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ORIGINAL ARTICLE

The Ecology and Conservation of Urban Insects

Urban intensity gradients shape community structure, life-history traits and performance in a multitrophic system

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Abstract

1. Urban ecosystems are formed by pronounced socio-ecological gradients, which are distinct from other ecosystems and can simultaneously filter and promote taxa, ultimately affecting their interactions. However, the strength of the effect of filtering and facilitation across the different trophic levels could vary among biotic and abiotic factors.
2. Here, we investigate the effects of habitat amount, temperature and host-enemy biotic interactions in shaping communities of cavity-nesting bees and wasps and their natural enemies. We installed trap-nests in 80 sites distributed along urban intensity gradients in five European cities (Antwerp, Paris, Poznan, Tartu and Zurich). We quantified the species richness and abundance of hosts and their natural enemies, as well as two performance traits (survival and parasitism) and two life-history traits (sex ratio and number of offspring per nest for the hosts). We analysed the importance of the abiotic and biotic variables using generalised linear models and multi-model inference.

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3. We found that habitat amount was the main driver of multiple host responses, with larger habitat amounts resulting in higher species richness and abundance for hosts and natural enemies, as well as a larger probability of survival and a larger number of brood cells for hosts.
4. Local resources proxies shaped both bees and wasps and indicate different uses of existing vegetation between bees and wasps. Temperature proxies had a minor role in shaping host and natural enemies.
5. Biotic interactions were a main driver of host and enemy community structure, with natural enemies being strongly affected by host availability, that is, with direct density-dependence between hosts and their natural enemies.
6. Overall, our study highlights the importance of habitat amount and temperature in shaping urban food webs, as well as on biotic interactions through direct effects on hosts responses and the subsequent consequences for their natural enemies. As cities prepare to tackle the consequences of global change, strategies that make it possible to maintain habitat and mitigate urban overheating emerge as a key urban adaptation for biodiversity conservation.

KEYWORDS
urbanisation cavity-nesting bees and wasps, ecological rate, parasitism, sex ratios, survival, trap-nest

INTRODUCTION

Urbanisation both filters and promotes biodiversity, providing challenges and opportunities for urban wildlife management. Understanding the drivers of urban diversity patterns and ecological processes across urban ecosystems has therefore become a central topic to promote biodiverse cities (Uchida et al., 2021). Understanding the impact of urbanisation on multitrophic biodiversity, specifically performance traits (e.g., parasitism, mortality) and life-history traits (e.g., sex ratio, number of eggs), can shed light on species fitness, survival and occupancy responses. This knowledge is crucial for implementing targeted management strategies. Species assemblages and the fitness of single species are determined by environmental conditions, such as habitat amount (i.e., the total area of suitable habitats at a defined space; sensu Fahrig, 2013), food resource availability and temperature, in combination with biotic interactions, such as top–down control by higher trophic levels (Dainese et al., 2018), and bottom–up control by lower trophic levels (Steffan-Dewenter & Schiele, 2008). All these drivers are expected to vary substantially along urban intensity gradients.

Habitat amount has been identified as a main driver of ecosystem biodiversity (Fahrig, 2013; Hutchinson, 1957), but the relationship between habitat amount and biodiversity might be more complex in cities than in other ecosystems. At the community level, species richness generally increases when the amount of habitat within an appropriately defined area is larger (Fahrig, 2013). Moreover, habitat amount can also influence life-history traits. For instance, habitat loss can result in male-biased sex ratios in several Hymenoptera species (Fitch et al., 2019). In cities, as urban intensity increases, the habitat amount becomes scarcer, particularly large habitat patches. However, cities differ from other ecosystems as, rather than being characterised by large habitat patches, habitat is typically distributed in small patches with variable local features (Aronson et al., 2017). Thus, it is unclear what are the effects on the community structure, life history traits and performance traits in urban taxa.

The landscape effects of urbanisation through habitat amount on biodiversity might be counteracted by the local habitat and resources present in existing patches within the cityscape (Diamond et al., 2023). Greater plant diversity often results in more food resources (e.g., nectar), enhancing the abundance and richness of consumers directly, and of higher trophic levels indirectly (Fabian et al., 2014; Srivastava & Lawton, 1998). For example, management activities can alter plant community structure within urban habitats by adding or removing species, also affecting the properties of food webs (Burks & Philpott, 2017; da Rocha-Filho et al., 2020). How food resources influence the life-history traits, performance traits and community structure of urban species is less known than in other ecosystems but this is of major importance for biodiversity management in urban areas.

Temperature gradients and their effects on biodiversity are well documented in communities outside cities (Mayr et al., 2020; Orr et al., 2021). However, cities can also have pronounced local temperature gradients (Zumwald et al., 2021). Different densities and impermeable materials and the presence of blue-green spaces can form urban heat or cooling islands at the points of greatest or fewest accumulation of heat and energy, respectively. High temperatures are expected to favour ectothermic taxa, by increasing insect activity, enhancing interactions, and potentially boosting their diversity (Banaszak-Cibicka, 2014; Geppert et al., 2022; Hamann et al., 2020; Jamieson et al., 2012). However, excessively high temperatures, above a species' physiological threshold at different life stages, could enhance desiccation and reduce survival and reproduction success (Dale & Frank, 2018), as well as creating a phenological mismatch with the plant hosts (Papanikolaou et al., 2017). Further, because of the positive association between temperature and grey surfaces, warmer areas can correspond to smaller amounts of green habitat and less availability of food resources. The effects of broad temperature gradients on biodiversity have been studied previously (Trøjelsgaard & Olesen, 2013), yet local temperature effects, particularly in cities, have been less investigated.

Biotic interactions between hosts and their natural enemies are an additional driver of diversity. Natural enemies include predators and parasites, which can indirectly favour species richness by alleviating competitive pressure by dominant species (i.e., top–down regulation Steffan-Dewenter & Schiele, 2008, Levi et al., 2019). Focusing on parasitism, interactions between hosts and their natural enemies can be either directly density-dependent (Dainese et al., 2018), when larger numbers of hosts result in increased parasitism (Hassell, 2000), or inversely density-dependent, when larger numbers of hosts result in decreased parasitism (Rosenheim, 1990; Steffan-Dewenter & Schiele, 2008), ultimately affecting the diversity of hosts and natural enemies. The dynamics between hosts and their natural enemies might be altered in cities, as the urban environment can affect the behaviour, distribution, physiology and community structure of both hosts and natural enemies, due to the combined action of multiple socio-ecological factors and processes (Classen-Rodríguez et al., 2021). However, studies on the effects of biotic interactions in cities are still scarce (Theodorou, 2022).

Here, we studied the effects of habitat amount, resources, temperature and biotic interactions between the hosts and their natural enemies on multitrophic diversity. In particular, we considered effects on the community structure (i.e., species richness, abundance) of cavity-nesting bees and wasps (CNBWs) and their natural enemies (e.g., parasites, parasitoids, cleptoparasites), as well as on the performance traits (i.e., parasitism, survival) and life-history traits (i.e., sex ratio, number of offspring cells per nest) of CNBW across urban ecosystems. We tested the following non-mutually exclusive hypotheses:

1. For hosts and natural enemies, habitat loss at the landscape (i.e., when urban intensity is high) reduces species richness and abundance. This effect might be stronger in wasps than in bees, as loss of habitat particularly affects arthropod prey diversity and abundance at higher trophic levels (Attwood et al., 2008; Mayr et al., 2020). Moreover, for hosts, small amounts of habitat also reduce the number of offspring per nest, the offspring survival, and reduce the number of females.
2. Higher local resources (inferred with plant richness and cover of specific habitat types) positively influence community structure, life history traits and survival of hosts. Bees and wasps are central place foragers and thus, the available resources in the vicinity of their nesting sites are critical for their persistence (Kendall et al., 2022; Rosenberg & McKelvey, 1999).
3. Increasing temperatures, below physiological thresholds where it becomes excessive, positively affect the foraging activity of CNBW. This results in a higher number of eggs laid per nest, offspring survival, number of females and overall abundance hatched (Geppert et al., 2022; Mayr et al., 2020). Alternatively, excessive temperatures above physiological thresholds will reduce survival (Ricklefs & Wikelski, 2002).
4. Biotic interactions (host–natural-enemy interactions) might positively shape both hosts and natural enemies. Regarding hosts, higher parasitism rates and a larger number of parasitized brood cells might increase host populations of bees and wasps by reducing competition among dominant species, thus increasing species richness. Regarding natural enemies, increased host availability (i.e., more nests and higher host species richness) increases natural enemy population sizes, resulting in enhanced species richness and the number of parasitized cells by providing more resources (Dainese et al., 2018; Hassell, 1982; Rosenheim, 1990).
5. Conversely, biotic interactions might negatively influence both hosts and natural enemies. Regarding hosts, higher parasitism rates and a larger number of parasitized brood cells might reduce host population sizes. Regarding natural enemies, increased host availability (i.e., more nests and higher host species richness) might result in a greater probability of detection of natural enemies by the host, less time for natural enemies to lay eggs, and enhanced collective defences by hosts, ultimately reducing natural-enemy species richness and the number of parasitized cells (Rosenheim, 1990).

MATERIALS AND METHODS

Study cities and sites

Our study was set in five European cities: Antwerp (Belgium), Greater Paris (France, hereafter referred to as Paris), Poznan (Poland), Tartu (Estonia), and Zurich (Switzerland), covering a large part of the climatic variability in mainland Europe (Figure S1). Site selection was done using an orthogonal gradient of patch size and patch isolation (Text S1, see also Casanelles-Abella et al., 2022). Overall, the final selection included 80 sites, 32 in Zurich and 12 in each of the remaining four cities (Figure S1 and Table S1). Sites were at least 500 m apart from each other, except for two sites in Zurich that were 260 m apart (see Text S1 for additional details).

Insect sampling

We sampled CNBW and their natural enemies (parasites, parasitoids, kleptoparasites, nest destroyers; see Text S2) using trap-nests, which were placed in the study sites. This enabled us to study their individual- and community-level responses in standardised nesting conditions (Figure 1b; Staab et al., 2018; Tscharntke et al., 1998). To avoid vandalism, we installed trap-nests at 2.5–3.5 m height in sun-exposed South East or South West- expositions for the period of January–October 2018. In October, we collected the trap-nests and

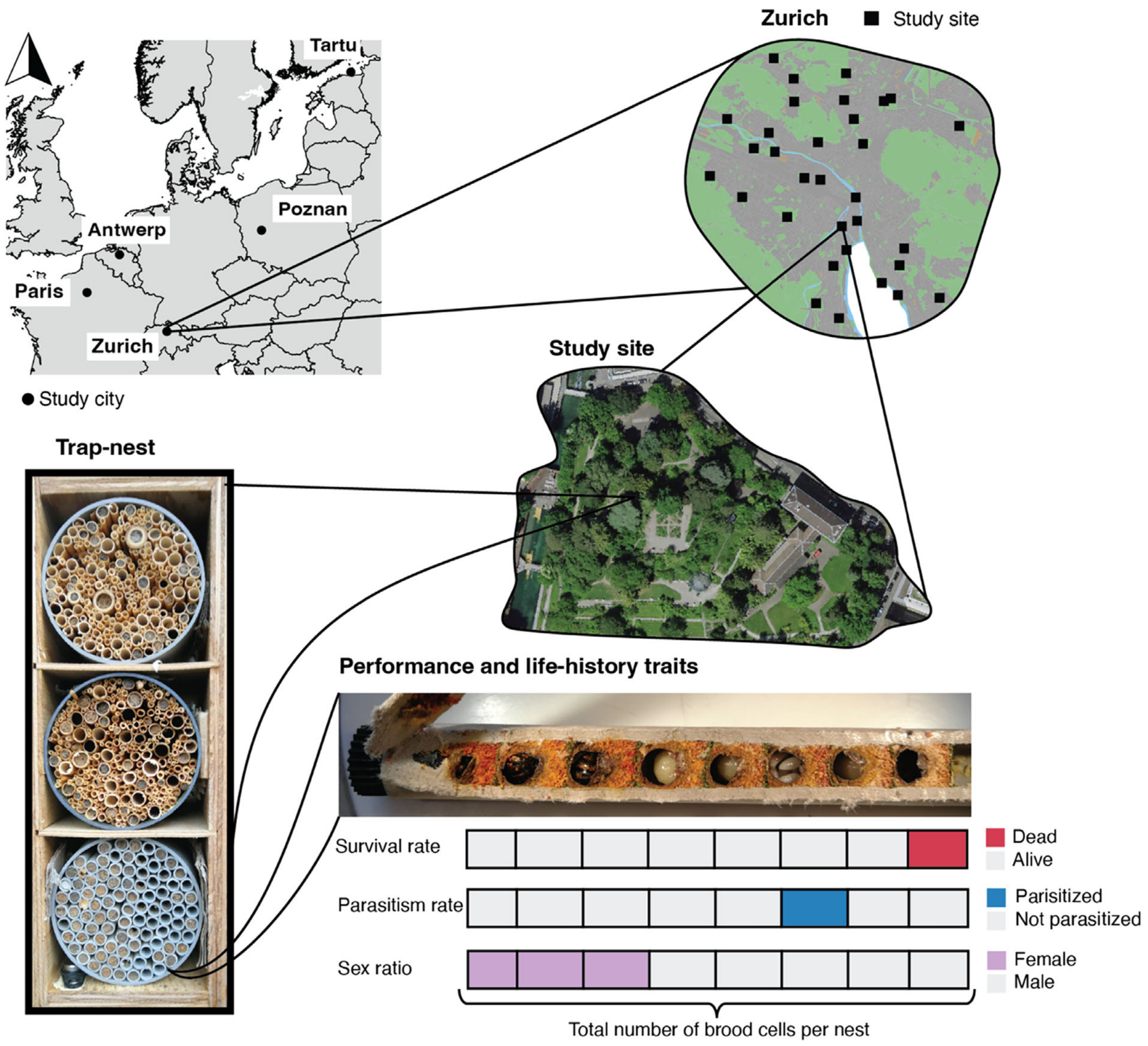

FIGURE 1 Summary of the study design and calculation of the performance traits (survival rate and parasitism rate) and life-history traits (sex ratio and number of cells per nest) using a nest from *Osmia leaiana* (Kirby, 1802) in Zurich as an example. Each rectangle represents an individual cell in the nest.

stored them at c. 5°C. Between November and December 2018, we opened all reed internodes to detect brood cells. We counted the number of brood cells in the bee and wasp nests and noted the occurrence of natural enemies (cleptoparasites, parasites, parasitoids and predators). We then placed the reeds individually into glass tubes and closed the tubes with cotton wadding to collect emerging insects. We stored the tubes at 5°C until February 2019, when we transferred the tubes to a room at ambient temperature.

During spring and summer 2019, bees, wasps and their natural enemies emerged. We identified bees, wasps and enemies to the species level or to the lowest taxonomic rank possible (Table S2), using existing identification keys (Text S3). In addition, we identified the sex of all emerged bees and wasps and calculated the sex ratio at the nest level (i.e., for each reed tube). When no adult hosts emerged from a nest, we used the nest features (sealing material, diameter, larval food type) to identify the host genus or the family. Finally, some natural enemy species could only be identified to morphospecies (Table S3).

Community structure, performance traits and life history traits

We calculated community structure, performance traits and life-history traits (sensu Violle et al., 2007) to study the effects of habitat amount, resources, temperature and biotic interactions between the hosts and their natural enemies on multitrophic community diversity. Concerning the community structure, at each site, we calculated species richness, abundance of hatched hosts and number of nests of the hatched hosts separately for bees and wasps. We calculated the abundance of hatched hosts as the number of brood cells where an individual emerged, that is, the total number of brood cells minus the number of parasitized cells and the number of cells with no emergence for reasons other than parasitism. Abundance was calculated as the total community abundance. We calculated the number of nests as the total number of colonised reeds. The abundance of hatched hosts and number of nests were highly correlated (Pearson correlations from 0.81 to 0.92). Thus, we only included the abundance of hatched hosts in the analyses, as it reflects the actual number of individuals that will constitute the next generation. For natural enemies, we calculated the species richness and abundance. We estimated the abundance of natural enemies as the number of parasitized brood cells rather than the total number of emerging individual enemies, to account for differences in the number of eggs laid per cell across different enemy species.

We assessed performance traits, that is, survival and parasitism, at the individual cell level. Specifically, for each cell within a nest, we noted whether the cell was alive or dead (survival; Figure 1c), and whether it had a parasite or not (parasitism; Figure 1c). Further, we calculated the parasitism rate as the number of cells with a parasite divided by the total number of cells. However, the scales at which parasitism operates can vary among natural enemies. For instance, some might attack the first or last cells in a nest, whereas others might attack an entire sequence of cells in a nest. Therefore, to account for the variability in the parasitism modes of the natural enemy community, we also calculated and studied parasitism at the nest level, as the number of cells parasitized.

Concerning life-history traits, we calculated the total number of brood cells per nest as the total number of brood cells within a single nest, regardless of whether the larvae were dead, alive or parasitized (Figure 1c). Finally, we used the probability that a female host emerged from a given cell as a proxy for sex ratio. To do so, we first identified the sex of the individual hosts. Then, we noted it in a binary way to indicate whether the host was a female or not (Figure 1c). We could identify the sex of all hatched hosts. Further, because CNBW first lay females and then males, on some occasions we could also identify the host sex in dead and parasitized cells, that is, when we had already identified the sex of the preceding and the following cells.

Predictors

We used four sets of variables representing (1) habitat amount at the landscape scale, (2) local habitat and resources, (3) temperature and (4) biotic interactions (Figure S2).

We inferred habitat amount at the landscape scale using a combination of landcover data and remote-sensing-based indices. First, we estimated habitat amount using metrics based on land-cover data. Using the European Urban Atlas (EEA, 2012), we calculated the local patch size (total area of the study site) and patch isolation (using the proximity index, which weights the contribution of the area of neighbouring patches by the distance to the focal patch within a given search radius) (Gustafson & Parker, 1994). We considered as favourable habitat all patches with high probability of having trees (that is, urban green areas: urban forest and grey urban land-cover with less than 30% impervious surface, as defined in EEA, 2012). Further, following the habitat amount hypothesis (Fahrig, 2013), which defines habitat amount as the total area of habitat at a defined distance from the nest, we used the European Land Cover Map at 10 m resolution (Venter & Sydenham, 2021), which enable accounting for small habitat patches. We calculated the amount of green and grey covers using 50, 100, 200, 400 and 800 m buffers from the focal trap-nests, to infer the habitat amount at each site. The selected buffer sizes are expected to be relevant for the studied organisms (Gathmann & Tscharntke, 2002). Due to the high correlations between buffers, we used 100 and 800 m in our analyses. Additionally, we also used remote-sensing-based indices, calculated at the same buffers. In particular, we used the normalised difference vegetation index (NDVI) and the Urban Index (UI) within the five buffers (Text S4). Due to the high correlations with the amount of green surfaces, the amount grey surfaces, NDVI and UI (Figures S3 and S4), we only used the amount of green surfaces at 100 and 800 m in our analyses.

We used the floristic inventories from Casanelles-Abella et al. (2021) to further characterise habitat amount in terms of food resource availability, inferred as plant species richness. Additionally, we computed plant Shannon diversity but due to the high correlations with species richness, we did not include it in the models. Briefly, we performed the floristic inventories in standardised plots, documenting the occurrence of all entomophilous plants (excluding families Poaceae and Cyperaceae) within a 100 m buffer of the trap-nests. Floristic inventories took place on four occasions between April and July 2018. In addition, we used the local landcover map developed by Alós Ortí et al. (2022). This local landcover map distinguishes between vegetation and build-up types (grasslands, woody vegetation, and impervious surfaces within 32 m) and can be used as an indirect proxy for food resource availability for bees and wasps as both taxa are central-place foragers and, thus, highly affected by the vegetation composition and availability within the vicinity of their nesting sites (see also, Text S5). Due to the high correlation between the proportion of woody vegetation and grasslands at 32 m, we only used the proportion of grasslands in our models.

We measured temperature at the trap-nest level and within an 800 m buffer from the trap-nests. At the trap-nest level, data loggers (1-Wire/Data Logger model DS1921G-F5, Analog Devices, Wilmington, MA, USA) recorded temperature hourly between February and June 2018 overlapping with the nesting activity of the majority of CNBW species, and we calculated the mean temperature per study site over this period (local temperature). We expect this scale of measurement to reflect the local thermal nesting conditions. However, because the studied cities followed a latitudinal gradient, we further transformed the local temperature by computing temperature anomalies for each city, by substracting the temperature measurement in a site by the average from all the sites in each city (hereinafter referred as local temperature). Within the 800 m buffer (landscape temperature), we inferred temperature using remote sensing indices of land surface temperature (LST; Text S4), from the USGS/Earth Explorer website (https://earthexplorer.usgs.gov/). We expect this scale of measurement to reflect the thermal landscape surrounding our study sites. Additionally, we calculated LST for 50, 100, 200 and 400 m buffers, but ultimately did not use these estimates due to high intercorrelations (Pearson $r > 0.8$). The distribution of values of the used predictors can be found in Figure S2.

To assess the role of biotic interactions on the studied responses, we used both top–down and bottom–up proxies. Specifically, we used the number of parasitized cells and the species richness of natural enemies as top–down proxies Moreover, as bottom–up proxies, we used the number of nests and the species richness of hosts.

Finally, we performed a principal component analysis (PCA) on the explanatory variables to define new meaningful underlying variables while reducing the dimensionality of the data set. The first PCA axis explained ca. 40% of the variation in the data, and was largely influenced by landscape level variables, that is, the amount of green areas at 100 and 800 m, and LST at 800 m (Figure S5). Thus, we referred to this first PCA axis as 'urban intensity', and used it for data visualisation, while we used the specific proxies of habitat amount, local resources, temperature and biotic interactions for modelling.

Statistical analyses

We used R version 4.0.2 (R Core Team, 2022) and RStudio v.07.1 (RStudio Team, 2020) for all analyses and statistical figures, using the packages glmmTMB v.1.1.3 (Brooks et al., 2017), MuMIn v.1.46.0 (Bartoń, 2023), evaluate v.015 (Wickham & Xie, 2022), performance v.0.9.2 (Lüdecke et al., 2021), DHARMa v.0.4.5 (Hartig, 2022) and ggplot2 v.3.3.6 (Wickham, 2016).

We used generalised linear mixed-effects models (GLMMs) to assess the influence of temperature, habitat amount and host–natural-enemy interactions (biotic interactions) on host and natural-enemy responses. For hosts, we considered the response variables species richness, abundance hatched, survival (probability that the host in a cell survived), parasitism at the cell level (probability that the host in a cell was parasitized), parasitism at the nest level (number of parasitized cells in a nest), sex ratio (probability that the host in a cell was female) and number of brood cells per nest. For natural enemies, we considered the response variables species richness and number of parasitized cells (proxy for enemy abundance). We modelled each response in hosts and natural enemies individually. One site in Antwerp (An057) was not colonised and was excluded from the analyses, leading to a sample size of 79 sites.

We ran models separately for bees and wasps and for the natural enemies of bees and wasps. We modelled species richness and abundance responses with a Poisson error structure when there was no overdispersion, and a negative binomial error structure and a log-link when we detected overdispersion. In the end, all species richness models were modelled with a Poisson error structure, and all abundance models were run with a negative binomial error structure. We built the models using city as a random term and a variable number of fixed effects (see below). For host parasitism, host survival and host sex-ratio, we used cell-level data, encoding each variable as a binary output (1 = non-parasitized/alive/female; 0 = parasitized/dead/male). We used a binomial distribution with a logit-link (Zuur et al., 2010), using a nested random term (individual nest within site within city) and a variable number of fixed effects. For the number of brood cells per nest and parasitism at the nest level, we used a negative binomial error structure, as overdispersion was detected, using a nested random term (site within city) and a variable number of fixed effects (see below).

For all variables, we ran all possible combinations of models using the function *dredge* from the MuMIN package. Then, we used the Akaike information criterion corrected for small sample sizes (AICc; Burnham et al., 2011) and selected the model with the lowest score. While we concentrate our inference on the best-supported model, to account for model uncertainty all models with ΔAICc <3 (following prior studies, Mayr et al., 2020) were also considered plausible and are presented in the Supplementary Information. Furthermore, in the additional models, we performed model averaging, computing the full-model averaged parameter estimates for each predicting variable in the candidate model set, using zero when predictors were not included in a particular model (Symonds and Moussali, 2010). We checked collinearity among the predictors using the variance inflation factor (VIF) and the Pearson correlation coefficient. We discarded variables with VIF >3 and a Pearson correlation coefficient >0.7 (Dormann et al., 2013; Zuur et al., 2010, Text S6, Figure S2). Prior to the analyses, we standardised all predictors by *z*-transformation (Schielzeth, 2010). We calculated the pseudo-R^2 following Nakagawa and Schielzeth (2013). We used diagnostic plots to estimate model performance and test for spatial autocorrelation. All *p*-values were adjusted with the Holm correction (Holm, 1979) to correct for multiple comparisons.

RESULTS

Our trap-nests sampled a total of 4392 nests of cavity-nesting bees (1998 nests) and wasps (2394 nests), containing 16,617 brood cells from 16 bee and 45 wasp species (Table S5), and 4 bee and 14 wasp morphospecies (Figure S6). Four species (*Chelostoma florisomne*, *Hylaeus communis*, *Osmia bicornis* and *Osmia cornuta*) accounted for about 80% of the total number of bee brood cells (Table S2), whereas for wasps the total number of brood cells was more evenly distributed across species. *Passaloecus eremita* was the only species representing more than 10% of the total wasp brood cells, indicating a greater dominance of certain species in cavity-nesting bees than in wasps (Table S2). All species were native, with the exception of the sphecid wasp *Isodontia mexicana* (Saussure, 1867), which was recorded in Antwerp, Paris and Zurich. Further, we identified a total of 47 natural enemy species or morphospecies in 812 nests and 1500 brood cells (Table S3 and S4), representing taxa from three insect orders (Hymenoptera, Coleoptera, Diptera) and mites (*Chaetodactylus* spp.).

Effect of urbanisation

A first exploration of the data revealed that several of the community structure metrics, performance traits and life history traits of CNBW and their natural enemies to be structured along urban intensity gradients (i.e., with increasing temperature and grey surfaces in the landscape Figure 2). Urban intensity tended to decrease the community structure (i.e., richness and abundance) of CNBW and their natural enemies, as well as reducing host survival rates and altering sex ratios to more male-biased (Figure 2). Conversely, parasitism at the cell and nest level was relatively unaffected by urban intensity (Figure 2).

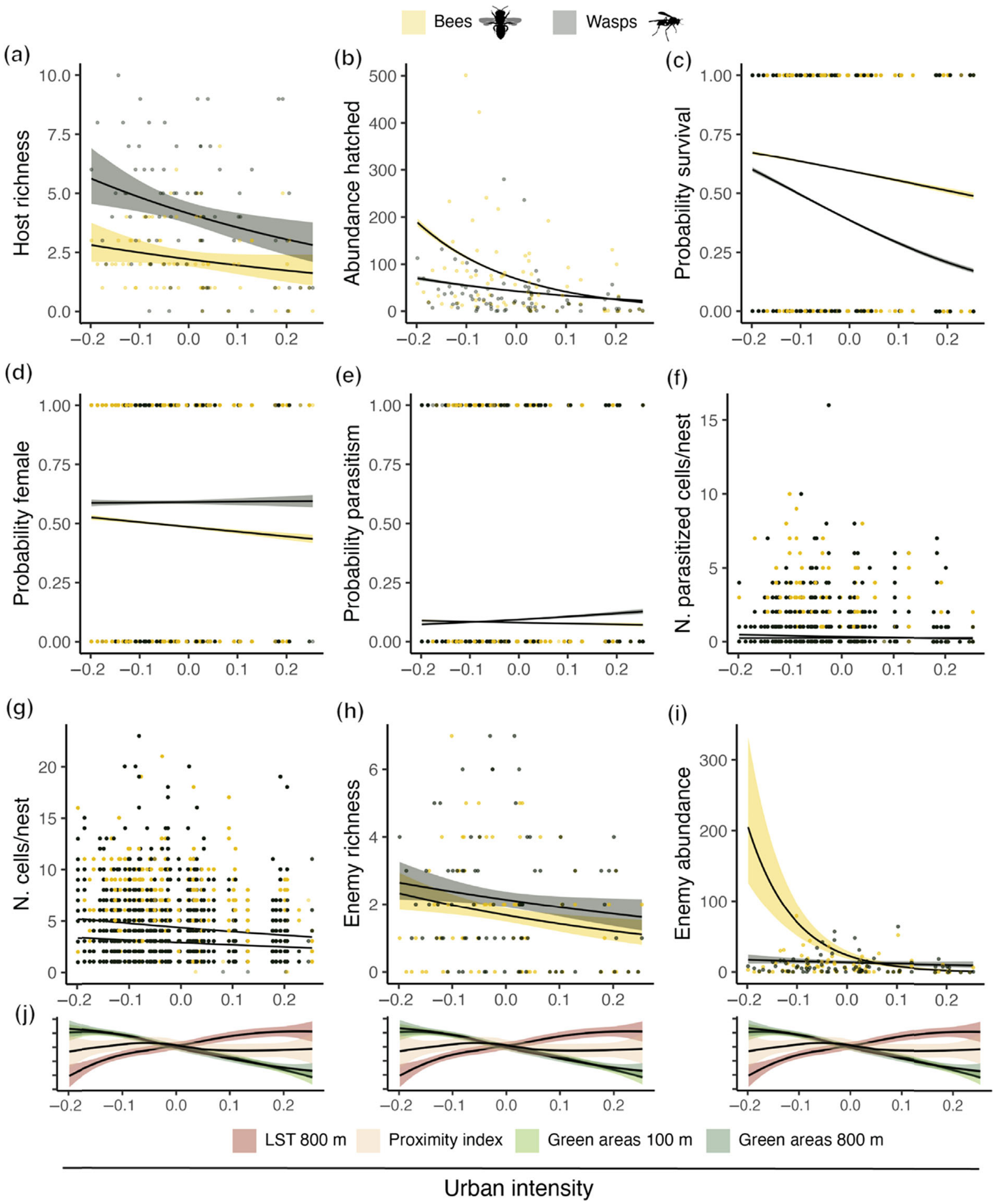

FIGURE 2 Changes in the community structure (a, b, h and i), performance traits (c, e and f) and life-history traits (d and g) of cavity-nesting bees and wasps and their natural enemies, along urban intensity gradients. Points represent the observed data and solid lines represent the predicted values obtained using the best generalised linear mixed-effects models; coloured bands indicate 95% confidence intervals. (j) Loess smoothing between urban intensity and the predictor variables depicting environmental changes at the landscape scale. Urban intensity is inferred through the first PCA axis (see Figure S5) performed on the explanatory variables, which explained ca. 40% of the variability in the data. The influence of specific drivers used to model the responses is shown in Figures 3–5. Credit bee silhouette: Melissa Broussard (Atribution 3.0 Unported).

Effect of habitat amount at the landscape scale

We found host community structure (species richness and abundance hatched) to be strongly associated with proxies for habitat amount (i.e., amount of green spaces within a given buffer from the trap-nest) for both bees and wasps (Table 1 and Figure 3). In particular, sites surrounded by larger amounts of green areas (i.e., with less urbanisation) had higher host species richness and abundance of the hatched hosts (Tables 1 and S6 and Figure 3). Moreover, habitat amount proxies had the largest estimate for host species richness, when compared with proxies for local resources or biotic interactions (Table 1). The influence of habitat amount proxies was also supported by multimodel inference, where these proxies were retained in most plausible models (Table S7 and Data S1 and S2). In addition, the amount of green areas also influenced the species richness for natural enemies of bees and wasps and the abundance for the natural enemies of wasps (Tables 1 and S6 and Figure 3), but the effect of habitat amount proxies was less clear after averaging plausible models. Specifically, park size and the amount of green areas in 800 m were retained in the vast majority of plausible models for the species richness of natural enemies of bees (Table S7 and Data S1 and S2).

Habitat amount also shaped several of the performance traits and life-history traits of hosts. Habitat amount proxies (i.e., the amount of green areas at 100 and 800 m) were the main drivers of bee and wasp survival, having the highest estimates (Tables 1 and S6 and Figure 3). However, the spatial scales were different for bees (800 m) and wasps (100 m). Particularly, the probability of survival increased with higher amounts of green areas (Figure 3).

Moreover, we found habitat amount to have the largest effect (based on the estimate, Table 1) on both parasitism at the nest level (i.e., number of parasitized cells per nest and number of cells per nest in bees), with a positive effect (Tables 1 and S6 and Figure 3). The influence of habitat amount on these performance and life-history traits was confirmed with multimodel inference, with the proxies selected in all plausible models and significant in the averaged model (Table S7 and Data S2). Strikingly, while we found habitat amount proxies to also have the largest effect on the sex ratio of wasps, we found it reduced the probability of a cell being a female (Tables 1 and S6). However, it is important to note that the effect of habitat amount was lost after averaging the other plausible models (Table S7 and Data S1 and S2).

Local resources

We found local resources to influence host and natural enemy responses. Regarding bees, plant species richness had a positive effect on bee species richness in both GLMMs (Tables 1 and S6 and Figure S7) and after model averaging (Table S6), with a similar effect size to habitat amount proxies (i.e., similar estimate, Tables 1 and S6). In contrast, we found the abundance of natural enemies of bees was negatively influenced by plant species richness (Table 1). Regarding wasps, local resource proxies had a negative effect on wasp responses. Higher plant species richness led to male-biased sex ratios and to a reduced number of cells per nest (Tables 1 and S6). However, these effects were lost after model averaging (Table S7 and Data S2). Furthermore, we found the amount of grasslands within 32 m to negatively influence wasp abundance, whereas positively boosting parasitism at the nest level (Tables 1 and S6 and Figure S7) in both GLMMs and after model averaging (Table S7 and Data S2).

Effect of temperature

Temperature was an important driver of some of the host and enemy responses (Figure 4). First, we found local temperature negatively influenced the number of cells per nest for wasps in the GLMMs (Tables 1 and S6 and Figure 4), but the effect was lost after model averaging. Second, the temperature at the landscape scale increased the number of parasitised cells per nest for bees (Tables 1 and S6 and Figure 4). Regarding natural enemies, the temperatures at the local scale reduced the abundance of the natural enemies of wasps, and at the landscape scale (LST at 800 m), increased the richness of bee natural enemies (Tables 1 and S6 and Figure 4), both for GLMMs and after model averaging (Table S6).

Effect of biotic interactions

Biotic interactions shaped host and enemy community structure both in GLMMs and after model averaging (Tables 1, S6 and S7 and Figure 5). Furthermore, proxies of biotic interactions had the largest effect on bee and wasp abundances (Table 1). Specifically, larger parasitism rate negatively impacted the abundance of both bees and wasps (Tables 1 and S6 and Figure 5). Conversely, a larger number of parasites were positively associated with host species richness and abundance (Tables 1 and S6 and Figure 5). Finally, both the abundance and the species richness of natural enemies of both bees and wasps increased with a larger number of nests per site and with a higher host species richness (Tables 1 and S6 and Figure 5).

DISCUSSION

Our results stress the importance of habitat amount, temperature, resources and biotic interactions in enhancing multitrophic biodiversity in urban ecosystems. However, the size of the effect of the different drivers varied depending on the response. Habitat amount turned to have a larger effect on several responses of CNBW than temperature, local resources and biotic interactions. For example, sites covered by larger amounts of green surfaces, and thus, with higher vegetation cover and heterogeneity, had more CNBW species and individuals, with higher survival rates. Greater vegetation cover has been found to be linked with higher abundances and richer communities of insect pollinators (Albrecht et al., 2007) and predators (Fabian et al., 2014). Moreover, our study supports the relevance of focusing on overall habitat amount, as proposed by Fahrig (Fahrig, 2013),

TABLE 1 Summary of the estimates of the proxies for temperature, habitat amount, resource availability and biotic controls from the GLMMs on the responses of cavity-nesting bees and wasps and their natural enemies.

			Temperature			Habitat amount			Local resources			Biotic interactions						
			Local temperature	LST 800	Park area	Prox. Index	Green areas 100	Green areas 800	Grasslands 32	Impervious 32	S	Par. rate	N. parasites	Host richness	Host nest	ΔAICc	R^2_m	R^2_c
Hosts	Bees	Richness					**0.234**				**0.210**					0.153	0.207	0.207
		Abundance			−0.294			0.374				**−0.659**	**0.911**			0.046	0.520	0.573
		Survival	0.223			0.234		**0.717**								0.099	0.052	0.676
		Parasitism cell														1.291	0.000	0.956
		Parasitism nest		**0.356**	0.079		−0.205	**0.409**		−0.196						1.067	0.020	0.792
		Sex ratio			−0.145											0.015	0.021	0.443
		N. cells						**0.11**		−0.054						0.426	0.038	0.452
	Wasps	Richness				−0.210	**0.341**		−0.116				**0.013**			0.754	0.449	0.548
		Abundance	−0.175				**0.422**		**−0.298**			**−0.705**	**1.004**			0.304	0.718	0.722
		Survival					**0.532**		**−0.389**	**−0.324**						0.576	0.062	0.592
		Parasitism cell		0.119						0.029						0.080	0.002	0.258
		Parasitism nest	−0.184		−0.201				**0.318**		−0.211					1.134	0.070	0.269
		Sex ratio		−0.155				**−0.203**			**−0.170**					0.214	0.015	0.217
		N. cells	**−0.072**	**−0.095**	**−0.076**						**−0.107**					0.027	0.053	0.519
Enemies	Bees	Richness		**0.338**				**0.352**						**0.473**	**0.330**	0.414	0.469	0.469
		Abundance			**−0.498**			0.258			**−0.36**				**1.79**	0.099	0.658	0.658
	Wasps	Richness						**0.197**						**0.397**	**0.141**	0.625	0.459	0.459
		Abundance	**−0.303**	0.214					0.301					**0.503**	**0.49**	1.186	0.622	0.627

Note: Plus signs indicate a positive estimate, whereas minus signs indicate a negative estimate. Estimates in bold indicate statistically significant effects ($p < 0.05$). For each model, the difference in the delta-corrected Akaike Information Criterion (AICc) between the best and the second best performing model, and the marginal R^2 and conditional R^2 are provided. Model estimates are provided in Table S5. For the results on multimodel inference, see Table S6 and Data S1 and S2.

Abbreviations: Grasslands 32, proportion of grasslands within a 32 m buffer; Host nest, Number of host nests; Host richness, host species richness; Impervious 32, proportion of impervious surfaces within a 32 m buffer; LST 800, land surface temperature within 800 m; N. parasites, number of parasitized brood cells; Par. rate, parasitism rate; Prox. index, proximity index; S, plant species richness.

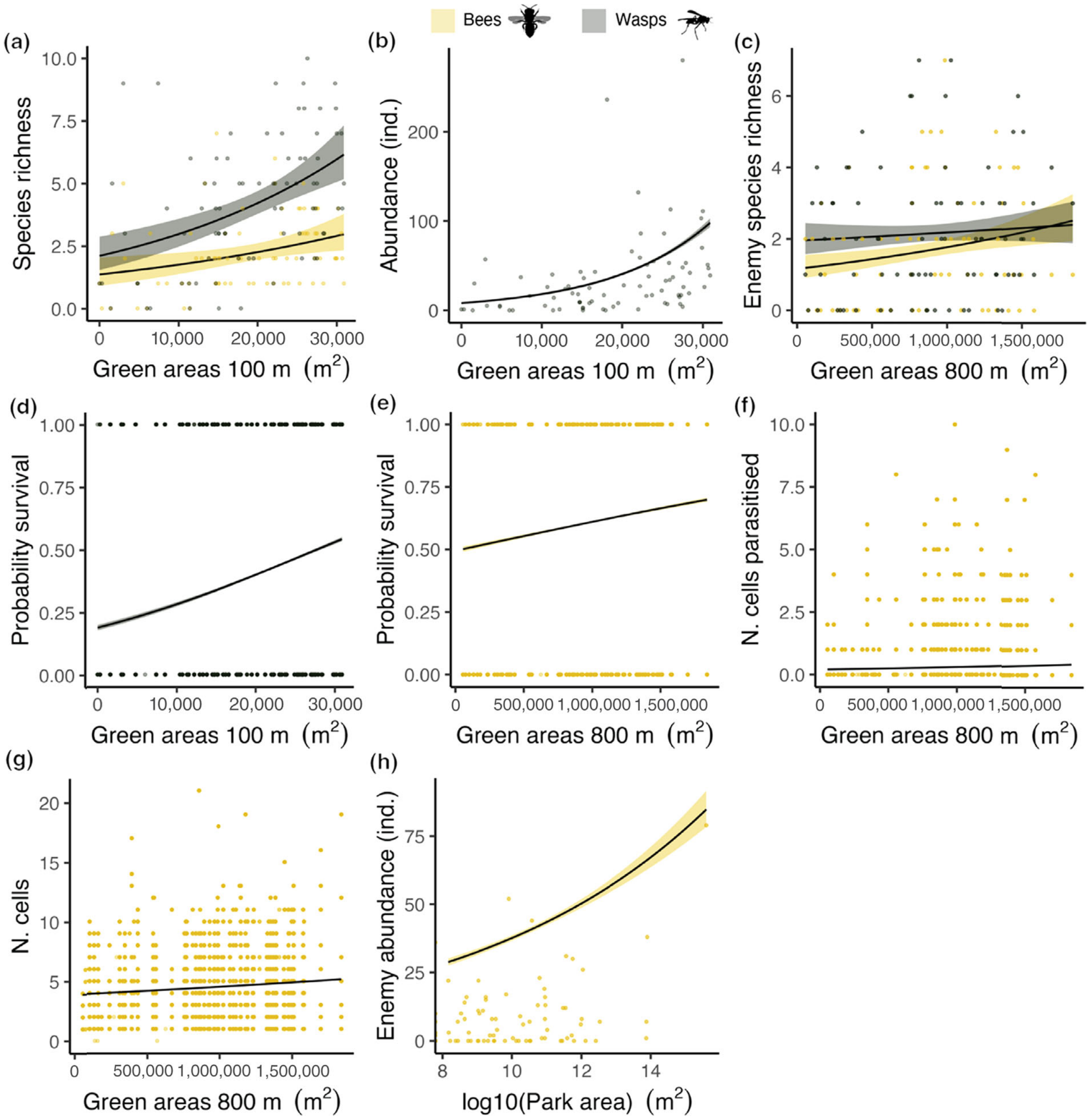

FIGURE 3 Generalised linear mixed-effects models (GLMMs) depicting the relationship between proxies of habitat amount (amount of green areas at 100 and 800 m, and park area) and (a and b) host community structure, (c and h) enemy community structure, (d–f) host performance traits, and (g) life-history traits. Note that habitat amount proxies did not affect natural enemies. Points represent the observed data and solid lines represent the predicted values obtained using the best GLMMs; coloured bands indicate 95% confidence intervals. Model results are shown in Table S6. Additional relationships can be found in Figures S8–S10. Credit bee silhouette: Melissa Broussard (Atribution 3.0 Unported).

rather than on specific, more classical metrics of patch size and isolation (e.g., the proximity index), which in our study had a much minor role in shaping the CNBW and their natural enemies. The *habitat amount hypothesis* (Fahrig, 2013) is very useful for understanding urban biodiversity patterns, as cities are characterised by a large number of relatively small, diverse, not necessarily adjacent patches (Aronson et al., 2017), explaining why certain cityscapes can still harbour relatively high diversity levels (Fournier et al., 2020; Vega & Küffer, 2021). Our research reinforces the notion that, particularly in cities with a long urban history like ours, the entirety of urban habitats—rather than just natural ones—plays a vital role in preserving diverse species assemblages across various trophic levels. This occurs through habitat supplementation and complementation, as discussed by Colding (2007). This contrasts with what has been observed in regions or cities with shorter land-use-change histories (e.g., Brazil; da Rocha-Filho et al., 2017, 2020), where the amount of natural habitat, rather than overall urban habitats, has been found to strongly shape bee and wasp diversities.

The effects of habitat amount are complex and often indirect, and can vary across trophic levels (Mayr et al., 2020; Steffan-Dewenter &

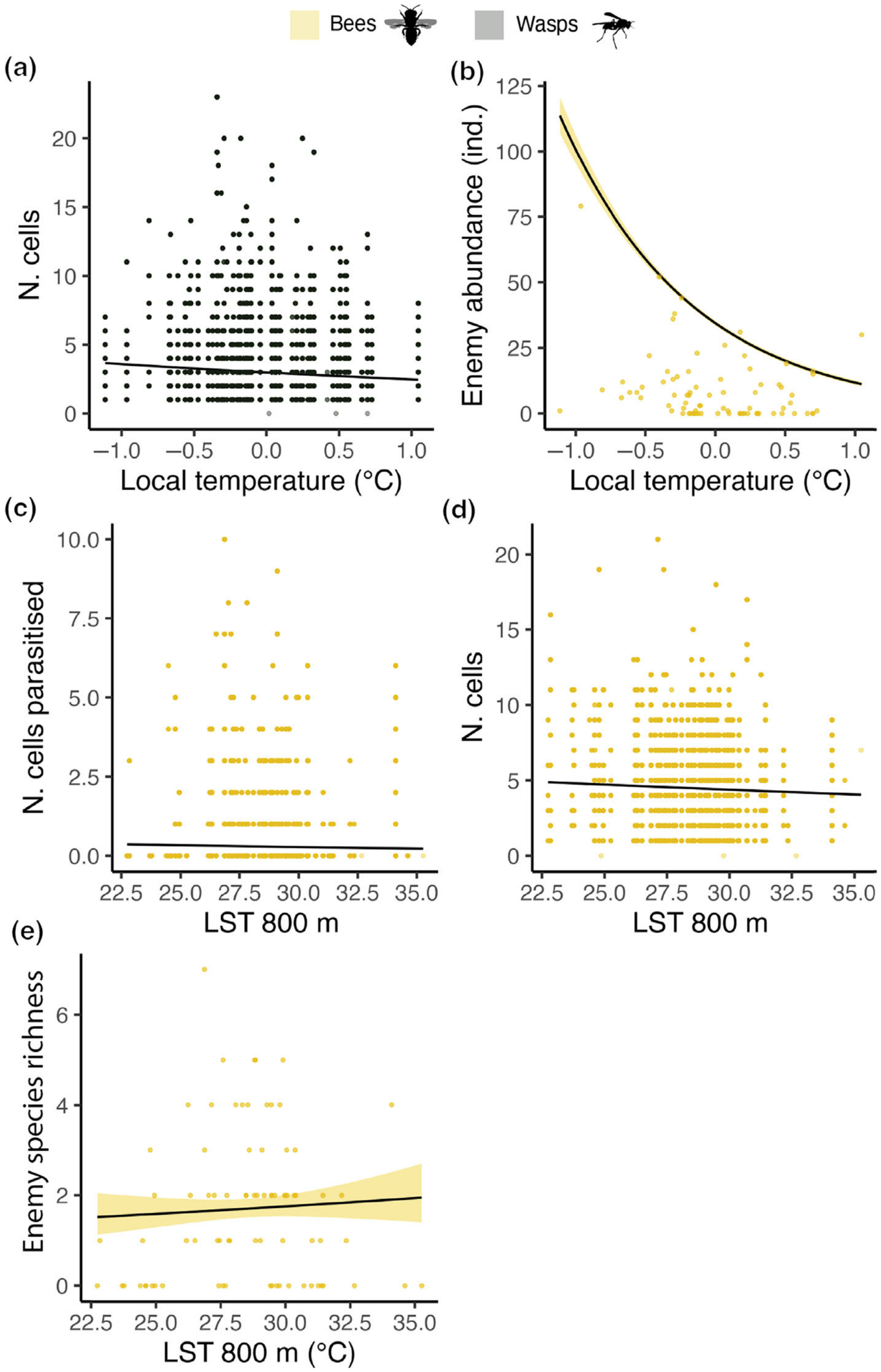

FIGURE 4 Generalised linear mixed-effects models (GLMMs) depicting the relationship between proxies of temperature (local temperature and LST at 800 m) and (a–c) host performance traits, (d and e) natural enemy community structure. Points represent the observed data and solid lines represent the predicted values obtained using the best GLMMs; coloured bands indicate 95% confidence intervals. Model results are shown in Table S6. Additional relationships can be found in Figures S8–S10. LST, land surface temperature; local temperature depicts the anomalies of the local temperature, see the Materials and Methods section. Credit bee silhouette: Melissa Broussard (Attribution 3.0 Unported).

Schiele, 2008). In our study, habitat affected the richness of bee and wasp enemies and the abundance of bee enemies. However, the magnitude of the effects was always smaller than the ones for proxies for biotic interactions with their hosts, assessed using metrics representing the availability of hosts (i.e., number of nests, host species richness) as observed in other studies (Dainese et al., 2018; Fabian et al., 2014). Nonetheless, the effects of habitat amount cannot be disregarded, as host communities depended strongly on the amount of habitat, hence indirectly affecting higher trophic levels. Indirect effects of habitat loss have been documented across food webs

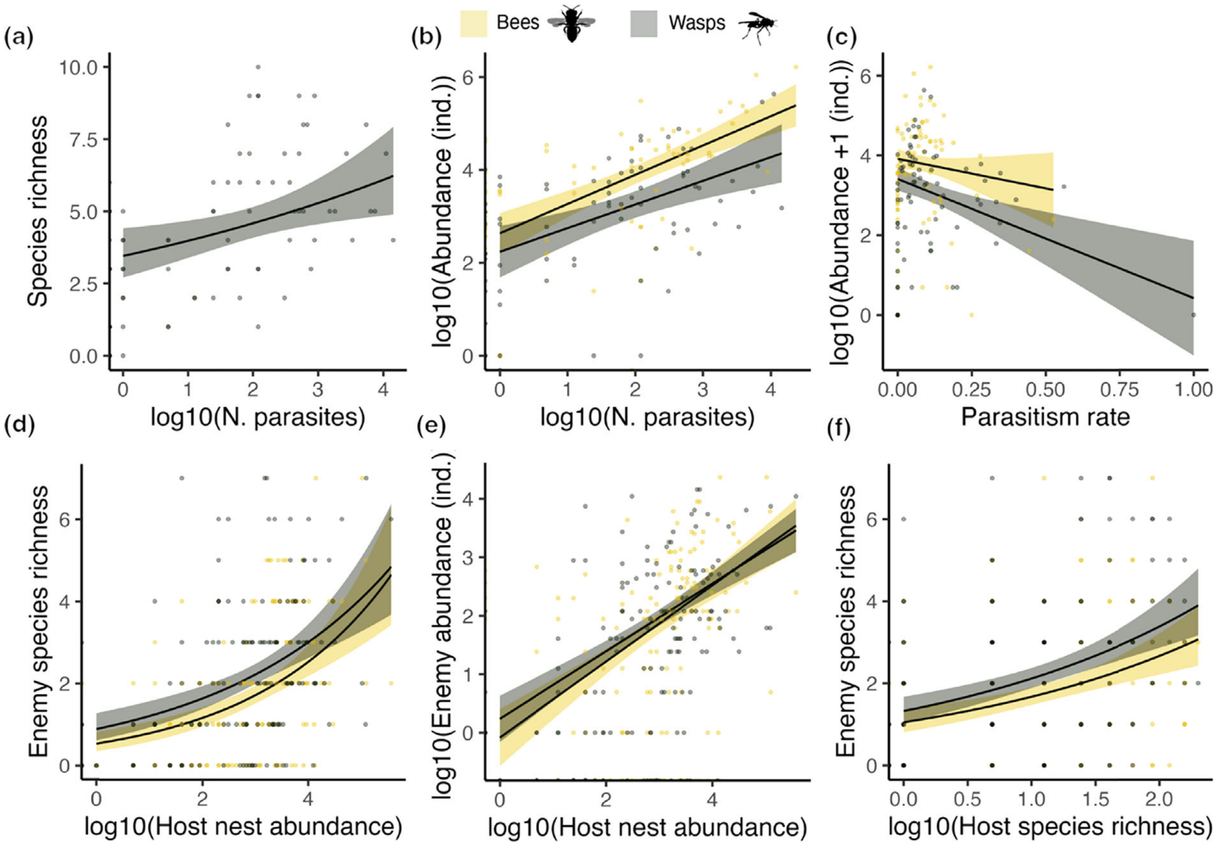

FIGURE 5 Generalised linear mixed-effects models (GLMMs) depicting the relationship between proxies of biotic interactions for hosts (a–c) and natural enemies (d–f). Points represent the observed data and solid lines represent the predicted values obtained using the best GLMMs; coloured bands indicate 95% confidence intervals. Model results are shown in Table S6. Additional relationships can be found in Figures S8–S10. Credit bee silhouette: Melissa Broussard (Attribution 3.0 Unported).

(Bascompte et al., 2003; Ryser et al., 2019), with negative effects occurring particularly for taxa from higher trophic levels (Melian & Bascompte, 2002).

Our metrics of plant diversity and vegetation composition, which we used as local resources, shaped several wasp responses and strikingly, only bee species richness. In the case of wasps, higher amounts of grasslands and plant species richness had a negative effect on wasp community structure, life history traits and performance traits. Larger amounts of grasslands imply lower amounts of woodlands (i.e., shrubs and trees). Similarly, larger plant species richness might be occurring in local landscapes with larger cover of grasslands. Cavity-nesting wasp prey on several insects to feed their larvae and often require certain compounds to build their nest (e.g., resin; Requier & Leonhardt, 2020) that are found in woodlands (Beyer et al., 2023), which might explain our results. In any case, local food resource availability has been found to have a variable effect on the structure of CNBW communities in non-urban ecosystems, with studies finding positive effects of plant species richness on CNBW (Albrecht et al., 2007; Mayr et al., 2020; Tscharntke et al., 1998) and no effects (Ebeling et al., 2012; Fabian et al., 2014). In that regard, the quantity and quality of the food resource (e.g., in terms of nutritional values) might mediate the effects of plant diversity on higher trophic levels (Lihoreau et al., 2015; Parreño et al., 2022; Raubenheimer et al., 2009; Vaudo et al., 2015).

Temperature can directly influence insect metabolism (Zuo et al., 2012) and can further regulate species richness and abundance, yet we only found evidence of temperature effects in a handful of responses and with complex and contrasting effects. Moreover, the magnitude of the effect was always smaller than habitat amount, local resources and biotic interaction drivers. Warmer environments have been found to enhance wild bee diversity in cities (e.g., in Rome; Geppert et al., 2022), while less is known about wasps. However, temperatures in cities are highly influenced by the amount and distribution of impervious surfaces, the density of buildings and the type of artificial materials. Therefore, higher temperatures can be also indicative of smaller habitat amounts and likely of lower food resource availability, which ultimately negatively impact biodiversity responses across ecological levels, as we observed. Finally, while our results provide new evidence on the effects of local temperature, there are some limitations. Particularly, we did not measure the temperature during the months when the larval or pupal stages of many species are developing, that is, from late summer to the following spring. Temperature sensitivity can vary during ontogeny (Rombough, 2003), and thermal conditions during the larval and pupal stages can therefore be critical for later CNBW development and emergence (Ostap-Chec et al., 2021; Rombough, 2003). Hence, future studies should extend temperature measurements to also include all developmental stages of CNBW.

How biotic interactions influence the properties of host communities in cities remains poorly understood. In our study, biotic interactions had the largest effect on several host community structure responses. This contrasts with findings from prior studies on cavity-nesting wasps in non-urban ecosystems, where resource availability (Steffan-Dewenter & Schiele, 2008) together with temperature (Mayr et al., 2020) were stronger drivers of CNBW diversity. In addition, our results showed that wasp richness is positively regulated by their natural enemies, which could indicate a possible top–down regulation from natural enemies for wasps through reduced competition (Levi et al., 2019). However, it is worth noticing that the effect size was much smaller than other drivers, limiting the importance of the top–down regulation of wasp diversity. Regarding bees, our finding of a lack of influence of top–down controls on bee richness should be interpreted with caution, as other top–down factors, such as predation, were not assessed and could be more important (Vidal & Murphy, 2018). It is also possible that habitat, and subsequently resource availability, represent a greater limitation than parasitism pressure on bee hosts. In this regard, we only find evidence of the effects of habitat amount and local resources on bee species richness, which had a similar estimate. For example, our results agree with a study on populations of the cavity-nesting bee *Osmia bicornis* in agricultural areas in Germany showed that resource availability was the primary driver, rather than regulation from natural enemies (Steffan-Dewenter & Schiele, 2008).

Biotic interactions exerted also the largest pressure in the species richness and abundance of natural enemies, with a direct density-dependence on their hosts. Previous studies have also reported direct density-dependence (Krewenka et al., 2011; Mayr et al., 2020). Thus, this suggests that the factors thought to promote inversely density-dependent parasitism, like limited handling time by natural enemies or improved defence and guarding capacities of aggregated hosts (Rosenheim, 1990), do not apply to the organisms studied. Moreover, our findings underpin the dependence of natural enemies on their resources (hosts), supporting the idea that higher trophic levels are severely limited by their food resources (Mayr et al., 2020). In that regard, natural enemies are vulnerable to the decline in host availability and to the drivers responsible for these declines, such as habitat reduction, loss of key resources and the spread of novel pathogens or diseases, which are well-known drivers of insect decline and are becoming more severe worldwide (Wagner et al., 2021).

Finally, our study opens some questions regarding other dimensions and scales of diversity that could not be developed here. First, regarding scale, studying how community restructuring (i.e., beta diversity metrics) occurs along urban socio-ecological gradients could help assess the degree of filtering of the communities of hosts and enemies across the studied cities, as shown in other studies (Fournier et al., 2020). Second, because biodiversity conservation and management requires information on all its complexity (Villalta et al., 2022), adding additional dimensions, such as functional and phylogenetic diversity, could provide complementary information on how diversity is structured within and among cities.

CONCLUSIONS

Our study shows how urban intensity shapes multitrophic diversity through different drivers. Particularly, our study highlights the importance of habitat amount and temperature in urban food webs, through the direct effects on hosts responses and the subsequent consequences on their natural enemies. Ongoing climate change and its interaction with the urban fabric (Müller et al., 2014), together with urban intensification scenarios in the face of a growing urban population (Liu et al., 2020), therefore represent two main challenges for the survival of urban CNBW communities, as well as the interacting species in higher or lower trophic levels. Ongoing adaptation plans to reduce overheating through targeted greening and the expansion of novel and restored habitats represent an opportunity to maintain urban biodiversity (Butt et al., 2018), including the studied food webs. Overall, the study of multitrophic diversity improves our understanding of the contributions of different drivers to multiple dimensions of biodiversity, which in turn helps us to monitor ecological conditions and anticipate future challenges for biodiversity conservation.

AUTHOR CONTRIBUTIONS

Joan Casanelles-Abella: Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; data curation; resources. **Loïc Pellissier:** Supervision; writing – review and editing; conceptualization. **Cristiana Aleixo:** Methodology; software; data curation; resources; writing – review and editing; writing – original draft. **Marta Alós Orti:** Conceptualization; data curation; resources; methodology; software; writing – review and editing; writing – original draft. **François Chiron:** Writing – review and editing; conceptualization; methodology; funding acquisition. **Nicolas Deguines:** Software; writing – review and editing; visualization. **Lauri Laanisto:** Funding acquisition; conceptualization; methodology; writing – review and editing. **Łukasz Myczko:** Methodology; writing – review and editing. **Stefanie Müller:** Resources; methodology; writing – review and editing. **Ülo Niinemets:** Funding acquisition; conceptualization; writing – review and editing. **Pedro Pinho:** Conceptualization; resources; methodology; writing – review and editing; investigation. **Roeland Samson:** Funding acquisition; project administration; writing – review and editing; conceptualization. **Piotr Tryjanowski:** Conceptualization; funding acquisition; methodology; writing – review and editing. **Lucía Villarroya-Villalba:** Methodology; resources; writing – review and editing. **Marco Moretti:** Supervision; writing – review and editing; writing – original draft; conceptualization; funding acquisition; methodology; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ENVIDAT at https://www.doi.org/10.16904/envidat.460.

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REFERENCES

Albrecht, M., Duelli, P., Schmid, B. & Müller, C.B. (2007) Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, 76, 1015–1025.

Alós Ortí, M., Casanelles-Abella, J., Chiron, F., Deguines, N., Hallikma, T., Jaksi, P. et al. (2022) Negative relationship between woody species density and size of urban green spaces in seven European cities. *Urban Forestry & Urban Greening*, 74, 127650.

Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S. et al. (2017) Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15, 189–196.

Attwood, S.J., Maron, M., House, A.P.N. & Zammit, C. (2008) Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography*, 17, 585–599.

Banaszak-Cibicka, W. (2014) Are urban areas suitable for thermophilic and xerothermic bee species (Hymenoptera: Apoidea: Apiformes)? *Apidologie*, 45, 145–155.

Bartoń, K. (2023). MuMIn: Multi-Model Inference. R package. https://CRAN.R-project.org/package=MuMIn

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 9383–9387.

Beyer, N., Kulow, J. & Dauber, J. (2023) The contrasting response of cavity-nesting bees, wasps and their natural enemies to biodiversity conservation measures. *Insect Conservation and Diversity.*, 16, 468–482.

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Burks, J.M. & Philpott, S.M. (2017) Local and landscape drivers of parasitoid abundance, richness, and composition in urban gardens. *Environmental Entomology*, 46, 201–209.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.

Butt, N., Shanahan, D.F., Shumway, N., Bekessy, S.A., Fuller, R.A., Watson, J.E.M.M. et al. (2018) Opportunities for biodiversity conservation as cities adapt to climate change. *Geo: Geography and Environment*, 5, e00052.

Casanelles-Abella, J., Frey, D., Müller, S., Aleixo, C., Alós Ortí, M., Deguines, N. et al. (2021) A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. *Data in Brief*, 37, 107243.

Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., Alós Orti, M., Chiron, F. et al. (2022) How wild bees find a way in European cities: pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. *Journal of Applied Ecology*, 59, 457–470.

Classen-Rodríguez, L., Tinghitella, R. & Fowler-Finn, K. (2021) Anthropogenic noise affects insect and arachnid behavior, thus changing interactions within and between species. *Current Opinion in Insect Science*, 47, 142–153.

Colding, J. (2007) 'Ecological land-use complementation' for building resilience in urban ecosystems. *Landscape and Urban Planning*, 81, 46–55.

da Rocha-Filho, L.C., Montagnana, P.C., Boscolo, D. & Garófalo, C.A. (2020) Green patches among a grey patchwork: the importance of preserving natural habitats to harbour cavity-nesting bees and wasps (Hymenoptera) and their natural enemies in urban areas. *Biodiversity and Conservation*, 29, 2487–2514.

da Rocha-Filho, L.C., Rabelo, L.S., Augusto, S.C. & Garófalo, C.A. (2017) Cavity-nesting bees and wasps (Hymenoptera: Aculeata) in a semi-deciduous Atlantic forest fragment immersed in a matrix of agricultural land. *Journal of Insect Conservation*, 21, 727–736.

Dainese, M., Riedinger, V., Holzschuh, A., Kleijn, D., Scheper, J. & Steffan-Dewenter, I. (2018) Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. *Journal of Applied Ecology*, 55, 195–204.

Dale, A.G. & Frank, S.D. (2018) Urban plants and climate drive unique arthropod interactions with unpredictable consequences. *Current Opinion in Insect Science*, 29, 27–33.

Diamond, S. E., Bellino, G., & Deme, G. G. (2023). Urban insect bioarks of the 21st century. *Current Opinion in Insect Science*, 57, 101028. https://doi.org/10.1016/j.cois.2023.101028

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G. et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

EEA. (2012). Urban Atlas. Retrieved from http://land.copernicus.eu/local/urban-atlas/urban-atlas-2012

Ebeling, A., Klein, A.M., Weisser, W.W. & Tscharntke, T. (2012) Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia*, 169, 453–465.

Fabian, Y., Sandau, N., Bruggisser, O.T., Aebi, A., Kehrli, P., Rohr, R.P. et al. (2014) Plant diversity in a nutshell: testing for small-scale effects on trap nesting wild bees and wasps. *Ecosphere*, 5, 1–18.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663.

Fitch, G., Glaum, P., Simao, M.C., Vaidya, C., Matthijs, J., Iuliano, B. et al. (2019) Changes in adult sex ratio in wild bee communities are linked to urbanization. *Scientific Reports*, 9, 1–10.

Fournier, B., Frey, D. & Moretti, M. (2020) The origin of urban communities: from the regional species pool to community assemblages in city. *Journal of Biogeography*, 47, 615–629.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71, 757–764.

Geppert, C., Cappellari, A., Corcos, D., Caruso, V., Cerretti, P., Mei, M. et al. (2022) Temperature and not landscape composition shapes wild bee communities in an urban environment. *Insect Conservation and Diversity*, 16, 1–12.

Gustafson, E.J. & Parker, G.R. (1994) Using an index of habitat patch proximity for landscape design. *Landscape and Urban Planning*, 29, 117–130.

Hamann, E., Blevins, C., Franks, S. J., Jameel, M. I., & Anderson, J. T. (2020). Climate change alters plant–herbivore interactions. *New Phytologist*, 229(4), 1894–1910. https://doi.org/10.1111/nph.17036

Hartig, F. (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package: https://CRAN.-R-project.org/package=DHARMA

Hassell, M.P. (1982) Patterns of parasitism by insect parasitoids in patchy environments. *Ecological Entomology*, 7, 365–377.

Hassell, M.P. (2000) Host-parasitoid population dynamics*. *Journal of Animal Ecology*, 69, 543–566.

Holm, S. (1979) A simple sequentially rejective multiple test procedure a simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.

Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, 160, 1719–1727.

Kendall, L.K., Mola, J.M., Portman, Z.M., Cariveau, D.P., Smith, H.G. & Bartomeus, I. (2022) The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology*, 103, e3809.

Krewenka, K.M., Holzschuh, A., Tscharntke, T. & Dormann, C.F. (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation*, 144, 1816–1825.

Levi, T., Barfield, M., Barrantes, S., Sullivan, C., Holt, R.D. & Terborgh, J. (2019) Tropical forests can maintain hyperdiversity because of enemies. *Proceedings of the National Academy of Sciences*, 116, 581–586.

Lihoreau, M., Buhl, J., Charleston, M.A., Sword, G.A., Raubenheimer, D. & Simpson, S.J. (2015) Nutritional ecology beyond the individual: a conceptual framework for integrating nutrition and social interactions. *Ecology Letters*, 18, 273–286.

Liu, X., Huang, Y., Xu, X., Li, X., Li, X., Ciais, P. et al. (2020) High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. *Nature Sustainability*, 3, 564–570.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. (2021) Performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139.

Mayr, A.V., Peters, M.K., Eardley, C.D., Renner, M.E., Röder, J. & Steffan-Dewenter, I. (2020) Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. *Journal of Biogeography*, 47, 854–865.

Melian, C.J. & Bascompte, J. (2002) Food web structure and habitat loss. *Ecology Letters*, 5, 37–46.

Müller, N., Kuttler, W. & Barlag, A.B. (2014) Counteracting urban climate change: adaptation measures and their effect on thermal comfort. *Theoretical and Applied Climatology*, 115, 243–257.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.

Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D. & Ascher, J.S. (2021) Global patterns and drivers of bee distribution. *Current Biology*, 31, 451–458.e4.

Ostap-Chec, M., Kierat, J., Kuszewska, K. & Woyciechowski, M. (2021) Red mason bee (Osmia bicornis) thermal preferences for nest sites and their effects on offspring survival. *Apidologie*, 52, 707–719.

Papanikolaou, A.D., Kühn, I., Frenzel, M. & Schweiger, O. (2017) Semi-natural habitats mitigate the effects of temperature rise on wild bees. *Journal of Applied Ecology*, 54, 527–536.

Parreño, M.A., Alaux, C., Brunet, J.-L., Buydens, L., Filipiak, M., Henry, M. et al. (2022) Critical links between biodiversity and health in wild bee conservation. *Trends in Ecology & Evolution*, 37, 309–321.

R Core Team. (2022) *R: a language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria.

Raubenheimer, D., Simpson, S.J. & Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, 23, 4–16.

Requier, F. & Leonhardt, S.D. (2020) Beyond flowers: including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, 24, 5–16.

Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17, 462–468.

Rombough, P. (2003) Modelling developmental time and temperature. *Nature*, 424, 268–269.

Rosenberg, D.K. & McKelvey, K.S. (1999) Estimation of habitat selection for central-place foraging animals. *The Journal of Wildlife Management*, 63, 1028.

Rosenheim, J.A. (1990) Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Annals of the Entomological Society of America*, 83, 277–286.

RStudio Team. (2020) *R studio: integrated development for R*. RStudio Inc, Boston, MA. Available at www.Rstudio.com

Ryser, R., Häussler, J., Stark, M., Brose, U., Rall, B.C. & Guill, C. (2019) The biggest losers: habitat isolation deconstructs complex food webs from top to bottom. *Proceedings of the Royal Society B: Biological Sciences*, 286, 286.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.

Srivastava, D.S. & Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-Hole communities. *The American Naturalist*, 152, 510–529.

Staab, M., Pufal, G., Tscharntke, T. & Klein, A.-M.M. (2018) Trap nests for bees and wasps to analyse trophic interactions in changing environments—a systematic overview and user guide. *Methods in Ecology and Evolution*, 9, 2226–2239.

Steffan-Dewenter, I. & Schiele, S. (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, 89, 1375–1387.

Symonds, M. R. E., & Moussalli, A. (2010). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Theodorou, P. (2022) The effects of urbanisation on ecological interactions. *Current Opinion in Insect Science*, 52, 100922.

Trøjelsgaard, K. & Olesen, J.M. (2013) Macroecology of pollination networks. *Global Ecology and Biogeography*, 22, 149–162.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, 35, 708–719.

Uchida, K., Blakey, R.V., Burger, J.R., Cooper, D.S., Niesner, C.A. & Blumstein, D.T. (2021) Urban biodiversity and the importance of scale. *Trends in Ecology & Evolution*, 36, 123–131.

Vaudo, A.D., Tooker, J.F., Grozinger, C.M. & Patch, H.M. (2015) Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, 10, 133–141.

Vega, K.A. & Küffer, C. (2021) Promoting wildflower biodiversity in dense and green cities: the important role of small vegetation patches. *Urban Forestry & Urban Greening*, 62, 127165.

Venter, Z.S. & Sydenham, M.A.K. (2021) Continental-scale land cover mapping at 10 m resolution over Europe (ELC10). *Remote Sensing*, 13, 2301.

Vidal, M.C. & Murphy, S.M. (2018) Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. *Ecology Letters*, 21, 138–150.

Villalta, I., Bouget, C., Lopez-Vaamonde, C. & Baude, M. (2022) Phylogenetic, functional and taxonomic responses of wild bee communities along urbanisation gradients. *Science of the Total Environment*, 832, 154926.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007) Let the concept of trait be functional! *Oikos*, 116, 882–892.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118, 1–10.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.

Wickham, H. & Xie, Y. (2022) evaluate: parsing and evaluation tools that provide more details than the default. R package: https://CRAN.R-project.org/package=evaluate

Zumwald, M., Knüsel, B., Bresch, D.N. & Knutti, R. (2021) Mapping urban temperature using crowd-sensing data and machine learning. *Urban Climate*, 35, 100739.

Zuo, W., Moses, M.E., West, G.B., Hou, C. & Brown, J.H. (2012) A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1840–1846.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

SUPPORTING INFORMATION

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

Data S1. Retained models multi-model inference.

Data S2. Results of model averaging.

Data S3. Supporting Information.

Text S1. Site selection.

Text S2. Details on the studied organisms.

Text S3. Insect sampling and identification.

Text S4. Details on remote sensing metrics.

Text S5. Details on local landcover map.

Text S6. Discarded variables.

Table S1. Study sites.

Table S2. List of cavity-nesting bee and wasp species.

Table S3. List of natural enemy species.

Table S4. Shared enemies.

Table S5. Community composition.

Table S6. Results GLMM.

Table S7. Variable importance multimodel inference.

Figure S1. Map study sites.

Figure S2. Predictors across cities.

Figure S3. Correlations between predictors.

Figure S4. Relationship between NDVI, UI, amount of green surfaces and amount of gray surfaces.

Figure S5. Principal Component Analyses.

Figure S6. Community composition.

Figure S7. Results biotic interactions.

Figure S8. Species richness and abundance of hosts plotted against predictors.

Figure S9. Species richness and abundance of natural enemies plotted against predictors.

Figure S10. Performance traits and life-history traits plotted against predictors.

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