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Title: Phylogenetic, functional and taxonomic responses of wild bee communities along urbanisation gradients

Irene Villalta[1], Christophe Bouget[2], Carlos Lopez-Vaamonde[1&3], Mathilde Baude[4,5]

[1] : IRBI, UMR 7261 – Université de Tours – Tours, France
[2] : INRAE, UR EFNO – Nogent-sur-Vernisson, France.
[3] : INRAE, UR0633 Zoologie Forestière – Orléans, France.
[4] : Université d'Orléans, INRAE USC 1328, LBLGC EA 1207, Orléans, France.
[5] : Current address : Institute of Ecology and Environmental Sciences-Paris (iEES-Paris),
Sorbonne Université, CNRS, IRD, INRAE, Université Paris Cité, UPEC, Paris, France.

Introduction

The last century has witnessed a widespread loss of diversity due to the anthropisation of natural habitats (Barnosky et al., 2011; Ceballos et al., 2015; Dirzo et al., 2014). Terrestrial insects have suffered a drastic decline (Hallmann et al., 2017; Wagner et al., 2021), and pollinators are no exception (Biesmeijer, 2006; Duchenne et al., 2020; Ollerton et al., 2014; Powney et al., 2019; Zattara and Aizen, 2021). Pollinator decline has been closely coupled with the intensification of agriculture and its management practices as well as with the increasing urban development, both of which result in an effective loss of natural habitats for pollinator's forage and nesting sites (Duchenne et al. 2020; Ollerton et al. 2014; Potts et al., 2010; Vanbergen et al., 2013; Winfree et al. 2009). By 2050, approximately two-thirds of the world's population will be living in urban areas, and this population increase will inevitably increase the metropolitan land area (Seto et al., 2012). In Europe, although a modest reduction over the last decade, land use for urban purposes still amounted to 711 km2/year between 2012-2018 (European Environment Agency, 2019).

Wild bees are essential for reproducing many wild plants and crops of high economic interest (Klein et al., 2007; Ollerton et al., 2011). With the loss of natural habitats, a growing concern in the potential resilience of cities to host a certain degree of pollinator biodiversity has emerged (reviewed by Buchholz and Egerer, 2020; Wenzel et al., 2020). This interest in urban ecosystems has the additional advantage of bringing unique opportunities to increase citizen engagement with nature and biodiversity conservation (Stevenson et al., 2020).

The quality of the urban environment for sustaining bees depends on multiple biotic and abiotic factors. It worsens with the increase in impervious surfaces and the reduction in green spaces, leading to decreased habitat amount and further landscape fragmentation (reviewed in Baldock, 2020; Harrison and Winfree, 2015). These effects, combined with less studied drivers such as the urban heat island (Fisogni et al., 2020; Hamblin et al., 2017), non-native plants (Koyama et al., 2018; Lentola et al., 2017; Staab et al., 2020), pesticides and other pollutions including chemical, light, noise, fumes and heavy metal residues (reviewed in Phillips et al., 2020) might have varying effects on bee populations. The response of wild bee communities to the degree of urbanisation ranges from those species showing a positive or neutral response (Baldock et al., 2019; Baldock et al., 2015; Hall et al., 2017) to those showing a deleterious effect (Banaszak-Cibicka and Żmihorski, 2020; Choate et al., 2018; Fortel et al., 2014; Geslin et al., 2013; Geslin et al., 2016; Pereira et al., 2021). In addition to impacts on species richness, urbanisation can induce compositional changes filtering out wild bee communities depending on the species functional traits (Banaszak-Cibicka and Żmihorski, 2020; Fortel et al., 2014; Geslin et al., 2016). Identifying the mechanisms involved in differences in species composition can indicate whether urbanisation allows the establishment of specific urban species (i.e. spatial turnover, which is the replacement of some species by others from sites to sites) or whether it filters species from a richer regional pool (i.e. nestedness, a pattern characterized by the poorest sites being a subset of the richest ones).

The environment where a species lives can be favourable to it on the basis of abiotic and biotic factors (Cohen et al., 2021; Gámez-Virués et al., 2015; Hamblin et al., 2017; Hung et al., 2019). Since these environmental factors differ between urban and peri-urban environments, cities will exert a different environmental filter for wild bees than peri-urban or agricultural environments. These factors will determine the potential ecological niche of a species, since what is beneficial to some species may be detrimental to others (Bartomeus et al., 2013; Tucker and Rehan, 2018; Williams et al., 2010). As a result the combination of functional traits exhibited by each bee species will determine their ability to persist in an urban or peri-urban environment. (Banaszak-Cibicka and Żmihorski, 2012; Bartomeus et al., 2013; Buchholz and Egerer, 2020; Geslin et al., 2016; Harrison et al., 2018; Normandin et al., 2017). The growing understanding of the relationships between bee functional traits and urban attributes is essential for establishing conservation and management practices in urban spaces (reviewed in Buchholz and Egerer, 2020). The resilience of cities to perturbations and their ability to provide pollination services could therefore be inferred from the study of the functional diversity of wild bee communities (Banaszak-Cibicka and Dylewski, 2021; Buchholz et al., 2020).

Since functional traits evolve in response to the environmental context, species with a shared evolutionary history are expected to have similar functional traits (Losos, 2008; Wiens & Graham, 2005). Urban-induced species loss is expected to be non-uniform in the phylogeny of the community and depend on the suitability of certain functional traits to the urban environment. In this sense, those traits with a phylogenetic signal are expected to be shared and conserved in urban communities, thus conditioning the presence of some lineages in response to land-use changes. The extent to which changes in land use impact the evolutionary history of wild bee communities has been studied in the agricultural context (Grab et al., 2019). However, few studies have addressed the effect of urbanisation on the phylogenetic diversity of wild bees (Harrison et al., 2018).

The objective of our study was to investigate the effects of urbanisation on the multiple components of wild bee diversity sampled through a replicated and standardized design of 29 sites located along urbanisation gradients of three medium-sized cities in the Loire valley (France). A functional and phylogenetic community approach was used to infer the effect of the urban landscape on wild bees. We benefited from the availability of wild bee published time-calibrated molecular phylogenies (Cardinal and Danforth, 2013; Peters et al., 2017) and a DNA barcode library for the studied wild bee community (Villalta et al. 2021). Specifically, we addressed the following questions : (i) does urbanisation lead to a decline in the abundance and richness of wild bee communities? (ii) Does urbanisation induce changes in the composition of wild bee communities, and what is the mechanism most involved in site dissimilarities? (iii) Does urbanisation favour wild bees on the basis of their biological traits? And (iv) does it lead to a loss of functional and phylogenetic diversity?

Methods

1. Study sites

We conducted the insect sampling in three mid-sized cities of the Loire valley (Orleans, Tours and Blois) located in the administrative region Centre-Val de Loire in France. The city populations are 45000 in Blois, 115000 in Orleans and 136000 inhabitants in Tours. The area's climate is temperate, with persistent rainfalls even during the driest months of the year. The average temperature and precipitation per year in the three cities are similar, around 12 °C and 650 mm, respectively. The Loire riverbanks offer a relatively homogeneous local habitat to set up the sampling facilities while moving away from each city's centre._We chose six sampling sites in Blois, 11 sites in Orleans and 12 in Tours. The number of plots was chosen according to the percentage of urbanisation, which differs between cities. The sampling sites varied in their urban area's extent (Fig. 1; Table S1).

2. Bee sampling and identification

Bees were collected at each of the 29 monitoring sites using a combination of pan traps and net sampling (O'Connor et al., 2019). Three triplets of coloured (yellow, blue and white UV-reflecting) pan traps spaced at 50 m apart were placed at each sampling site for an exposure time of 96 h, repeated for 5 sessions from April 23rd to July 17th 2018. At the end of each trapping session, the traps were lifted and filtered. Bees were conserved in 96° ethanol and stored at -20°C until identification. Pan trapping was completed with five netting sessions of ten minutes each on a 100m transect at the end of each trapping session.

All 2944 wild bee specimens collected were pinned and photographed. Bee identification was based on a combination of morphology and DNA barcodes of 2419 wild bees published in a recent study (Villalta et al., 2021). In addition, we also used these published COI barcodes to calculate bee genetic diversity (see below).

3. Landscape composition

To characterize land uses in a 500m-radius landscape around sampling sites, we used land cover maps OSO 2017 (Inglada et al., 2017; https://www.theia-land.fr/ceslist/ces-occupation-des-sols/) which were generated from Landsat 8 to Sentinel-2 into a 10m resolution land use database for the whole of metropolitan France. We choose a 500m radius to keep buffer zones surrounding sites as entities independent of each other while maximizing the landscape area attributed to each point and encompassing the average flight distance of most wild bees as in (Geslin et al., 2016). From the 17 land classes provided by OSO 2017 and after photo-interpretation of each site to validate the assignment of the surfaces, we determined the area of six simplified land uses of interest towards insects at a 500m radius surrounding sites, including urban landscape cover (Table S2). Based on their land-use composition, sites were also classified as “urban” vs “peri-urban” (Fig S1) following Ward's hierarchical clustering (hclust function) carried out on principal components (prcomp function) from R Statistical Software (v4.1.2; R Core Team 2020).

4. Local floral resources

We recorded the flowering vegetation present locally on each site in June 2018 by arranging 75 quadrats (50 x 50 cm) so that 25 quadrats at 5m apart were placed around the three sampling triplets (except when arranging the quadrat was too dangerous such as in riverbanks or roads). Since the triplets were arranged in open vegetation made up of herbaceous plants showing little covering, quadrats could be photographed from the top for later identification of flowering plants and count of floral units. A floral unit was defined as a single flower head or part of multiple heads, from which a medium-sized bee has to fly rather than walk to reach another floral unit of the same species (Dicks et al., 2002). The sum of floral units of all species per square meter was used as a proxy of local floral abundance. In addition to the species encountered in the quadrats, the flowering plants present locally were identified to the species or morphospecies level. Plant species richness was used as a proxy of local floral diversity.

5. Insect metrics

Our data set comprises each sampling site unit, including the pooled data from all three pan traps and net samplings per study site and all sampling periods in 2018.

5.1 Taxonomic diversity

5.1.1 Abundance and species diversity

For each sampling site, we have recorded the abundance (n) and the number of species (nsp) for the whole dataset and by family. In addition to the species richness, we estimated bee diversity through the Simpson diversity index (Simpson, 1949) to account for the species presence and their relative abundance in sampling sites and the Chao1 diversity index (Chao, 1984) to account for the diversity of undetected species. Both indices were calculated with the R vegan package v. 2.5 6 (Oksanen et al., 2020).

5.1.2 Genetic diversity

We used 2419 barcodes out of 2944 collected specimens obtained from a recently published study (Villalta et al., 2021) to calculate the total number of haplotypes (nhap) and the number of haplotypes per family at each sampling site. The number of COI haplotypes per species corresponds to the number of unique sequences that differ from others at one or more base pairs. It was calculated with the R Pegas package v.0.14 (Paradis, 2010). They were summed to calculate the total number of haplotypes and the number of haplotypes per family at each sampling site.

5.2. Community compositional changes

We visualized the dissimilarity in the species composition of wild bee communities using Non-metric Multidimensional Scaling (NMDS; metaMDS function of the R vegan package v. 2.5-6, Oksanen et al., 2020) based on Bray-Curtis distances for the abundance weighted community matrices. We tested whether dissimilarity was explained by the urban landscape class through Permutational Multivariate Analysis of Variance with 999 permutations (PERMANOVA; adonis function of the R vegan package). We checked that geographic distance between sites did not significantly explain dissimilarity by carrying out a Procrustes analysis using the protest function of the R vegan package .

We used the “nestedbetasor” function of the R vegan package to evaluate the contribution of nestedness and turnover to community dissimilarity. Overall community dissimilarity was evaluated by calculating the Sørensen dissimilarity, split into the turnover component evaluated by calculating the Simpson dissimilarity and the nestedness-resultant component (Baselga, 2012).

To explore the pattern by which species would be lost across the urban gradient, we also calculated the abundance weighted NODF (Nestedness metric based on overlap and decreasing fill) of the bee communities ordered along the urbanisation gradient (nestednodf function from the bipartite package; Dormann et al., 2008) which was then compared to what would be expected by chance using null models, as in Grab et al., 2019 (File S1).

The species involved in the partition of sites in urban vs peri-urban (Fig. S1) were identified through the “multippatt” function of the R indicspecies package (De Cáceres et al., 2011).

Beta diversity analyses were carried out with the R vegan package v 2.5-6 (Oksanen et al., 2020) for the overall wild bee community data and separately by city (results by each city in File S2).

5.3 Functional traits

Functional traits of bee species (Table S3) were selected according to the possible response to floral resource availability, landscape composition and bee social behavior. They included female body size, duration of activity per year (flight period length in months), sociality (*sensu stricto*) regarding the presence of a reproductive caste (i.e., ‘solitary’, ‘social’, ‘polymorphic’, ‘social parasite’ or ‘kleptoparasite’), nesting structure ('ground', ‘cavities’, ‘dead stems or ‘carder’), diet (‘opportunist’ or ‘specialised’) and voltinism (“univoltin”, “bivoltin” and “partly bivoltin”). All functional traits were retrieved from the literature (Table S3) and completed in some cases by expert's evaluation.

Changes in the functional composition of wild bee communities were measured by computing at each site the community-level weighted means of trait values (CWM) and functional dispersion (FDis from the dbFD function, FD package in R, Laliberté and Legendre, 2010) for each quantitative trait separately and by calculating trait frequencies for nominal or binary traits.

5.4 Phylogenetic tree

Representative COI sequences for each species (153 species out of 156) in the study area (Table S4; File S3) were aligned with Geneious v. 8.0 (Kearse et al., 2012) using the MAFFT plugin (Katoh, 2002) with the auto option and other parameters set as default. BEAUTI v.1.8.1 (Drummond et al., 2012) was used to create input files for BEAST v.1.8.1 (Drummond et al., 2012). Time-calibrated phylogeny contruction details can be found in File

S1. The maximum clade credibility newick tree file obtained (File S4) was used to calculate the subsequent metrics related to phylogenetic diversity.

5.5 Functional and phylogenetic diversity

Three different metrics of the phylogenetic and functional community structure were calculated at each sampling site: the Faiths' diversity (PD for phylogenetic diversity and FD for functional diversity), the mean nearest taxon distance (MNTD) and the mean pairwise distance (MPD). The Faiths' diversity index is related to species richness (Schweiger et al., 2008). PD represents the evolutionary relatedness within a community and is calculated by summing the total lengths of the branches of the phylogenetic tree of the species present in the community (Faith, 1992). Similarly, FD is the total branch length of the functional dendrogram (Petchey and Gaston, 2002) computed from functional dissimilarity among species based on the Gower distance. MNTD represents the mean of the branch lengths connecting each species to its closest relative in the dendrogram (Webb, 2000). The MPD index calculates the mean pairwise phylogenetic (or functional) distance among all species in a community, is equivalent to the average taxonomic distinctiveness and is independent of species richness.

We also used richness-independent standardized effect sizes for PD and FD (hereafter sesPD and sesFD), MPD (hereafter sesMPD) and MNTD (hereafter sesMNTD) metrics using a null model for each city that maintains species richness and abundance constant while randomizing species from the set of species occurring in at least one community of the city transect (sample.pool option) 999 times through the “ses.pd”, “ses.mpd” and “ses.mntd” functions of the R Picante package v.1.8.2. (Kembel et al., 2010).

6. Statistics

We tested the effect of landscape land-use variables at 500 m radius surrounding sites and local floral resources on aboved insect metrics using generalised linear mixed effects models (GLMMs) with the R package glmmTMB (Brooks et al., 2017), using the city as a random factor. Since some land-use variables were correlated (Table S5), we included the proportion of urban surfaces and uncorrelated variables only, such as the proportion of water, the proportion of forests and the proportion of sandbanks and dunes at a 500m buffer. Local floral resources factors included the scaled 'local floral abundance' and 'local floral richness'. Haplotypic and taxonomical analyses were carried out for (i) the entire dataset and (ii) separately for each of the six bee families.

From the list of models with combinations of fixed effect terms in the global model, we selected the top best model (dredge and get.models functions of the R MuMIn package, Bartoń, 2019) on the basis of the second-order Akaike Information Criterion (AICc; Anderson and Burnham, 2004). Poisson error distribution (or negative binomial when overdispersion was detected) with a log link function were used for count data (abundance, number of species and number of haplotypes). Gaussian error distribution with an identity link function were used for the following variables species diversity indices (Simpson and Chao1), functional and phylogenetic diversity indices (PD and FD, MTD, sesPD and sesFD, sesMPD and sesMNTD) and quantitative trait-related indices (CWM and FDis). Gaussian error distribution with a log link was used for the MNTD metrics. Betabinomial error structures with a logit link function were used to analyse the shifts in the frequencies of categorical traits (nesting, sociality, lectism, parasitism, voltinism). To validate the goodness of the fit and the assumptions of each GLMM, simulated residuals were plotted using the '*simulateResiduals*' function in the 'DHARMa' package (Hartig, 2020).

Results

1. Wild bee community description

Over the year of the survey, a total of 2944 wild bee specimens were collected, 647 from Blois (85 species), 1673 from Orleans (115 species) and 624 from Tours (82 species). They were assigned to six families, 25 genera and 156 species. The Halictidae was the most abundant family and represented 50% to 71% of samples depending on the city (Table S6).

Out of 2944 specimens, 382 belonging to 75 species were netted, of them only 16 species were exclusively caught by netting. Eleven out of these sixteen species were represented by singletons (10) and doubletons (1). Given that the abundance estimates for pan trap and netting samples could be very different we assessed whether analysing the data with and without considering netting samples had any impact on the results obtained before using the complete database.

The species accumulation curve reaches saturation, indicating that we captured most of the species in our study area (Fig. S2). Notwithstanding, the haplotype accumulation curve did not reach saturation, thus reflecting an incomplete capture of the genetic diversity in our sampling with a total number of 666 haplotypes (Andrenidae 122, Apidae 92, Colletidae 28, Halictidae 375, Megachilidae 41, Melittidae 8).

2. Does urbanisation lead to a decline in wild bee abundance and richness?

Overall wild bee abundance was not explained by the urban landscape cover or any other landscape factor (Table 1; Fig. 2). A significant reduction of both Melittidae and Megachilidae bee abundance associated with the urban landscape cover was found (Table 1; Fig. S3).

The overall species richness and the Simpson and Chao1 indices of wild bees responded strongly to the urban landscape cover. (Table 1; Fig. 2). They showed a significant decrease with the increase in the proportion of urban landscape cover (p-value <.001), revealing a negative effect of urbanisation on wild bee taxonomic diversity, whether we consider dominant or account for undetected species. Since the effect of urban landscape cover on wild bee species richness remains significant even after the inclusion of abundance as a co-variable (estimate= -0.877191, se=-0.191015, p-value = 4.38e-06), this indicates that this trend is independent of the sample size. As expected, the proportion of water surrounding sites negatively influenced the species richness of collected wild bees (but not the Simpson and Chao1 indices) since water also constitutes an impervious surface. The drop in the overall species number with the proportion of urban landscape cover is mainly driven by a significant reduction in Andrenidae and Halictidae species (Table 1; Fig. S3). This overall species reduction is not concomitant with a significant decrease in the total number of haplotypes (Table 1). Despite the variation in haplotypes number for each family mirrored the abundances trends, we did not find a significant relationship between urban landscape cover and the number of haplotype in any family (Table 1; Fig. S3).

Local floral abundance and plant species richness did not significantly influence overall wild bee abundance or taxonomic richness. Floral abundance was, however, positively associated with the Chao1 diversity index, with the abundance of Halictidae and Apidae as well as with the number of haplotypes in Halictidae. Plant species richness was only positively associated with the number of haplotypes in Apidae (Table 1).

3. Does urbanisation induce changes in species composition of wild bee communities?

The NMDS reveals strong dissimilarity in species composition between urban vs peri-urban classes (Fig. 3a). Bee communities from the urban sites are taxonomically different from the peri-urban ones (Permanova, F(1,29)=2.31, p-value = 0.003). From Procrustes analysis, geographic and community dissimilarity matrices are not significantly correlated (p-value =

0.177, Procrustes correlation= 0.415), indicating that species community dissimilarity is not a function of the Euclidean distance between communities.

The decomposition of overall community dissimilarity in turnover and nestedness components (0.875 and 0.039, respectively) indicates that species turnover is the main contributing factor in community dissimilarity overall (Fig. 3b).

We found that the ordered matrix's observed value of weighted NODF is significantly lower than the nestedness values obtained with null models (t=66.14, df=99, p-value<2.2e-16), confirming that the ordered matrix does not present a nested structure. Hence, urban sites do not contain a subset of species from the more complete communities present in peri-urban landscapes but seem to harbour a set of urban species distinct from the peri-urban ones.

Nine species were found to be involved in the partitioning of sites into urban and peri-urban classes. Species associated with urban sites are *Lasioglossum laticeps*, *L. nitidulum* and *Andrena pusilla.* In contrast, species associated with peri-urban sites are *L. zonulum, Halictus maculatus A. haemorrhoa, Dasypoda hirtipes, L. marginatum, and Panurgus calcaratus.* Beta diversity analyses carried out separately on each city reveal similar results (File S2).

4. Does urbanisation favour wild bees on the basis of their biological traits?

We found a significant negative relationship between the urban landscape cover and the community weighted mean of body size of wild bees (Table 2, Table S7), suggesting that smaller species dominate urban wild bee communities compared to periurban communities although the functional dispersion of body size remains similar. The community weighted mean of bee size also significantly decreased with the proportion of water and increased with forests. A significant increase in the community weighted mean of the duration of activity with urban landscape cover and local floral richness was also found (Table S7), suggesting that urban wild bee communities have a broader period of activity compared to periurban ones

(Table 2). This relationship was however depended on the netted samples, since the relationship disappeared when netted individuals were excluded from analysis. The frequency of solitary bees significantly decreased with an increase in urban landscape cover and local floral abundance (Table 2; Table S7). Contrary to our expectations, the frequency of ground-nesting bees was not significantly influenced by the urban landscape cover (Table 2). Also, none of the frequency of specialist and univoltine bees showed a significant response to urban landscape cover (Table S7).

5. Do favoured traits lead to a loss of functional and phylogenetic diversity?.

The functional and phylogenetic Faith diversity (FD and PD) of wild bee communities were significantly reduced by an increase in urban landscape cover (Table S8, Fig. 2). This reduction was accompanied by a significant increase in the functional and phylogenetic MNTD but not in MPD (Table S8), suggesting that urbanisation did not influence functional nor phylogenetic diversity when decorrelated from species richness. Moreover, we did not find any significant relationship between the urban landscape cover and functional or phylogenetic sesPD, sesFD, sesMPD or sesMNTD (Table S8, Fig. 2).

Discussion

We investigated the effect of urbanisation on the taxonomic, functional and phylogenetic diversity of wild bees in three medium-sized cities along the Loire river in France. The wild bee community sampled was relatively diverse, with 156 species representing about 60 % of the regional bee fauna (Villalta et al., 2021).

The total abundance recorded in our study was not related to the urban landscape cover. However, consistent with previous research we observed a drop in species richness (44 %) and taxonomical diversity indices with increasing urban landscape cover (Banaszak-Cibicka and Żmihorski, 2020; Bates et al., 2011; Geslin et al., 2013; Geslin et al., 2016; McCune et al., 2020; Hostetler and Mcintyre, 2001).

In addition to changes in species diversity, cities as well as and peri-urban sites seem to select taxonomically and functionally different communities from an overall species pool. While Banaszak-Cibicka and Żmihorski (2020) found a nested structure in their wild bee communities, indicating that urban sites have a subset of species from the more complete communities present in rural and suburban landscapes, here it seems that urban sites harbour a set of species distinct from the peri-urban ones. In our study, the spatial turnover of species was the main contributing factor in overall community dissimilarity. *L. laticeps*, *L. nitidulum* and *A. pusilla* were the species that most represent the urban assemblage, and together with *L. morio* responded positively to the urban landscape cover (Table S9). These "winner" species are among the most numerous overall. Therefore, an increase in their abundance associated with urbanisation contributes substantially to reduce the differences in the total abundance between urban and peri-urban areas. On the contrary, we found *L. zonulum, H. maculatus, A. haemorrhoa, D. hirtipes, L. marginatum, and P. calcaratus* as the peri-urban related species.

Shifts in bee communities towards smaller, social bees with extended flight periods were found, resulting in a modification of the functional composition of bee communities with urbanisation. The flight distance to forage is positively correlated with bee body size (Greenleaf et al., 2007). In urban areas with a more fragmented landscape, larger species would potentially benefit from foraging in patches of distant resources, and would therefore be expected to be selected. Although it is found in some studies (Birdshire et al., 2020), there is evidence across the literature that urbanisation filters for smaller species (Ahrné et al., 2009; Banaszak-Cibicka and Żmihorski, 2012; Hamblin et al., 2018) and large body-size are rare in cities (Banaszak-Cibicka et al., 2018a, 2018b; Glaum et al., 2017). In our case, small bee species seems to be favoured in urban areas, where small-bodied bees such as

Lasioglossum display shorter flight ranges. The advantage of being small in an urban environment has been related to the reduction of resources needed to survive in these areas of potentially reduced nutrient availability (Fortel et al., 2014). On the other hand, it has also been related to diverse and abundant floral patches that would ensure the foraging needs of small species without the need to fly long distances (Buchholz and Egerer, 2020). In addition, a warmer environment caused by the urban heat island effect promotes ectotherms' increased metabolic costs that are expected to drive shifts to smaller body sizes (Scheffers et al., 2016) and select for small ectotherm species with reduced metabolic costs (Merckx et al., 2018).

The phenology of bee populations in urban areas is closely linked with the presence of native or exotic floral resources (Wilson and Jamieson, 2019), the effect of temperature on the overwintering period of bee species (Schenk et al., 2018) and the phenology of native plants (Fisogni et al., 2020). Several studies have shown that urban environments favour wild bee species with later spring emergence dates and extended flight periods (Banaszak-Cibicka and Żmihorski, 2012; Harrison et al., 2018; Wray and Elle, 2015). In our design, we have found a predominance of bees with extended and less variable flight periods in urban areas. Unlike native flora, ornamental flora is selected for longer flowering and renewal several times a year, contributing to the establishment and selection of bee species with extended foraging periods (Harrison and Winfree, 2015).

Social bees were positively associated with the increase in urban landscape cover as found in other urban areas studied (Banaszak-Cibicka et al., 2018b; Banaszak-Cibicka and Żmihorski, 2012; Hinners et al., 2012). Social bees are ecologically dominant for resource foraging compared to solitary bees, thus facilitating their behavioural and ecological versatility and, consequently, their survival in urbanised environments (Banaszak-Cibicka and Żmihorski, 2012).

We did not find differences in the dietary breadth of wild bee communities according to urbanisation. Shifts in community composition from specialist to generalist species (Deguines et al., 2016; Matteson et al., 2008) might be expected once again because of the abundance of ornamental plants in urban environments. However, there is no clear consensus in the literature as trait-based selection for specialist or neutral trends have been reported with urbanisation (Buchholz and Egerer, 2020). Finally, the expected decrease in ground-nesting bees with increasing urbanisation (Banaszak-Cibicka and Dylewski, 2021; Geslin et al., 2016; Matteson et al., 2008) was not detected in our study. Locally, the presence of bare soil, cobblestone paving and sandbanks alongside the Loire might provide nesting resources for ground-nesting bees, especially *Lassioglossum* species with colonies often found in the crevices of cracked pavements, well adapted to disturbed environments and with a rapid response to the appearance/disappearance of nesting niches. The significant increase of 3 *Lasioglossum* species with urbanisation could also dilute the abundance of other soil nesting bee species in urban sites.

A few studies considered the functional diversity of wild bees in urban environments (reviewed in Buchholz and Egerer 2020). While functional dispersion has been found to decrease with urbanisation (Hung et al., 2019; Banaszak-Cibicka and Dylewski 2021), other studies reported functional diversity to be greater in urban gardens compared to semi-natural habitats (Martins et al., 2017), and no effects of urbanisation were detected in the studies conducted by Buchholz et al., 2020, and Zaninotto et al., 2021. In spite of several responses to urbanisation of individual traits in mean and variance in our study, they seem to be not sufficient to contribute to significant response of overall multi-trait functional metrics.

Along with the reduction in the number of species associated with the increase in the urban landscape area, we found a decrease in Faith’s diversity (FD and PD) and an increase in MNTD while no effect on MPD, both for functional and phylogenetic dendrograms.

However, these effects appear to be purely due to the reduction of specific richness with increasing urbanisation. The lack of significant differences in the phylogenetic metrics (sesPD, sesMPD and sesMNTD) with urban landscape cover for observed assemblages and those expected from simulated communities indicates that the effect of urbanisation on functional and phylogenetic diversity between sites do not differ from that resulted from a random loss of species. In our study, despite the decline in species richness, species turnover contributes to maintaining taxonomically and functionally distinct communities between urban and peri-urban sites, thereby compensating to some degree for the negative effects of urbanisation on taxonomic diversity and contributing to the maintenance of functional and phylogenetic diversity.

The availability of floral resources has been shown to increase the diversity and abundance of bees in urban environments (Baldock et al., 2015; Bennett and Lovell, 2019; Hülsmann et al., 2015; Matteson and Langellotto, 2010; Threlfall et al., 2015) and has the potential to help compensate for the negative effects of urbanisation (Wilson and Jamieson, 2019). Despite having no significant effect on total wild bee abundance or the number of species, floristic abundance was positively associated with the Chao1 richness index. This pattern suggests an essential role of floral abundance in conserving rare bee species, either because they benefit from an increase in net floral resources or a decrease in competition. These results underline the importance of maintaining floral resources in cities to alleviate other adverse effects of urbanisation.

Conclusion

The analysis of bee communities in a replicated design along three urbanisation gradients has allowed us to show that urbanisation leads to a strong decline in species richness while maintening an overall abundance. This might be explained by family-dependent responses to urbanisation, with few dominant species benefiting from the urban area. The urban environment favours wild bees based on their body size, flight phenology and social structure. The trait-based approach of wild bee communities has allowed us to highlight some urban drivers potentially involved in trait filtering, including the urban heat island effect and abundance of ornemental plants. However, this trait-based filtering does not lead to a non-random loss of evolutionary history in the urban environment. The species turnover between urban and periurban areas contributes to maintaining a relatively stable phylogenetic and functional diversity when considered independently from the reduction in species number along the urbanisation gradient.

Our data show that the city provides a markedly different environment from peri-urban areas, which exert a contrasting mode of selection. Consequently, cities and peri-urban areas appear to filter bee communities that are taxonomically and functionally different. These results underline the key role of wild bee functional traits in assisting conservation policies and habitat management in anthropised landscapes.

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Figure and Table captions

Figure 1: Location of the 29 sampling sites across 3 cities in France (Orleans in yellow, Blois in green, and Tours in red)

Figure 2: Wild bee variation in abundance (a), richness (b) functional and phylogenetic diversity observed metrics FDobs (c) or PDobs (d) and standardized effect sizes metrics sesFD (e) or sesPD (f) computed from both functional and phylogenetic dendrograms in the three cities as a function of the urban landscape cover (ULC). The black line represents the overall predicted values from the generalized linear mixed model, and the grey ribbon represents the calculated standard errors of the predictions. The coloured dashed lines represent trends in the three cities. Signif. codes: "***" 0.001; "**" 0.01 ;"*" 0.05.

Figure 3: a) Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarities for the periurban and urban bee communities. Sites were classified as "urban" or "periurban" land cover classes based on ward hierarchical clustering depending on their simplified land use classification proportions (Fig. S1). b) Partition of overall dissimilarity among sites (Sørensen dissimilarity index) between the turnover (Simpson dissimilarly) and the nestedness-resultant components.

Table 1: Summary of the generalised mixed-effects models (glmmTMB) testing for the effects of urban landscape cover and other land classes at a 500m radius surrounding sites on abundance and diversity metrics of wild bees. Overall abundance, species richness, Simpson index, Chao1 index, and haplotype numbers are presented in (a). Per family abundance, species and haplotype richness are shown in (b).

Table 2: Landscape and floral traits effect on functional bee community traits. Significant relationships in community weighted means (CWM) and functional dispersion (FDis) of quantitative traits, and in frequencies of categorical traits are denoted by arrows denoting the direction of change.

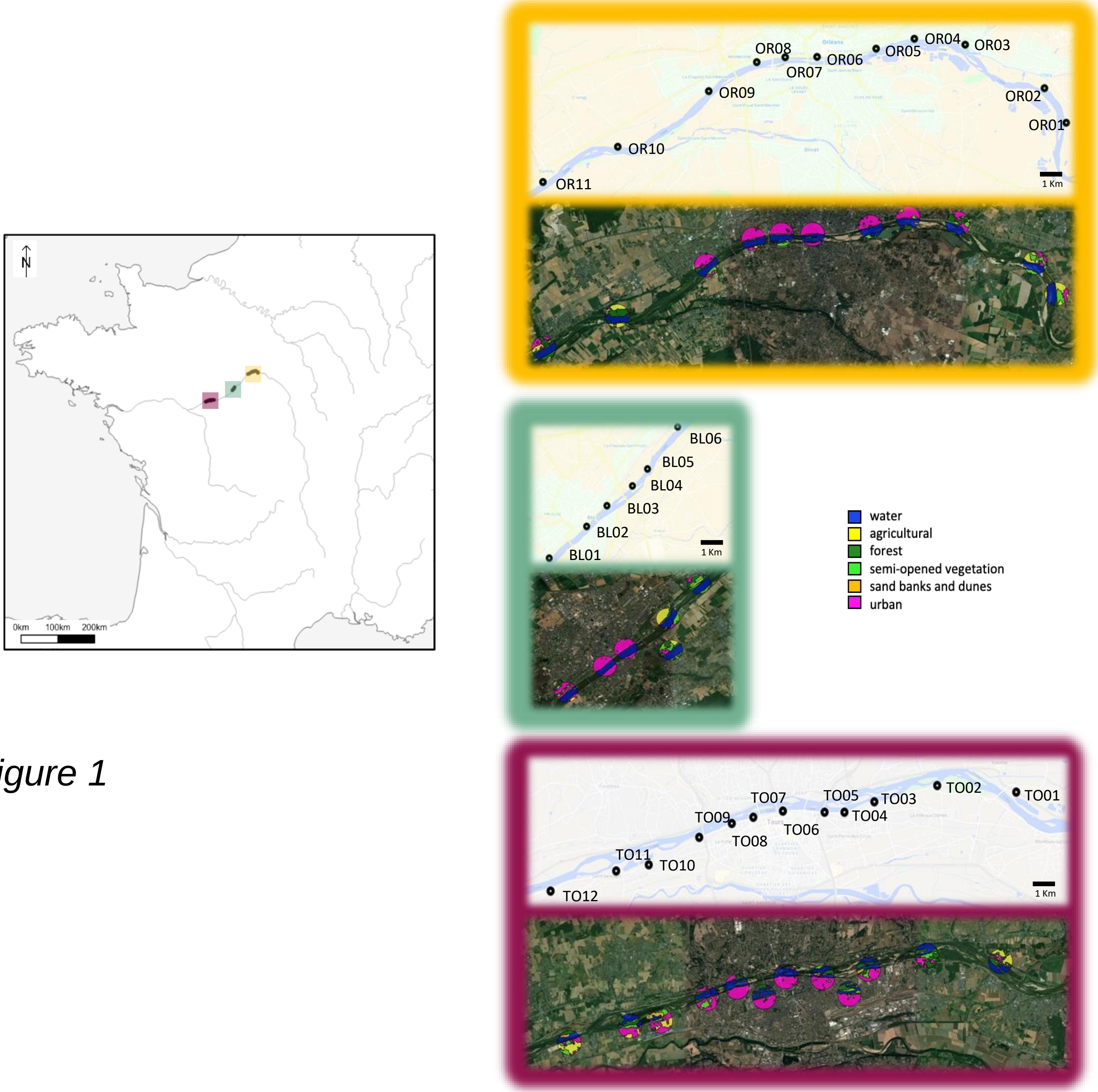

N
0km
100km
200km
OR01
OR02
OR03
OR04
OR05
OR06
OR07
OR08
OR09
OR10
OR11
1 Km
BL01
BL02
BL03
BL04
BL05
BL06
1 Km
TO01
TO02
TO03
TO04
TO05
TO06
TO07
TO08
TO09
TO10
TO11
TO12
1 Km
water
agricultural
forest
semi-opened vegetation
sand banks and dunes
urban

Figure 1

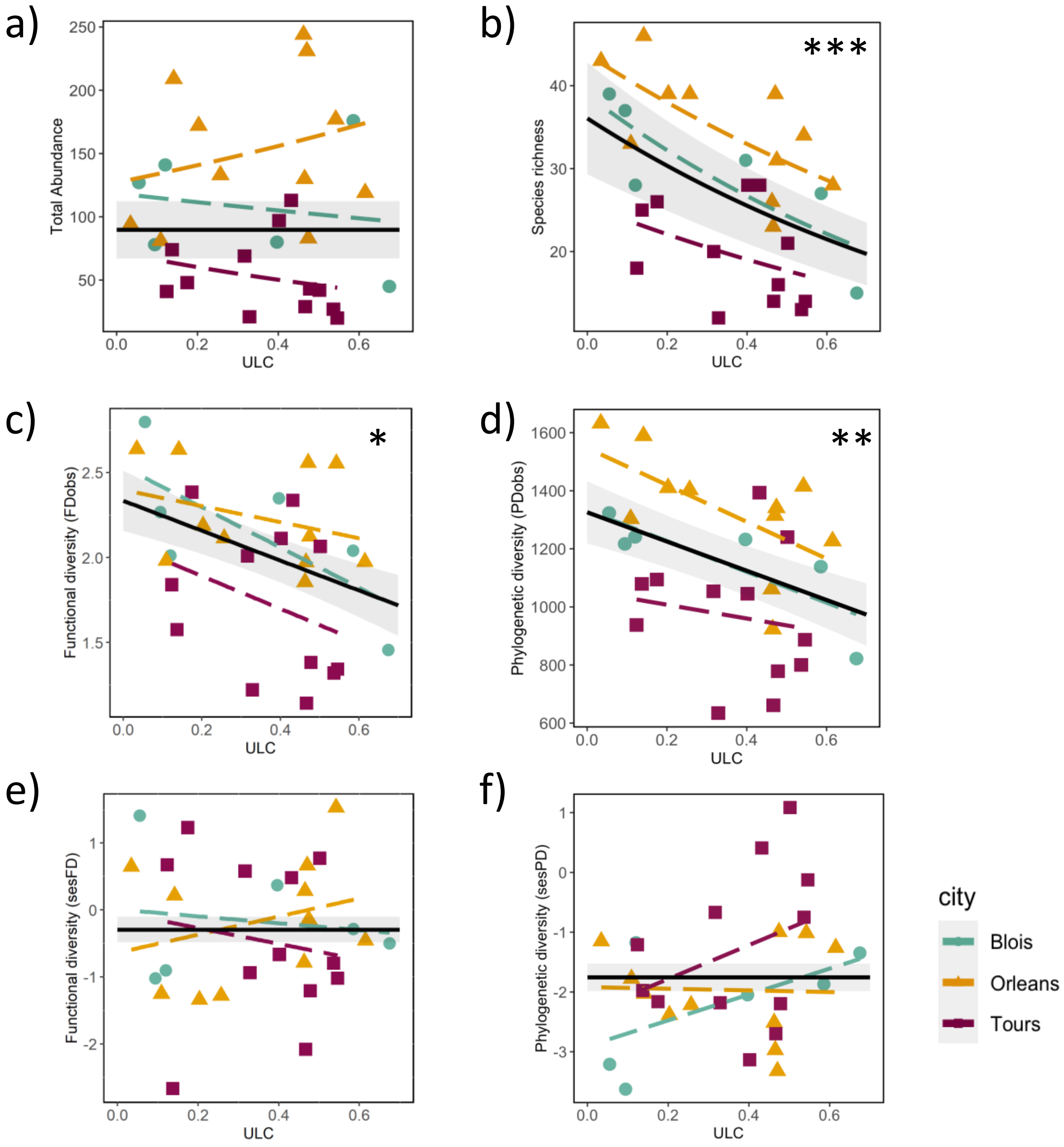

a)
Total Abundance
250
200
150
100
50
0.0
0.2
0.4
0.6
ULC
b)
***
Species richness
40
30
20
0.0
0.2
0.4
0.6
ULC
c)
*
Functional diversity (FDobs)
2.5
2.0
1.5
0.0
0.2
0.4
0.6
ULC
d)
**
Phylogenetic diversity (PDobs)
1600
1400
1200
1000
800
600
0.0
0.2
0.4
0.6
ULC
e)
Functional diversity (sesFD)
1
0
-1
-2
0.0
0.2
0.4
0.6
ULC
f)
Phylogenetic diversity (sesPD)
1
0
-1
-2
-3
0.0
0.2
0.4
0.6
ULC
city
Blois
Orleans
Tours

Figure 2

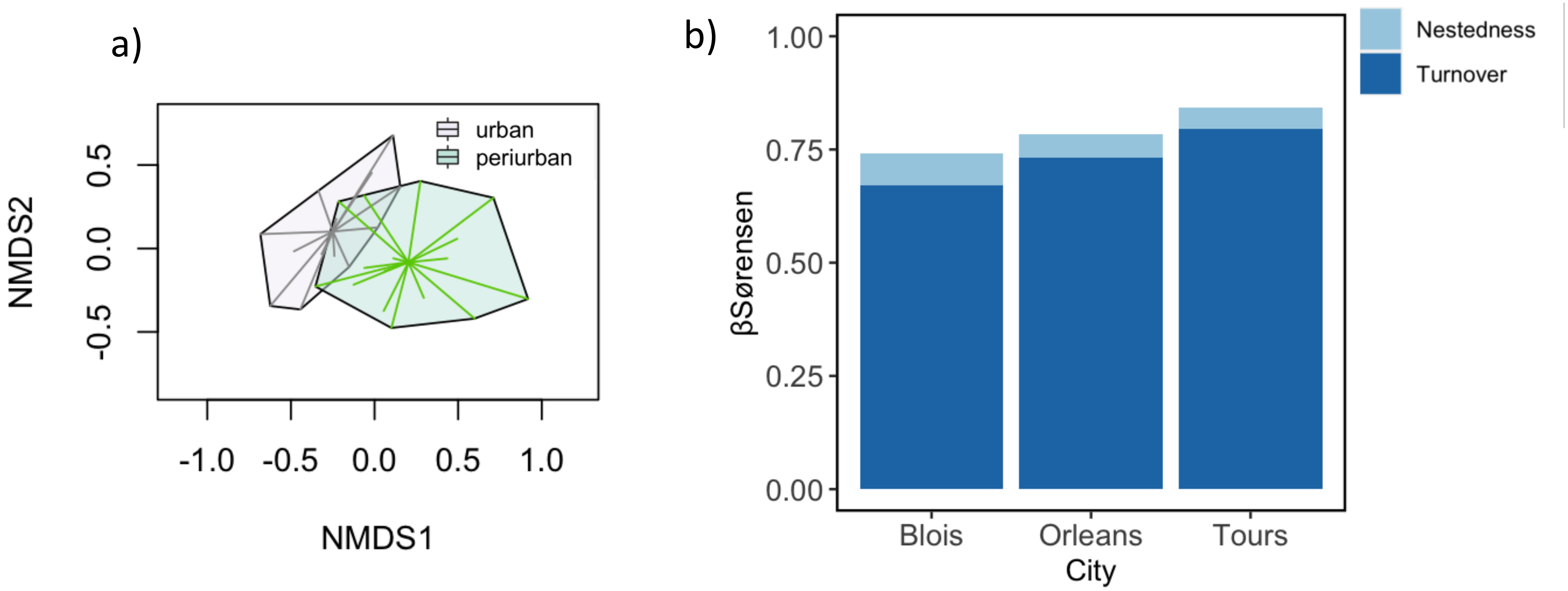
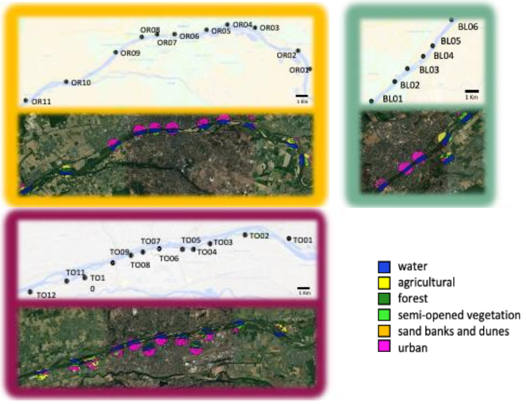
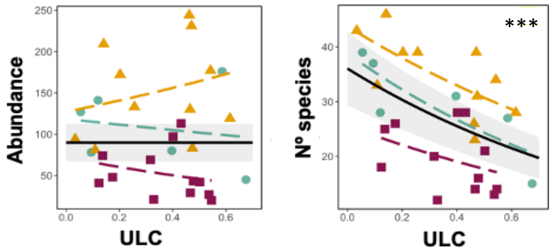

a)
NMDS2
0.5
0.0
-0.5
urban
periurban
-1.0
-0.5
0.0
0.5
1.0
NMDS1
b)
1.00
0.75
0.50
0.25
0.00
βSørensen
Nestedness
Turnover
Blois
Orleans
Tours
City

Figure 3

Urban landscape cover (ULC) effect on wild bees

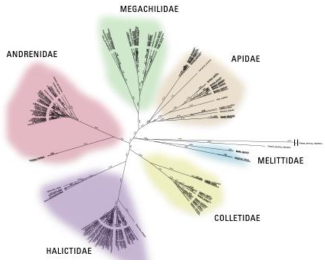


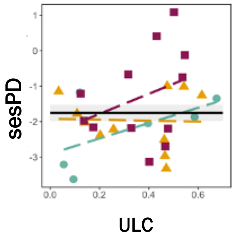
Species abundance and diversity



↓ Null models

Phylogenetic diversity





↓↑

Community composition

-High species turnover
-Functional structure response

social	solitary
small	big
Long flight period	Short flight period

Urban — Peri-urban

Functional diversity