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A trait-based framework to understand and predict the response of wild bee functional groups to anthropogenic landscapes

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Abstract

1. Wild bees play a vital role as pollinators in ecosystems, yet their existence is increasingly threatened amidst ongoing biodiversity declines driven by land use change.
2. This study examined how wild bee functional traits relate to landscape composition in urban and agricultural settings across Central Europe (Czechia), aiming to understand how these traits influence patterns of abundance and occurrence.
3. Eighteen functional groups were defined based on ecological traits related to foraging and nesting behaviours, and multivariate species distribution models were applied to analyse their associations with different land use variables.
4. Our results showed that functional groups exhibit distinct and complex responses to landscape composition, often differing in how they respond to environmental change, even among groups with similar trait profiles.
5. These findings underscore that the relationship between traits and the environment cannot be generalised across functional groups and that interpreting wild bee community patterns requires integrating multiple ecological dimensions such as nesting type, diet breadth, sociality and seasonality.
6. The study highlights the need for conservation strategies that are tailored to functional diversity and landscape context, as efforts that support one group may not benefit others, and may even be counterproductive. Promoting diverse functional communities is essential for sustaining pollination services and ecosystem resilience under environmental change.

KEYWORDS
biodiversity, conservation, functional groups, functional traits, landscape, pollination, wild bees

INTRODUCTION

Wild bees play a key role in the functioning of both natural and anthropogenic ecosystems, serving as the primary pollinators of many wild plants and crops (IPBES, 2016; Potts et al., 2016). As such, conserving wild bee populations and their habitats is crucial, particularly in light of current insect declines (Wagner et al., 2021). To date, over 20,000 species of wild bees have been described (Orr et al., 2021), highlighting their remarkable diversity and ecological importance. However, effective conservation strategies aiming to conserve the importance of their diversity for ecosystem functioning should go beyond simply maximising species richness; instead, they should incorporate functional traits that link species to their ecological roles and environmental preferences (Carré et al., 2009; Hamblin et al., 2018; Nunes et al., 2024; Rotondi et al., 2024). Studying functional traits, defined as the key targets of natural selection, that is, characteristics relevant for the response and persistence of an organism to the environment or ecosystem (Violle et al., 2007), allows for a deeper understanding of the effect of ecosystem-level impacts on biodiversity (Cadotte et al., 2011; Carmona et al., 2021). For example, it is becoming clear that pollination efficiency and yield are driven by pollinator diversity, particularly their functional diversity (Chase et al., 2023; Greenop et al., 2023), including their morphology, phenology, behaviour and floral preferences (Turo et al., 2024). Ultimately, the effective conservation of wild bees requires an understanding of how environmental factors and landscape composition influence the abundance and occurrence of species with particular functional traits (Ostwald et al., 2024).

Research into wild bee functional traits has increased substantially in recent decades, leading to a wide range of trait quantifications and methodological approaches. This is exemplified by the differing perspectives on trait categorisation and the selection of species used as trait representatives (e.g., see for multiple studies on urban bee functional traits: Normandin et al., 2017; Buchholz et al., 2020; Villalta et al., 2021; Brasil et al., 2023). Consequently, there is a growing need for standardisation in trait definition and categorisation to enable meaningful comparisons across geographical and temporal scales (Ostwald et al., 2024). However, functional trait datasets are often limited by the availability of traits, particularly for rare and less studied species (De Bello et al., 2021; see also Marshall et al. (2024) for an EU-wide perspective on biodiversity shortfalls and impediments associated with wild bees). These limitations can lead to oversimplified or ill-designed trait groupings, reliance on coarse classifications or analyses based on a subset of species. For example, nesting behaviour is commonly subdivided into just two broad types, namely belowground and above-ground (Buchholz & Egerer, 2020; Montoya-Pfeiffer et al., 2020). This binary classification overlooks key ecological differences, such as the diversity of nest locations above ground (e.g., stems, wood cavities, galls) and the nest building strategies (e.g. renting an existing cavity versus actively excavating a cavity). A higher trait resolution is essential for accurately assessing trait diversity and thereby gaining more fine-grained insights into how species interact with their environment. Achieving this, however, requires large datasets based on extensive sampling, high taxonomic coverage and comprehensive trait databases.

When such data are available, an alternative trait-based approach can be applied to describe the functional structure of wild bee communities, namely by creating functional groups (FGs). In studies of other taxa, organisms are often grouped together into FGs based on shared trait combinations, allowing researchers to analyse ecological responses of species and communities across different spatial scales (Benedetti et al., 2018; Campos et al., 2017; Cortois et al., 2016; Jansen et al., 2018), even when species cannot be identified to species level but can be assigned an ecological role (Baldrighi & Manini, 2015). The use of FGs over individual traits reflects more closely how traits and trait combinations interact with the environment, a vitally important aspect for landscape conservation and restoration aimed at wild bees. Knowing which trait combinations are beneficial or detrimental in certain natural, or perhaps more importantly, anthropogenic landscapes should guide conservation actions. Unfortunately, the term 'functional group' is frequently incorrectly applied in wild bee studies, for example when all bee species sharing a single trait (e.g., all parasitic species) are classified as one 'functional group' (Beyer et al., 2020; Braman et al., 2023; Graf et al., 2022; Wu et al., 2018). In reality, FGs should reflect a combination of species that are grouped together based on all of their known and relevant traits rather than a single characteristic (Montoya-Pfeiffer et al., 2020).

The systematic delineation of FGs, using a combination of all measured traits, refines the analysis of wild bee associations with the surrounding landscape. When incorporated with information on the suitable habitat patches where bees occur and the matrix between them, we can develop a more comprehensive understanding of how trait groups relate to their environment. This approach is vital for targeted conservation and restoration actions, moving beyond analyses based on a single species or trait by providing a robust generalisation of a group of species that share a common mix of traits and are thus more likely to share an ecological niche. Therefore, this study aims to advance our understanding of how landscape composition influences wild bee functional traits by providing the first extensive analysis of the relationship between wild bee FGs and their surrounding landscapes. Specifically, we aim to (i) define wild bee FGs based on relevant species' functional traits, (ii) assess how these FGs are associated with land use variables across anthropogenic landscapes and (iii) determine whether FGs respond similarly or differently to changes in landscape compositions. We hypothesise that FGs will exhibit distinct associations with landscape composition, with greater differences in association among groups that are more functionally divergent. From a conservation perspective, we anticipate that habitat restoration and management strategies for wild bees will involve trade-offs, as optimising conditions for one FG may not benefit or could even disadvantage others.

METHODOLOGY

Study locations

To answer our research questions, we selected 32 sampling sites in Czechia, 16 in and around the city of Prague and 16 in and around the city of Brno. Half of the sites were located within agricultural landscapes, primarily dominated by rapeseed (*Brassica napus*), and the other half within urban landscapes. We defined agricultural and urban landscapes as landscapes where the dominant land use matrix between natural habitat types consisted of rapeseed croplands in the case of agricultural sites and built-up impervious areas for urban sites. Natural land cover types in this study were grasslands, shrublands and forests (similar to, e.g., Graf et al., 2022), since these offer foraging and nesting opportunities for the entire gamut of wild bee species.

These natural land cover types included both semi-natural habitats as well as anthropogenic ones such as production forests and a cemetery; therefore, we refer to them as suitable bee habitats as opposed to semi-natural habitats. The sites were chosen in such a way that the suitable habitats were of comparable quality as much as possible (e.g., similar forest type in all agricultural landscapes), as well as varied in both the total amount of suitable habitat (from 12% to 96%) and the relative composition of the suitable habitat types (Appendix S5). A similar suitable habitat composition existed between both anthropogenic matrices and between each city. To quantify landscape composition, we created land cover maps in QGis (QGis Development Team, 2024). These maps integrated data on farmland, impervious surfaces, grassland cover (defined as open spaces dominated by herbaceous vegetation), tree cover and small woody features (SWF), such as shrubs and hedgerows (Figure 1). Farmland 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). For each study site, we delineated a circular buffer zone with a 1 km radius around the sampling location. Within each buffer, the amount of suitable habitat was calculated as the combined area of grasslands, tree cover and SWF.

Sampling

Sampling on all 32 sites was performed monthly from April to August 2022 and 2024. Additionally, a single round of sampling was conducted in April 2023 to compensate for pan trap removal and destruction at one location in Prague and one in Brno during the April 2022 sampling round. Wild bees were collected using a standardised pan trapping protocol: at each site, nine pan traps were deployed, arranged in three triplets consisting of one white, one blue and one yellow pan trap (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, and remained in the field for five consecutive days. The pan traps were filled up to 2 cm from the top with water that contained a few drops of detergent to reduce surface tension of the water. Even though pan trapping has been shown to have inherent biases in which species and traits are collected (Portman et al., 2020), this methodology does allow the collection of a large number of specimens across many locations and can be effectively used to compare bee communities between landscape compositions. 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 (Schmid-Egger & Scheuchl, 1997; Amiet et al., 2001, 2004, 2007, 2014; Scheuchl, 2006; Bogusch & Straka, 2012; Dathe et al., 2016; Smit, 2018). The *Bombus terrestris* group (*B. terrestris*, *B. magnus* and *B. cryptarum*) was all labelled as *B. terrestris*.

Functional trait selection

We selected eight widely used wild bee functional traits (Buchholz & Egerer, 2020; Ostwald et al., 2024) for analysis and subdivided them to capture the full range of interspecific variation (Appendix S1). Of these traits, three relate to foraging, three to nesting and the remaining two link foraging and nesting behaviour. All traits were weighted equally in the analyses. For trait correlation see Appendix S7.

Foraging-related traits

The first trait connected to foraging is tongue length. Wild bees collect nectar from a wide variety of flowers with different shapes, and the length of their tongue indicates from which flowers they are able to extract nectar. We estimated tongue length using the 'BeeIT' package in R (Cariveau et al., 2016; Kendall et al., 2019), which predicts values based on intertegular distance (ITD, see below) and family affiliation. When empirically known values were available, we replaced the estimates with these known values.

The second trait connected to foraging is pollen specialisation. Wild bees are often classified as being generalist (polylectic) or specialist (oligo- or monolectic), depending on the diversity of plant taxa used to provision their brood cells. We used a two-category system: polylectic species gather pollen from multiple plant families, while oligolectic species specialise in a single family or genus. Although monolecty (specialisation on a single plant genus) and various gradients of oligolecty are also reported in the literature (Cane, 2021), the ecological implications of these categories have been questioned (see, e.g., Cane, 2021) and therefore we included them within a broader definition of the oligolectic category. For parasitic bee species, which are directly dependent on the pollen that the host collects, we assigned pollen specialisation based on the known preference of their host(s).

The third trait connected to foraging is the method of pollen transport which varies across bee families and reflects how much pollen they are able to gather, and how effectively they can transport it. Because some species use multiple transport methods, we treated this trait as binary, indicating presence/absence across several body parts. This approach avoided misclassifying multifunctional strategies as unique categories (e.g., 'legs and metasoma') (Benedetti et al., 2018). The final categories were: (i) via hairs on legs, (ii) via hairs on mesosoma, (iii) via hairs on metasoma, (iv) via specialised pollen baskets (corbiculae) on legs, (v) carried only within the crop and (vi) accidental transport by parasitic species.

Nesting-related traits

The first trait connected to wild bee nesting is the type of nest they construct, that is, the type of substrate or structure used for nesting. Again, this trait was treated as binary to account for species with multiple nesting strategies. Categories for this trait were (i) soil,

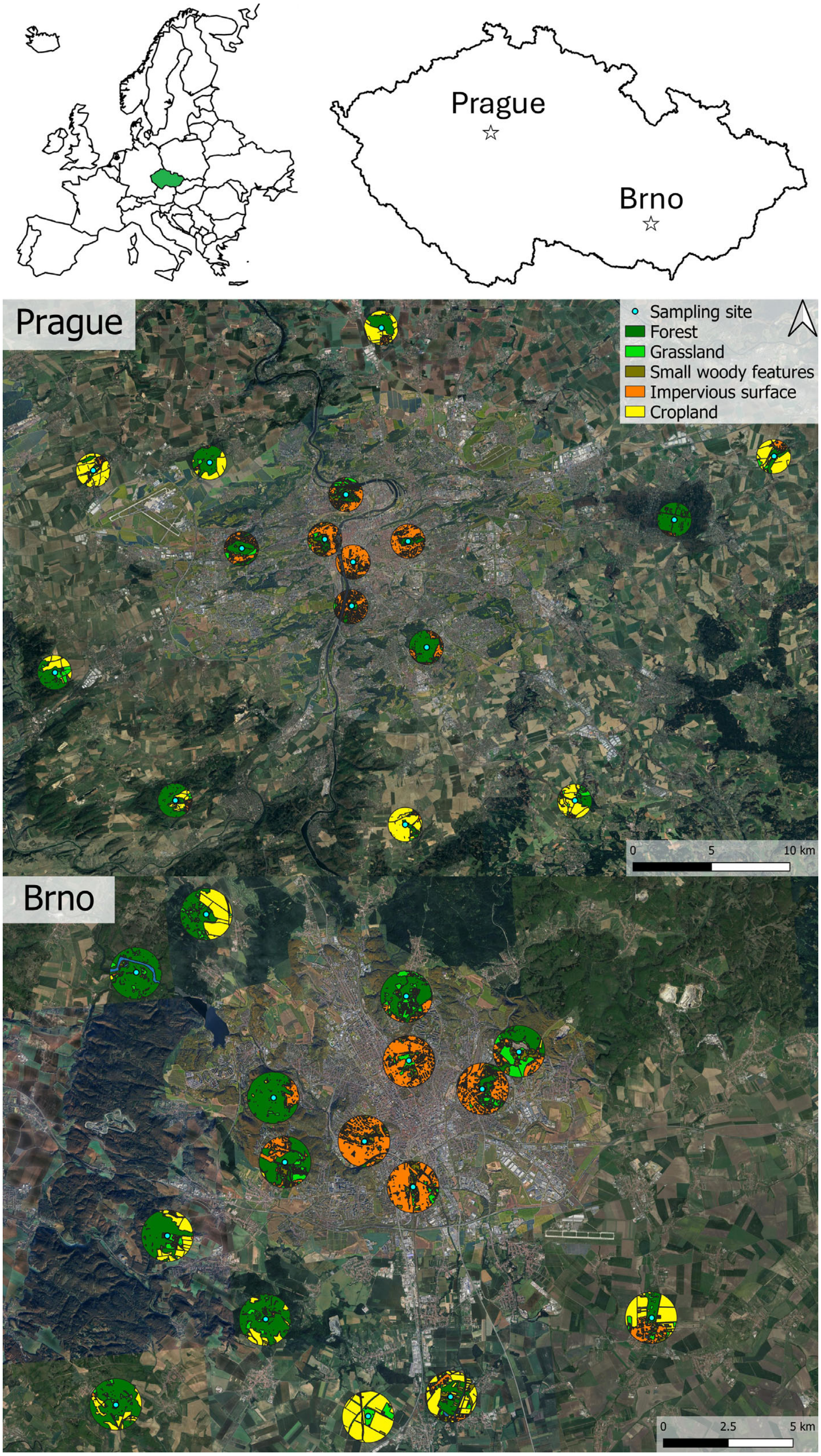

FIGURE 1 Sampling locations in Prague (above) and Brno (below). In each city, 16 locations were selected of which half were in agricultural landscapes and the other in urban landscapes. This categorisation was defined based on the dominant anthropogenic matrix between the patches of natural habitat. A 1 km buffer zone was then drawn around each sampling location after which the relative cover of agricultural land (yellow), impervious surface (orange), tree (dark green), grassland (light green) and small woody features (brown) was calculated.

(ii) above-ground cavities (wood and stone), (iii) stems, (iv) galls, (v) empty snail shells, (vi) resin structures and (vii) open nests in grass or low vegetation.

The nesting strategy trait was defined by how the nest is constructed or acquired. Categories included (i) excavators (actively digging nests), (ii) renters (reusing existing nests), (iii) builders (constructing above-ground structures) and (iv) carders (collecting plant fibres). Parasitic species were classified as renters as they rely on existing host nests.

The third trait connected to nesting is sociality, which describes whether and how bees interact with one another while nesting. For our dataset, we distinguished: (i) solitary species, (ii) obligatorily primitively eusocial species, (iii) biparental species, (iv) social parasites (which take over nests of social species) and (v) kleptoparasites (which steal the host's resources i.e., brood parasites). Species with facultative sociality were categorised as having (vi) variable sociality.

Traits linking foraging and nesting

The interplay between foraging and nesting is created by the time period in which the bees are active and how far they fly from their nests to their foraging locations. The seasonality or flight period of bees can be defined by the number of generations they have in a single year (voltinism), but this can vary within a species depending on the climatic conditions in which a population lives. Here, we defined three types of seasonal activity based on flight periods: (i) spring (March–June), (ii) summer (June–August) and (iii) both periods. The third group includes bivoltine species and social species with multiple generations per year. Seasonality was also coded as binary data.

The second trait is foraging distance, approximated via ITD, a widely used proxy for body size and flight capacity (Greenleaf et al., 2007). ITD is measured as the average distance between the tegulae of females of a species. For our species, all ITD values were obtained from literature and trait databases.

Trait data sources

The functional traits were obtained via multiple sources. First and foremost we used the preliminary trait database for the ORBIT project (https://orbitproject.wordpress.com/) which derives from the 'European bee traits database' (established by ALARM, www.alarm-project.ufz.de, developed by STEP, www.STEP-project.net, and maintained and updated by S. P. M Roberts) and is in part available from Naturalis Biodiversity Centre (https://beetraits.linnaeus.naturalis.nl). For missing trait data, we gathered information from https://www.wildbienenwelt.de and https://wildebijen.nl as well as from the keys that were used for the identifications (Schmid-Egger & Scheuchl, 1997; Amiet et al., 2001, 2004, 2007, 2014; Scheuchl, 2006; Bogusch & Straka, 2012; Dathe et al., 2016; Smit, 2018).

Statistical analysis

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

To investigate how combinations of functional traits respond to landscape composition, we first defined wild bee FGs based on a systematic and statistically robust clustering of traits. Unlike previous studies that grouped wild bees using a predefined combination of traits (e.g., Montoya-Pfeiffer et al., 2020), we employed a data-driven approach. We began by calculating a Gower's distance matrix using the *gowdis* function from the FD package (version 1.0-12.1) (Laliberté et al., 2014), which accommodates mixed data types (quantitative and qualitative). Since many traits were binary, we first computed a separate distance matrix for each of the eight traits individually. These eight distance matrices were then averaged to create a single composite distance matrix following the procedure outlined by De Bello et al. (2021). Next, we used hierarchical clustering with Ward's linkage method (Legendre & Legendre, 2012) via the *hclust* function to group species based on trait similarity and visualised the resulting functional dendrogram using the *fviz_dend* function from the factoextra package (version 1.0.7) (Kassambara & Mundt, 2020). To determine the optimal number of FGs, we used the silhouette width index via the NbClust package (version 3.0.1) (Charrad et al., 2014) and the *fviz_nbclust* and *fviz_silhouette* functions from the factoextra package. The final number of FGs (clusters) was chosen to ensure that groups were functionally homogeneous and ecologically meaningful, avoiding over- or under-clustering and ensuring adequate representation of trait variation. We visualised the multivariate distribution of species traits using a principal coordinates analysis (PCoA) via the *pcoa* function in the ape package (version 5.7-1) (Paradis & Schliep, 2019) and assessed the quality of the functional space via the *quality.fspaces* function in the mFD package (version 1.0.7) (Magneville et al., 2021). Subsequently, we evaluated the internal dispersion of each FG using a PERMDISP analysis via the *betadisper* function from the vegan package (version 2.6-4) (Oksanen et al., 2022), which evaluates differences in trait variability among groups, showing whether the FGs are significantly different from one another.

To assess how the FGs relate to landscape composition, we constructed a multivariate species distribution model (MSDM) using the *traitglm* function from the mvabund package (version 4.2.1) (Wang et al., 2022). This approach fits a set of negative binomial generalised linear models (GLMs) to test the associations between FG abundance and the five landscape variables. A LASSO (Least Absolute Shrinkage and Selection Operator) penalty (method = glm1path) was applied to retain only significant associations by shrinking non-significant coefficients to zero. Lastly, to further evaluate how different FGs respond to changes in landscape composition relative to one another, we used the *boral* function in the 'BORAL' (Bayesian Ordination and Regression Analysis) package (version 2.0) (Hui, 2015). This Bayesian ordination method fits GLMs with a negative binomial distribution (without latent variables), testing whether groups respond similarly or divergently to environmental gradients. Specifically, we used this model to test for directional correlations in group responses to variation in grassland, forest and SWF cover. To assess how these patterns differed across anthropogenic land use contexts, we also repeated the analyses separately for agricultural and urban landscapes.

RESULTS

After removing all records of *Apis mellifera*, the final dataset contained 26,607 wild bee specimens, consisting of 283 species across 6 families. Halictidae was the most abundant 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%).

Functional trait grouping

The trait-based distance matrix for the 283 species was converted into a dendrogram (Figure 2), and our clustering analysis identified 18 FGs as the optimal partition (see Appendix S2 for results of silhouette analyses). The PERMDISP analysis based on the PCoA (Appendix S3) confirmed that these FGs were significantly different from each other ($F_{17} = 17.1$, $p < 0.01$). The number of species per FG varied between 4 and 32, and the number of specimens varied between 10 and 11.058 (Figure 2).

The dendrogram was first split into two major clusters: bee genera containing parasitic species (FGs 13–18) and all non-parasitic species (FGs 1–12).

Within the parasitic cluster, the first split separated the large, long-tongued bumblebees (FGs 13–14) from smaller, short-tongued parasitic species (FGs 15–18). Specifically, FG 13 included all socially parasitic bumblebees (subgenus *Psithyrus*), and FG 14 contained all non-parasitic social bumblebees (the only non-parasitic lineage in this part of the dendrogram). The remaining parasitic bees were split into exclusively spring-active species (FGs 15–16) and species exclusively or also active in summer (FGs 17–18). Among the spring-active species, FG 15 included oligolectic species and FG 16 included polylectic ones. Summer-active species were further divided based on the nesting behaviour of their host: FG 17 consisted of species whose host(s) nest in cavities, whereas FG 18 included species whose host(s) nest in the soil.

Within the non-parasitic cluster, the first division separated oligolectic species (FGs 1–3) from polylectic species (FGs 4–12). FG 1 was made up of cavity-nesting oligolectic species, FG 2 consisted of spring-active, soil-excavating oligolectic species and FG 3 included oligolectic species that excavate soil nests and are only active in summer.

The polylectic species (FGs 4–12) were initially divided into renters and excavators of cavities, along with species with soil-excavators with large tongues or that only fly in summer (FGs 4–7), and short-tongued soil and stem excavators (FGs 8–12). Specifically, FG 4 was comprised only of *Hylaeus* spp. which nest in stems and/or in galls and transport pollen in their crop. The remaining groups (FGs 5–7) were split first between exclusively summer-active species (FG 7) and species that (also) fly in spring (FGs 5–6), with FG 5 consisting of long-tongued bees that excavate their nest in cavities or soil and transport pollen on their legs, and FG 6 consisting of short-tongued bees that transport pollen on their metasoma and that nest in rented cavities.

The last cluster (FGs 8–12) was initially divided based on sociality. Firstly, into solitary species (FGs 8–10) and non-solitary species (FGs 11–12). The solitary species were further divided by flight season: FG 8 contained species only active in spring and FGs 9–10 contained species also active in summer, which were subsequently differentiated by pollen transport. FG 9 consisted of species that transport pollen on the legs and/or metasoma, and FG 10 of species that transport pollen on the legs and metasoma. Parallel to that, the non-solitary species were split into species that are facultatively social (i.e., having variable sociality) in FG 11, and obligatorily (primitively) eusocial species in FG 12.

The association of FGs with the surrounding landscape

The MSDM revealed that wild bee FGs are differentially associated with specific types of landscapes (Figure 3) (see Appendix S5 for the abundance of the FGs per site).

When comparing the two anthropogenic landscape types, agricultural and urban, clear differences in association between FGs emerge. Indeed, while some FGs are more prevalent in agricultural settings, others are more strongly associated with urban areas. Among parasitic groups, the polylectic, soil-nesting, spring-active kleptoparasites of FG 16 showed a positive association with urban landscapes but no association with agricultural landscapes. Conversely, the cavity-nesting, summer-active kleptoparasitic species of FG 17 were negatively associated with urban landscapes but positively associated with agricultural ones. Among non-parasitic groups, four FGs showed a negative association with urban landscapes, and four showed a positive association. For agricultural landscapes, one non-parasitic FG showed a negative association and two showed a positive one. Finally, two FGs, FG 9 (summer-active Lasioglossum, Ceratina and Hoplitis species) and FG 14 (social bumblebees) had no association with the anthropogenic landscapes.

Our analyses also revealed strong and contrasting associations with semi-natural habitat components across FGs. For example, grasslands were strongly negatively associated with FG 14 (bumblebees, i.e., social and polylectic species active in spring and summer), contrary to FG 4 (*Hylaeus* spp.) which showed a strong positive association. For cavity nesters, the responses were mixed: polylectic cavity-nesting FGs were slightly negatively associated with grasslands, while FG 1 (the only oligolectic cavity-nesting group) was positively associated. Parasitic groups also differed: FG 15 and FG 16 (spring-active kleptoparasites) showed positive associations with grasslands, whereas FG 17 (summer-active, cavity-nesting kleptoparasites) was negatively associated. Tree cover was also linked to FG identity. Among parasitic bees, only FG 17 (cavity-nesting kleptoparasites)

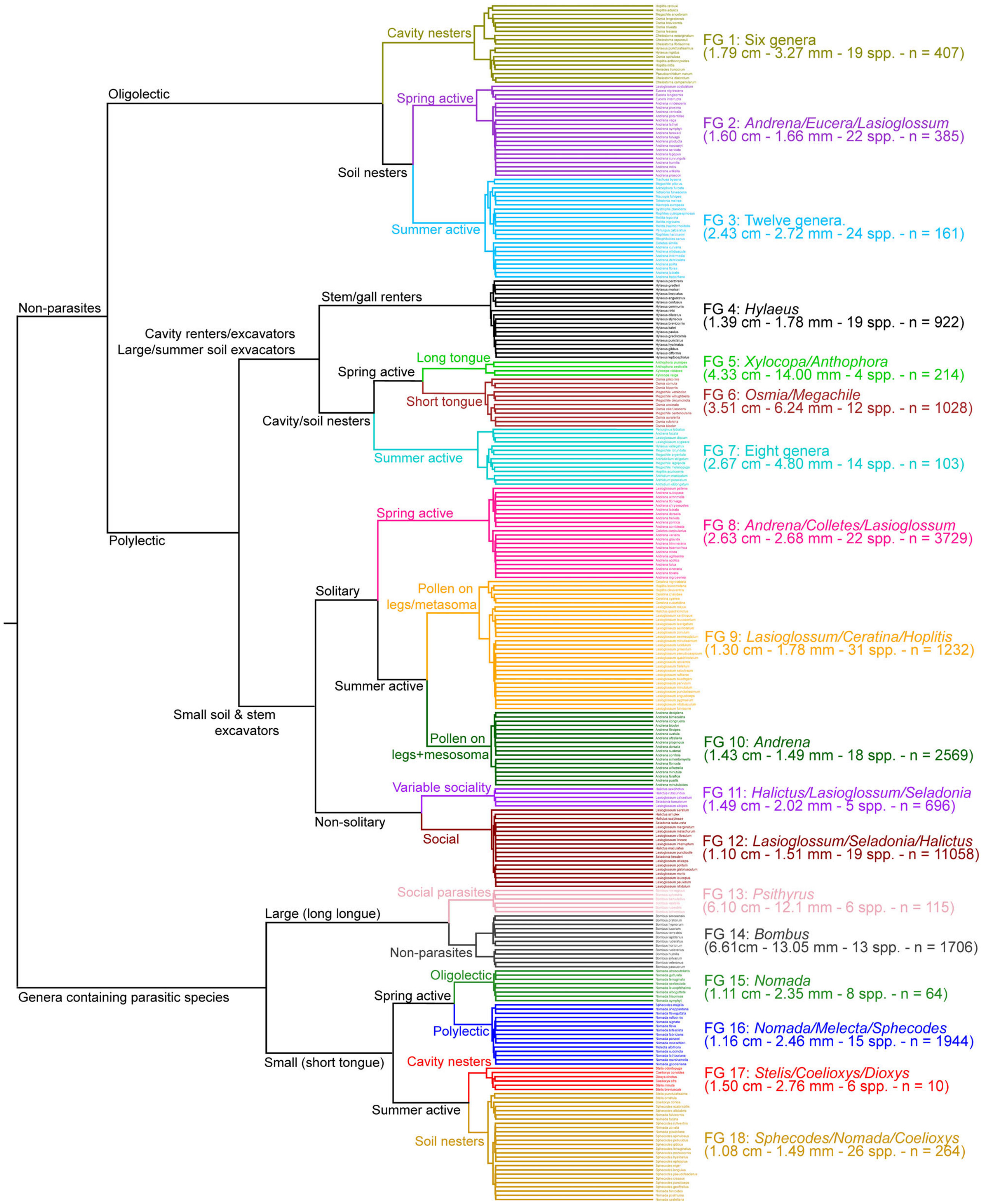

FIGURE 2 Functional dendrogram showing clustering of the species into 18 functional groups based on their traits. Functional groups are coloured and the most important characters for each of the dendrogram branches are shown. Genera for each group are indicated, unless exceeding three, as well as mean intertegular distance (cm), tongue length (mm), number of species and number of specimens per group in brackets. Note that groups characterised as spring-active are always exclusively active in spring (univoltine), whereas groups characterised as summer-active may be exclusively active in summer (FG 3 and FG 7) or active in both spring and summer (FG 9, FG 10, FG 17 and FG 18).

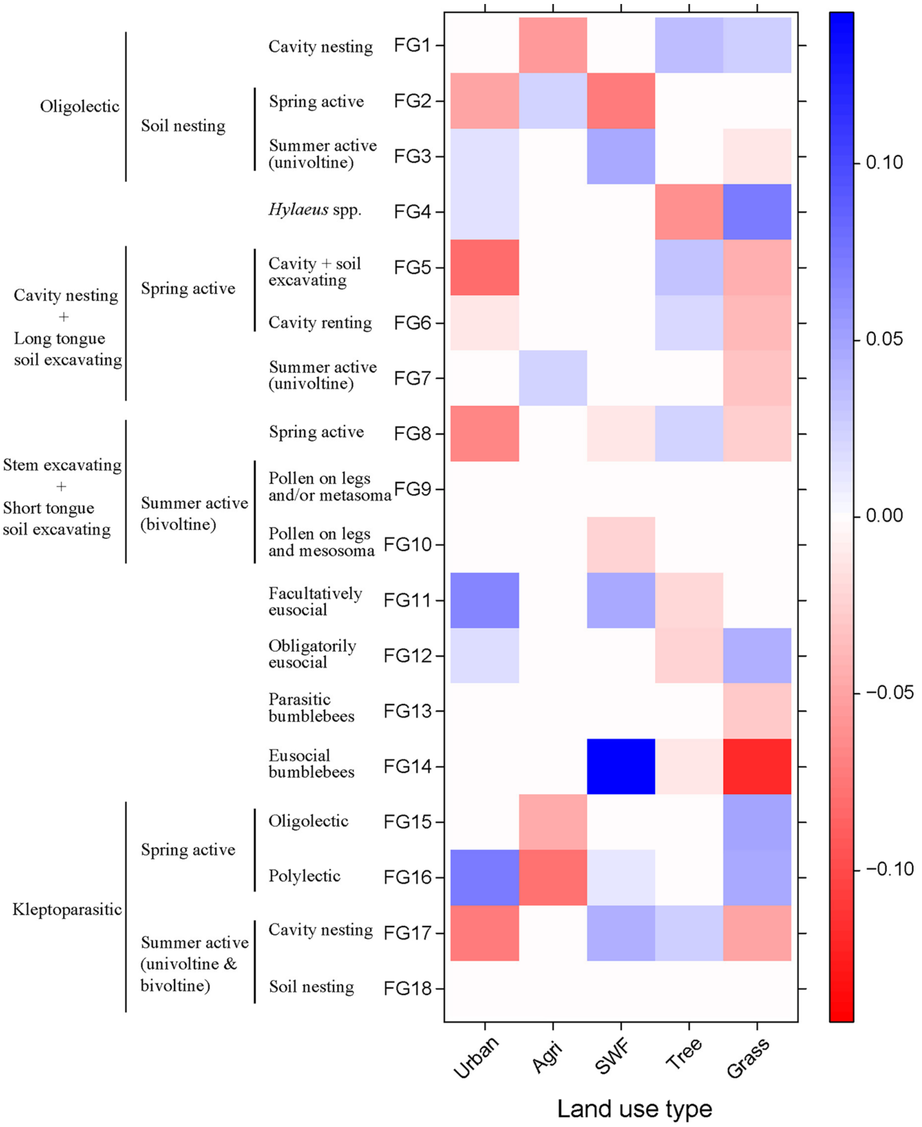

FIGURE 3 Multi species distribution model (MSDM) showing the association of the functional groups (FGs) with the five land use types. Only significant associations are shown, with positive associations in blue and negative associations in red. The results of the MSDM show that the FGs are associated with different types of habitats and anthropogenic landscapes. FGs that are closely related based on their traits can also show different associations, highlighting the importance of splitting large trait groups (e.g., all parasitic bees) into smaller groups, based on their other traits (details in Discussion).

showed a notable positive association. Negative associations with tree cover were observed for FG 4 (*Hylaeus* spp.), and for the non-solitary groups FG 11 (facultatively social species) and FG 12 (obligatory eusocial species). In contrast, positive associations with tree cover were recorded for FG1, FG 5, FG 6 (cavity-nesting, polylectic species) and FG 8 (spring-active, soil-nesting, polylectic species). Finally, SWF such as shrubs and hedgerows were important for FG 14 (social bumblebees) and FG 3 (oligolectic, summer-active species). By contrast, FG 2 (spring-active oligolectic species) was negatively associated with SWF. Notably, while FG 3 (oligolectic summer-active species) positively associated with SWF, its polylectic counterpart FG 10 showed a slightly negative association. Finally, FG 17 (summer-active, cavity-nesting kleptoparasitic species) also displayed a positive association with SWF.

In extension to the MSDM, the Boral analysis reveals how FGs respond to changes in suitable habitat composition in relation to one another (Figure 4). When not accounting for the surrounding anthropogenic matrix (Figure 4a), several strong positive and negative correlations emerge, some of which occur between functionally dissimilar groups. Among the strongest correlations in landscape responses across all sites, FG 16 (spring-active, polylectic kleptoparasites) showed (i) positive correlations with FG15 (functionally related oligolectic kleptoparasites), FG 4 (*Hylaeus* spp.), FG 11 and FG 12 (facultatively and obligatorily eusocial species, respectively), but also (ii) negative correlations with FG 2 (spring-active, oligolectic soil-nesters), FG 5 (*Xylocopa* and *Anthophora* spp.) and FG 8 (spring-active, polylectic soil-nesters). Interestingly, despite FG 16 consisting of *Nomada* species, kleptoparasites of (mostly) *Andrena*, its strongest

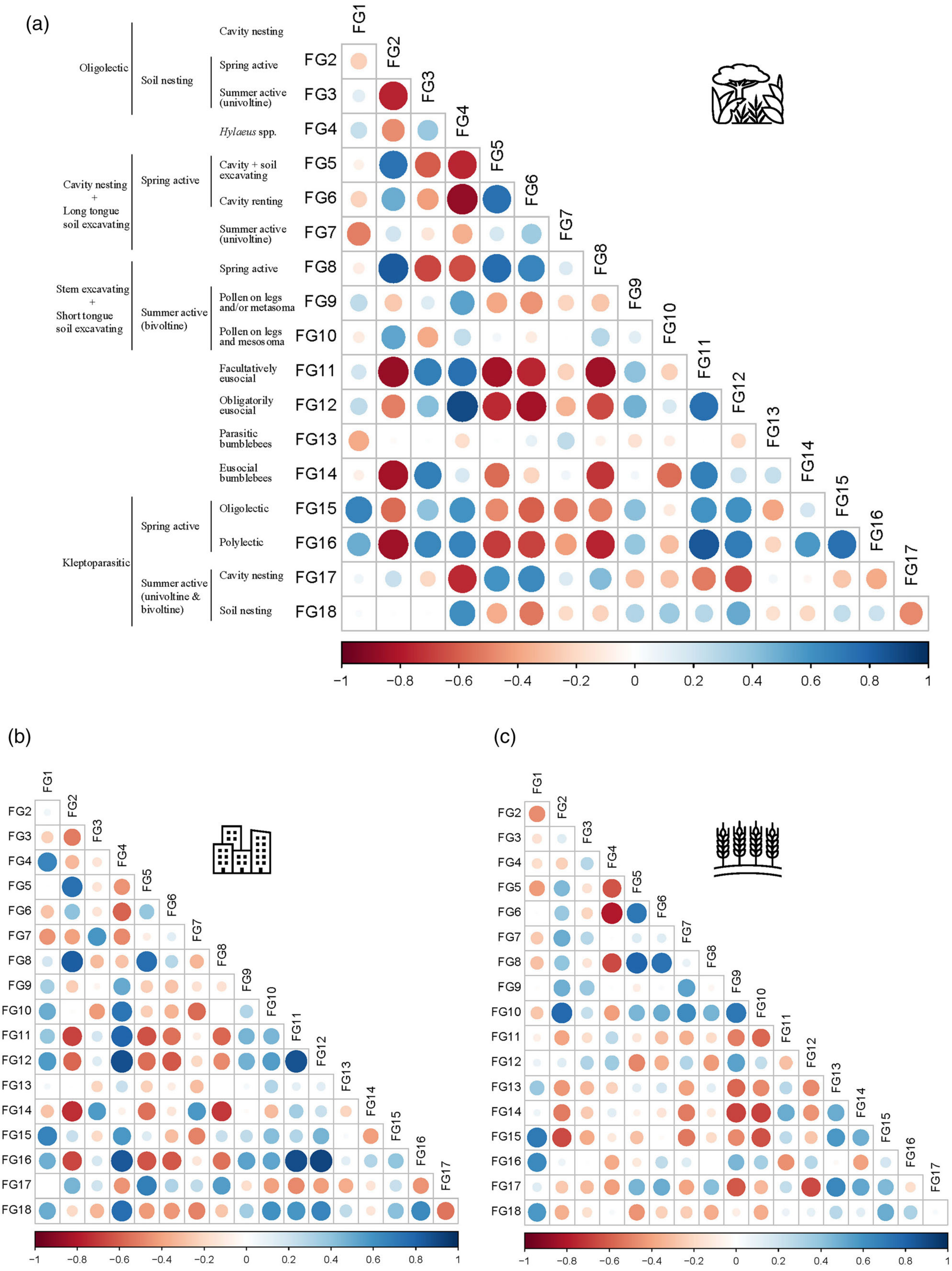

FIGURE 4 Legend on next page.

positive correlations are not with host-containing FGs, while several negative correlations are with groups that do include host species. Another group that showed interesting patterns is FG 14 (social bumblebees) which exhibited two strong positive correlations, namely with FG 11 (facultatively social species) and with FG 3 (summer-active oligolectic soil-nesters). In contrast, FG 14 also showed strong negative correlations with FG 2 and FG 8, both spring-active *Andrena*-dominated groups. Other notable patterns include FG 12 (obligatorily social species) which positively correlates with FG 11 and FG 4 (the latter also correlating with each other). In contrast, FG 11 showed several negative correlations, including with FG 2 (oligolectic spring-active soil-nesters), FG 5 (large-bodied bees such as *Xylocopa* spp. and *Anthophora* spp.), FG 6 (spring-active Megachilidae cavity nesters) and FG 8 (polylectic spring-active soil-nesters). Last, FG 6 (spring-active Megachilid cavity nesters) showed a positive correlation with FG 5 (large-bodied bees) and a negative correlation with FG 4 (*Hylaeus* spp.); similarly, FG 4 is negatively correlated with FG 5.

Since the results of the MSDM showed that FGs associate differently with urban versus agricultural landscapes, we further explored the BORAL analysis by separating the correlations by anthropogenic landscape context (Figure 4b,c). This comparison revealed that the strength and even direction of the correlation can differ markedly between contexts. Examples of context-specific patterns include FG 2 (spring-active oligolectic soil-nesters) and FG 10 (summer-active polylectic soil-nesters), which show a strong positive correlation in agricultural landscapes but no correlation in urban landscapes. Similarly, FG 18 (summer-active kleptoparasites) and FG 11 and FG 12 (facultatively and obligatorily social species, respectively) are positively correlated in urban landscapes but not correlated in agricultural settings. Even more striking are cases of reversed correlations, such as (i) between FG 18 and FG 10 (*Andrena* spp., which include host species for FG 18) with a positive correlation in urban landscapes but a negative correlation in agricultural landscapes, (ii) a similar flip in correlation between FG 10 and FG 1 (oligolectic cavity nesters) and FG 11 (facultatively social species) and (iii) likewise between FG 14 (social bumblebees) and FG 13 (social parasites) with again a positive correlation in urban settings but a negative correlation in agricultural landscapes.

DISCUSSION

In this study, we grouped wild bee species based on combinations of functional traits to better understand how landscape composition influences the presence and abundance of FGs. This, in turn, provided new insights into the functional basis of environmental filtering targeting wild bees in anthropogenic landscapes, that is, how each FG's trait combination confers advantages in some environments but not others.

Wild bee FGs show distinct landscape associations

While most studies indicate that open grassland increases wild bee abundance and species richness (Buchholz et al., 2020; Ekroos et al., 2020; Morandin et al., 2007), our results show that grasslands indeed do favour multiple FGs, but not all of them. Some of the important trade-offs highlighted in our study include groups like FG 4 (*Hylaeus* spp.), which nest in stems and which benefit from grassland habitats that offer suitable nesting sites. Likewise, oligolectic groups such as FG 1 and FG 15 depend on the presence of specific floral resources typically (or more frequently) found in grasslands. Conversely, species that rely on shrubs or trees for nesting or foraging are negatively impacted by an excess of open space (Carrié et al., 2017). This includes groups such as FG 5, FG 6 and FG 17 (cavity-nesting groups), which are positively associated with tree cover or SWF, suggesting that nesting site availability rather than floral diversity may be the primary limiting factor for these bees (Rivers-Moore et al., 2020). Some FGs rely specifically on forested habitats, such as the spring-active, soil-nesting polylectic species of FG 8, which depend on the flowering early-season undergrowth typically found in forests (Sevenello et al., 2020). The presence of SWF, such as hedgerows and shrubs, was particularly important for FG 14 (social bumblebees). Many bumblebee species nest beneath shrubs and rely on flowering shrubs like blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus* spp.) as key food sources (Mola et al., 2021). Mola et al. (2021) also report the importance of forests for social bumblebees, which is not reflected by our results. This is most likely due to some bumblebees preferring forests, while others prefer open habitats (Diaz-Forero et al., 2011). Additionally, many of the SWF in agricultural landscapes in Czechia are present in the form of hedgerows, which bumblebees use as navigational aids when foraging (Brebner et al., 2021). This may also in part explain the positive association of FG 3 (summer-active oligolectic species) with SWF, despite their lack of specialisation on shrub species. Since these bees are active after most shrubs have flowered, this association points to additional landscape-level factors, such as pesticide exposure, mowing regimes or pollution, that may influence habitat suitability (LeBuhn & Vargas Luna, 2021). Interestingly, FG 2, the group of spring-active, soil-nesting oligolectic species, showed a negative association with SWF, suggesting that these features may have different ecological value in spring and summer, especially for oligolectic bees. Crucially, since different bees are associated

FIGURE 4 Correlation matrices from the Bayesian Ordination and Regression Analysis for (a) all habitats, (b) only the agricultural landscapes, and (c) only the urban landscapes. Blue circles indicate a similar of the functional groups (FGs) response to changes in landscape composition, while red circles indicate an opposite response to changes in landscape composition. These results show that FGs can have very different responses to changes in the landscape context, and that the anthropogenic matrix between the habitat patches influences the difference in response for many groups.

with distinct types of landscapes, integrating complementary habitat types, for example, open grasslands adjacent to wooded areas, can maximise both floral diversity and nesting opportunities and therefore wild bee diversity (Cavigliasso et al., 2022; Hass et al., 2018; Rivers-Moore et al., 2020).

In agricultural landscapes, the contrasting responses of FG 1 and FG 2 are especially striking. Both groups are oligolectic, but FG 1 (cavity nesters) is negatively associated with agricultural landscapes, whereas FG 2 (soil- nesters) is positively associated. This contrast suggests that nesting site availability, rather than floral resources, may drive functional distribution across agricultural areas (Morandin et al., 2007). For urban landscapes, a seasonal pattern emerges: spring-active groups tend to be negatively associated, while summer-active groups are positively associated. Since nesting conditions are unlikely to change between seasons, this suggests that floral availability and diversity may be higher or more suitable to wild bees in summer within urban settings, possibly due to human-managed gardens and green spaces (Sponsler et al., 2020; Zaninotto et al., 2023).

FGs respond differently to land use change

Beyond simple presence or absence in specific habitats, our results also show that FGs respond differently to landscape composition changes, even when they share similar trait profiles. Specifically, our study illustrates that FGs with closely related traits do not always exhibit positively correlated responses to environmental gradients, something known for other organisms but until now not for bees (Benedetti et al., 2018; Cordero & Jackson, 2023; Wong et al., 2020). For example, as expected, closely related FG 5 and FG 6 (spring-active cavity nesters) and FG 11 and FG 12 (social species) responded similarly to changes in landscape context; however, other related groups did not. This is particularly evident among kleptoparasitic FGs, which showed divergent landscape associations. For some groups, this association even differed from those of their hosts, a disconnect sometimes observed between the occurrence of hosts and parasites (Chaverri & Samuels, 2013; Tylianakis et al., 2007; Wullschleger & Jokela, 1999). A striking case is FG 16, a group of spring-active polylectic kleptoparasites whose hosts are mainly in FG 2 and FG 8. Despite this host association, FG 16 only shows a positive correlation with unrelated groups such as FG 4, FG 12, and FG 15, likely due to a shared connection to forested environments. In contrast, we argue that negative correlations between FGs may reflect (i) different nesting strategies (e.g., FG 4 versus FG 6), (ii) differences in pollen specialisation (e.g., FG 14 versus FG 2) or even (iii) competition for nesting sites and/or floral resources (Brazeau & Schamp, 2019). Collectively, these results emphasise the complexity of species-environment interactions, even within functionally defined groups, and underscore the need to consider multiple ecological dimensions (all nesting and foraging traits combined) when interpreting trait-based patterns in wild bee communities.

The anthropogenic matrix between patches of suitable habitats matters

The results from the MSDM, complemented by the BORAL analysis stratified by land use type, highlight the critical role of the anthropogenic matrix, the landscape between suitable habitat patches, in shaping wild bee functional community structure. Our findings indicate that FGs, and by extension species, are influenced not only by the habitat types they use for foraging and nesting, but also by the nature of the landscape they traverse to access their key resources and micro-habitats. The majority of bees will not move between patches, and this movement decreases strongly with patch isolation (Harmon-Threatt & Anderson, 2023) but also with inter-patch matrix quality (Jauker et al., 2009). Furthermore, De Palma et al. (2015), who used broader trait categories, showed that different traits are affected differently by the anthropogenic matrix, which we also found for our FGs. Moreover, we observed inverse responses of FGs to habitat composition across anthropogenic landscapes, suggesting that when conditions are favourable for one FG, they can also be for another FG in a particular anthropogenic landscape, but not necessarily in the other. This decoupling suggests that factors beyond habitat composition per se influence these dynamics. Potential explanations include differences in dispersal ability (Hopfenmüller et al., 2014; Hofmann et al., 2020; Grüter & Hayes, 2022), susceptibility to pesticides (Arena & Sgolastra, 2014; Chan & Rondeau, 2024), competition with other soil-nesters (Cane, 1991) or fine-scale microhabitat variation (Landsman et al., 2019; Peeters et al., 2012) and has profound consequences for conservation efforts aimed at wild bees. Additionally, wild bee habitat types themselves can differ across anthropogenic matrices. For example, forests within Prague and Brno are often remnants of old-growth woodlands, offering diverse understorey vegetation and decaying wood, valuable for cavity nesters. In contrast, forests in surrounding agricultural regions are frequently production forests composed of even-aged stands lacking structural complexity. These forests are also more likely to be adjacent to fertilised croplands, where nutrient enrichment promotes competitive species like *Urtica dioica*, reducing understorey floral diversity (Chytrý, 2012; Global Forest Watch, 2025). This underscores how landscape context alters the quality and ecological function of habitat types.

Functional traits versus FGs

Clustering of species into FGs assumes that the species within the groups respond similarly to environmental variables, but the methods used to group species greatly affect the interspecific trait variation captured within them. Crucially, basing the grouping of species on a single trait instead of a combination of all available traits can lead to oversimplification of trait responses to environmental variables and an underestimation of interspecific variation within the FGs (Appendix S4). Commonly, existing studies group species together based on (i) pollen specialisation, (ii) size category and (iii) parasitic behaviour (Ostwald et al., 2024).

Grouping bees together based on their pollen specialisation entails grouping all oligolectic (and monolectic) bees together into the specialist group and all polylectic bees into the generalist group (e.g., Brasil et al., 2023; Graf et al., 2022; Montoya-Pfeiffer et al., 2020). However, this grouping forgoes the nuances that exist within these groups and their association with certain landscape compositions. This is exemplified by the fact that some studies report that urban gardens benefit polylectic species the most (Fetridge et al., 2008; Buchholz et al., 2020), while others report that specialists are the ones present in higher numbers at these locations (Baldock et al., 2015; Martins et al., 2017). These differing results may be caused by the type of generalists or specialists that were sampled, since they were all grouped together into one 'functional group'. Our clustering analysis, however, grouped non-parasitic generalists in nine distinct FGs containing only polylectic bee species. Importantly, these FGs vary greatly in their other traits. For example, the *Hylaeus* species of FG 4 have no other trait than polylectism in common with the *Andrena*, *Colletes* and *Lasioglossum* species of FG 8. The difference between these FGs is exemplified by their opposite response to changes in landscape composition. Similarly, for specialist bees, the cavity-nesting oligolectic species of FG 1 have the same narrow pollen preference as the other two non-parasitic oligolectic groups, but they have different nesting strategies and types. Even FG 2 and FG 3, which are very similar in most of their traits, are negatively correlated in their response to changes in the composition of the landscape.

Another common way to group bees is by size category (e.g., Brasil et al., 2023; Weber et al., 2023; Wu et al., 2018), specifically when analysing the response of bees to fragmented landscapes (Hofmann et al., 2020) such as cities with disconnected urban green spaces. Our results show, however, that not all large bees react the same to the landscape context. The FGs that contain *Xylocopa* spp. (FG 5) and *Bombus* spp. (FG 14) are the ones with the largest bees, and it is specifically in urban areas where their reaction to changes in the composition of suitable habitat is opposite.

Finally, in studies where socially parasitic and kleptoparasitic bees are not a priori excluded from analysis (Beyer et al., 2020; Bogusch et al., 2020), they are commonly grouped together as "parasites" (e.g., Ferrari & Polidori, 2022; Graf et al., 2022; Weber et al., 2023). The term "parasitic" is sometimes even adopted for multiple trait categories. For example, in Buchholz et al. (2020), the authors used it to define both the sociality trait, as well as the nesting site trait, while Lanner et al. (2025) categorised bees as being parasitic in both the sociality and pollen selectivity (i.e., pollen preference) traits. However, parasitic bees vary as widely in their nesting and foraging traits as their hosts (Bogusch et al., 2006; Peeters et al., 2012; Sedivy et al., 2013; Sick et al., 1994; Smit, 2018) and grouping them all together can lead to (over)simplified assumptions about their association with the landscape. As an example, Graf et al. (2022) found that kleptoparasites benefit from an increase in landscape diversity and from an increase in vegetation cover (grassland, shrubs and trees combined). Indeed, a higher proportion of vegetation cover will increase overall kleptoparasite abundance, but our study shows that the type of vegetation that is (relatively) increased results in a turnover of different types of parasites. Therefore, we argue that it is important to separate parasites by firstly differentiating between social parasites (i.e., the parasitic bumblebees, subgenus *Psithyrus*) and kleptoparasites, which have a completely different lifecycle (Lhomme & Hines, 2018). Secondly, kleptoparasites are strongly dependent on their host's food source and nesting behaviour and therefore vary within these traits. Kleptoparasites that have a host which nests in cavities have different environmental needs than those that have a host which nests in the soil, which is exemplified by the difference in landscape association between FG 17 and FG 16. Similarly, kleptoparasites that have a host which is oligolectic are more dependent on the availability of specific food sources than those that have a host which is polylectic (e.g., the only host of *Nomada atroscutellaris* is *Andrena viridescens*, a species that is oligolectic on *Veronica* spp. (Smit, 2018)).

Because of the large trait variation within the group of "parasites" it is imperative that parasitic species, as well as specialists and generalists, and large and small bees are not just grouped together by their one defining trait, but by the entire gamut of their functional traits. This will reduce interspecific variation within the groups and more clearly show the difference in association with environmental variables between the groups. By contributing our results to this broader context, we show that by avoiding these oversimplifications a more nuanced understanding of the association of trait groups to the landscape context can be achieved.

CONCLUSION

This study represents the first comprehensive analysis of how wild bee FGs, defined through clustering of multiple functional traits, respond to landscape composition. Our approach offers a more realistic representation of wild bee ecological strategies by accounting for trait combinations rather than isolated attributes. We demonstrate that wild bee FGs exhibit distinct and sometimes opposing responses to changes in landscape composition. These responses are shaped not only by the presence of suitable habitats, but also by the anthropogenic matrix between them. Even closely related or host–parasite-linked groups may respond divergently across different landscape contexts. Since conservation efforts inevitably involve trade-offs, decisions must be made about which species or trait groups to prioritise. Prioritisation of species may depend on criteria such as conservation status, historical presence or their role as indicators of ecosystem health (Arponen, 2012) and may conflict with other targets such as climate mitigation through forest carbon storage (Littlefield & D'Amato, 2022). Crucially, our study provides evidence-based guidance for managing and restoring landscapes to support wild bee diversity. By moving beyond simplistic trait categories and accounting for the full range of ecological strategies, we can develop more targeted and effective conservation actions for one of the planet's most important pollinator groups.

AUTHOR CONTRIBUTIONS

Johannes T.C. Visser: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation; resources. **Leon Marshall:** Methodology; visualization; writing – review and editing; supervision; software; conceptualization; investigation. **Jakub Straka:** Writing – review and editing; methodology; supervision. **Nicolas J. Vereecken:** Conceptualization; investigation; writing – review and editing; visualization; supervision; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15879302. (Visser, 2025). [Correction added on 12 August 2025 after first online publication: The Data Availability Statement has been updated.]

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SUPPORTING INFORMATION

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

Appendix S1. Supporting Information.

Appendix S2. Establishing the optimal number of clusters.

Appendix S3. PCoA and PERMDISP.

Appendix S4. Variation between species within functional groups.

Appendix S5. Supporting Information.

Appendix S7. Correlation between traits.

Appendix S8. Supporting Information.

Data S1. Supporting Information.

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