefore, designed seed mixtures for supporting wild bees by incorporating specific plant traits (e.g., variation in phenology and flower shapes and colors) proves to be an optimal strategy for increasing the ecological value of restored urban grasslands (Fornoff et al., 2017; Dietzel et al., 2022; Blüthgen and Klein, 2011). Nonetheless, plant trait redundancy and larger patch sizes are prerequisites to provide sufficient forage quantity for the local wild bee fauna over space and time (Uyttenbroeck et al., 2017). Taking spatial and phenological variation of bee-plant interactions into account is essential at the trait level, as apparently less attractive or functionally redundant plant species can make a difference for rare wild bee species even in urban areas (Burkle et al., 2020; Moens et al., 2023).

Landscape-scale factors altered the dispersion of traits within the communities in our experiment. Several studies investigated trait-based filtering, but only a few used functional indices (Buchholz and Egerer,



**Fig. 4.** Between species correlations, visualized as ordination of the two centered latent variables of the gllvm, the environmental variables (blue), and 15 wild bee ‘indicator’ species, as groups of most correlated species common at specific sites. Environmental variables: veg.shan: vegetation diversity; land.shan: landscape diversity; dist\_center: distance from the city center; p/a.green: perimeter-area-ratio of urban green space. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

**Table 2**

Species and their traits co-occurring at patches with high urban green edge availability. Colors indicate similar traits or dependence on structures or plants.

Species	Phenology/Sociality	Nesting trait	Nesting structure	Diet
<i>Hoplitis mitis</i>	Univoltin, solitary	Aboveground	Cavity	Oligolect: Campanulaceae
<i>Hoplitis adunca</i>	Univoltin, solitary	Aboveground	Cavity	Oligolect: <i>Echium</i> spp.
<i>Hoplitis leucomelana</i>	Univoltin, solitary	Aboveground	Rubus stem	Polylectic, preferably <i>Lotus</i> spp.
<i>Bombus hypnorum</i>	Social	Aboveground	Large cavities	Polylectic, preferably Rosaceae (Rubus)
<i>Halictus rubicundus</i>	Partially bivoltine, facultative social	Belowground	Substrate ubiquist	Polylectic

2020). Here, we present first evidence that functional filtering occurs very close to heavily used urban roadsides and that bee communities are functionally depleted in areas with increasing landscape homogenization. Other than bee abundance and richness, functional dispersion was independent of the sampling year, highlighting the relative importance of the urban landscape that shapes urban wild bee communities by urban trait filtering. A decrease in functional diversity is commonly accompanied by reduced ecological functionality, e.g., pollination in the case of wild bees (Wong et al., 2019; Dietzel et al., 2023). Furthermore, it leads to the reduced ability of wild bee communities to buffer ecological disruptions or changes, such as climate-change-induced impacts of heat waves and the forming of urban heat islands (Hamblin et al., 2018; Kammerer et al., 2021). Besides, functional homogenization increased towards the inner city, highlighting the importance of habitat stepping-stones in urban areas (Buchholz et al., 2020). Overall, enhanced roadsides can be a tool to efficiently support species dispersal and habitat connectivity and can locally improve the quantity and quality of wild bee forage, as bee abundance, richness and functional diversity increased on the wildflower patches (Sydenham et al., 2017).

#### 4.3. Trait-environment interactions

In the fourth corner analysis, enhanced roadside vegetation in general positively affected wild bee communities, in line with the results of the glmm's. However, increased vegetation diversity possibly triggered resource competition for small bees with larger species. Body sizes correlate with wild bees' competitive capabilities, as large bees exploit food resources more effectively by covering high distances between nesting and foraging sites (Kendall et al., 2022). They also can carry greater loads of pollen and nectar, which decreases local resources for less effective species and affects their reproduction (Page and Williams, 2023). For example, body sizes in four common bumblebee species were significantly reduced in situations of high competition with honeybees (Goulson and Sparrow, 2009). Due to their lower foraging ranges, small bees rely on their host plants adjacent to their nesting sites. Thus, planting wildflower patches in isolated areas could favor large species over small ones (Harrison and Winfree, 2015).

Additionally, we found lower numbers of univoltine and short-lived species at patches with high vegetation and landscape diversity. Bees that are socially organized or produce a second generation in summer have an advantage concerning their seasonal abundances and more effective pollen and nectar exploitation (Page and Williams, 2023; Brasil et al., 2023). Even in diverse landscapes, univoltine bees showed a negative trend in our experiment. Urbanization, in general, favors generalist, social species with long flight periods, and the here-used inner-city gradient was most likely not able to cover broader phenological shifts on the landscape scale (Padilla and Sutherland, 2019). The same applies to food and nesting specialists and parasitic bees, which were rare in the samples. However, except for seasonal variation, urbanization impacts on phenological traits still need to be better understood (Buchholz and Egerer, 2020).

Solitary bees are more prone to negative effects of urbanization. For example, Banaszak-Cibicka and Dylewski (2021) found that solitary

bees decrease in most urban habitats, and Ropars et al. (2019) reported that solitary bees are outcompeted in sites with intensive urban beekeeping. In our study, solitary bees were associated with the availability of green space edges. Along the linear landscape elements of hedges and shrubs, borders of parks, dikes, and lawns, species sensitive to urbanization can still find niches that provide structures for nesting as well as sufficient forage (Tward et al., 2021). This highlights the importance of these secondary habitats for wild bees within structurally poor urban environments (Tward and Banaszak-Cibicka, 2019). It also stresses the importance of conserving and enhancing those habitats for species prone to intense land use and anthropogenic disturbance (Sile et al., 2023).

#### 4.4. Species co-occurrence and trait-based conservation

Local vegetation, urban landscape composition, and configuration shaped the functional diversity of the wild bee communities. We identified five indicator species co-occurring at patches with increased availability of urban green space edges, and certain functional commonalities can be recognized. Knowing their habitat requirements and given that these species were bound to green space edges in urban areas, nest site restoration is a tool to foster urban wild bee populations locally and support their dispersal with roadside enhancements, such as wildflower patches (Winfree, 2010). In addition, creating open soil nesting structures supports a large proportion of ground-nesting bee species that are limited in their dispersal, e.g., the found *Halictus rubicundus* (Neumüller et al., 2022). Yet, research on artificially introduced nesting hills as stepping-stones at urban sites or gradients and the influence of different substrates and exposures is lacking, and so it is for other structures like shrub stems and dead wood (Antoine and Forrest, 2021).

For an optimization of urban floral restoration, using native seed material and designing mixtures for different purposes and types of green spaces in future-changing urban climates is promising (Dietzel et al., 2022; Rojas-Botero et al., 2023b; Staab et al., 2015). Information on plant attractiveness for wild bees is abundant (Westrich, 2019; Kuppler et al., 2023). Combining ecological knowledge about specific site conditions, e.g., at roadsides, and taking floral specializations of wild bees into account is necessary to successfully establish pollinator-friendly green space that supports species groups affected by ongoing urbanization. Therefore, a mechanistic understanding of urban filtering processes helps to predict trait-based changes in species distributions (Green et al., 2022). More systematic urban restoration approaches at a landscape scale are needed to mitigate biodiversity losses caused by urbanization (Harvey et al., 2020; Klaus and Kiehl, 2021).

#### 5. Conclusions

Increased vegetation diversity along urban roadsides positively affects individual and species numbers and the functional diversity of wild bee communities. Enhancement of roadside vegetation can be achieved by different strategies, e.g., changing management or using seed mixtures, implying differences in costs and practical effort on different time scales. Sowing species-rich mixtures is specifically advantageous for

newly established roadsides, after reconstruction, when soil seed banks are depleted in native species or dominated by invasive neophytes. Designing seed mixtures for urban green spaces requires expert knowledge of the ecological ranges of plants, their suitability for specific urban habitats, and particular knowledge about the pollinator species adapted to those plants. Analyzing trait–environment interactions supports a more accurate monitoring of restoration measures in urban areas. Additionally, by understanding the interactions of bee species and their environment, groups of species discriminated by urban landscape change are identified, and the role of specific habitat types and landscape elements is determined. In doing so, conservation action can be taken more systematically and efficiently to mitigate local species extinctions and global biodiversity declines driven by urbanization.

## Funding

This study was funded by the non-profit Regina-Bauer-Foundation and the Bavarian State Ministry of the Environment and Consumer Protection (KP01KPB-73852).

## CRediT authorship contribution statement

**Simon Dietzel:** Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Sandra Rojas-Botero:** Data curation, Investigation, Methodology, Validation, Writing – review & editing. **Anja Dichtl:** Data curation, Investigation, Visualization, Writing – review & editing. **Johannes Kollmann:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Christina Fischer:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgements

We thank the students Corinna Lieberth, Carmen Meyer, Franz Haertel, Julia Hiller, and Phoebe Koppendorfer, who greatly supported insect sampling and sorting in the lab. We are also grateful to Gudrun Kloos (Department for Public Green Space, Munich) who provided permission for our experiment. The seed producer Johann Krimmer (Pulling, Germany) provided local seed material, the landscape engineer Andreas Schweiger ('Grüne Aussichten', Ismaning) prepared the experimental sites and gave valuable practical advice. We thank Silvia Gonzales, Sebastian Gardt and Christian Grundmann from Green City e. V. for the cooperation within the project.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110480>.

## References

- Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2001. Fauna Helvetica. Apidae 3. *Halicus, Lasioglossum*. Centre Suisse de Cartographie de la Faune, Neuchâtel.
- Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2004. Fauna Helvetica. Apidae 4. *Anthidium, Chelostoma, Coelioxys, Dioryx, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Centre Suisse de Cartographie de la Faune, Neuchâtel.
- Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2007. Fauna Helvetica. Apidae 5. *Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetrabronia, Thyreus, Xylocopa*. Centre Suisse de Cartographie de la Faune, Neuchâtel.
- Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2010. Fauna Helvetica. Apidae 6. *Andrena, Melliturga, Panurginus, Panurgus*. Centre Suisse de Cartographie de la Faune, Neuchâtel.
- Amiet, F., Müller, A., Praz, C., 2017. Fauna Helvetica. Apidae I. *Apis, Bombus*, 2nd ed. info fauna Centre suisse de cartographie de la faune, Neuchâtel, Suisse.
- Anderson, M., Crubaugh, F., Greenslit, C., Hill, E., Kroth, H., Stanislawski, E., Ribbons, R., Del Toro, I., 2023. B.Y.O. Bees: managing wild bee biodiversity in urban greenspaces. *PLoS One* 18, e0281468. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0281468>.
- Antoine, C.M., Forrest, J.R., 2021. Nesting habitat of ground-nesting bees: a review. *Ecol. Entomol.* 46, 143–159. <https://resjournals.onlinelibrary.wiley.com/doi/full/10.1111/een.12986>.
- Baldock, K.C., 2020. Opportunities and threats for pollinator conservation in global towns and cities. *Curr. Opin. Insect Sci.* 38, 63–71. <https://www.sciencedirect.com/science/article/pii/S2214574520300201>.
- Banaszak-Cibicka, W., Dylewski, Ł., 2021. Species and functional diversity - a better understanding of the impact of urbanization on bee communities. *Sci. Total Environ.* 774, 145729. <https://www.sciencedirect.com/science/article/pii/S0048969721007968>.
- Bavarian State Statistics Office, 2020. Flächenerhebung nach Art der tatsächlichen Nutzung zum Stichtag 31.Dezember 2019. <https://www.statistik.bayern.de/presse/mitteilungen/2020/pm307/index.html> (27 August 2023).
- Blüthgen, N., Klein, A.-M., 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* 12, 282–291. <https://www.sciencedirect.com/science/article/pii/S1439179110001350>.
- Brasil, S.N.R., Ayers, A.C., Rehan, S.M., 2023. The effect of urbanisation and seasonality on wild bee abundance, body size and foraging efforts. *Ecol. Entomol.* 48, 499–507. <https://resjournals.onlinelibrary.wiley.com/doi/full/10.1111/een.13243>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400. <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>.
- Buchholz, S., Egerer, M.H., 2020. Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. *Biodivers. Conserv.* 29, 2779–2801. <https://link.springer.com/article/10.1007/s10531-020-02003-8>.
- Buchholz, S., Gathof, A.K., Grossmann, A.J., Kowarik, I., Fischer, L.K., 2020. Wild bees in urban grasslands: urbanisation, functional diversity and species traits. *Landscape. Urban Plan.* 196, 103731. <https://www.sciencedirect.com/science/article/pii/S0169204619306693>.
- Burkle, L.A., Delphia, C.M., O'Neill, K.M., 2020. Redundancy in wildflower strip species helps support spatiotemporal variation in wild bee communities on diversified farms. *Basic Appl. Ecol.* 44, 1–13. <https://www.sciencedirect.com/science/article/pii/S1439179120300153>.
- Dániel-Ferreira, J., Berggren, Å., Wissman, J., Öckinger, E., 2022. Road verges are corridors and roads barriers for the movement of flower-visiting insects. *Ecography* 2022.
- Dathe, H.H., Scheuchl, E., Ockermann, E., 2016. Illustrierte Bestimmungstabelle für die Arten der Gattung *Hylaeus* F. (Maskenbienen) in Deutschland, Österreich und der Schweiz. Supplement 1. *Entomologica Austriaca. Zeitschrift der Österreichischen Entomologischen Gesellschaft*, 1–51.
- deBello, F., Botta-Dukát, Z., Lepš, J., Fibich, P., 2021. Towards a more balanced combination of multiple traits when computing functional differences between species. *Methods Ecol. Evol.* 12, 443–448. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.13537>.
- Dietzel, S., Rojas-Botero, S., Fischer, C., Kollmann, J., 2022. Aufwertung urbaner Straßenräder als Anpassung an den Klimawandel und zur Förderung bestäubender Insekten. *ANLiegend Natur* 44, 31–42.
- Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023. Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecol. Indic.* 147, 109980. <https://www.sciencedirect.com/science/article/pii/S1470160X2300122X>.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1600-0587.2012.07348.x>.
- EEA, 2018. Corine Land Cover. Copernicus Land Monitoring Service. European Environment Agency, EU Copernicus Land Monitoring Service.
- Esri Inc, 2020. ArcGIS Desktop. Esri Inc., USA.
- Eurostat, 2023. Statistical Atlas. Eurostat Census population grid. [https://ec.europa.eu/eurostat-atlas/viewer/?config=REF-GRID.json&mids=2,3,POPGRDEST2021,CNT\\_OVL&o=1,0,5,1,0,7&ch=POP,POPGRDGST&center=45.49798,15.7194,4&lcis=POPGRDEST2021&](https://ec.europa.eu/eurostat-atlas/viewer/?config=REF-GRID.json&mids=2,3,POPGRDEST2021,CNT_OVL&o=1,0,5,1,0,7&ch=POP,POPGRDGST&center=45.49798,15.7194,4&lcis=POPGRDEST2021&) (17 October 2023).
- Fauvieu, A., Baude, M., Bazin, N., Fiordaliso, W., Fisogni, A., Fortel, L., Garrigue, J., Geslin, B., Goulnik, J., Guillaud, L., Hautekèete, N., Heiniger, C., Kuhlmann, M., Lambert, O., Langlois, D., Le Féon, V., Lopez Vaamonde, C., Maillet, G., Massol, F.,

- Michel, N., Michelot-Antalik, A., Michez, D., Mouret, H., Piquot, Y., Potts, S.G., Roberts, S., Ropars, L., Schurr, L., van Reeth, C., Villalta, I., Zaninotto, V., Dajoz, I., Henry, M., 2022. A large-scale dataset reveals taxonomic and functional specificities of wild bee communities in urban habitats of Western Europe. *Sci. Rep.* 12, 18866. <https://www.nature.com/articles/s41598-022-21512-w>.
- Felderhoff, J., Gathof, A.K., Buchholz, S., Egerer, M., 2022. Vegetation complexity and nesting resource availability predict bee diversity and functional traits in community gardens. *Ecol. Appl.* e2759. <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eaap.2759>.
- Ferrari, A., Polidori, C., 2022. How city traits affect taxonomic and functional diversity of urban wild bee communities: insights from a worldwide analysis. *Apidologie* 53, 1–23. <https://link.springer.com/article/10.1007/s13592-022-00950-5>.
- Fischer, L.K., Eichfeld, J., Kowarik, I., Buchholz, S., 2016. Disentangling urban habitat and matrix effects on wild bee species. *PeerJ* 4, e2729. <https://pubmed.ncbi.nlm.nih.gov/27917318/>.
- Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. *Oikos* 126, 1020–1030.
- Fox, J., 2022. Polycor. Polychoric and polyserial correlations. <https://CRAN.R-project.org/package=polycor>.
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winquist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceed. Biol. Sci.* 282, 20142620.
- Gathof, A.K., Grossmann, A.J., Herrmann, J., Buchholz, S., 2022. Who can pass the urban filter? A multi-taxon approach to disentangle pollinator trait-environmental relationships. *Oecologia* 199, 165–179. <https://link.springer.com/article/10.1007/s00442-022-05174-z>.
- Goulson, D., Sparrow, K.R., 2009. Evidence for competition between honeybees and bumblebees: effects on bumblebee worker size. *J. Insect Conserv.* 13, 177–181. <https://link.springer.com/article/10.1007/s10841-008-9140-y>.
- Green, S.J., Brookson, C.B., Hardy, N.A., Crowder, L.B., 2022. Trait-based approaches to global change ecology: moving from description to prediction. *Proc. Biol. Sci.* 289, 20220071.
- Hamblin, A.L., Youngsteadt, E., Frank, S.D., 2018. Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosyst.* 21, 419–428. <https://link.springer.com/article/10.1007/s11252-018-0731-4>.
- Harrison, T., Winfree, R., 2015. Urban drivers of plant-pollinator interactions. *Funct. Ecol.* 29, 879–888. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12486#fec12486-bib-0012>.
- Hartig, F., 2021. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://CRAN.R-project.org/package=DHARMA>.
- Harvey, J.A., Heinen, R., Armbrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E.E., Dicke, M., Dijkstra, K.-D.B., Dyer, L., Ellers, J., Fartmann, T., Forister, M. L., Furlong, M.J., García-Aguayo, A., Gerlach, J., Gols, R., Goulson, D., Habel, J.-C., Haddad, N.M., Hallmann, C.A., Henriquez, S., Herberstein, M.E., Hochkirch, A., Hughes, A.C., Jepsen, S., Jones, T.H., Kaydan, B.M., Kleijn, D., Klein, A.-M., Latty, T., Leather, S.R., Lewis, S.M., Lister, B.C., Losey, J.E., Lowe, E.C., Macadam, C.R., Montoya-Lerma, J., Nagano, C.D., Ogan, S., Orr, M.C., Painting, C.J., Pham, T.-H., Potts, S.G., Rauf, A., Roslin, T.L., Samways, M.J., Sanchez-Bayo, F., Sar, S.A., Schultz, C.B., Soares, A.O., Thancharoen, A., Tscharntke, T., Tylianakis, J.M., Umbers, K.D.L., Vet, L.E.M., Visser, M.E., Vujic, A., Wagner, D.L., WallisDeVries, M.F., Westphal, C., White, T.E., Wilkins, V.L., Williams, P.H., Wyckhuys, K.A.G., Zhu, Z.-R., Kroon, H.d., 2020. International scientists formulate a roadmap for insect conservation and recovery. *Natur. Ecol. Evol.* 4, 174–176. <https://www.nature.com/articles/s41559-019-1079-8>.
- Herrmann, J., Buchholz, S., Theodorou, P., 2023. The degree of urbanisation reduces wild bee and butterfly diversity and alters the patterns of flower-visitation in urban dry grasslands. *Sci. Rep.* 13, 2702. <https://www.nature.com/articles/s41598-023-9275-8>.
- Kammerer, M., Goslee, S.C., Douglas, M.R., Tooker, J.F., Grozinger, C.M., 2021. Wild bees as winners and losers: relative impacts of landscape composition, quality, and climate. *Glob. Chang. Biol.* 27, 1250–1265. <https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15485>.
- Kendall, L.K., Mola, J.M., Portman, Z.M., Cariveau, D.P., Smith, H.G., Bartomeus, I., 2022. The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* 103, e3809. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.3809#>.
- Klaus, V.H., Kiehl, K., 2021. A conceptual framework for urban ecological restoration and rehabilitation. *Basic Appl. Ecol.* 52, 82–94. <https://www.sciencedirect.com/science/article/pii/S1439179121000372>.
- Knapp, S., Aronson, M.F.J., Carpenter, E., Herrera-Montes, A., Jung, K., Kotze, D.J., La Sorte, F.A., Lepczyk, C.A., MacGregor-Fors, I., MacIvor, J.S., Moretti, M., Nilon, C.H., Piana, M.R., Rega-Brodsky, C.C., Salisbury, A., Threlfall, C.G., Trisos, C., Williams, N.S.G., Hahs, A.K., 2021. A research agenda for urban biodiversity in the global extinction crisis. *BioScience* 71, 268–279. <https://academic.oup.com/bioscience/article/71/3/268/6009693?login=false>.
- Kowarik, I., Fischer, L.K., Kendal, D., 2020. Biodiversity conservation and sustainable urban development. *Sustainability* 12, 4964. <https://www.mdpi.com/2071-1050/12/4964>.
- Kratschmer, S., Kriechbaum, M., Pachinger, B., 2018. Buzzing on top: linking wild bee diversity, abundance and traits with green roof qualities. *Urban Ecosyst.* 21, 429–446. <https://link.springer.com/article/10.1007/s11252-017-0726-6>.
- Krewenka, K.M., Holzschuh, A., Tscharntke, T., Dormann, C.F., 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biol. Conserv.* 144, 1816–1825. <http://www.sciencedirect.com/science/article/pii/S00632071100108X>.
- Kuppler, J., Neumüller, U., Mayr, A.V., Hopfenmüller, S., Weiss, K., Prosi, R., Schanowski, A., Schwenninger, H.-R., Ayasse, M., Burger, H., 2023. Favourite plants of wild bees. *Agr. Ecosyst. Environ.* 342, 108266. <https://www.sciencedirect.com/science/article/pii/S0167880922004157>.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-2244.1>.
- Marshall, A.J., Grose, M.J., Williams, N.S., 2019. From little things: more than a third of public green space is road verge. *Urban Forest. Urban Green.* 44, 126423. <https://www.sciencedirect.com/science/article/pii/S1618866719300718>.
- Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosyst.* 20, 1359–1371. <https://link.springer.com/article/10.1007/s11252-017-0688-8>.
- Moens, M., Biesmeijer, J.C., Klumpers, S.G.T., Marshall, L., 2023. Are threatened species special? An assessment of Dutch bees in relation to land use and climate. *Ecol. Evol.* 13, e10326. <https://onlinelibrary.wiley.com/doi/10.1002/ece3.10326#pane-pw-figures>.
- Munich city administration, 2023. Population, area and population density in the city districts. <https://stadt.muenchen.de/infos/statistik-bevoelkerung.html> (17 October 2023).
- Muñoz, P.T., Torres, F.P., Megías, A.G., 2015. Effects of roads on insects: a review. *Biodivers. Conserv.* 24, 659–682.
- Neumüller, U., Burger, H., Mayr, A.V., Hopfenmüller, S., Krausch, S., Herwig, N., Burger, R., Diestelhorst, O., Emmerich, K., Haider, M., Kiefer, M., Konicek, J., Kornmilch, J.-C., Moser, M., Saure, C., Schanowski, A., Scheuchl, E., Sing, J., Wagner, M., Witter, J., Schwenninger, H.R., Ayasse, M., 2022. Artificial Nesting Hills promote wild bees in agricultural landscapes. *Insects* 13, 726. <https://www.mdpi.com/2075-4450/13/8/726>.
- Niku, J., Brooks, W., Herliansyah, R., Hui, F.K.C., Taskinen, S., Warton, D.I., 2019a. Efficient estimation of generalized linear latent variable models. *PLoS One* 14, e0216129. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0216129>.
- Niku, J., Hui, F.K.C., Taskinen, S., Warton, D.I., 2019b. gllmv: fast analysis of multivariate abundance data with generalized linear latent variable models in r. *Methods Ecol. Evol.* 10, 2173–2182. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.13303>.
- Niku, J., Hui, F.K.C., Taskinen, S., Warton, D.I., 2021. Analyzing environmental-trait interactions in ecological communities with fourth-corner latent variable models. *Environmetrics* 32, e2683. <https://onlinelibrary.wiley.com/doi/10.1002/env.2683>.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borchard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., O'Hill, M., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J., Weedon, J., 2022. vegan: community ecology package. <https://CRAN.R-project.org/package=vegan>.
- Open Street Map Contributors, 2020. Geofabrik download server. Upper Bavaria. <http://download.geofabrik.de/europe/germany/oberbayern.html> (22 January 2020).
- Padilla, B.J., Sutherland, C., 2019. A framework for transparent quantification of urban landscape gradients. *Landscape Ecol.* 34, 1219–1229. <https://link.springer.com/article/10.1007/s10980-019-00858-z>.
- Page, M.L., Williams, N.M., 2023. Evidence of exploitative competition between honey bees and native bees in two California landscapes. *J. Anim. Ecol.* 92, 1802–1814. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2656.13973>.
- Palacio, F.X., Callaghan, C.T., Cardoso, P., Hudgins, E.J., Jarzyna, M.A., Ottaviani, G., Riva, F., Graco-Roza, C., Shirey, V., Mammola, S., 2022. A protocol for reproducible functional diversity analyses. *Ecography* 2022, e06287. <https://onlinelibrary.wiley.com/doi/full/10.1111/ecog.06287>.
- Parris, K.M., Amati, M., Bekessy, S.A., Dagenais, D., Fryd, O., Hahs, A.K., Hes, D., Imberger, S.J., Livesley, S.J., Marshall, A.J., Rhodes, J.R., Threlfall, C.G., Tingley, R., van der Ree, R., Walsh, C.J., Wilkerson, M.L., Williams, N.S., 2018. The seven lamps of planning for biodiversity in the city. *Cities* 83, 44–53. <https://www.sciencedirect.com/science/article/pii/S0264275117314245>.
- Phillips, B.B., Wallace, C., Roberts, B.R., Whitehouse, A.T., Gaston, K.J., Bullock, J.M., Dicks, L.V., Osborne, J.L., 2020. Enhancing road verges to aid pollinator conservation: a review. *Biol. Conserv.* 108687. <http://www.sciencedirect.com/science/article/pii/S000632072030745X>.
- Ricotta, C., Carboni, M., Acosta, A.T., 2015. Let the concept of indicator species be functional! *J. Veg. Sci.* 26, 839–847.
- Rojas-Botero, S., Dietzel, S., Kollmann, J., Teixeira, L.H., 2023a. Towards a functional understanding of rehabilitated urban road verge grasslands: effects of planting year, site conditions, and landscape factors. *Flora* 152417. <https://www.sciencedirect.com/science/article/pii/S0367253023002062>.
- Rojas-Botero, S., Teixeira, L.H., Kollmann, J., 2023b. Low precipitation due to climate change consistently reduces multifunctionality of urban grasslands in mesocosms. *PLoS One* 18, e0275044. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0275044>.
- 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. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0222316>.

- Scheuchl, E., 2000. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band I: Anthophoridae. 2. extended edition, self-published. Velden, pp. 1–158.
- Scheuchl, E., 2006. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band II: Megachilidae, Mellitidae, 2. extended edition. Apollo Books, Stenstrup.
- Schmack, J.M., Egerer, M., 2023. Floral richness and seasonality influences bee and non-bee flower interactions in urban community gardens. *Urban Ecosyst.* 1–14. <https://link.springer.com/article/10.1007/s11252-023-01353-9>.
- Schmid-Egger, C., Scheuchl, E., 1997. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band III: Andrenidae. Self-published. Velden.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsemair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674. <https://www.nature.com/articles/s41586-019-1684-3.pdf>.
- Staab, K., Yannelli, F.A., Lang, M., Kollmann, J., 2015. Bioengineering effectiveness of seed mixtures for road verges: functional composition as a predictor of grassland diversity and invasion resistance. *Ecol. Eng.* 84, 104–112. <https://www.sciencedirect.com/science/article/pii/S0925857415301221>.
- Stoklosa, J., Blakey, R.V., Hui, F.K.C., 2022. An overview of modern applications of negative binomial modelling in ecology and biodiversity. *Diversity* 14, 320. <https://www.mdpi.com/1424-2818/14/5/320>.
- Sülie, G., Kovács-Hostyánszki, A., Sárospataki, M., Kelemen, T.I., Halassy, G., Horváth, A., Demeter, I., Báldi, A., Szegedi, V., 2023. First steps of pollinator-promoting interventions in Eastern European urban areas – positive outcomes, challenges, and recommendations. *Urban Ecosyst.* 1–15. <https://link.springer.com/article/10.1007/s11252-023-01420-1>.
- Sydenham, M.A.K., Moe, S.R., Kuhlmann, M., Potts, S.G., Roberts, S.P.M., Totland, Ø., Eldegard, K., 2017. Disentangling the contributions of dispersal limitation, ecological drift, and ecological filtering to wild bee community assembly. *Ecosphere* 8, e01650. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1650>.
- Theodorou, P., Radzevičiutė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E., Paxton, R.J., 2020. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11, 1–13. <https://www.nature.com/articles/s41467-020-14496-6.pdf>.
- Tward, L., Banaszak-Cibicka, W., 2019. Wastelands: their attractiveness and importance for preserving the diversity of wild bees in urban areas. *J. Insect Conserv.* 23, 573–588. <https://link.springer.com/article/10.1007/s10841-019-00148-8>.
- Tward, L., Sobieraj-Betlińska, A., Szefer, P., 2021. Roads, railways, and power lines: are they crucial for bees in urban woodlands? *Urban Forest. Urban Green.* 61, 127120. <https://www.sciencedirect.com/science/article/pii/S161886672100145X>.
- Uyttenbroeck, R., Piqueray, J., Hatt, S., Mahy, G., Monty, A., 2017. Increasing plant functional diversity is not the key for supporting pollinators in wildflower strips. *Agr. Ecosyst Environ.* 249, 144–155. <https://www.sciencedirect.com/science/article/pii/S016788091730364X>.
- Vega, K.A., Küffer, C., 2021. Promoting wildflower biodiversity in dense and green cities: the important role of small vegetation patches. *Urban For. Urban Green.* 62, 127165. <https://www.sciencedirect.com/science/article/pii/S1618866721001904>.
- Verboven, H.A., Uyttenbroeck, R., Brys, R., Hermy, M., 2014. Different responses of bees and hoverflies to land use in an urban-rural gradient show the importance of the nature of the rural land use. *Landscape Urban Plan.* 126, 31–41. <http://www.sciencedirect.com/science/article/pii/S0169204614000528>.
- Wenzel, A., Grass, I., Belavadi, V.V., Tscharntke, T., 2020. How urbanization is driving pollinator diversity and pollination – a systematic review. *Biol. Conserv.* 241, 108321. <https://www.sciencedirect.com/science/article/pii/S0006320719307761>.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* 78, 653–671. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/07-1292.1>.
- Westrich, P., 2019. Die Wildbienen Deutschlands, 2, aktualisierte Auflage. Ulmer, Stuttgart (Hohenheim).
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291. <http://www.sciencedirect.com/science/article/pii/S0006320710001138>.
- Winfree, R., 2010. The conservation and restoration of wild bees. *Ann. N. Y. Acad. Sci.* 1195, 169–197.
- Wong, M.K.L., Guénard, B., Lewis, O.T., 2019. Trait-based ecology of terrestrial arthropods. *Biol. Rev.* 94, 999–1022. <https://onlinelibrary.wiley.com/doi/full/10.1111/brv.12488>.