Larger cities host richer bee faunas, but are no refuge for species with concerning conservation status: Empirical evidence from Western Europe

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Larger cities host richer bee faunas, but are no refuge for species with concerning conservation status: empirical evidence from Western Europe.

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Abstract

In the context of worldwide biodiversity and wild bee decline, it is increasingly important to better understand the effect of land-use changes on wild bee communities at a global scale. To do so, we studied the effect of city area and urban green spaces layout on wild bee species richness and community composition, as well as on wild bee species with an unfavorable UICN conservation status. This study was based on a large European dataset encompassing 20 cities from France, Belgium and Switzerland. We found a mean wild bee species richness in cities of 96 ± 48 (SD), showing that this species richness was highly variable among cities. The main factor positively influencing wild bee species richness in cities was the area of the city. Conversely, species richness was not significantly related to the total area of urban green spaces in a given city, measured as the spatial extent of urban parks, wastelands and other semi-natural habitats, excluding urban private gardens. Species with conservation status were quite scarce in urban environments, especially when compared to the European Red List of Bees, and we could not link their presence to either city or urban green space area. Dissimilarities in wild bee species community compositions were not associated with any of the studied characteristics of cities. We found that the dissimilarity of wild bee community composition among cities was mainly driven by the rarest species, as the most common ones were found in a majority of the cities sampled. Overall, these results emphasize that larger cities host more wild bee species, but are no refuge for the ones with concerning conservation status. Thus, stakeholders are encouraged to design their cities in favor of biodiversity to better support wild bee communities, and perhaps mitigate the established effect of the urban ecological filter.

Introduction

By 2030, anthropic disturbances of habitats, such as agricultural and urban use, are scheduled to increase, especially in developing countries where agricultural intensification and urban development are still low (Seto et al., 2012; Zabel et al., 2019). This underlines the need to better understand how urbanization impacts on biodiversity. Therefore, given the importance of wild bees as pollinators, a better understanding of their current state in urban environments is strongly needed. This is especially true at a time in which citizens' needs for nature and biodiversity in their surroundings are growing, such as for local food production, and pollinating insects and flowering plants are at risk of parallel declines (Biesmeijer et al., 2006; Schleuning et al., 2016).

Urban environments can be challenging for wild bee communities for several reasons. First, these areas are highly impervious, resulting in the loss and fragmentation of habitats that are suitable for wild bees, as well as the reduction of their floral and nesting resources (Geslin et al., 2016; Hamblin et al., 2018; Potts et al., 2010). Moreover, a large part of the floral resources found in cities are provided by ornamental flowers, in private gardens and public parks, that can be less attractive to pollinators than native plants (Erickson et al., 2020; Garbuzov et al., 2017; Garbuzov & Ratnieks, 2014). Cities experience higher temperatures compared to the surrounding environment due to the urban heat island effect, which can be harmful to wild bees, leading to decline in their abundance (Hamblin et al., 2018; Martinet et al., 2021). Cities are also polluted in various ways, such as soil or air pollution, which can have negative impacts on pollinators and plants-pollinators interactions, including wild bees (Baldock, 2020; Harrison & Winfree, 2015).

Despite these challenges, cities have been reported to host a substantial number of wild bees and other pollinators. Some authors even describe cities as “refuges” for pollinators, particularly when compared to surrounding agricultural landscapes (Hall et al., 2017). Cities can also be considered as biodiversity “hotspots” (Baldock et al., 2019; Theodorou, Radzevičiūtė, et al., 2020), making wild bee conservation in urban environments even more critical. Indeed, several studies have found a high wild bee diversity in different cities spanning over a wide geographic range (Banaszak-Cibicka et al., 2018; Felderhoff et al., 2022; Fortel et al., 2014; Gruver & CaraDonna, 2021; Zaninotto & Dajoz, 2022). However, the complexity of the relationship between urban habitats and pollinators is highlighted by the contrasting trends recorded in a meta-analysis that gathered 141 studies of pollinator communities in urban environments (with 99 out of 141 studies based exclusively on bees). Most often, pollinator community diversity and urbanization were not correlated, less frequently they were positively correlated, and most rarely, negatively correlated (Wenzel et al., 2020).

In the light of these contrasting trends and by comparing multiple cities within a single study, our aim is to understand which characteristics of urban environments influence the diversity of wild bee communities. Wild bees are the best-studied pollinator group and thus the easiest to find information on, making it particularly appropriate for large-scale studies. Currently, most studies concentrate on a single city (Dylewski et al., 2019; Geslin et al., 2015; Hamblin et al., 2018; Zaninotto & Dajoz, 2022) or on urban-rural gradients (Banaszak-Cibicka et al., 2018; Banaszak-Cibicka & Żmihorski, 2012; Fortel et al., 2016; Geslin et al., 2016; Villalta et al., 2022; Zaninotto et al., 2020, 2021). Although these studies provide extensive results of the sites they examine overall, they remain of local interest and are difficult to generalize about. More comprehensive analyses are starting to emerge, such as one conducted by Ferrari and Polidori (2022), who studied the relationships between city characteristics and wild bee community diversity from taxonomic and functional viewpoints in 55 cities worldwide. In their study, they found relationships between city size and wild bee species traits, with fewer parasitic and oligolectic species in larger cities. Moreover, the fragmentation of urban green space led to fewer oligolectic species, and cities with the highest impervious surfaces held less ground nesting species.

Wild bee studies in urban environments also are of particular importance given that an ever-increasing number of cities seek to develop pollinator-friendly initiatives and action plans throughout their administrative districts. Pioneering cases on this topic include the city of Lyon (France), with the European UrbanBees program (Fortel et al., 2014), the *Get Bristol Buzzing* in Bristol (UK), launched in 2015 (Howard, 2015) and at a larger scale a European Commission guide for the design of pollinator-friendly cities (Wilk et al., 2020). In western Europe, local elected officials and land managers support city action plans that aim to promote the suitability of urban green spaces for pollinators, in order to host pollinator communities as diverse as possible within their administrative boundaries. This is usually carried out through the development of alternative management practices (Daniels et al., 2020). However, most actions are carried out at green space level with effects on the local diversity (Zaninotto et al., 2023), and with no information on how many bee species may be expected to occur in a focal city, and how this potential species pool may be related to broader urban features such as the size of the city and its land-use characteristics. In this respect, species-area relationships (SARs) have proven to be a useful tool to help predict species richness variation among cities, e.g. bird species richness (Ferenc et al., 2014). SARs describe how species richness found in a habitat increases with the area of that habitat - inasmuch as larger habitats hold more species than smaller ones (Guilhaumon et al., 2008). Typical SAR curves display a first steeply ascending part as new species rapidly accumulate with increasing areas, followed by a ceiling as the species accumulation rate diminishes when richness approaches the regional species pool. This pattern is usually well described by asymptotic functions such as power laws. Therefore, they are adequately linearized using logarithmic scales, which facilitates the implementation of additional environmental covariates into empiric models and ultimately improves species richness predictions.

SARs have been primarily developed in traditional oceanic island-colonization systems (MacArthur & Wilson, 1967), where species richness increases over time through successive migrations and establishments. Later on, SARs have been used as an effective tool to predict species richness in habitat island systems, i.e. including fragments of formerly continuous habitats where species richness has been on a downward trend. We hypothesize here that a SAR approach applied to city areas may give insights into the bee species richness in cities, along with other components of urban land use, such as urban green space (hereafter UGS) cover and layout.

In addition to the richness of the city species pool, we will evaluate two indicators that may provide useful information on wild bee species communities in cities. First, we computed the species beta-diversity, which indicates whether a given city’s pool of species is more or less unique compared to other cities (i.e. the diversity turnover among cities). We aim to test if different cities host similar wild bee communities due to the strong environmental filter already studied in literature (Deguines et al., 2016; Fauviau et al., 2022). Secondly, we want to assess if bee species with concerning conservation status (i.e., judged to be endangered, vulnerable, threatened or nearly so, Nieto et al., 2014), are found within our dataset and if their occurrence is similar to the one found in all habitats of Europe. Indeed, wild bee species with a conservation status have already been recorded in several cities (Grossmann et al., 2023; Zaninotto & Dajoz, 2022). Therefore, assessing their presence at a larger scale could give a baseline for what can be expected in cities.

To answer these questions, we focus here on a large-scale dataset, encompassing wild bee species diversity across 20 cities of Western Europe (France, Belgium and Switzerland), that differ in their areas of UGS. Our study differs from other large-scale studies that have already been published (e.g. Fauviau et al., 2022; Ferrari & Polidori, 2022; Wenzel et al., 2020). Firstly, we here compare dense urban environments rather than analyzing bee community changes along an urban to non-urban gradient. Secondly, our study is conducted at a different scale than the one of Ferrari and Polidori (2022), and takes into account the sampling heterogeneity of communities. Last, we will tackle on the wild bee community differences among cities, as well as considering conservation status of wild bees in urban places, which has not been done in other large-scale studies.

We will first (i) investigate the wild bee species richness in the aforementioned 20 different cities of western Europe, expecting variation among cities in the species richness of wild bee communities (Banaszak-Cibicka et al., 2018; Felderhoff et al., 2022; Fortel et al., 2014; Gruver & CaraDonna, 2021; Zaninotto & Dajoz, 2022). Then, using SAR, we will determine if, and how wild bee species richness covaries with (ii) city area and (iii) UGS area, supposing that it will more likely be related to UGS area (Buchholz et al., 2020; Steffan-Dewenter, 2003; Zaninotto et al., 2023), as most of the urban habitat consists of buildings and impervious surfaces that are devoid of feeding or nesting habitats for pollinators. Next, (iv) we will examine the impact of UGS layout (number of patches, size and connectivity) on wild bee species richness, knowing that sites management, that we cannot study here, will likely affect wild bee communities (Lerman et al., 2018; Wastian et al., 2016; Zaninotto et al., 2023). We expect that UGS layout will impact wild bee communities, with UGS size and connectivity affecting positively the wild bee species richness (Buchholz et al., 2020; Graffigna et al., 2023; Zaninotto et al., 2023). Moving on, we will investigate (v) whether the species composition of wild bee communities varies among cities, and if UGS layout may be responsible for these variations. Despite a functional homogenization of wild bee communities in cities (Deguines et al., 2016; Fauviau et al., 2022), we wonder if cities can still harbor distinct species assemblages, and if these differences arise from differences in UGS layout. Finally, we will study (vi) how wild bee species with conservation status are faring in urban habitats. Since there is evidence from several parts of the world that cities can provide habitats for species with concerning conservation status, we will investigate if urban habitats of

Western Europe could be viewed as refuges for wild bee species with such a conservation status, and if city size or UGS area could also positively affect their number.

Materials and Methods

Study area and data collection

The study focuses on a set of 20 cities from three western European countries: France, Belgium and Switzerland. Data on bee species diversity was gathered for each city from wild bee specialists affiliated with the GDR *Pollinéco,* a group of pollination-expert scientists from France, Belgium and Switzerland. Most of these experts are part of the INPN (*Inventaire National du Patrimoine Naturel*), a scientific network that aims to evaluate biodiversity within metropolitan France.

All of the data collected were documented in terms of timing and location, and all wild bee species were identified to the species level by expert taxonomists. The original dataset (Fauviau et al., 2022) included wild bee surveys carried out in France, Belgium and Switzerland, and spanning a wide range of habitats, from highly urbanized to semi-natural areas. Since this study focuses on the landscape drivers of wild bee diversity in urban habitats, a subset of the original dataset was used, focusing on samples from cities. We implemented this dataset with information on the bee fauna of two more cities: Nancy Métropole in France and Uccle in Belgium.

City definition, sampling coverage and selection

All wild bee surveys were assigned to a city based on city administrative boundaries. We selected from the initial dataset a subset of wild bee surveys which met criteria of data robustness and ecological relevance. First, to ensure that the cities under consideration were of substantial size, we selected those with more than 20,000 inhabitants (40 cities), which is the statutory population size threshold for a "medium-sized" city in France (Floch & Morel, 2011). From the 40 cities in our initial dataset that met this criterion, we further narrowed down the list to 38 cities, excluding the two for which detailed land use data were not available.

Finally, we selected city surveys whose spatial sampling coverage and species sampling completeness were judged satisfactory. Spatial coverage refers to the percentage of city surface covered by wild bee samples, considering a given sample may, to some extent, include information on species occurring within up to a 1-km radius (Zurbuchen et al., 2010). For each city, we delineated 1 km buffers around each sampling point using the R package sf v1.0-7 (Pebesma et al., 2023). These buffers were then merged to determine the spatial sampling coverage for a given city. For each city, we then calculated a sampling coverage value (%) by dividing the area covered by the merged sampling buffers within the administrative boundary of a city by the total city area.

We then restricted our data set to cities that were adequately sampled, which was defined as having more than a 30% sampling coverage and/or 5 sampling sites. This resulted in a final list of 20 cities: 17 in France, 2 in Belgium, and 1 in Switzerland (see Appendix A).

Estimated species richness

To account for unequal sampling effort among cities, we computed the estimated bee species richness in each of the 20 cities using bootstrap analyses in the R package iNEXT v2.0.20 (*iNEXT* function, Hsieh & Chao, 2022), from abundance data in each city. This function computes rarefaction curves for each city, that are then extrapolated to give an estimated species richness. Working with estimated values allows to overcome the differences in sampling efforts among cities. Additionally, observed species richness may be expressed as a percentage of the estimated richness values, providing an indicator of sampling completeness - i.e. the proportion of expected richness actually observed by samples. This ratio gives an idea of the actual extent of bee species sampling completeness in each city. We then checked the sampling completeness of the 20 studied cities. Overall, the mean completeness was 67.2% ± 16.1% (SD), maximum completeness was 94.5%, and only 3 cities had a completeness below 50% (33.5%, 42.9% and 46.9%).

(Near-)threatened species

To assess the conservation status of the wild bee species reported from our city surveys, we used the Red List Status of European Bees (Nieto et al., 2014). This status comprises five categories: *Least concern, Near-threatened, Vulnerable, Endangered* and *Data deficient* species. We combined the *Near-threatened, Vulnerable and Endangered* categories to create a *(Near-)threatened* category, as opposed to *Least Concern* species. The former category thus represents species with a concerning conservation status.

City area and land cover composition and layout

Following the objective of identifying the most appropriate Species-Area relationships (SAR) to predict wild bee species richness in cities, we focused on the size of cities and the total area of UGS within cities as area metrics. We used the Urban Atlas (Copernicus) layers to get access to the landcover characteristics. Urban Atlas is a comprehensive land use dataset for European cities (European Environment Agency, 2012) that provides finely detailed information at the city level, rendering it easy to compare land-use among cities, even from different countries.

We created one vector layer for each city, that comprised two categories: UGS and non-UGS. In the UGS category, we included the following land-use categories: *Green Urban Areas, Permanent crops, Pastures, Forest* and *Herbaceous vegetation associations*. We excluded *Arable lands* and *Open spaces* *with little or no vegetation* to avoid land uses such as intensive fields, beaches or bare rocks with no vegetation, as these are unsuitable habitats for wild bees. We also excluded *Land without current use*, because these spaces are highly variable in their use and may be used differently today since the publishing of the Urban Atlas in 2012 (*Urban Atlas Land Cover/Land Use 2012 (Vector), Europe, 6-Yearly*, 2012). Private gardens were not included in our definition of UGS. These are not referred within the Urban Atlas landcover categories, which only focuses on public green spaces.

Following Prastacos et al. (2017), we merged all UGS located within 20m of each other. This ensured an accurate representation of UGS city metrics.

In a final step, we extracted city metrics using the VecLI landscape index calculation software, v3.0.0 (Yao et al., 2022). For each city, we computed the city area (ha), the UGS total area (ha) within each city, the mean Euclidean nearest neighbor distance between UGS (in m, as a measure of connectivity), the number of UGS patches, the proportion of UGS cover (%), and the UGS average size (ha).

Statistical analyses

All statistical analyses were conducted using R v4.1.1 (R Core Team, 2021).

We first wanted to make sure that our estimated species richness was not correlated to latitude, since in France, more wild bee species are expected in the south, especially in the Mediterranean region (Nieto et al., 2014). To do so, we built a simple linear model (*lm*) comparing the estimated species richness with latitude and percent coverage of city sampling.

We used a Species-Area Relationship (SAR) framework to analyze links between city characteristics and the species richness of wild bee communities. In all of our models, we controlled for the city spatial sampling coverage (calculated beforehand) by introducing it as a covariate in the model, to control for differences in the sampling coverage of each city.

We computed two different candidate SARs with linear models (*lm*), using city area and UGS area separately, given that they are highly correlated ($r = 0.95$). The first model (1) was a log-log relationship between city area (in ha) and estimated species richness, taking into account the log of city sampling coverage. The second model (2) was similar, but instead of using city area, we used the total UGS area, also in log scale (in ha). These models allowed for testing of the effect of city area, and the role of UGS area in explaining variations in wild bee species richness among cities.

A new analysis was carried out to assess possible impacts of UGS layout on wild bee species richness among cities. To do so, we computed a *lm* model (3), taking into account the UGS connectivity, average UGS size, city sampling coverage and city size.

To assess the ability of wild bee species with conservation status to establish in urban environments, we first used a chi² test comparing the distribution of the number of (Near-)threatened species and the number of least-concern species between the data from the 20 selected cities, and the overall data from the European Red List of Bees (Nieto et al., 2014). We further summarized the patterns of urban conservation status by computing the ratio between the number of Least Concern species and the number of (Near-)threatened species. This statistic may provide a better outlook of species with conservation status within urban bee communities.

Then, we computed models similar to (1) and (2) to evaluate if city characteristics have an effect on the number of (Near-)threatened species reported to occur in cities. The first model (4) tested for the effect of the log of city area on the log of (Near-)threatened species, while controlling for the log of city sampling coverage. The second model (5) was similar, but instead of using city area, we used the UGS area. These models were computed using the linear model *lm* function.

To test whether wild bee community composition varies among cities, we first computed a Latent Block Model (R package sbm, v0.4.5,Chiquet et al., 2023) to get an accurate representation of our wild bee species distribution across the cities considered. This model is descriptive and clusters into blocks the lines and columns of a matrix based on their numerical values. In our case, we used this model on a presence absence species by site matrix. This allowed to distinguish three groups of species based on their occurrence: (i) species that occurred in most cities; (ii) species that occurred in a limited number of cities and (iii) species that occurred in only one of the 20 investigated cities.

We then conducted a distance-based redundancy analysis (db-RDA) using Jaccard distance index to test the influence of UGS layout on differences in the composition of wild bee species communities across cities (R package vegan v.2.5-7,Oksanen et al., 2022). The db-RDA was first built using city area and sampling coverage, and then using the same variables as in model (3): namely, UGS connectivity, average size of UGS patches and total city area. We controlled for spatial positioning by adding a conditional term (*Condition* argument of the db-RDA function) containing spatial coordinates of the barycenter of the 20 studied cities. We favored the Jaccard distance index because we handled presence/absence data.

Limitations of the study

Large-scale analyses imply to deal with issues on data availability and data heterogeneity. Regarding data availability, information on city area and UGS area were available, but not on UGS type or management practices. We therefore chose to focus on a broad-scale approach, in line with the large spatial scale covered by our study. However, this prevented us to take into account other factors influencing wild bee diversity, such as UGS type or management (Lerman et al., 2018; Wastian et al., 2016; Zaninotto et al., 2023), or the area covered by private gardens (Levé et al., 2019), as this land-use category was not included in Urban Atlas, nor in other large-scale landcover datasets.

Another limitation of large-scale studies lies in the heterogeneity of the data. Here, our dataset gathers wild bee samplings from different sources. Therefore, we standardized the data-sets calculating the spatial coverage of the samplings in each city, as mentioned previously. A threshold value of 30% was applied, ensuring that a significant part of the city was sampled. We also calculated the estimated species richness for each city, that enabled to compute for each city a sampling completeness (observed species richness/estimated species richness).

As the mean sampling completeness value was 67% (which is relatively high, see Appendix A), this implies that analyses were carried out on a subset of the actual wild bee communities expected to occur in the sampled cities. This bias was partially accounted for in our SAR models (1) and (2), since we used the estimated species richness as dependent variable. However, we couldn't compute the estimated species richness for species with conservation status, thus models (4) and (5) use observed species richness, which is expected to vary with increasing sampling completeness. Indeed, we expect that the incomplete sampling might disproportionately concern the rarest species, which are arguably harder to detect compared to common species. On the other side, this incomplete sampling might also have an effect on the beta diversity results, since the most frequently sampled species will also be the most common ones. This might lead to an overestimation of biotic homogenization among cities.

Results

Number of species per city (observed species richness)

We found a total of 404 wild bee species recorded in our dataset, that included the 20 medium and large cities of Western Europe whose bee fauna was adequately sampled according to our criteria (Fig. 1, Appendix A).

The number of wild bee species in cities varied from 14 to 194 (mean of 96 species, standard deviation of 48, and a median of 92), with the maximum value for Lyon, France. Although the overall wild bee species richness found in the 20 selected cities can be quite high, there is arguably a large variation in wild bee species richness among these cities.

[Fig 1. About here]

Estimated wild bee species richness variation, city area and UGS cover

We found no effect of latitude on our estimated wild bee species richness ($p = 0.10$).

We found a significant positive relationship between total city area and estimated wild bee species richness, but no significant relationship between the UGS area and the estimated wild bee species richness (Table 1, Fig. 2). Also, the sampling coverage effect was not significant in both models (Table 1). Model (1) explained 25% of the variation in estimated wild bee species richness (Adjusted R^2= 0.249), and model (2) explained 4.5% of the variation in estimated wild bee species richness (Adjusted R^2 = 0.0456).

[Table 1 about here]

[Fig 2. About here]

Estimated species richness and UGS layout

No relationships were found between the estimated wild bee species richness and the UGS connectivity (p = 0.56) nor the mean UGS size (p = 0.29). However, we again found a positive relationship between wild bee estimated species richness and the total city area (p = 0.007).

Wild bee community differences among urban environments

The Latent Block Model divided the urban bee species assemblage into 3 blocks (Fig. 3). The left part of each block gathered the most common wild bee species, i.e. those that were found in the majority of cities, the right part of each block enclosing the least common wild bee species in the dataset. Cities that did not host a lot of wild bee species also hosted a small proportion of the most common wild bee species. Overall, this suggests that part of the wild bee communities in species-poor cities are nested communities within those of species-rich cities. However, we did not record this pattern for rarer wild bee species across cities: on the contrary, species turnover seemed to explain most of the community differences across cities.

In the two db-RDA models, there was no significant effect of the total city area nor of the UGS area on changes in wild bee species community composition (p = 0.17 and p = 0.47 respectively). Concerning the db-RDA evaluating the effects of UGS layout on wild bee species composition among cities, none of the aforementioned variables explained the variation. In all db-RDA models, the sampling coverage effect was also not significant.

[Fig 3. About here]

(Near-)threatened species in urban environments

In the 20 cities considered, we found 23 wild bee species out of 404 (5.6%) with a (Near-)threatened status, and 268/404 (66.3%) having a Least Concern Status. For comparison, in the European Red List of Bees, Nieto et al. found 171/1942 wild bee species (8.8%) with a (Near-)threatened status, and

663/1942 (34.1%) having a Least Concern Status, the majority having a Data Deficient status (1101/1942 = 56.7%).

These differences in the proportions of conservation status occurrences were highly significant (Chi²= 23.9, $p < 0.001$), meaning that there are overall proportionally less (Near-)threatened species compared to least-concern species in the 20 selected cities than what would be expected from the European Red List of Bees (Nieto et al., 2014). As an alternative way of illustrating the urban gap in terms of conservation status, we computed conservation status ratios and found that the sampled cities overall harbor 11.4 (262/23) Least Concern species for one (Near-)threatened species, while the European Red List of Bees returns 3.9 (663/170) Least Concern species for one (Near-)threatened species.

We found no significant effect of the total city area on the (Near-)threatened wild bee species richness (Table 2, Fig. 4). No effect was recorded either between the UGS area and the (Near-)threatened wild bee species richness (Table 2, Fig. 4). Again, the sampling coverage had no significant effect on the (Near-)threatened wild bee species richness, which was true for both models (4) and (5).

[Table 2 about here]

[Fig 4. About here]

Discussion

Our dataset of wild bee samplings from 20 cities of Western European confirms that urban habitats can host a diverse wild bee fauna, with a total of 404 wild bee species (representing 40% of the regional fauna, Rasmont et al., 2017), and that this species richness is highly variable among different cities. Here, the Species Area Relationships (SAR) related with Urban Green Spaces is not supported, contrarily to the SAR related with city area, indicating that species richness within a given administrative boundary is first and foremost dependent on total city area. We were unable to explain additional variation in species richness through other city characteristics such as UGS connectivity, or mean UGS size. Furthermore, we did not detect any significant effect of these city characteristics on dissimilarity of urban wild bee communities. Moreover, we showed that most cities share a common set of bee species, while some species are exclusively found in one or a few cities only. Finally, we found that cities host on average fewer species with conservation status, compared to what was expected from the European Red List of Bees, and their presence was not explained by city area or UGS area in a city, giving little support to the increasingly held belief that cities can serve as refuges for endangered wild bee species (Ives et al., 2016). However, it is important to note that none of the data used in this study had the objective of specifically finding species with concerning conservation status, nor we can know if these species are present in the regional species pool or not. Overall, these data are a first step to check if such species are present in dense urban habitats. A more complete and dedicated sampling may be needed to ensure that those species are detected in urban habitats. This would also increase the sampling completeness, resulting in more accurate information on the wild bee communities in each city.

Wild bee species richness variation and city characteristics

Using Species-Area relationship (SAR) approaches highlighted that city area is the key factor influencing wild bee diversity in urban areas of Western Europe. Analogous results have been reported for birds not only at the city-scale (Ferenc et al., 2014), but also at the patch scale (MacGregor-Fors et al., 2011; Murgui, 2007). Concerning bees, although there is evidence for links between species numbers and habitat area, studies have not been carried out in the urban environment (Krauss et al., 2009; Steffan-Dewenter, 2003; Taki et al., 2018). Furthermore, to our knowledge, SAR has never been applied to bee species richness in cities at such a large-scale, with the exception of the recent study by Ferrari and Polidori (2022), who report interesting new results on the functional characteristics of urban bee species pools, notably revealing differential occurrence of bee species depending on their life history traits. However, unlike our study, the richness of urban species pools they reviewed was independent of city surfaces, and these authors acknowledged that richness was primarily driven by unequal sampling efforts in their study, which is indeed a challenging point to deal with in large meta-analyses. Herein, for each city, we could compute species richness extrapolations using common estimates of species richness, so as to account for missing species in each urban bee survey.

Interestingly, our results show that wild bee species richness increases with total city area, which seems counterintuitive, as cities can be considered as limiting environments for pollinators (Geslin et al., 2016; Hamblin et al., 2018). The urban matrix is indeed mainly composed of impervious surfaces, lacking in floral and nesting resources, that are limiting factors for wild bees (Fortel et al., 2016; Potts et al., 2005; Theodorou, Herbst, et al., 2020). Previous studies have also shown that cities filter out numerous pollinator species, leading to biotic homogenization of pollinating insect communities among urban habitats (Deguines et al., 2016). Such is the case for urban wild bee communities, where life-history traits such as above-ground nesting and polylectic diets are favored (Buchholz & Egerer, 2020; Fauviau et al., 2022). Despite the ecological filtering, we found a non-negligible diversity of wild bees in cities, especially in the largest ones. Indeed, it can be assumed that larger cities provide numerous nesting sites for above-ground nesting species, resulting in greater abundance and diversity of this category of wild bees. Recently, it has also been shown that ground-nesting bees can nest between non-sealed paving stones, suggesting that at least some impervious soil in cities can host suitable nesting sites for ground nesting wild bee species (Noël et al., 2023). We can also hypothesize that larger cities carry more diverse habitats in terms of UGS management and vegetation, thus more diverse wild bee communities. Additionally, the increase in generalist polylectic species in cities that can feed on ornamental flowers (Threlfall et al., 2016) which are not suitable to specialist, oligolectic species (Erickson et al., 2020) and often not attractive to many pollinators (Garbuzov et al., 2017) can also contribute to the high wild bee diversity in cities.

In our study, total city area was a predictor of bee species richness but not UGS area. Furthermore, we did not detect any additional effect of UGS connectivity or UGS mean size on wild bee species richness, although, in a previous study, UGS connectivity has been shown to have a positive impact on pollinator abundance and richness (Graffigna et al., 2023). It is important to mention that the GIS layers we used for our land-use analysis (Urban Atlas), do not detect all green space in cities. In particular, they do not detect private gardens, small green spaces (< 250m²) or green spaces associated with private structures (such as green places near company buildings). Thus, our UGS category doesn't encompass every available green space in cities, which might explain why we fail to find relevant correlation between wild bee communities and UGS layout.

Moreover, parts of the urban matrix other than UGS can still be suitable habitats for some pollinators. For example, previous studies reported that urban trees planted along streets may provide important food resources for wild pollinators (Requier & Leonhardt, 2020; Somme et al., 2016). Also, tree pits along streets can host a diversity of plants and offer nesting sites for some pollinators (Lundquist et al., 2022). Finally, ornamental and native flora are also present in cities elsewhere than in UGS (Baldock et al., 2019; Levé et al., 2019), and the presence of both types of flora seems to be essential in maintaining pollinator biodiversity, according to Salisbury et al (2015). It is also worth noting that we did not consider UGS management, which can have a significant impact on wild bee diversity and thus could explain its variability between cities. For example, Shwartz et al (2013) found that in the city of Paris, gardens labelled "biodiversity-friendly" hosted significantly more pollinator and bird richness compared to classical gardens, due to the use of different management measures. Other studies also highlight the importance of UGS management on biodiversity (Daniels et al., 2020; Fortel et al., 2016; Threlfall et al., 2015; Wastian et al., 2016), and that not all UGS are equally valuable to pollinators (Dylewski et al., 2019). Indeed, it has been shown that local scale management practices can have important impacts on diversity of urban pollinator assemblages: for example, local richness of flowering plants and floral density along urban roadsides was positively correlated with pollinator abundance in the urban habitat (Dietzel et al., 2023).

Thus, according to our results and the previously mentioned studies, the area and layout of UGS may not be as crucial as we previously thought. Considering local UGS management practices may be more critical to apprehend wild bee diversity at the city scale. Unfortunately, we could not get this information for the 20 cities considered herein. This is indeed a challenging issue given the difficulty to get consistent information to properly characterize UGS management practices in cities.

Overall, even though UGS are not the only habitats for pollinators in urban environments, they are still important to develop, and attention should be paid to favor alternative management practices, to support urban wild bee communities.

Wild bee community differences among urban environments

We did not find any significant effect of city area or UGS area on the variation of wild bee community composition among our 20 western European cities. Considering results from the Latent Block Model, we observed differences in wild bee community composition across cities, either due to nestedness (for the most common wild bee species), or due to turnover, especially in rarer species. This suggests that a part of urban wild bee species community is constituted of common species, but also that part of it differs among cities, with distinct wild bee species in each city.

Banaszak-Cibicka & Zmihorsk (2020) studied beta diversity of wild bee communities in rural, urban and suburban habitats, and found higher dissimilarity among rural areas, with the lowest dissimilarity among habitats in urban environments. On the contrary, Fournier et al. (2020) found that the majority (65%) of total bee gamma taxonomic diversity among sites within the city of Zurich was due to beta diversity. This result suggests that, in addition to having high diversity turnover across cities, it might also be significant within cities (Janvier et al., 2022). However, as of today, large scale studies on wild bee beta diversity among cities are lacking, as most of them are based on a comparison between urban and non-urban environments (Deguines et al., 2016; Gruver & CaraDonna, 2021; Villalta et al., 2022). Our study tried to fill this gap by giving insights into wild bee diversity among cities, and attempting to understand if city area or UGS area could explain differences in wild bee communities between cities.

(Near-)threatened) species in urban environments

Cities have been previously described as “hotspots” for threatened species compared to non-urban areas in Australia (Ives et al., 2016). However, we did not find many threatened species in our set of 20 European cities, and their proportion was significantly lower compared to expectations from the European Red List of Bees. In our study, the presence of these (Near-)threatened species was not conditioned by city variables such as city area or UGS area of each city, which is not surprising given the low number of (Near-)threatened species in the dataset, leading to limited variability in their distribution. This does not necessarily mean that endangered wild bee species are absent or unaffected by city characteristics, but rather that more sampling at a smaller scale may be needed to detect them in urban habitats. Indeed, Grossmann et al. (2023) analyzed the impacts of alternative grassland management practices within the urban matrix and showed that endangered wild bee species responded positively to the local presence of pollinator-friendly plant species. It is worth noting that Grossmann et al. (2023) used a local red list of bees, and conservation status might differ from the European Red List of Bees (Nieto et al., 2014) that we used in this study. Last, it is also worth mentioning that the European Red List of Bees contains many Data Deficient (DD) species, and that it is actually under revision.

Conclusion & perspectives

Our study has established a formal Species-Area Relationship between city area and wild bee species richness, and highlighted that UGS area is not the main factor in predicting wild bee species richness in urban habitats. We, unfortunately, found fewer (Near-)threatened wild bee species than expected in the sampled cities, and failed to explain what could drive their presence or absence in cities. We emphasized that urban wild bee community dissimilarity is driven both by nestedness (for the most frequently found wild bee species), and by turnover (for the rarest species). Thus, we ask that managers and decision makers from different cities join their efforts and collaborate through city networks aimed at promoting global bee diversity through public awareness of the taxonomic uniqueness and complementarity of their respective city species pools. This study could be viewed as a baseline reference for stakeholders to assess how wild bee species diversity at a city-scale compares to the SAR expectations established herein.

To help them even further, it will be crucial in future studies to consider management practices of UGS in analyzing wild bee diversity at the city-scale, as we previously highlighted that not all UGS are equally beneficial to wild bees and to pollinators in general. We, however, couldn't assess these factors in our study due to the limitation of our data. Thus, we recommend examining wild bee community variation at the city level with respect to UGS characteristics and management practices, in order to have a better understanding the factors shaping wild bee communities in cities. Overall, this should help improve the design and management practices of urban green spaces in favor of biodiversity.

Authors contribution

A.F., I.D. and M.H. conceptualized the study; A.F. conducted the statistical analyses and wrote the manuscript; I.D. and M.H. extensively reviewed the manuscript. All other authors contributed to the manuscript by providing data, and all have read and approved the manuscript.

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Data Availability Statement

Data will be available upon request.

Appendix A: Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Figure captions

Fig. 1. *Map of the study area, representing the 20 selected cities. Each polygon in the main map and in panels A and B represents a single sampled city. Numbers refer to the observed wild bee species richness in the corresponding city.*

Fig. 2. *Representation of the relationships between wild bee species richness and (A) total city size or (B) total urban green spaces area. The lines and shaded areas stand for the model prediction and its 95% confidence interval. A full line indicates a significant relationship, a dashed line a non-significant relationship ($p < 0.05$).*

Fig. 3. *Results of the Latent Block Model. Each of the 20 horizontal lines represents the bee fauna found in one of the 20 studied cities. Each black square represents the occurrence of a species in a city. A grey square means the species has not been found in the corresponding city. Each figure represents one species block identified by the model. The Block 1 includes 53 bee species, most commonly found in the 20 cities. Block 2 includes 115 species less commonly found in the 20 cities, and Block 3 includes 236 species that were not shared among cities. Cities (y axis), are the same across the 3 blocks.*

Fig. 4. *Representation of the relationships between (Near-)threatened wild bee species richness and (A) total city size or (B) total urban green spaces area. The dashed lines (associated to a non-significant variable) and shaded areas stand for the model prediction and its 95% confidence interval.*

Fig. 1

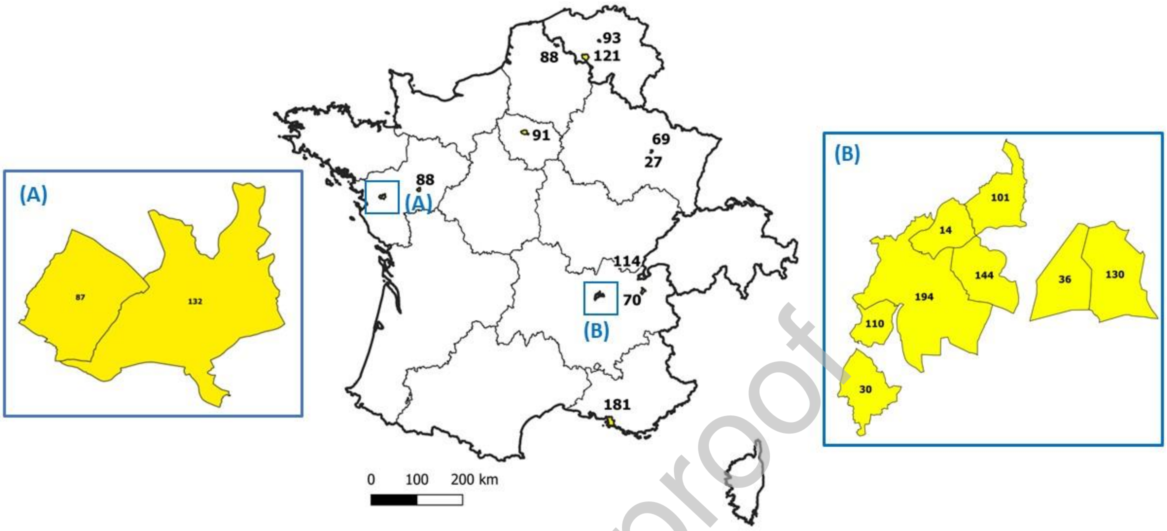
93
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Fig. 2

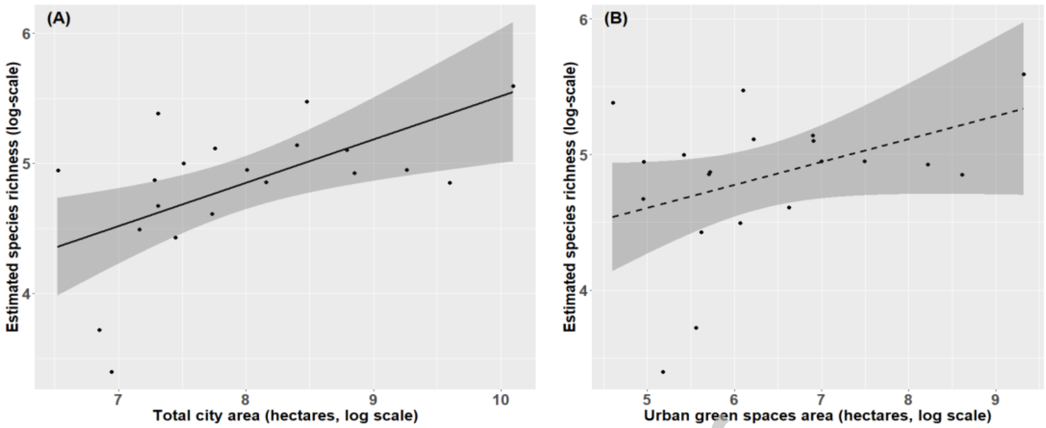
(A)
Estimated species richness (log-scale)
Total city area (hectares, log scale)
(B)
Estimated species richness (log-scale)
Urban green spaces area (hectares, log scale)

Fig. 3

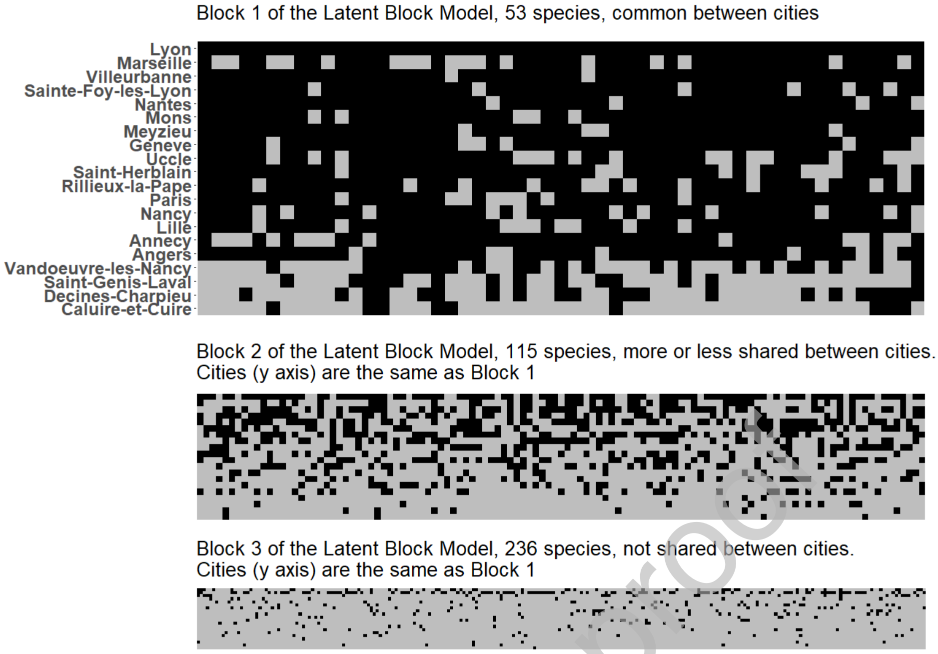
Block 1 of the Latent Block Model, 53 species, common between cities
Lyon
Marseille
Villeurbanne
Sainte-Foy-les-Lyon
Nantes
Mons
Meyzieu
Geneve
Uccle
Saint-Herblain
Rillieux-la-Pape
Paris
Nancy
Lille
Annecy
Angers
Vandoeuvre-les-Nancy
Saint-Genis-Laval
Decines-Charpieu
Caluire-et-Cuire
Block 2 of the Latent Block Model, 115 species, more or less shared between cities.
Cities (y axis) are the same as Block 1
Block 3 of the Latent Block Model, 236 species, not shared between cities.
Cities (y axis) are the same as Block 1

Fig. 4

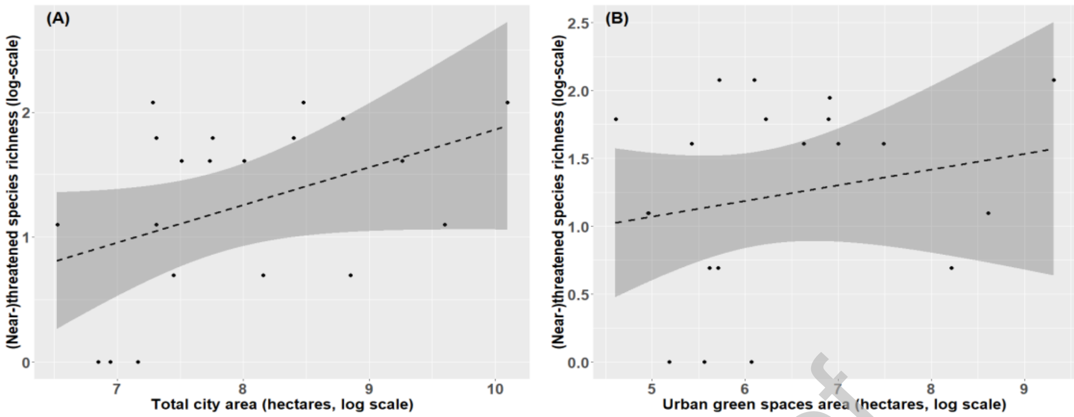
(A)
(Near-)threatened species richness (log-scale)
Total city area (hectares, log scale)
(B)
(Near-)threatened species richness (log-scale)
Urban green spaces area (hectares, log scale)

Table 1. *Summary table of the wild bee species richness -area relationship curves for models (1) and (2). P-values in bold indicate a significant relationship.*

Model (1): ***total species***	**Estimate (± SE)**	**t-value**	**p-value**
Total city area (log)	0.33 (0.12)	2.88	**0.01**
Sampling coverage (log)	0.25 (0.27)	0.93	0.37
Model (2): ***total species***	**Estimate (± SE)**	**t-value**	**p-value**
UGS area (log)	0.17 (0.1)	1.7	0.11
Sampling coverage (log)	0.17 (0.3)	0.57	0.58

Table 2. *Summary table of the (Near-)threatened wild bee species-Area relationships for models (4) and (5).*

Model (4): *(N)T species*	**Estimate (± SE)**	**t-value**	**p-value**
Total city area (log)	0.30 (0.17)	1.76	0.097
Sampling coverage (log)	-0.10 (0.39)	-0.26	0.79
Model (5): *(N)T species*	**Estimate (± SE)**	**t-value**	**p-value**
UGS area (log)	0.12 (0.14)	0.83	0.42
Sampling coverage (log)	-0.22 (0.43)	-0.51	0.62

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Arthur FAUVIAU, on behalf of all authors.