



Pollinator functional group responses to urban land cover in Merseyside, UK

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Abstract

Pollinators are declining globally, partly due to habitat loss and fragmentation - which may be exacerbated by urbanisation. Species differ in functional traits that can influence their ability to persist in cities, and understanding these differences may be key to effective urban insect conservation. This exploratory study examines how bee and hoverfly functional groups respond to urban land cover change and which land cover categories best support pollinator populations. Continuous predicted habitat suitability maps were created for each functional group to identify the most suitable urban land cover categories. The majority of pollinator functional groups showed moderate to high predicted suitability across diverse urban land-cover types, with the notable exceptions of leafcutter bees and hoverflies with phytophagous larvae. Dense urban fabric showed unexpectedly high predicted suitabilities for some functional groups, while green urban areas showed unexpectedly low predicted suitabilities for several groups, suggesting that conservation focus should shift beyond green spaces to encompass more diverse urban habitat types. We also recommend long-term standardised monitoring to better understand trends across functional groups and guide urban conservation strategies. Implications for insect conservation: Urban pollinator conservation strategies should expand beyond their focus on green spaces to include diverse habitat types such as industrial areas and heavily developed land. Management interventions should provide functional group-specific resources including supplementing nesting resources and varied floral resources to support diverse pollinator communities.

Keywords Conservation · Entomology · Pollinators · Urban ecology

Introduction

Pollinators play a critical role in ecosystems, with 87.5% of flowering plants globally dependent on animal pollination, primarily by insects (Ollerton et al. 2011; Potts et al. 2016). One-third of these plants fail to produce seeds without insect pollinators (Rodger et al. 2021). Pollinators also underpin global food systems, with 35% of crops—providing essential nutrients such as vitamins A and C, plant-based proteins, and livestock fodder—relying on their services (Klein et al. 2006; Eilers et al. 2011; Devkota et al. 2024). A global pollinator collapse could result in 1.42 million additional deaths annually due to nutrient deficiencies (Smith et

al. 2015). Although current shortages have not yet reduced yields, increasing reliance on pollinator-dependent crops poses future risks (Aizen et al. 2008).

Despite debate about the existence of a global “pollinator crisis” (Ghazoul 2005), declines are well documented. In Germany, flying insect biomass has declined by over 75% in 27 years (Hallmann et al. 2017). In the US, some bumblebee species have declined by up to 96% (Cameron et al. 2011). In the UK, a third of wild pollinator species declined between 1980 and 2013 (Powney et al. 2019), although hoverfly richness has increased in some regions (Biesmeijer et al. 2006). Butterfly populations have halved since 1976, and significant proportions of species have gone extinct in parts of Europe (Warren et al. 2021). Local trends, however, may diverge due to factors such as climate, land use, and pesticide exposure (Vanbergen 2013). Historic biodiversity records can provide valuable insights into regional change. Habitat loss is a major driver of pollinator decline (Jauker et al. 2018; Goulson et al. 2015), often due to urbanisation, which causes fragmentation and degradation of natural

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areas (McKinney 2002; Harrison and Winfree 2015). Urban land cover is expected to expand by 1.5 million km² by 2030 (Seto et al. 2011), with more than two-thirds of the global population living in cities by 2050 (United Nations, n.d.). Urbanisation negatively impacts terrestrial arthropod diversity and insect biomass (Fenoglio et al. 2020; Svenningsen et al. 2024), although its effects on pollinators remain debated. Green spaces in urban environments, including parks (Threlfall et al. 2015) and gardens (Matteson et al. 2008) as well as transport infrastructure such as railways (Twerd et al. 2021) and road verges (New et al. 2020) could help reduce negative effects of urbanisation on pollinator populations (Svenningsen et al. 2022).

Bee responses to urbanisation vary. Some studies report increased abundance and richness (Fortel et al. 2014; Baldock et al. 2015; Theodorou et al. 2020), while others find declines (Bates et al. 2011). Recent work suggests urbanisation may have a limited effect overall (Nunes et al. 2024), with species- and functional group-specific responses. Solitary bees, for instance, may benefit (Persson et al. 2020; Wilson and Jamieson 2019), and over half of UK solitary bee taxa have been found in city centres (Sirohi et al. 2015). Responses of bumblebees are inconsistent (Wilson and Jamieson 2019; Hernandez et al. 2009), and generalists appear less affected than specialists such as *Andrena semi-laevis* (Bates et al. 2011). Cavity-nesting species benefit more than ground-nesting bees (Fortel et al. 2014; Matteson et al. 2008; Wenzel et al. 2020). Some urban habitats favour specialists like *Lasioglossum smeathmanellum* (nesting in mortar) and *Bombus hypnorum* (bird boxes) (Bates et al. 2011).

Non-bee pollinators such as *Lepidoptera* and *Diptera* are often underrepresented in urban studies (Wenzel et al. 2020; Senapathi et al. 2017). Yet, they play a key role, with non-bee insects accounting for 38% of crop flower visitations, contributing to fruit and seed set (Rader et al. 2015). *Diptera*, especially hoverflies, are second only to bees in pollination importance (Larson et al. 2001). Hoverflies pollinate over 70% of both food crops and wildflowers (Doyle et al. 2020), and transport pollen farther than bees due to their high mobility (Rader et al. 2011; Wotton et al. 2019). Their larvae also provide pest control and aid decomposition (Pekas et al. 2020; Moquet et al. 2017). Urban impacts on hoverflies remain unclear. Some studies show greater sensitivity to urbanisation than bees (Verboven et al. 2014; Baldock et al. 2015), while others suggest hoverflies tolerate land-use change well (Dunn et al. 2020). Diversity may decline with increasing urbanisation, particularly where larval habitats like water bodies and tree cavities are lacking (Grossmann et al. 2022; Persson et al. 2020; Ulrich and Sargent 2025). However, their mobility may buffer against fragmentation (Doyle et al. 2020).

Although urbanisation may be a driver of pollinator decline, long-term data from urban environments is limited, and existing research offers no clear consensus on how different pollinator functional groups may respond. Functional traits such as nesting strategy, sociality and dietary preferences (Graf et al. 2022; Wilson and Jamieson 2019; Braman et al. 2023; Aguirre-Gutiérrez et al. 2016) may affect how pollinators respond to urbanisation - although responses may vary among species within the same functional group (Cariveau and Winfree 2015; Buchholz and Egerer 2020). Nevertheless, examining functional group responses may provide insight into traits that confer resilience to urban environments. Examining urban land cover types may help identify which urban environments best support pollinator communities, allowing more effective targeting of conservation efforts. We predict that green urban spaces and transportation infrastructure (such as railways and roads) will provide the highest predicted suitable habitat across functional groups (Threlfall et al. 2015; Twerd et al. 2021; New et al. 2020). Additionally, due to their higher tolerance for fragmented habitats, we hypothesise that discontinuous low density urban fabric will also prove a suitable predicted habitat for hoverfly functional groups (Doyle et al. 2020).

This exploratory study evaluates predicted habitat suitability of different urban land cover categories for bee and hoverfly functional groups. We will use continuous predicted suitability maps to identify the most suitable land cover categories by functional group. We will make recommendations for improving long-term urban pollinator data collection and reducing sampling and observer bias.

Methods

Historical data

Historical species occurrence data covering the Merseyside area of the UK were collected from verified recording schemes (Merseyside BioBank, Lancashire Wildlife Trust and NBN Atlas), which include identification verification.

Merseyside is a predominantly urban region of North-west England (Fig. 1) (81% urban land cover; Natural England, 2026 and population density: 2,262 people/km²; Office for National Statistics, 2025) with substantial green infrastructure including parks and gardens, and a relatively high proportion of woodland (5%). Merseyside also encompasses industrial areas such as docks, agricultural land and coastal habitats including sand dunes and mudflats (Natural England, 2026). Merseyside has mean annual temperatures ranging from 7.5 °C to 13.6 °C and mean annual rainfall of 824 mm (Met Office, n.d.).

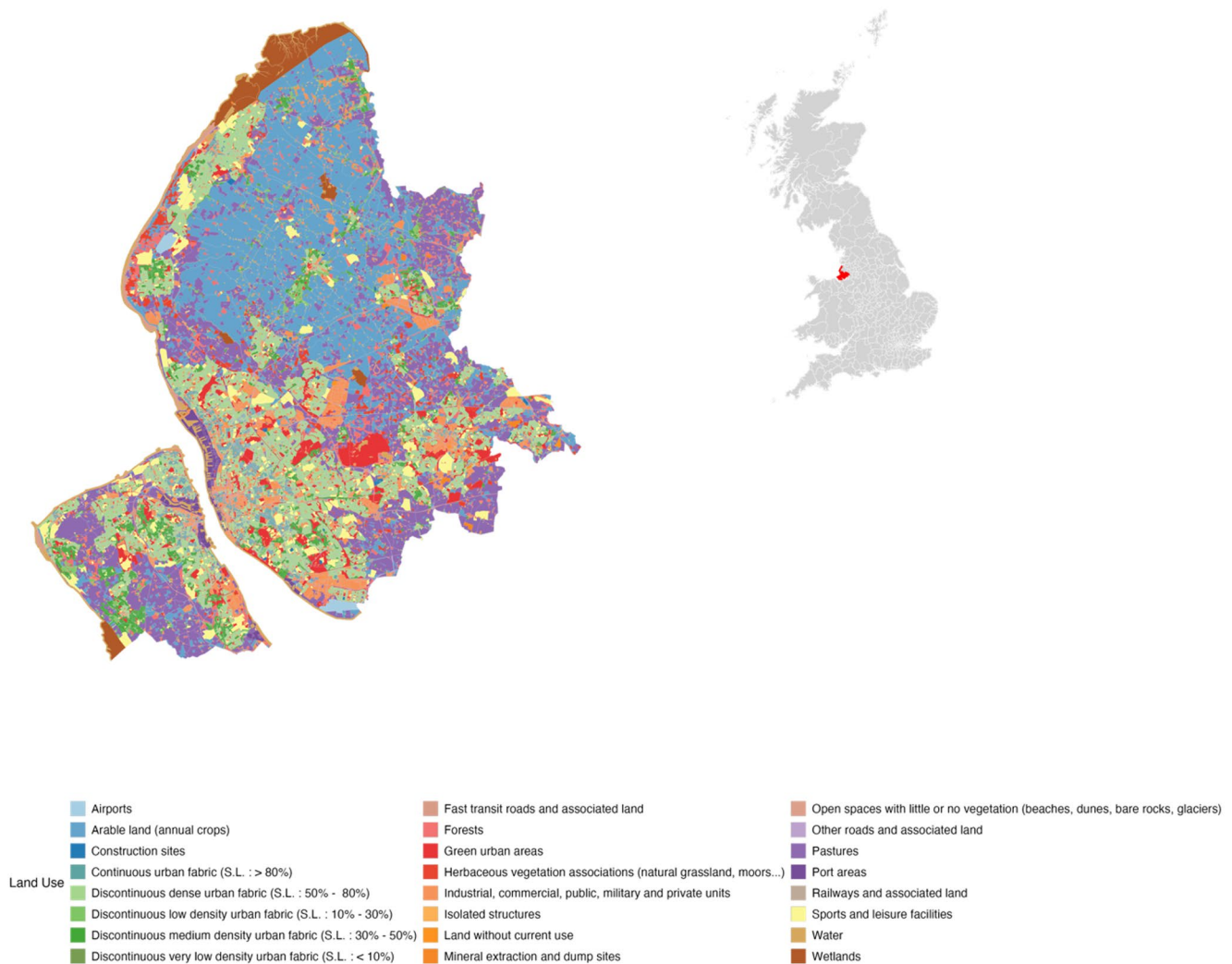


Fig. 1 Location of Merseyside within the UK, with zoomed in map showing distribution of land use by category

Occurrence records were initially filtered using Quick-OSM in QGIS to include only records within the boundaries of Merseyside. Records were then manually cleaned in Microsoft Excel to remove data from non-target species, duplicate records (defined as identical species, date and coordinates), records not identified to species level, and observations missing location or date. Only records marked as accepted in the source databases (indicating expert validation of species identification) were retained; records marked as unconfirmed or incorrect were excluded. Due to uncertainty about reliability of individual counts in some records, all observations were treated as single occurrences. Observations of bees were classified into taxonomic groups in Excel (bumblebee, carder bee, cuckoo bee, flower bee, honey bee, leafcutter bee, mason bee, mining bee, sweat bee, yellow-faced bee) according to traits such as nesting strategy, sociality and foraging behaviour; Michener 2007). Hoverflies were classified into functional groups based on

larval feeding strategy (microphagous mycophagous, phytophagous, saprophagous, scavenger, zoophagous; Miličić et al. 2021; Rotheray 1993; National Biodiversity Data Centre, n.d.; Hoverfly Recording Scheme, n.d.). Both bee and hoverfly classifications are referred to collectively as functional groups for brevity. The taxonomic composition of these functional groups is provided in Table S1.

Data analyses

All data analysis was conducted in R (v4.5.1; R Core Team, 2025), using the packages *dismo* (v.1.3.16; Hijmans et al. 2024), *raster* (v3.6.32; Hijmans 2025), *sf* (v1.0.21; Pebesma 2018; Pebesma and Bivand, 2023), *caret* (v7.0.1; Kuhn 2008), *exactextractr* (v0.10.0; Baston 2023) and *glmmTMB* (v1.1.13; Brooks et al. 2017; McGillicuddy et al. 2025).

Functional group distribution models

To model functional group distributions, the 2018 Land Cover Map (LCM 2018; 25 m raster; Morton et al. 2020) was downloaded and cropped to Merseyside boundaries using Local Authority District (December 2018) shapefiles (Office for National Statistics, 2024). Topographical data was obtained from the OS Terrain 50 ASCII files (Ordnance Survey, 2025) and filtered to British National Grid squares SJ and SD, which cover the Merseyside region. Land cover and terrain were combined by resampling to 25 m resolution using linear interpolation. All spatial data was projected to a consistent coordinate reference system (British National Grid, EPSG:27700). Final analysis used 25 m resolution. Historical records were filtered to 2016–2020, to align with the 2018 Land Cover Map. As all occurrence records had both land cover and elevation data available, no records were excluded due to missing environmental values. Presence data was randomly split into training (75%) and testing (25%) datasets.

All functional groups were initially modelled using MaxEnt. However, groups with very small sample sizes (<50) were excluded, as small training datasets have been shown to reduce model reliability in presence-only species distribution models (Wisiz et al. 2008; van Proosdij et al. 2015; Liu et al. 2018). To account for spatial sampling bias, background points were generated using a target group approach (Phillips et al. 2009), with occurrence records from all other bee and hoverfly functional groups (excluding the group being modelled) used as background points rather than randomly sampled locations. As the focal group was excluded from the background for each model, the background points used differed for each functional group. This approach reduces the influence of spatial sampling bias by ensuring that background points reflect sampling effort distribution rather than assuming uniform sampling effort across the landscape. Background points were also split into training (75%) and testing (25%) datasets. MaxEnt models were trained using background and training data, with models projected across the Merseyside area. MaxEnt was run using default settings in the dismo package (v.1.3.16; Hijmans et al. 2024) with the following parameters: feature types: linear, quadratic, product and hinge; regularisation values: linear/quadratic/product: 0.05, categorical: 0.25, threshold: 1.0, hinge: 0.5. All environmental layers were treated as continuous variables, with the exception of land cover class which was treated as categorical.

To assess model stability, each model was run three times using different random seeds (42, 123, 456), producing three predicted suitability maps for each functional group. Mean predicted suitability values across the three runs were calculated and used to produce a single continuous suitability

map for each group, which was used in subsequent zonal statistics analysis. Model performance was assessed using area under the receiver operating characteristic curve (AUC-ROC), the True Skill Statistic (TSS, calculated as sensitivity + specificity - 1) and the Continuous Boyce Index (CBI). CBI is particularly recommended for presence-only models as it does not require true absence data (Hirzel et al. 2006). Model performance metrics were calculated from continuous suitability predictions. All performance metrics, including sensitivity and specificity at the maximum TSS threshold (the threshold maximising the sum of sensitivity and specificity), are reported for each functional group in Table S2. Binary suitability maps were not generated as threshold values varied across model runs, producing inconsistent classifications of suitable and unsuitable habitat (Table S2). This is consistent with known limitations of threshold selection in presence-only species distribution models (Hirzel et al. 2006). All analyses were therefore based on continuous suitability predictions. Predicted habitat suitability was modelled using MaxEnt with two environmental predictors: categorical land cover (LCM 2018; 25 m raster; Morton et al. 2020) and continuous elevation (OS Terrain 50 ASCII files; Ordnance Survey, 2025). No additional topographical predictors (e.g. slope) or landscape-level variables (e.g. distance to natural habitats) were used. Elevation is commonly incorporated in species distribution models, although its usefulness is debated (Hof et al. 2012). Nevertheless, topographic metrics such as elevation can act as surrogates for climatic factors, and their omission has been shown to reduce model performance (Kosicki 2017). Additionally, although elevation varies relatively little across Merseyside (-3.5 m to 208.5 m; OS Terrain 50; Ordnance Survey, 2025), and we acknowledge that climatic variation across this range may also be limited, elevation contributed substantially to model gain for some functional groups (Table S3). A consistent set of predictors was maintained across all functional group models to ensure comparability. Continuous functional group distribution maps were overlaid with the Urban Atlas Land Cover/Land Use 2018 dataset (European Union's Copernicus Land Monitoring Service, 2020) in QGIS, and the zonal statistics tool used to calculate mean predicted habitat suitability for each category within the Artificial Surfaces class.

Results

A total of 43,744 historical records were analysed, covering 1896 to 2025. 41% of records were observations of hoverflies, and 59% of bees. Carder bees (26 records), yellow-faced bees (39 records) and hoverflies with microphagous (1 record) and mycophagous (9 records) larvae were excluded

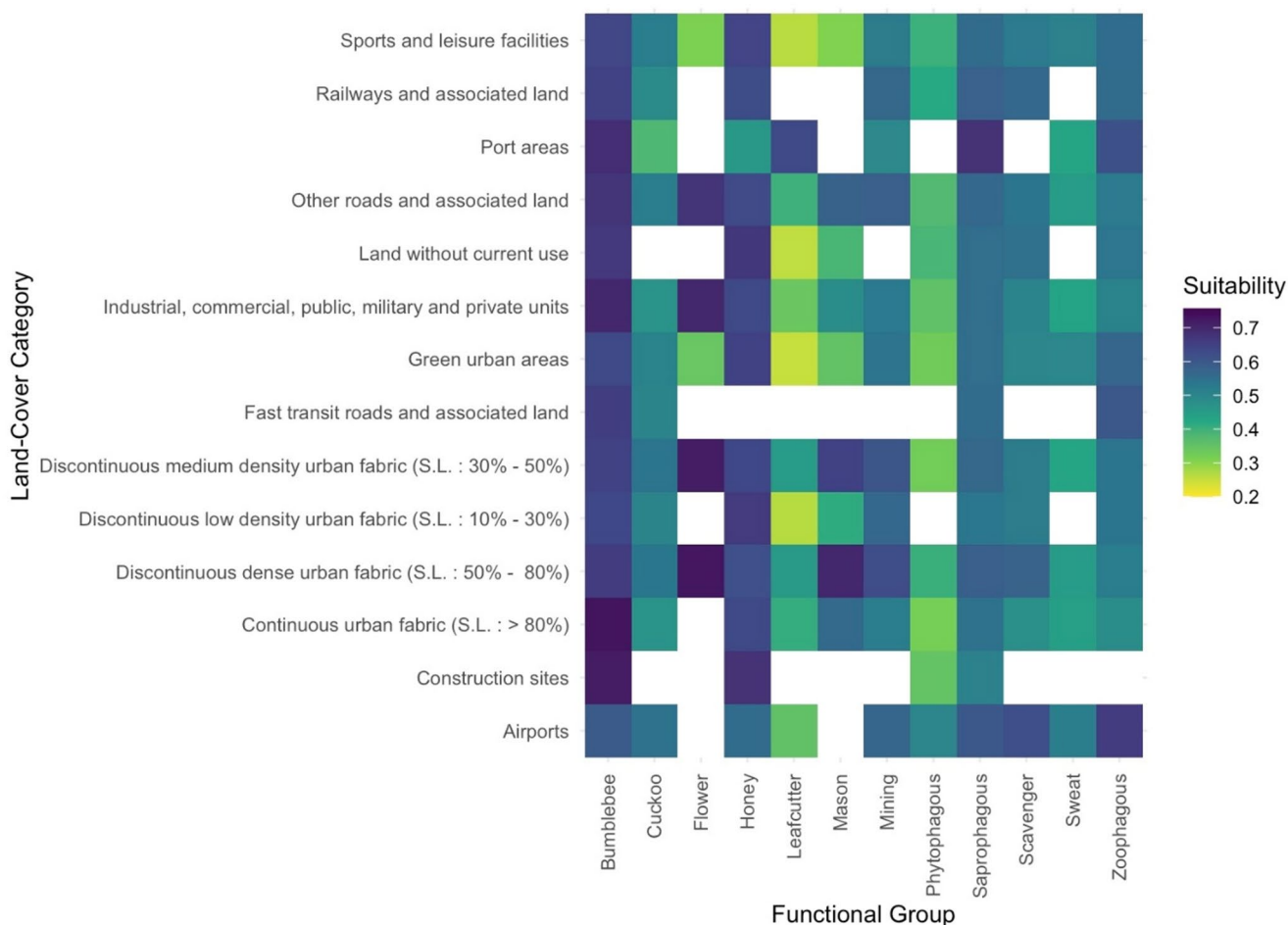


Fig. 2 Mean predicted habitat suitability scores across urban land cover categories by functional group. Land cover categories with fewer than 20 occurrence records were excluded. *Note: Airports ($N=38$) and

port areas ($N=34$) had limited sample sizes; results for these categories should be interpreted with caution

from analysis due to small sample sizes. The number of records peaked in 2016. Most functional groups showed moderate-high suitability across multiple urban land cover categories (Fig. 2).

Discussion

This exploratory study evaluated predicted habitat suitability of different urban land cover categories for bee and hoverfly functional groups. The results suggest that the majority of functional groups show moderate to high predicted suitabilities across diverse urban land cover categories, with the exception of leafcutter bees and hoverflies with phytophagous larvae which demonstrated low predicted suitability across most categories.

Zonal statistics were used to identify which urban land cover categories had the highest mean predicted suitabilities for each functional group. It was predicted that green urban

spaces and transportation infrastructure would provide the highest predicted suitable habitat for multiple functional groups, and that discontinuous low density urban fabric would provide a suitable habitat for hoverfly functional groups. While data was limited for some transport land cover categories (notably fast transit roads), port areas and other roads and associated land did show moderate to high predicted suitabilities across multiple functional groups. However, predicted suitabilities of green urban areas were moderate to low for many functional groups. Low density urban fabric did not provide highly suitable predicted habitat for hoverfly functional groups, instead showing more moderate predicted suitabilities; however, no occurrence data was available for hoverflies with phytophagous larvae in this category.

Bumblebee and honey bee models showed highly variable performance across runs (bumblebee CBI: $-0.20, -0.30, -0.80$; honey bee CBI: $0.26, -0.05, 0.19$; Table S2),

suggesting unstable and unreliable predictions. Results from these functional groups are therefore not interpreted further.

Mining bees demonstrated consistently moderate predicted suitabilities across most urban land cover categories. This is notably as many ground-nesting species require bare soil for nesting, which is often replaced by impermeable surfaces in urban areas (Government Office for Science, 2024; Arnold and Gibbons 1996). It is also in contrast to previous research suggesting that cavity-nesting species benefit more from urban environments than ground-nesting species (Fortel et al. 2014; Matteson et al. 2008; Wenzel et al. 2020). We hypothesise that urban areas in Merseyside may be providing more bare ground nesting opportunities than expected. Mason bees demonstrated a gradient of predicted suitabilities across urban land cover categories, with lower predicted suitabilities in green urban areas and sports and leisure facilities, and higher predicted suitabilities in dense and medium density urban fabric. We hypothesise that this may reflect use of man-made structures such as walls for nest-building (Falk 2019). This is also consistent with findings from other European cities, which have found mason bees to be flexible and well-adapted to urban environments (Zajdel et al. 2021; Everaars et al. 2011). The highest predicted suitabilities were found for flower bees in medium density and dense urban fabric. We hypothesise that this may reflect the availability of nesting opportunities in mortar (Else 2021) and pavements (Weber et al. 2024), as well as the prevalence of suitable foraging plants such as daffodils, primroses and ivy in urban gardens (Else 2021). However, flower bee models showed some instability across runs (Table S2), and these results should therefore be interpreted with caution.

Two notable exceptions to the broad moderate to high habitat suitabilities are found in leafcutter bees and hoverflies with phytophagous larvae, which showed low predicted suitabilities across nearly all urban land-cover categories. Many species of hoverflies with phytophagous larvae have complex larval host plant requirements. Females may be highly selective about which plants they lay eggs on, and larval development may be tied to seasonal changes (Rotheray and Gilbert 2011) - conditions that may not be met in many urban environments. Similarly, leafcutters have preferences for plants of certain families (such as Fabaceae; Sinu and Bronstein 2018) - with their presence in urban environments therefore depending on availability of suitable plant communities. It is important to note, however, that hoverflies with phytophagous larvae (particularly *Cheilosia*) can be difficult to identify without microscopic analysis (Rotheray and Gilbert 2011), so may be historically underrecorded. It is also possible, however, that Merseyside represents generally poor habitat for these groups, irrespective of land cover type.

Port areas showed unexpectedly high predicted suitabilities across multiple functional groups, including leafcutter bees and hoverflies with saprophagous larvae. Port areas could be considered brownfield land (Ministry of Housing, Communities and Local Government, 2012), which has previously been identified as potentially valuable pollinator habitat (Goulson et al. 2010). However, these areas often have restricted access, meaning pollinator recording efforts may have been limited and occurrence records consequently sparse. Results for this land cover category should therefore be interpreted with caution. Conversely, urban green areas showed surprisingly low predicted suitabilities for several functional groups, including flower, leafcutter and mason bees, and hoverflies with phytophagous larvae. This suggests that these spaces may not provide the floral and/or nesting resources required by these more specialist species (Fortel et al. 2014; Poole et al. 2025). This has important implications for pollinator conservation, which often focuses on urban green areas (Ranalli et al. 2025). It may be possible to improve urban pollinator conservation by provisioning these spaces with additional resources - whether that is artificial nests for cavity-nesting solitary bees (Prendergast 2023; Christman et al. 2022) or incorporating specific forage plants known to support specialist species, such as plants from the Fabaceae family for leafcutter bees (Sinu and Bronstein 2018) and lungwort and comfrey for flower bees (Else 2021; Poole et al. 2025). However, the effectiveness of artificial nesting structures is debated (Geslin et al. 2020).

There are several limitations which may have affected the findings of this study. To address spatial sampling bias, a target group background approach was employed using occurrence records from all other bee and hoverfly functional groups as background records. However, this approach assumes consistent recording effort across functional groups. Visual pollinator surveys are naturally biased towards larger, more mobile species, with smaller, less-conspicuous species potentially underrepresented (Kremen et al. 2011; O'Connor et al. 2019). Sampling effort was not evenly distributed across land cover types (Table S4), which may affect the reliability of model predictions across urban land cover categories. Additionally, the MaxEnt models used in this study only used land cover class and elevation (terrain) as environmental predictors, and did not capture fine-scale habitat characteristics such as floral resource availability and soil type. The study also did not account for landscape-scale factors such as proximity to green spaces and green space size, which may have contributed to suitability scores. These results may therefore reflect modelling limitations, rather than true predicted habitat suitability.

Results for functional groups with lower model stability across runs, including sweat bees and flower bees, should

be interpreted with caution. Bumblebee and honey bee models showed highly variable performance across runs, and so were not interpreted further. MaxEnt results for functional groups with lower numbers of records (Table S5) must also be interpreted with caution, as limited presence data may affect model reliability. This study did not check for georeferencing accuracy or spatial clustering of records, or remove coordinates for records at institutional locations (e.g. records found in museums rather than collection sites), which may have affected model predictions. Models were not cross-validated using multiple splits, and MaxEnt default settings were used without testing alternative configurations.

While some of these limitations may be difficult to fully resolve without additional data, several could be mitigated in future studies through incorporation of additional environmental predictors such as soil type and floral resource availability, spatial thinning of occurrence records, and inclusion of landscape-scale variables such as distance to green spaces. We also recommend targeted field surveys for rarer land cover types (such as ports and airports) to improve record availability. More broadly, long-term standardised monitoring of pollinators in urban areas is essential. One promising approach may be the UK Pollinator Monitoring Scheme, which already includes a number of urban habitat categories (such as brownfield sites and gardens) (UK Pollinator Monitoring Scheme, 2025). Expansion of this scheme to encompass more areas could provide essential long-term data on urban pollinators. Another possible approach may be found in the recent developments of insect camera traps (Naqvi et al. 2022; Droissart et al. 2021; Bjerger et al. 2024), which in combination with AI could help reduce observer and sampling bias. Implementing these systematic monitoring approaches and using more comprehensive modelling approaches, would allow us to determine whether observed predicted habitat suitabilities are ecologically meaningful or simply reflect sampling biases and limitations.

Conclusion

This exploratory study evaluated predicted suitability of different types of urban land cover for bee and hoverfly functional groups. Results revealed moderate to high predicted habitat suitability across functional groups and land cover types, including port areas and urban fabric of multiple densities. Unexpectedly, urban green areas showed relatively low predicted suitabilities for several functional groups. These results suggest that conservation measures should extend beyond urban green spaces to encompass more diverse urban spaces. However, data and modelling limitations including uneven sampling effort, absence

of landscape-scale variables and recorder bias, may have impacted on results. To address these limitations, long term urban monitoring, integration of unbiased recording technologies such as AI camera traps and use of improved modelling methods are essential to validate whether the predicted urban habitat suitabilities are ecologically meaningful, or simply a result of data limitations.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-026-00774-z>.

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Author contributions K.H. : Writing – original draft (lead); methodology (equal); project administration (lead); formal analysis (lead). D.H.: Conceptualisation (lead); methodology (equal); supervision (lead); review and editing (lead).

Data availability Data used in this manuscript is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dr7sqvbbp>.

Declarations

Competing interests The authors declare no competing interests.

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