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Using wild bees as indicators of landscape composition and bee diversity: Insights from contrasting clustering approaches

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ABSTRACT

Global insect declines and pronounced spatial and taxonomic sampling biases highlight the need for efficient biodiversity monitoring tools. Indicator species offer a promising solution, yet wild bees remain underexplored in this context. To address this gap, we evaluated the applicability of wild bees as indicators of landscape composition and bee diversity across urban and agricultural environments. Using standardised pan trap sampling, we collected 26,607 wild bees representing 283 species from 32 sites in and around Prague and Brno (Czech Republic), spanning two biogeographical regions. We compared two clustering approaches: a top-down method based on landscape composition and a bottom-up method based on bee community composition. Indicator species were identified for each cluster, and co-occurrence analyses were used to characterise typical wild bee communities. Both approaches produced moderately similar groupings but differed substantially in the indicator species identified. Clustering based on bee abundances yielded more ecologically coherent indicators and clearer differentiation between urban and agricultural landscapes, while capturing effects of habitat composition and regional species pools. Analyses revealed distinct bee communities associated with forests, urban greenspaces, agricultural landscapes, and both urban and agricultural wastelands. Most indicator species were specific to a region, but a select number of species proved effective as indicators on larger scales. Our results demonstrate that selected wild bee species can serve as effective indicators of landscape composition and bee diversity. We recommend bee-based clustering where comprehensive data are available, as it better incorporates species' ecological requirements and supports efficient monitoring and conservation planning in heterogeneous anthropogenic landscapes.

1. Introduction

The current global loss of insect biodiversity (Raven and Wagner, 2021; Outhwaite et al., 2022), together with the large bias in how and where it is being measured (Troudet et al., 2017; Marshall et al., 2024), has underlined the importance of extensive monitoring of population trends and species distributions. Monitoring insects is resource-intensive, requiring standardised sampling methodologies, deep taxonomic knowledge, and extensive fieldwork, particularly when extrapolating results over large biogeographical areas (Ebach et al., 2011; Engel et al., 2021). One strategy to reduce sampling effort is the use of indicator species as proxies for certain ecological or environmental variables, or for biodiversity itself (Siddig et al., 2016). Effective indicators should be sensitive to environmental variation (Osborn, 2022), ecologically relevant (Stork and Eggleton, 1992), representative of other taxa (Siddig et al., 2016), and easy to collect, monitor, and identify (Stork and Eggleton, 1992; Turner and McGraw, 2015; Carignan and Villard, 2002).

Several insect taxa have been successfully employed as indicator species (Gerlach et al., 2013). For example, Odonata as indicators of freshwater systems (Samways and Sharratt, 2010; Rosset et al., 2013), Coleoptera to investigate changes in the landscape (Filgueiras et al., 2011; Escobar et al., 2008), and Lepidoptera as indicators of habitat quality (Maes and Van Dyck, 2005) and richness of other taxa (e.g. beetles, Bhardwaj et al., 2012). Within Hymenoptera, ants have received most attention as indicators, especially for restoration projects (e.g.

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Gollan et al., 2011; Lawes et al., 2017; Majer, 1992). Concerning bees, studies have largely focussed on the honey bee (*Apis mellifera*) as an indicator of pollution due to its well-known biology (Porrini et al., 2003; Rabea et al., 2010; Quigley et al., 2019). Wild bees remain underexplored (Gerlach et al., 2013), despite their high diversity and range of life-history traits that suggest strong potential as indicators (Demeter et al., 2024). To date, studies using wild bees have shown that bee communities differ between types of croplands and with variation in the surrounding semi-natural landscape (Schindler et al., 2013; Martins et al., 2018; Maurer et al., 2022; Demeter et al., 2024), yet their role as indicators in urban environments remains unknown. A crucial step in indicator species research is specifying the method for site clustering. Clustering can follow either a top-down, land-use focussed approach that uses predetermined site clusters based on environmental factors (McGeoch et al., 2002; Bazelet and Samways, 2011; Birkhofer et al., 2018), or a bottom-up, taxon-abundance-focussed approach where sites are grouped according to community composition after which environmental variables are analysed (Carvalho et al., 2011; Murawski, et al., 2018; Marshall et al., 2023). The choice of clustering method can have a profound effect on the outcome of the final analysis (Gelbard et al., 2007; Hennig, 2022).

After indicator species are selected, they can be associated with other species to elucidate the composition of the typical community. Species co-occurrence is shaped by interspecific interactions and environmental preferences (Cordero and Jackson, 2021, 2023; Pozsgai et al., 2023). Interspecific interactions such as competition (Brazeau and Schamp, 2019; Page and Williams, 2023), predation (Bu et al., 2016; Ramesh et al., 2017), and parasitism (Ferreira et al., 2018; Veitch et al., 2020) influence whether species are able to coexist, which in turn is modulated by their traits (Elo et al., 2021; Cordero and Jackson, 2023). In bees, competition is mainly for floral resources and, to a lesser extent, nest sites. Specialisation in either resource can facilitate coexistence, even among species that share pollen sources (Johnson and Hubbell, 1975; Steffan-Dewenter and Tscharntke, 2000). In such cases, occurrence is bound by the distribution of the host plant as well as the species' competitive strength (Wood et al., 2016). Another determinant of co-occurrence is the regional species pool (Ilmonen et al., 2009; Cooper et al., 2016; Renner et al., 2018), which reflects the set of species available within biogeographical regions and the connectivity between them (Cornell and Harrison, 2014). Local environmental filters select species from this pool, resulting in distinct community compositions. This combination of interspecific interactions, trait-mediated constraints, and regional filtering creates complex co-occurrence patterns that are often difficult to interpret. Nonetheless, when sampling design is robust and species are carefully selected, co-occurrence analysis can effectively reveal typical bee communities and their association with landscape composition (Swengel and Swengel, 1997; Bu et al., 2016; Drever et al., 2019; Han et al., 2020; Marshall et al., 2023).

This study investigates the applicability of wild bees as indicator species of landscape composition and bee diversity across urban and agricultural landscapes in two Czech cities located in distinct biogeographical regions and compares the results of the analysis between the two beforementioned methods. We used standardised sampling, collecting an extensive dataset of wild bees and applying both clustering methods to compare results. We then conducted indicator species and co-occurrence analyses to characterise typical bee communities. We hypothesise that at least a subset of wild bee species can serve as effective indicator species. We expect that the two approaches yield different results, with the bee approach emerging as the preferred methodology. Additionally, we hypothesise that wild bee communities differ significantly between agricultural and urban landscapes, as well as between different landscape compositions of (semi-)natural habitats.

Our findings aim to inform future wild bee monitoring, conservation planning, and the development of efficient indicator assessment tools to protect our most important pollinators.

2. Methodology

2.1. Study sites

In order to investigate indicator species and co-occurrence patterns, we sampled 32 sites in and around Prague and Brno in the Czech Republic (Fig. 1). Each city included 16 sites, half of which were embedded within urban matrices and half within agricultural matrices with mainly oilseed rape (*Brassica napus*). We defined urban and agricultural landscapes as being landscapes where the dominant land-use matrix between natural habitat types consisted of built-up impervious areas for urban sites and croplands in the case of agricultural sites. Prague and Brno are situated in different biogeographical regions that have their own distinct regional species pool (Zettler et al., 2013). Brno is located in Moravia, on the edge of the Pannonian region, while Prague is located in Bohemia, in the Continental biogeographical region. The Pannonian region is seen as a wild bee diversity hotspot (Nieto et al., 2014) with approximately 600 species having been reported from Moravia, while from Bohemia approximately 400 species have been reported (Straka and Bogusch, 2017). These regions are separated by highlands that form a barrier for many species, which results in some species only being found at the Brno sites (e.g. *Andrena susterai, Ceratina chalybea, Seladonia kessleri,* and *Systropha planidens*).

Around each site, we delineated a 1 km radius circular buffer zone, approximating the average foraging distance of most wild bees (Greenleaf et al., 2007; Hofmann et al., 2020). Within each buffer, we quantified suitable bee habitats as the relative presence of grassland cover, cover of shrubs, and tree cover (similar to e.g. Graf et al. (2022)), since these offer foraging and nesting opportunities for all wild bee species. For this purpose, land cover maps were created in QGis (QGis development team, 2024) by integrating data on cropland, impervious surfaces, grassland cover (defined as open spaces dominated by herbaceous vegetation), tree cover, and small woody features (SWF), such as shrubs and hedgerows (Fig. 1). Cropland data were imported from OpenStreetMap (OSM) via the QuickOSM plugin in QGis, while the layers for impervious surfaces, grasslands, tree cover, and SWF were downloaded from the Copernicus Land Monitoring Service. The latter datasets were collected in 2018 and consist of high-resolution raster files with a 10-meter spatial resolution (https://land.copernicus.eu/pan-european/high-resolution-layers). Detailed information for all sites can be found in Appendix A1.

2.2. Sampling

Sampling was conducted by pan trapping from April to August in 2022 and 2024, with a compensatory round in April 2023 to account for irregularities encountered during the April 2022 sampling round (removal of pan traps from two sites). The oval pan traps used had a length of 15 cm, a width of 13 cm, and a depth of 4 cm, and coated UV-reflective white, blue or yellow paint. Each site was sampled once per month during a period of five contiguous (semi-)sunny days with similar temperatures. Pan traps were placed at eight sites during one day, resulting in one round taking eight days and the pan traps remaining at each site for five days. Ultimately, every site was sampled for a total of 55 days. Pan trapping was conducted with a standardised protocol by deploying nine traps at each site, arranged in three triplets consisting of one white, one blue, and one yellow pan trap each (Vereecken et al., 2021). These triplets were placed on a clear space on the ground near the centre of the site, within 100 m of each other. The pan traps were filled with 3 cm of water that contained a few drops of detergent to reduce the surface tension of the water up to 2 cm from the top. After collection, all bee specimens were first stored in a freezer before being washed, pinned, labelled, and identified to species level using available keys for central Europe (Amiet et al., 2001, 2004, 2007, 2014; Bogusch and Straka, 2012; Dathe et al., 2016; Scheuchl, 2006; Schmid-Egger and Scheuchl, 1997; Smit, 2018). Specimens from the *Bombus terrestris* group

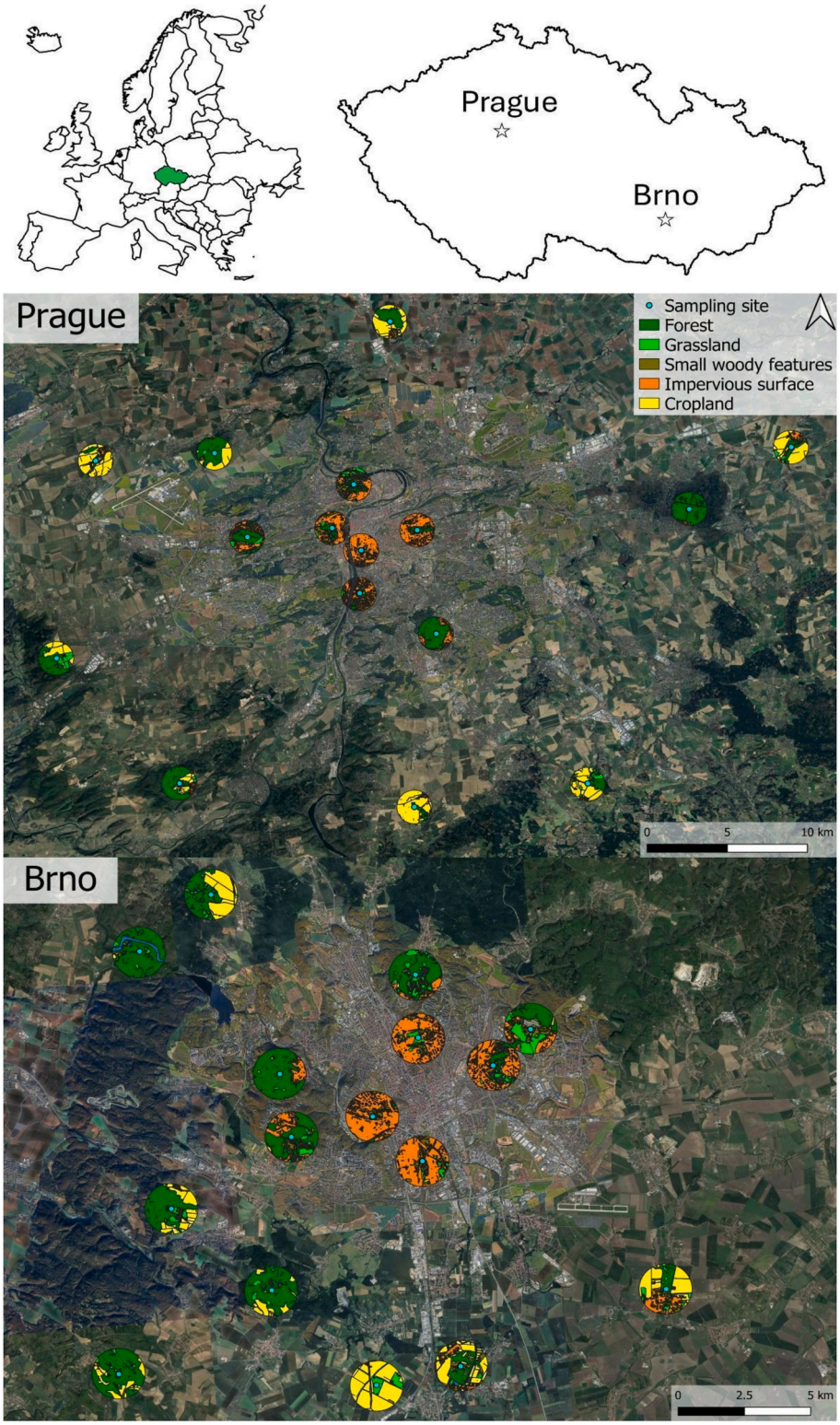

Fig. 1. Sampling sites in Prague (top) and Brno (bottom). In each city, 16 sites were selected, half in agricultural landscapes and half in urban landscapes. This categorisation was based on the dominant anthropogenic matrix between patches of natural habitat. A 1 km buffer zone was delineated around each sampling site, within which the relative cover of agricultural land (yellow), impervious surfaces (orange), tree cover (dark green), grassland (light green), and small woody features (brown) was calculated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(*B. terrestris*, *B. magnus*, *and B. cryptarum*) were all labelled as *B. terrestris*.

2.3. Clustering methods

All statistical analyses were performed in RStudio (2024.9.0.375) (Posit Team, 2024) for R (version 4.3.1) (R Core Team, 2023).

Since Prague and Brno are situated in two distinct biogeographical regions, we first split the data between the two cities. We then performed a clustering analysis for each city using two different approaches. For the first approach (hereafter "land-use approach"), the

sites were clustered together based on the composition of the landscape (i.e. the five land-use types). Clustering was performed with the scaled land-use type percentages (*scale* function in base R), and with Ward's linkage (Legendre and Legendre, 2012) via the *hclust* function in base R. For the second approach (hereafter "bee approach"), we clustered the sites together based on hierarchical clustering of the Hellinger transformed bee abundance per site using Ward's linkage (Legendre and Legendre, 2012). The Hellinger transformation, which reduces the influence of highly abundant species, was done with the *dist* function, and the clustering was performed with the *hclust* function. Based on the results of the clustering analyses, a dendrogram was created for each approach with the *fviz_dend* function, after which the optimal number of clusters was investigated with the *fviz_nbclust* and *fviz_silhouette* functions. Visualisation of the clusters in multivariate space was done with the *fviz_cluster* function. All of the *fviz* functions are included in the factoextra package (version 1.0.7) (Kassambara and Mundt, 2020). Cluster robustness was assessed using bootstrap resampling with the *clusterboot* function of the package fpc (version 2.2–14) (Hennig, 2026). For each clustering analysis, 1000 bootstrap resamples were generated and reclustered after which cluster stability was quantified using mean Jaccard similarity coefficients, which measures the frequency with which clusters are recovered across bootstrap replicates. Detailed cluster-wise stability estimates for all clustering analyses are provided in Appendix A3. Similarity between the clusterings of the two approaches was assessed by comparing the two resulting dendrograms with the *tanglegram* function and quantified via the Fowlkes-Mallows index with the *FM_index* function, both available in the dendextend package (version 1.19.1) (Galili, 2015). The Fowlkes-Mallows index measures the similarity between two clusterings by comparing the observed clustering with an expected value under fully random shuffling of both clusterings (Fowlkes and Mallows, 1983). The index can take values between 0 and 1, with a value of 0 indicating that the dendrograms are completely different (reshuffled) and a value of 1 indicating that the dendrograms are completely similar (no reshuffling).

2.4. Indicator species and co-occurrence

To find indicator species and analyse co-occurrence patterns, we continued with the results from the bee approach, since this inherently takes (hidden) ecological needs for the bees into account. Indicator species were selected for each cluster with the *multipatt* function from the indicspecies package (version 1.7.14) (De Cáceres and Legendre, 2009) with a maximum order of one, 999 permutations, and the IndVal.g function (which corrects for different cluster sizes). The *multipatt* function allows for the inspection of the individual components that the indicator value is composed of, called components 'A' and 'B' (De Cáceres and Legendre, 2009). Component 'A', known as the specificity, is an estimate of the probability that the surveyed site belongs to a designated cluster given the fact that the species has been found there. This shows the positive predictive value of the species as an indicator of the cluster. Specifically, a value of 1.00 for component 'A' entails that this species is only found in the associated site cluster but not in any others. Component 'B', the fidelity or sensitivity, is an estimate of the probability of finding the species at sites belonging to the cluster. In this case, a value of 1.00 means that the species is found in all of the sites within the cluster. After selecting the indicator species, we analysed their co-occurrence patterns with other wild bee species using the cooccur package (version 1.3) (Griffith et al., 2016). This analysis aimed to identify the species that consistently and significantly co-occurred with the indicator species, highlighting shared habitat preferences or biotic interactions. The main function of this package is the *cooccur* function, which accepts a binary presence-absence matrix and yields a list of indicator species for a given site cluster with their respective indicator value between 0 and 1. Positive co-occurrences with the indicator species were investigated by the *pair* function, which shows all significant co-occurrences of a selected species. Species co-occurrence and their interconnectedness was visualised with the 'visNetwork' package (version 2.1.2) (Almende and Contributors, 2022), which provides an illustration of bee community structure.

3. Results

Our dataset contained 26,607 wild bee specimens, of which 12,862 individuals (48%) were collected at the agricultural sites and 13,745 individuals (52%) at the urban sites. The total number of specimens from Prague was 12,794 (48%), which included 196 species, and the total number for Brno was 13,813 (52%) with 260 species. In total, 283 wild bee species were collected from six different families. Halictidae was the most common family with 48.5% of the specimens, followed by Andrenidae (24.9%), Apidae (16.7%), Megachilidae (6.1%), Colletidae (3.7%), and Melittidae (0.2%).

3.1. Comparison of clustering methods

When the data were split between Prague and Brno (Fig. 2), four clusters emerged for both cities under both approaches (see Appendix A1 for an overview showing which site belongs to which clustering for either approach and Appendix A3 for cluster robustness results). For Prague, clustering with the land-use approach first separated cluster PL1 (Fig. 2a**)** which consisted of two urban and two agricultural sites, characterised mainly by forests. Cluster PL2 comprised the remaining six agricultural sites with lower forest cover. Cluster PL3 included four urban sites with relatively high proportions of grassland and SWF, and cluster PL4 consisted of two sites with overall low amounts of suitable habitat. Clustering with the bee approach (Fig. 2b) resulted in a strict separation between agricultural and urban clusters. Cluster PB1 consisted of three urban sites with relatively high forest cover, while the four sites of cluster PB2 consisted mainly of agricultural sites with low grassland cover. The outlier in this cluster, with 13% grassland cover, contained grassland with poor flower diversity. Cluster PB3 included the remaining five urban sites with relatively lower forest cover and, finally, cluster PB4 consisted of four agricultural sites with a higher grassland cover or with flower-rich grassland. For Brno, a similar pattern was observed for both approaches, although the separation between urban and agricultural sites was less strict for the bee approach (Fig. 2c and d). Under the land-use approach (Fig. 2c), cluster BL1 consisted of three agricultural and one urban site with high forest cover, and cluster BL2 comprised the remaining five agricultural sites. Cluster BL3 included three urban sites with medium forest cover, while cluster BL4 comprised four sites where the cover of grassland and SWF exceeded that of the tree cover. Using the bee approach (Fig. 2d), cluster BB1 included two urban and four agricultural sites with high forest cover. Cluster BB2 consisted of two agricultural sites with low forest cover, and cluster BB3 comprised four urban sites with intermediate forest cover accompanied by grassland and/or SWF. The final cluster, cluster BB4, consisted of two urban and one agricultural site where the tree cover was lower than that of the other two habitat types.

When comparing the two approaches for both cities, the results were moderately similar. For Prague (Fig. 3), the main difference between the clustering methods resulted from the grouping of the agricultural sites (cluster PL2 compared to clusters PB2 and PB4). The urban sites were only slightly reshuffled between the approaches. Accordingly, the FM-index analysis showed an observed value of 0.42 with an expected value under random clusters of 0.22 and a variance of 0.005. Together with a Z-score of 2.71 ($p \approx 0.01$) this indicated that the two clusterings were moderately similar and that this similarity was significant. For Brno, the result was highly comparable (Fig. 4). In this case, however, the main reshuffling between approaches was caused by a difference in grouping of forested and non-forested sites (clusters BL2 and BL4 compared to clusters BB2 and BB4). The FM-index for Brno showed an observed Fowlkes-Mallows similarity between the two clusters of 0.40, while the expected value under random clustering was 0.23 with a

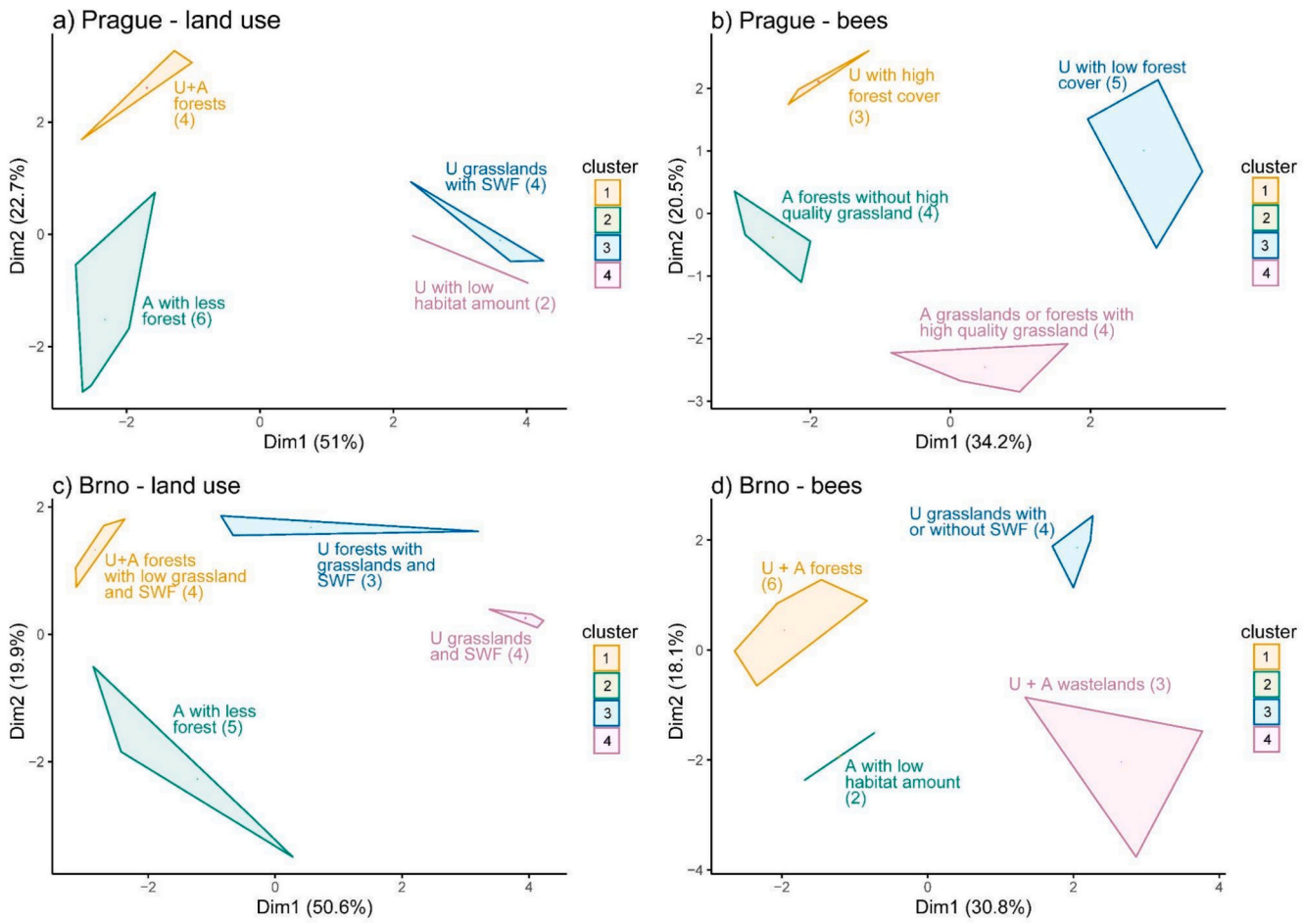

Fig. 2. Cluster maps of sampling sites for both cities based on landscape composition and wild bee community composition. site clusters are indicated with "A" for agricultural or "U" for urban, accompanied by a brief description of the site types included in each cluster. Numbers in parentheses indicate the number of sites per cluster. (a) Prague land-use approach, (b) Prague bee approach, (c) Brno land-use approach, and (d) Brno bee approach. Similar clusters within each city and approach are shown in the same colour.

variance of 0.005. Combined with a Z-score of 2.39 ($p \approx 0.02$) this showed that the two clustering methods were again moderately similar and that this similarity was significant.

3.2. Indicator species

Indicator species analysis of the site clusters based on the landscape composition identified nine indicator species across the four clusters in Prague and 20 in Brno (Table 1). In contrast, indicator species analysis based on the wild bee composition identified 21 indicator species for the four clusters in Prague and 29 indicator species for the four clusters in Brno (Table 2).

Even though the two clustering approaches resulted in statistically significant, albeit moderately similar site clusters, they differed considerably in their indicator species. For Prague, only three of the 27 indicator species (11%) were shared between the two approaches: *Andrena flavipes, Lasioglossum leucozonium,* and *Lasioglossum minutissimum*. For Brno, six of the 43 indicator species (14%) were shared between the two approaches, namely *Andrena strohmella, Bombus pascuorum, Bombus pratorum, Heriades truncorum, Lasioglossum glabriusculum,* and *Seladonia subaurata*. In addition, multiple species appeared as indicator species for similar clusters between cities when the same approach was used. Under the land-use approach, *Andrena nigroaenea* consistently indicated agricultural landscapes. Under the bee approach, *Heriades truncorum* indicated forested sites, while *Lasioglossum leucozonium* indicated lightly forested urban sites. Interestingly, under the bee approach, *Andrena helvola* indicated urban forests in Prague, while it indicated open agricultural landscapes in Brno. This alludes to differences in filtering from the regional species pool for this species, either based on differences in environmental factors or due to differences in species composition between the cities.

3.3. Co-occurrence

For the co-occurrence analysis, taking the moderate similarity between the clustering methods into account, we opted to use the indicator species derived from the bee approach to identify the typical wild bee communities, as this approach inherently incorporates the ecological requirements of the species.

Co-occurrence analysis for Prague, comprising 19,110 species combinations, resulted in the removal of 9919 (51.9%) combinations because the expected co-occurrence was <1. Out of the remaining 9191 pairs, 1.4% of all co-occurrence combinations were non-random, with 86 combinations being positive co-occurrences and 42 being negative co-occurrences. Further analysis of the positive co-occurrences with the selected indicator species revealed 21 species that co-occurred with the indicator species (Fig. 5) (see Appendix A2 for the full table of positive and negative co-occurrences). For cluster PB1 (urban forests), the typical wild bee community comprised 17 species, while cluster PB2 (agricultural forests) had a typical community of eight species. Clusters PB1 and PB2 were interconnected through two shared indicator species, *Sphecodes ephippius* and *Nomada panzeri*. Cluster PB3 (urban parks) had a

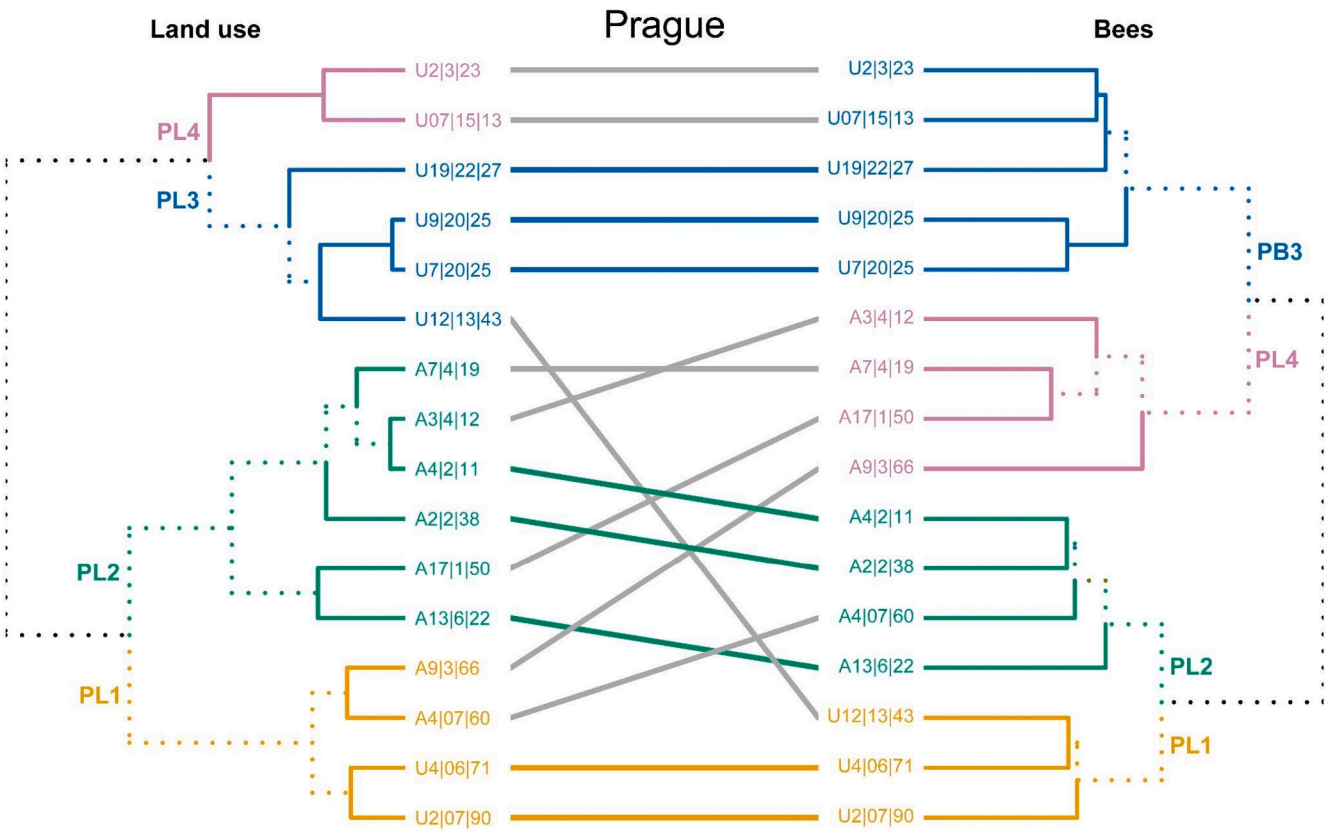

Fig. 3. Comparison of dendrograms for Prague derived from the land-use approach (left) and the bee approach (right). Cluster names are shown at the base of the first split for each cluster, and clusters are coloured as in Fig. 2. Dotted lines indicate splits present in both approaches, whereas solid lines indicate unique splits. Grey lines connecting sites show those assigned to different clusters between approaches, while coloured lines indicate consistent clustering. Most dissimilarity between dendrograms is driven by differences in the grouping of agricultural sites. Overall similarity between trees based on the FM-index is moderate but significant.

typical community consisting of only five species and finally, cluster PB4 (agricultural grasslands) contained 13 typical wild bee species. This cluster was connected to PB2 through a non-indicator species, *Lasioglossum parvulum*.

For Brno, 33,670 species combinations were analysed, with 18,965 pairs being removed due to the expected co-occurrence being <1. Again, 1.4% of the remaining pairs were non-random, resulting in 4705 of them being assessed. Out of those species combinations, 99 were positive co-occurrences, while 111 were negative. In total, 25 species co-occurred with the indicator species from Brno (Fig. 6) (see Appendix A2 for the full table of positive and negative co-occurrences). In cluster BB1 (urban and agricultural forests), 18 typical species were identified, while cluster BB2 (agricultural sites with low habitat amount) had eight typical species and included only a single non-indicator species, namely *Bombus hortorum*. For cluster BB3 (urban grasslands), 13 typical species were identified, and finally, cluster BB4 (wastelands) contained 14 species in the co-occurrence network. None of the clusters in Brno were interconnected.

4. Discussion

This study evaluated the use of wild bees as indicator species of different landscape compositions and assessed their potential as bio-indicators of typical wild bee communities. Understanding which species are positively or negatively affected by changes in landscape composition has important implications for wild bee conservation, as it guides trade-offs when selecting conservation or restoration targets (Siddig et al., 2016). Our results highlight clear differences between two clustering approaches, one based on landscape composition, and one based on wild bee abundances. While both approaches produced broadly similar site clustering, they differed substantially in the selected indicator species. Even though the approaches are interchangeable to an extent, clustering based on the bees themselves is recommended as it takes their ecological needs, as well as hidden, latent variables, into account. Overall, our findings demonstrate that a carefully selected subset of wild bees can function as effective indicator species of overall wild bee diversity and can support monitoring efforts in conservation and restoration projects. These results are consistent with previous studies that have reported differences in wild bee communities across anthropogenic landscapes (Choate et al., 2018; Nunes et al., 2024; Villalta et al., 2021) and underscore the importance of the regional species pool in shaping local diversity (Cornell and Harrison, 2014; Rivers-Moore et al., 2020).

4.1. Comparison of clustering methodologies

Using the land-use approach, sites were clustered together based on their landscape composition, whereas with the bee approach, the bee community composition formed the basis of the clustering. Despite these methodological differences, both approaches produced moderately similar site clusterings. However, the differences that were present substantially affected the outcome of indicator species analysis. This confirms that methodological choices can strongly influence the outcome of indicator species analysis (De Cáceres et al., 2010; Dufrêne and Legendre, 1997). Even moderate reshuffling of sites among clusters alters species abundances within clusters, an effect exacerbated when species are unevenly distributed or concentrated within a single site (Tichy and Chytry, 2006; Podani and Csányi, 2010). When such sites shift between clusters, relative abundances change and different species may be identified as indicators. Consequently, clustering methods and

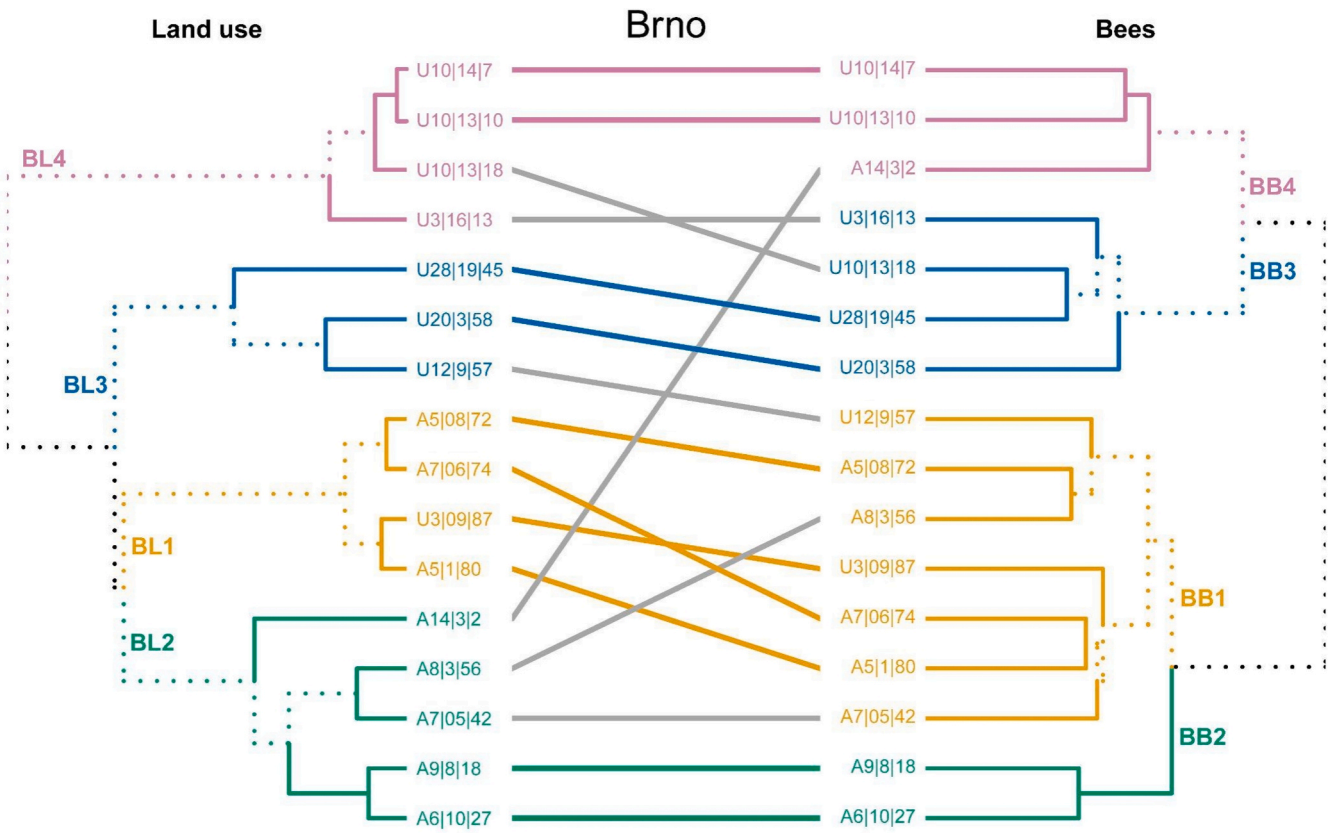

Fig. 4. Comparison of dendrograms for Brno derived from the land-use approach (left) and the bee approach (right). Cluster names are shown at the base of the first split for each cluster, and clusters are coloured as in Fig. 2. Dotted lines indicate splits present in both approaches, whereas solid lines indicate unique splits. Grey lines connecting sites show those assigned to different clusters between approaches, while coloured lines indicate consistent clustering. Most dissimilarity between dendrograms is driven by differences in the grouping of forested and non-forested sites. Overall similarity between trees based on the FM-index is moderate but significant.

resulting clusters must be critically evaluated. A possible solution for mitigating this problem is to increase the maximum order in the indicator species analysis (De Cáceres et al., 2010), allowing species that represent multiple clusters to be identified as an indicator of multiple clusters. However, species associated with multiple clusters may respond differently to landscape changes across clusters, and their habitat preferences should therefore be examined in a cluster-specific context (Elo et al., 2021). Finally, it is possible to combine the two approaches. Sites can be clustered together using broad landscape categories (e.g. urban versus agricultural) and biogeographic regions to identify typical species for these broad categories (Choate et al., 2018). Subsequent analyses can then assess shifts in community composition by analysing the habitat preferences of the indicators and their co-occurring species using multi-species distribution models. This integrated framework enables a clear assessment of changes in wild bee communities in response to landscape composition.

Overall, both approaches are usable, and the choice of method depends on the availability of data and the goal of the analysis. However, each approach has its distinct benefits and limitations. For the land-use approach, the main considerations are the type (Neumüller et al., 2020) and scale (Féon et al., 2013; Neokosmidis et al., 2016) of the landscape variables, as clustering needs to reflect ecologically relevant conditions for wild bees. Habitat classification can vary from very broad, as used in this study or by Graf et al. (2022), to more fine-scale classifications (e.g., broad-leaf forest versus coniferous forest). Interactions between these local factors and broader landscape composition can influence wild bee communities in a variety of ways (Neumüller et al., 2020). Here, we deliberately applied the broadest habitat classification to assess whether typical wild bee communities could be detected, since this approach minimises effort, cost, and time; all important factors for practical conservation efforts (Klaus et al., 2024). Moreover, in fragmented anthropogenic landscapes, the matrix between habitat patches plays a major role in shaping wild bee communities (Zurbuchen et al., 2010; Krewenka et al., 2011; Dorchin et al., 2012; Visser et al., 2026) and should therefore always be included among the selected land-use types. Conversely, the bee approach does not suffer from uncertainty regarding the ecological relevance of the resulting clusters for wild bees, as the clustering is directly based on the bees themselves. The main limitation of this approach, however, is the requirement for extensive abundance datasets collected using standardised sampling protocols (Klaus et al., 2024), which requires time, effort, and resources. In some cases, this limitation can be alleviated by using existing datasets, such as those derived from citizen science. However, such data must be used cautiously, as they may contain spatial, temporal, or taxonomic biases that can affect indicator species analyses (Petersen et al., 2021; Visser et al., 2025).

Ultimately, the choice of clustering approach depends on both data availability and on the intended application. When the objective is to identify indicator species that accurately represent wild bee communities and their associated landscape composition, clustering based on wild bee community composition is preferable because it directly captures the ecological relationships among species and their environment. Conversely, when comprehensive bee community data are unavailable, clustering based on landscape composition provides a practical alternative that can still identify useful indicator species, although these may differ from those obtained using bee community data. We therefore recommend landscape-based clustering as a first-step approach in data-poor situations, whereas bee community-based clustering should be

Table 1
Indicator species for Prague and Brno under the land-use clustering approach, with species abundances, the 'A' (specificity) and 'B' (fidelity) components, and the overall indicator value (indic.stat). All listed species are statistically significant indicators. Species in bold are shared between clustering approaches within each city.

City	Cluster	Indicator species	Abundance	A	B	Indic. stat
Prague	1	*Andrena floricola*	3	1.00	0.75	0.87
		Bombus bohemicus	18	0.64	1.00	0.80
		Andrena cineraria	296	0.54	1.00	0.74
	2	*Andrena nigroaenea*	39	0.89	1.00	0.94
		Andrena flavipes	274	0.65	1.00	0.81
		Lasioglossum minutissimum	19	0.61	1.00	0.78
	3	***Lasioglossum leucozonium***	53	0.61	1.00	0.78
		Seladonia subaurata	100	0.47	1.00	0.68
	4	*Sphecodes ferruginatus*	5	0.82	1.00	0.91
Brno	1	*Bombus sylvestris*	5	0.75	1.00	0.87
		Heriades truncorum	14	0.71	1.00	0.84
		Bombus pratorum	26	0.64	1.00	0.80
		Andrena strohmella	156	0.64	1.00	0.80
		Bombus pascuorum	207	0.63	1.00	0.79
		Hylaeus communis	15	0.57	1.00	0.76
		Nomada ferruginata	7	0.74	0.75	0.74
		Andrena dorsata	33	0.50	1.00	0.71
	2	*Andrena nigroaenea*	44	0.80	1.00	0.90
		Lasioglossum lineare	21	0.76	1.00	0.78
	3	*Osmia cornuta*	89	0.73	1.00	0.85
		Andrena intermedia	2	1.00	0.67	0.82
		Megachile circumcincta	9	0.93	0.67	0.79
		Eucera nigrescens	30	0.60	1.00	0.78
	4	*Anthidium manicatum*	13	0.86	1.00	0.93
		Lasioglossum glabriusculum	236	0.80	1.00	0.90
		Colletes cunicularius	30	0.75	1.00	0.86
		Seladonia subaurata	158	0.63	1.00	0.80
		Halictus scabiosae	42	0.62	1.00	0.78
		Hoplitis leucomelana	39	0.55	1.00	0.74

preferred whenever sufficiently robust datasets are available because it inherently accounts for species' ecological requirements and the regional species pool.

4.2. Indicator species and typical wild bee communities

When clustering sites based on wild bee abundances, the resulting clusters for Prague and Brno were broadly comparable but showed interesting differences in their landscape composition. The more pronounced separation between agricultural and urban sites in Prague, alongside the less strict separation in Brno, underscores the importance of the anthropogenic matrix for structuring bee communities in fragmented landscapes (Jauker et al., 2009; Visser et al., 2026). Agricultural and urban landscapes have previously been shown to host distinct bee communities that filter species differently from the regional species pool (Cornell and Harrison, 2014; Sydenham et al., 2014), a crucial

Table 2
Indicator species for Prague and Brno under the bee-based clustering approach, with species abundances for each city, the 'A' (specificity) and 'B' (fidelity) components, and the overall indicator value (indic.stat). All listed species are statistically significant indicators. Species in bold are shared between clustering approaches within each city.

City	Cluster	Indicator species	Abundance	A	B	Indic. stat
Prague	1	*Lasioglossum punctatissimum*	7	0.77	1.00	0.88
		Nomada panzeri	121	0.74	1.00	0.86
		Nomada flava	30	0.71	1.00	0.84
		Andrena helvola	257	0.67	1.00	0.82
		Heriades truncorum	11	0.63	1.00	0.79
		Nomada ruficornis	228	0.50	1.00	0.71
		Andrena haemorrhoa	425	0.47	1.00	0.69
	2	***Lasioglossum minutissimum***	19	0.60	1.00	0.77
		Hylaeus communis	47	0.56	1.00	0.75
		Sphecodes ephippius	19	0.52	1.00	0.72
		Nomada flavoguttata	552	0.51	1.00	0.72
		Andrena minutula	1126	0.51	1.00	0.71
	3	***Lasioglossum leucozonium***	53	0.61	1.00	0.79
		Andrena viridescens	9	0.74	0.80	0.77
		Lasioglossum morio	1002	0.69	1.00	0.77
	4	*Lasioglossum glabriusculum*	13	0.92	1.00	0.96
		Lasioglossum malachurum	413	0.80	1.00	0.90
		Andrena flavipes	274	0.70	1.00	0.84
		Nomada bifasciata	23	0.69	1.00	0.83
		Lasioglossum pauxillum	1662	0.69	1.00	0.83
		Nomada fucata	26	0.62	1.00	0.79
Brno	1	***Bombus pratorum***	26	0.72	1.00	0.85
		Bombus bohemicus	6	1.00	0.72	0.85
		Sphecodes geoffrellus	39	0.69	1.00	0.83
		Andrena strohmella	156	0.68	1.00	0.82
		Heriades truncorum	14	0.77	0.86	0.82
		Bombus pascuorum	207	0.63	1.00	0.79
		Andrena bicolor	147	0.62	1.00	0.79
	2	*Andrena chrysosceles*	7	0.90	1.00	0.95
		Andrena helvola	153	0.81	1.00	0.90
		Anthophora furcata	4	0.78	1.00	0.89
		Andrena subopaca	128	0.63	1.00	0.80
		Andrena haemorrhoa	239	0.62	1.00	0.79
		Osmia bicornis	314	0.53	1.00	0.73
		Hylaeus confusus	301	0.46	1.00	0.68
	3	*Lasioglossum marginatum*	1943	0.92	1.00	0.96
		Melecta albifrons	15	0.83	1.00	0.91
		Megachile rotundata	3	1.00	0.75	0.87
		Colletes similis	5	0.67	1.00	0.82
		Lasioglossum leucozonium	32	0.62	1.00	0.79
		Nomada bifasciata	79	0.89	1.00	0.77
		Lasioglossum laevigatum	23	0.57	1.00	0.76

(*continued on next page*)

Table 2 (*continued*)

City	Cluster	Indicator species	Abundance	A	B	Indic. stat
	4	***Lasioglossum glabriusculum***	236	0.83	1.00	0.91
			37	0.74	1.00	0.86
		Seladonia tumulorum	12	0.72	1.00	0.85
		Lasioglossum interruptum	24	0.68	1.00	0.82
		Ceratina nigrolabiata	2	1.00	0.67	0.82
		Andrena florea	6	1.00	0.67	0.82
		Hylaeus paulus	158	0.61	1.00	0.78
		Seladonia subaurata	57	0.58	1.00	0.76
		Ceratina cyanea				

consideration for wild bee conservation because species responses to landscape change differ markedly between agricultural and urban environments.

In Prague, two distinct agricultural bee communities were identified that differed in their composition of suitable habitats. Cluster PB2 comprised sites that were either mostly forested or characterised by low tree cover combined with flower-poor grasslands, whereas cluster PB4 consisted of less forested sites or forested sites accompanied by flower-rich grasslands. As no plant surveys were conducted, this interpretation is solely based on field observations during sampling. These patterns nevertheless indicate that local factors such as floral composition or management regime also partly influenced the differences between the two communities (Neumüller et al., 2020; Edelkind-Vealey et al., 2024; Nunes et al., 2024). Importantly, both clusters supported distinct wild bee communities. Agricultural cluster PB2 was characterised by small-bodied species with diverse traits, however, none of the species was (primitively) eusocial. In contrast, cluster PB4 included four primitively eusocial species (*Lasioglossum glabriusculum*, *Halictus scabiosae*, *Lasioglossum pauxillum*, and *Lasioglossum malachurum*) and one eusocial bumble bee (*Bombus sylvarum*). This contrast suggests differences in connectivity and inter-patch distances, as smaller species typically have shorter foraging ranges than larger bees (Greenleaf et al., 2007), and social bees forage over greater distances than similarly sized non-social species (Grüter and Hayes, 2022). The urban clusters in Prague differed both from the agricultural clusters and from one another. Cluster PB1, which included forested urban sites, was characterised by *Andrena* spp. and *Lasioglossum* spp., accompanied by *Nomada* spp., the brood parasite of the former, and by cavity-nesting species such as *Heriades truncorum*, which in our analysis served as the typical forest indicator due to its reliance on the presence of existing wooden cavities as nesting substrate (Peeters et al, 2012). Cluster PB3, representing urban parks, had the smallest bee community, indicating strong ecological filtering from the regional species pool. This may be due to more intense landscape management or increased competition for limited resources (Cornell and Harrison, 2014). Notably, two oligolectic species (*Andrena viridescens* and its brood parasite *Nomada atroscutellaris*) occurred in this cluster, despite oligolecty often being reported as particularly sensitive to habitat loss from urbanisation (Ferrari and Polidori, 2022; Prendergast et al., 2022).

In Brno, the separation between agricultural and urban landscapes was less distinct. Nevertheless, clusters consisting exclusively of a single anthropogenic matrix closely resembled their counterparts in Prague. Cluster BB2 comprised two agricultural sites with low forest cover, analogous to cluster PB2, and was characterised by a typical community dominated by solitary, ground-nesting *Andrena* spp., with *Hylaeus* sp. and *Osmia* sp. as non-ground-nesting additions. Cluster BB3 was the only exclusively urban cluster in Brno and included urban parks, grasslands, community gardens, and a cemetery. This cluster closely resembled Prague's PB3, with communities dominated by *Andrena* spp. and *Lasioglossum* spp., but additionally included several cavity-nesting *Megachile* spp. As in PB3, BB3 contained oligolectic species, namely *Colletes similis* and *Melitta haemorrhoidalis*, but these species specialise on different plants than the oligolectic species in PB3. Together, these findings do suggest that certain urban landscapes may benefit specific oligolectic bees, which is highly relevant for wild bee conservation. Cluster BB1 represented the first instance where urban and agricultural sites were grouped together, indicating that in Brno, forested landscapes are more strongly structured by tree cover than by the surrounding anthropogenic matrix. All sites in this cluster were heavily forested, with

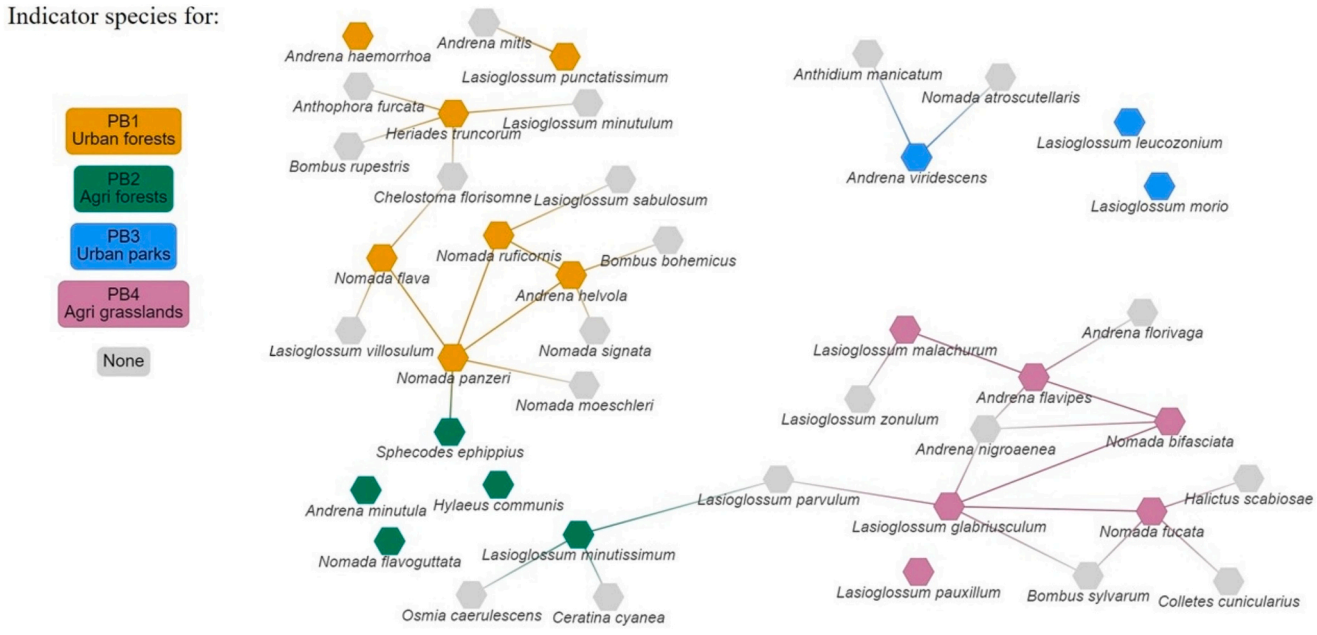

Fig. 5. Co-occurrence network for Prague showing the four site clusters. Indicator species are coloured according to cluster (as in Fig. 2), while non-indicator species are shown in grey. Cluster PB1 (urban forests) includes seven indicator species and a typical community of 17 species. PB1 is connected to PB2 through shared indicator species. Cluster PB2 includes five indicator species and a community of eight species; one non-indicator species (Lasioglossum parvulum) links PB2 to PB4. Cluster PB3 consists of three indicator species and a community of five species. Cluster PB4 includes six indicator species and a total community of 13 species.

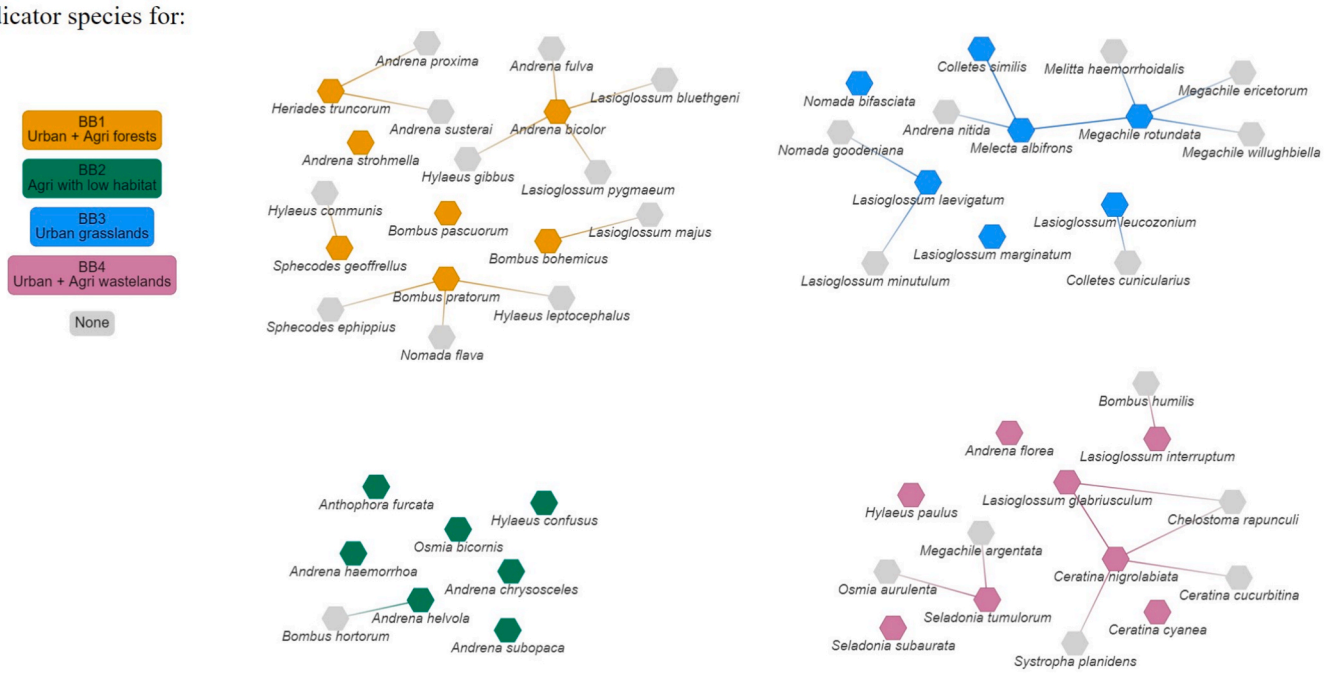

Fig. 6. Co-occurrence network for Brno showing the four site clusters. Indicator species are coloured according to cluster (as in Fig. 2), while non-indicator species are shown in grey. Cluster BB1 (urban and agricultural forests) includes seven indicator species and a typical community of 18 species. Cluster BB2 consists of seven indicator species and a community of eight species. Cluster BB3 includes seven indicator species and a community of 13 species. Cluster BB4 contains eight indicator species and a total community of 14 species.

tree cover comprising at least three times the area of other suitable habitat types. Forest-dominated landscapes are generally associated with lower wild bee diversity, with community composition depending on the complementarity of additional habitat types (Diaz-Forero et al., 2011; Eckerter et al., 2021; Rivers-Moore et al., 2020; Rubene et al., 2015; Török et al., 2022). While our results align with this pattern, they also indicate that in landscapes dominated by tree cover, the composition of other habitat types and the anthropogenic matrix becomes less influential. Cluster BB1 was characterised by forest-associated indicator species, including several *Bombus* spp. (Diaz-Forero et al., 2011; Mola et al., 2021), select *Andrena* spp., and *Heriades truncorum*. The presence of *H. truncorum* as an indicator in both BB1 and PB1 highlights its value as a cross-regional indicator species (Roberge and Angelstam, 2006; Fleishman et al., 2018). Cluster BB4 in Brno represented a distinct landscape type not captured by any other cluster. All three sites in this cluster had low tree cover relative to other habitat types and included two urban wastelands and one atypical agricultural site. Urban wastelands are characterised by low management intensity combined with frequent disturbance (Twerd and Banaszak-Cibicka, 2019) and, consistent with other studies, also supported the highest bee diversity in this study (Twerd and Banaszak-Cibicka, 2019; Vereecken et al., 2021). Interestingly, grouped together with the two urban wastelands was an agricultural site. This “agricultural wasteland” was formed by an extensively managed apple orchard bordered by a wheat field with wildflower margins and partially surrounded by hedgerows. The orchard was mown only once per year, resulting in a heterogeneous landscape with flowering shrubs, flower-rich field edges, and grasslands, while tree cover was limited to widely spaced apple trees and a small forest patch. Orchards are known to supplement floral resources in agricultural landscapes (Mandelik et al., 2012) and host bee communities that are distinctly different from those in other agricultural landscapes, with similar environmental filtering even across biogeographical regions (Kline et al., 2023; Leclercq et al., 2023). Our results indicate that this filtering closely resembles what takes place for urban wastelands, highlighting extensively managed orchards as potentially important conservation targets. The typical bee community in this cluster was highly diverse and included species with a wide range of traits, such as the social *Lasioglossum glabriusculum*; two social *Seladonia* species; cavity-nesting *Megachile argentata* and *Chelostoma rapunculi*; and the snail-nesting *Osmia aurulenta*. Additionally, three *Ceratina* species and *Hylaeus paulus*, all of which nest in plant stems, were present.

Finally, beyond *Heriades truncorum* and *Lasioglossum glabriusculum* serving as indicators for similar clusters across regions, *Andrena helvola* emerged as an indicator of markedly different clusters in Prague and Brno. This species was indicative of urban forests in Prague (PB1) and non-forested agricultural sites in Brno (BB2), underscoring the importance of biogeographical context in indicator species analysis. This pattern demonstrates that indicator species respond differently to climatic and environmental conditions (Zettler et al., 2013), regional floral composition (Neumüller et al., 2020; Weber et al., 2023), and competitive interactions (Wiens, 2011). Although *A. helvola* is a common and generalist species, its distribution and co-occurrence patterns are shaped by the interaction of these factors.

4.3. Limitations and conservation implications

The use of indicator species has great potential for wild bee conservation, as it may reduce the temporal and spatial effort required for comprehensive biodiversity monitoring. Depending on their ecological associations, indicator species can reflect habitat quality (Stork and Eggleton, 1992; Vallecillo et al., 2016; Chowdhury et al., 2023), detect changes in landscape composition (Fleishman et al., 2018), or serve as targets for restoration projects (Siddig et al., 2016). In addition, species that serve as indicators of biodiversity may be used to infer the presence of other species (Ferreira et al., 2018; Cordero and Jackson, 2023) or to assess shifts in community composition (Chu et al., 2022; Terrigeol et al., 2022). While focusing on a limited number of species can substantially reduce monitoring effort, this approach relies on the strength of indicator species as proxies for overall biodiversity (Carignan and Villard, 2002).

However, several limitations should be considered when interpreting the identified indicator species. First, the low overlap in indicator

species between clustering approaches highlights the sensitivity of indicator species analysis to the underlying site classification (Dufrêne and Legendre, 1997). Indicator species should therefore not be considered universally transferable but rather interpreted within the methodological and ecological context in which they are identified. Our results suggest that clustering based on the focal taxon may provide a more ecologically direct basis for indicator species analysis than clustering based solely on landscape composition. Secondly, indicator species identified in one biogeographical region cannot necessarily be generalised across regions, as species associations may be influenced by regional differences in species pools, abiotic conditions, and interspecific interactions (McGeoch et al., 2002). The occurrence of the same species as indicators for different habitat types in Prague and Brno likely reflects such context dependency. Thirdly, co-occurrence patterns should be interpreted cautiously, as they do not necessarily indicate direct ecological interactions but may instead reflect shared habitat preferences or sampling-related effects (Blanchet et al., 2020). Finally, as this study was conducted in only two cities (Beninde et al., 2015), extrapolation of the identified indicator relationships to other urban or agricultural landscapes should be made with caution. As such, performing the same analysis with the same methodology across larger scales and in multiple biogeographical regions is crucial for a deeper understanding of the connection between bees and the landscape.

Despite these limitations, consistent patterns emerged across both study regions, indicating that the observed clustering structure and associated indicator species indeed capture meaningful ecological organisation of bee communities at the landscape scale. Our results indicate that ecological filtering of wild bee communities is driven not only by the biogeographical region, but also by the composition of suitable habitats and the surrounding anthropogenic matrix. Landscape composition, together with the regional species pool, structured typical bee communities and resulted in distinct site clusters. Although wild bee conservation has mostly focused on (semi-)natural grasslands due to their high diversity and abundance of rare and specialised species (Buchholz et al., 2020), protecting overall bee diversity requires consideration of multiple landscape types. Urban and agricultural forests (Braman et al., 2023), urban wastelands (Vereecken et al., 2021), and agricultural orchards (Leclercq et al., 2023) each host distinct wild bee communities and contribute to regional diversity. However, since some (semi-)natural habitats complement anthropogenic matrices more effectively than others (Mandelik et al., 2012; Maurer et al., 2022; Ockermüller et al., 2023; Visser et al., 2026), this highlights the importance of landscape heterogeneity for wild bee conservation (Diaz-Forero et al., 2011; Eckerter et al., 2021; Rivers-Moore et al., 2020; Rubene et al., 2015; Török et al., 2022).

4.4. Conclusion

This study evaluated wild bees as indicator species by comparing land-use-based and bee community-based clustering approaches combined with indicator species and co-occurrence analyses. Although both clustering approaches produced moderately similar site groupings, the resulting indicator species differed markedly. Bee community-based clustering identified indicators that more closely reflected ecological differences among landscapes and was therefore used to characterise typical wild bee communities. Where sufficiently robust wild bee datasets are available, we recommend this approach for biodiversity monitoring and conservation planning, whereas landscape-based clustering provides a practical alternative when such data are unavailable. Applying this framework across broader geographic regions and larger datasets would further strengthen its robustness and support the development of efficient, indicator-based tools for pollinator monitoring and conservation in anthropogenic landscapes.

CRediT authorship contribution statement

Jaco J.T.C. Visser: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Leon Marshall:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Nicolas J. Vereecken:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Jakub Straka:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article includes the full sampling dataset, site information, co-occurrence analysis , and cluster robustnes and can be found online at https://doi.org/10.1016/j.jnc.2026.127384.

Data availability

Sampling data and appendices are available at https://doi.org/10.5281/zenodo.18399965

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