

## ORIGINAL ARTICLE

## The Ecology and Conservation of Urban Insects

Insect Conservation  
and Diversity

# Large uncertainty in trait responses across insects among overall declines in a subtropical city

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Research**Editor/Associate Editor:** Catherine Matilda  
(Tilly) Collins**Abstract**

1. Continued and rapid development of urban environments presents many challenges to organisms living in and around cities. Insects are among the most abundant and diverse class of animals but surprisingly little is known about how most species respond to urbanisation across clades with varying life histories, especially in the subtropics and tropics.
2. In this study, we sample insect abundance and diversity across an urbanisation gradient in a subtropical region to assess the impact of urbanisation on 43 phototactic species of insects representing eight distinct orders. We also attempted to determine which life history traits best explain how species respond to urbanisation.
3. We predicted an overall loss of abundance and richness with increasing urbanisation, with smaller, generalist species being the least impacted. We also predicted that species with above ground larval habitats would be less affected by urbanisation.
4. Overall, urban development decreased both species richness and the abundance of individuals per order, with abundance being most reduced for Hymenoptera but least reduced for Coleoptera. At a species-specific level, urban development negatively impacted most but not all species, although uncertainty around these estimates was high. We did not identify key traits that determined a species' sensitivity to urbanisation.
5. Our results showcase that urbanisation may impact ecosystem function given overall reduction in the number of individual insects per order, despite wide variability in species-specific responses. Our study also emphasises the importance of species selection when designing studies that examine responses of multiple taxa across an environmental gradient.

**KEYWORDS**

Bayesian modelling, insect declines, life history traits, uncertainty, urban ecology

**INTRODUCTION**

Growing human populations represent an increasing threat to biodiversity and ecosystem functions as cities expand and become more numerous (Simkin et al., 2022). Urbanisation impacts biodiversity by disrupting a variety of ecological processes, including increasing levels

of light pollution, reducing habitat quality, and warming temperatures compared with surrounding natural areas due to the urban heat island effect (Grimm et al., 2008; McDonnell & Hahs, 2015; Simkin et al., 2022). The ecological impact of urbanisation may differ depending on the spatial scale at which stressors are examined (Clergeau et al., 2006), and the level of disruption caused by each of these

processes typically scales with the level of urbanisation, ranging from minor impacts in more rural areas to strong effects in major cities (Grimm et al., 2008; McDonnell & Hahs, 2015). Cities, in particular, have developed and expanded rapidly since the industrial revolution; in 2018, more than 55% of the world's population resided in cities, and that number is projected to increase to two-thirds by 2050 (Baeumler et al., 2021). Urbanisation is, therefore, an ecological stressor that has rapidly emerged even when considering Anthropocene timescales (Faeth et al., 2011), and the impact this has on the environment and biodiversity is still being understood.

Urbanisation has been proposed as one of the many interacting stressors contributing to reductions in insect abundance, biomass and richness (Wagner et al., 2021), a phenomenon that has been widely documented in recent years (Montgomery et al., 2020; Wagner et al., 2021). Given the critical role insects play in ecosystems, for example, as pollinators, decomposers and as a food source (Schowalter et al., 2018), it is imperative to understand how urbanisation impacts insect population and community dynamics. Although most studies have found declines in insect richness and abundance in response to urbanisation (Fenoglio et al., 2020; Piano et al., 2020; Vaz et al., 2023), wide variation has been reported, and certain species and clades appear to be able to exploit urban environments (e.g., Baldock et al., 2015; Chatelain et al., 2023; Raupp et al., 2010). For example, Theodorou et al. (2020) found that Hymenoptera as a whole and particularly the Anthophila group of bees had higher richness within urban spaces compared with rural areas. Identifying the factors contributing to these varied responses is essential to informing urban planners tasked with designing cities that can support insects and their ecosystem services.

The subtropics and tropics are estimated to host the greatest diversity of insects (Stork, 2018) and are also facing the most rapid levels of urban development (United Nations, 2018). Although important contributions have documented the effect of urbanisation on tropical insect diversity (e.g., Gaona et al., 2021; Iserhard et al., 2019; Rocha-Ortega & Castaño-Meneses, 2015), our knowledge of how urbanisation is impacting insect diversity is less complete in low-latitude regions (Theodorou, 2022; Wenzel et al., 2020). The magnitude of urban stressors may differ in these regions compared with temperate areas. For example, the urban heat island effect, a phenomenon where urban areas with developed structured and limited green spaces become islands of higher temperatures relative to surrounding areas, is amplified in coastal, tropical and rapidly growing cities, possibly making urban areas even less hospitable to many insects in low-latitude areas (Diamond et al., 2023; Wenzel et al., 2020).

Previous work indicates that urban stressors likely interact with life-history traits to determine a species' vulnerability to urbanisation (Hahs et al., 2023). However, studies examining how traits condition the impacts of urbanisation on insect species and communities are heavily biased towards a few insect groups in temperate locations (Fenoglio et al., 2020). Insects in these regions are adapted to challenging seasonal conditions, which is not the case for lower latitude populations. Still, these studies have been important in identifying a few key traits, that is, body size, mobility, thermophily and diet

generalism that are important in determining the success of an insect species in an urban environment (Callaghan et al., 2021; Merckx, Kaiser, & Van Dyck, 2018; Piano et al., 2017). The diet type of insects may also impact how species respond to urbanisation. For instance, urban beetle species that rely on decaying organic materials tend to show reduced species richness, likely due to the active removal of decaying organic material from many urban areas (Magura et al., 2013). Additionally, species that spend part of their life stage underground may be more vulnerable to urbanisation, since urban soils are often highly compacted and topsoil disturbance is common (Schmitt & Burghardt, 2021). Concerted efforts are needed to expand the geographic focus of studies to the subtropics and tropics where different traits may emerge as important given the different physiological demands placed on insects in these environments.

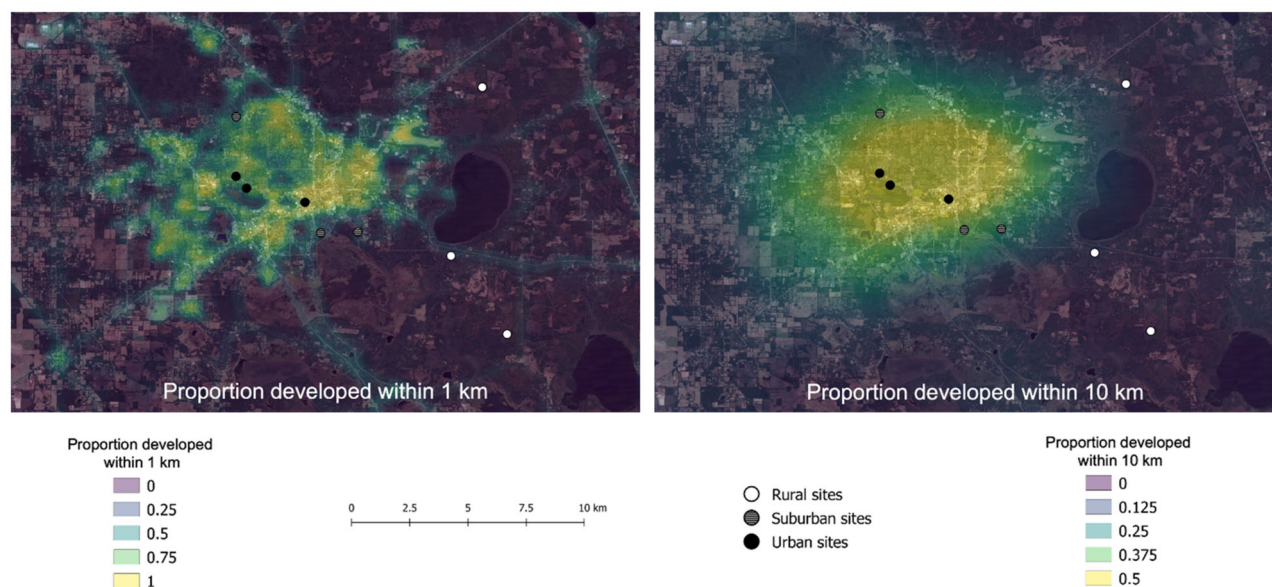
Here, we aim to explore a set of urbanisation hypotheses by quantifying abundance patterns in a unique dataset of nocturnal insects that were sampled along a local urbanisation gradient in a subtropical environment. Specifically, we examine the impact of urban development on species richness and abundance across a broad suite of nocturnally-active insect species. We also examine how life history traits predict species-specific responses to urbanisation. We analyse these trends across 43 species representing eight orders and diverse life history traits, allowing us to examine species and order-specific responses of key insect groups in an understudied region.

We predict a general reduction in species richness and a reduction of abundance across all orders with increasing urbanisation. Additionally, we expect that smaller species will be the least impacted, as they have lower metabolic costs that should be less sensitive to urbanisation-driven warming (Merckx, Souffreau, et al., 2018). Finally, we predict that species whose larvae develop above ground will be less sensitive to urbanisation related-changes, and especially increases in temperature directly, as other work has shown that the urban heat island effect may be amplified in below-ground environments, where larvae are exposed to greater environmental stressors (Menberg et al., 2013).

## METHODS

### Study sites

This study was carried out at nine study sites sampled extensively across the year, along an urbanisation gradient in Alachua County, FL, USA (Figure 1). All nine sites were located within forested conservation areas. We selected sites by first calculating the proportion of pixels within a 1- and 10-km neighbourhood that were classified as developed (including developed open space, low-intensity, medium-intensity and high-intensity classifications) based on the 2016 National Land Cover Database (NLCD) (Homer et al., 2020). We delineated three categories—urban, suburban and rural—and selected three sites within each category. Urban sites were those that had at least 60% of the area within 1 km, and 50% of the area within 10 km, defined as developed based on NLCD. Suburban sites had to have



**FIGURE 1** Location of study sites in relation to the urbanisation density of Alachua County, FL. The proportion of developed land cover within a 10-km buffer is represented by a colour gradient.

between 10% and 50% of the area within 1 km, and between 25% and 50% within 10 km, defined as developed. Rural sites needed to have less than 10% of the area around the site developed at both spatial scales. These delineations were determined by overlaying urban development layers on satellite imagery of the county, which showed a clear urban development decay (Figure 1).

## Species sampling and selection

Our study utilised adult insect by-catch collected at traps intended to target moths (see Belitz et al., 2023 for details of moth study). These insects were collected at a single light trap per site that was built following the blueprint of White et al. (2016). These are LED funnel traps that consist of a plastic funnel, plastic collecting container, plastic vanes and two strips of low-wavelength (395–405 nm) LED blacklights that are powered by a 12-volt battery. Sampling was conducted weekly over the course of 51 weeks (10 March 2019–February 28 2020). Each week, each light trap at all nine sites was connected to a battery, and the collecting containers were replenished with 70% isopropyl alcohol. With the battery connected, the LED blacklights would automatically turn on via a light sensor at dusk and would turn off again at dawn. Insects that were attracted to the light trap (i.e., phototactic insects) were collected from the container the following day and specimens were transferred from isopropyl into 50 mL conical tubes with 70% EtoH until they were later sorted into Lepidoptera and non-Lepidoptera species. These non-Lepidoptera species, termed by-catch, were used in this study.

Ideally, a study looking to examine community-level effects of an environmental stressor and estimate trait-level responses would be able to identify and count all insects captured. However, such an effort would be extremely costly in time, labour and expertise,

especially in species rich subtropical locales. Instead, we opted for an approach that would be tractable given monetary and logistical constraints, while still allowing us to examine urbanisation-trait interactions on a species-specific basis for a broad assembly of light-attracted insects. To assemble a final set of species examined in this study, we first constructed a list of taxa that were repeatedly being sampled when sorting specimens into Lepidoptera versus by-catch jars. We also utilised iNaturalist records (<https://www.inaturalist.org/>) in Alachua County, FL, as of May 2021, to determine additional species that are likely to be found at light traps in large enough quantities to facilitate analysis. From this list of possible species that might be found in such traps, we filtered down to those that can be identified without dissection and without the use of anything more than a hand-held magnifier. Combining these two filters left us with an initial species list representing 74 possible species across eight orders (7 Blattodea, 30 Coleoptera, 6 Diptera, 21 Hemiptera, 2 Hymenoptera, 2 Megaloptera, 3 Neuroptera and 3 Orthoptera), representing a variety of life history traits. After identifying and sorting the by-catch, and removing species never captured, our list consisted of 43 species (2 Blattodea, 19 Coleoptera, 2 Diptera, 11 Hemiptera, 2 Hymenoptera, 2 Megaloptera, 2 Neuroptera and 3 Orthoptera) for our analysis. We recognise the methods used to create our species set do not represent the full phototactic insect community and may be biased towards urban-exploiting species, and thus we view our results as a conservative estimate of the effect of urbanisation on insect abundance.

## Urbanisation variables

We used urban development at a 1-km scale as our urbanisation predictor variable in the analyses described below. Although the exact scale of urbanisation effect is not known for subtropical insect

communities and likely differs across species based on life history traits (Jackson & Fahrig, 2012), we choose to use urban development within 1 km as our urbanisation variable due to the proximity of sampling sites, and because urbanisation at this scale is known to strongly influence a wide array of insect orders and functional traits (González-Céspedes et al., 2021). Developed area surrounding the site at a 30-m resolution was retrieved from the National Land Cover Database (Homer et al., 2020), and we included areas classified as developed open space, low-intensity, medium-intensity and high-intensity developments as 'developed areas'.

## Trait data

We collected trait data for the 43 identified study species from both literature and web sources (<https://github.com/mbelitz/InsectUrbanization/blob/main/Data/TraitData.csv> for list of species and traits; Table S1.1). Specifically, we relied on BugGuide ([www.bugguide.net](http://www.bugguide.net)) and species profiles written and published online by the University of Florida Department of Entomology & Nematology, University of Wisconsin Milwaukee Field Station, and the Mississippi State University Extension. We assembled traits that were predicted to influence how species respond to urbanisation, which included (1) adult body size, (2) larval diet, (3) larval habitat and (4) temperature niche. Larval diet was categorised as herbivore, omnivore or carnivore. Larval habitat was divided into the categories of above ground, below ground, plant and freshwater. Body size was the mean of total length measurements available for each species, and for species in the family, Formicidae was measured for queens. Temperature niche values were calculated by first downloading occurrence records for each species from the Global Biodiversity Information Facility (GBIF, 2022), since temperature niche data are not available for most subtropical insect species. We then mapped these occurrence records and removed records that fell outside the known range of the species. Using these cleaned occurrence records, we extracted an annual temperature value (using the BIO1 bioclimatic variable available via WorldClim at a 30 s resolution; Fick & Hijmans, 2017) for each occurrence point. Temperature niche was the mean value among all annual temperature values. Spatial biases in insect GBIF data are well documented (Rocha-Ortega et al., 2021), with insects being better documented in North America, Western Europe, Australia, Japan, South Africa and New Zealand, and large gaps in biodiversity hotspots such as tropical South America, Africa and Asia (Rocha-Ortega et al., 2021). Thus, our temperature niche values may be biased towards northern temperature values, but given our analytical design, this variable is still useful in describing if a species primarily lives in a relatively warm or cool region.

## Statistical analyses

We counted the number of target species found at each site and used that value as a measure of species richness. We fit a Bayesian generalised linear model using the Gaussian distribution to estimate the

effect of urban development on taxonomic richness. The richness of a given site ( $Y_i$ ) was modelled as normally distributed with a conditional mean of  $\mu$  and standard deviation of  $\sigma$ ,

$$Y_i \sim N(\mu_i, \sigma), \\ \mu_i = \alpha + \beta_{Dev} X_{Dev_i},$$

where  $\alpha$  is the intercept,  $\beta_{Dev}$  is the effect of urban development and  $Dev_i$  is the proportion of developed land within 1 km of site  $i$ .

Next, we summed the total number of individuals sampled at each site for each order. To ensure orders were sufficiently represented across an urbanisation gradient, we only included orders with individuals sampled at five or more sites. Orders without any individuals sampled at a site were given the value zero, which occurred in 3 of 45 sites by order combinations. We quantified if the abundance of different orders was more impacted than others to urban development by using a hierarchical Bayesian framework. For this model, the total abundance of sampled individuals of order  $i$  at site  $j$  ( $y_{ij}$ ) was modelled using a negative binomial distribution,

$$y_{ij} \sim \text{NegBin}(\lambda_{ij}),$$

where  $\lambda_{ij}$  is the expected abundance of order  $i$  observed at site  $j$ . We modelled  $\lambda_{ij}$  as a function of the proportion of developed land within 1-km site  $j$  ( $Dev_j$ ) with varying slopes and intercepts for each order  $i$ .

$$\log(\lambda_{ij}) \sim \alpha_i + \beta_{1i} X_{Dev_j}.$$

Finally, we used a hierarchical Bayesian framework using a negative binomial distribution to quantify the effect of urban development, life history traits and the interactions among these variables on the abundance of individual insect species at a site. Species not captured at a given site were given an abundance of zero, and in total, we had abundance values for 43 species and 387 species by site combinations. For this model, ( $y_{ij}$ ) is the number of sampled individuals of species  $i$  at site  $j$ , which we model using a negative binomial distribution.

$$y_{ij} \sim \text{NegBin}(\lambda_{ij}),$$

where  $\lambda_{ij}$  is the expected number of individual species  $i$  observed at site  $j$ . We modelled  $\lambda_{ij}$  as a function of the proportion of developed land within 1 km of site  $j$  ( $Dev_j$ ), larval diet ( $LD_i$ ), larval habitat ( $LH_i$ ), body size ( $BodySize_i$ ), temperature niche ( $TempNiche_i$ ) and the interactions between urban development and these traits:

$$\log(\lambda_{ij}) \sim \alpha_i + \beta_{1i} X_{Dev_j} + \beta_{2i} X_{LD_i} + \beta_{3i} X_{LH_i} + \beta_{4i} X_{BodySize_i} + \beta_{5i} X_{TempNiche_i} + \beta_{6i} X_{Dev_j} X_{LD_i} + \beta_{7i} X_{Dev_j} X_{LH_i} + \beta_{8i} X_{Dev_j} X_{BodySize_i} + \beta_{9i} X_{Dev_j} X_{TempNiche_i}.$$

We included a random intercept for each species ( $\alpha_i$ ) and random slope for the development coefficient for each species ( $\beta_{1i}$ ). Phylogenetic relationships among species in trait-by-environment environmental modelling can inflate the chances of type I errors (Li & Ives, 2017). To address this, we checked for phylogenetic autocorrelation in our residuals by calculating Pagel's lambda (Pagel, 1999). We did not



find a phylogenetic signal in our residuals (Pagel's  $\lambda = 0.18$ ;  $p$ -value = 0.42), so we did not include a phylogenetic term in our model.

One species, *Hydaticus bimarginatus*, was highly abundant and represented ~34% of our total number of individuals collected. Thus, to examine the influence of this highly abundant species, we also ran our order-specific and species-specific abundance models on a subset of the data that did not include *H. bimarginatus*.

All analyses were developed in R version 4.1.1 (R Core Team, 2021). Data cleaning and manipulation scripts relied heavily on the Tidyverse packages (Wickham et al., 2019). Models were fit using brms (Bürkner, 2017), and tidybayes (Kay, 2023) was used for visualisation of posterior distributions. Models were fit with default priors, 2400 iterations, and 1000 warmup iterations. We used posterior predictive checks of all models to ensure the models fit our data assumptions (Table S1.1 and Figures S1–S3). Data and scripts to reproduce our results and figures can be found in the following GitHub repository (<https://github.com/mbelitz/InsectUrbanization>) and are permanently archived on Zenodo archive (<https://doi.org/10.5281/zenodo.10419482>).

## RESULTS

### Summary statistics

The overall abundance of individuals declined across the urbanisation gradient, with one notable outlier (Figure S4). The site with the second most urban development within 1 km had the fourth highest overall abundance (Table S1.1). However, nearly 74% of the individuals sampled at this site came from one species, *H. bimarginatus*, which was overall the most abundant species with ~34% of our total number of individuals consisting of this species (Table S1.1). Many other species were rarely sampled, with seven species only being sampled a single time at a single site (Table S1.1).

### Richness and total abundance

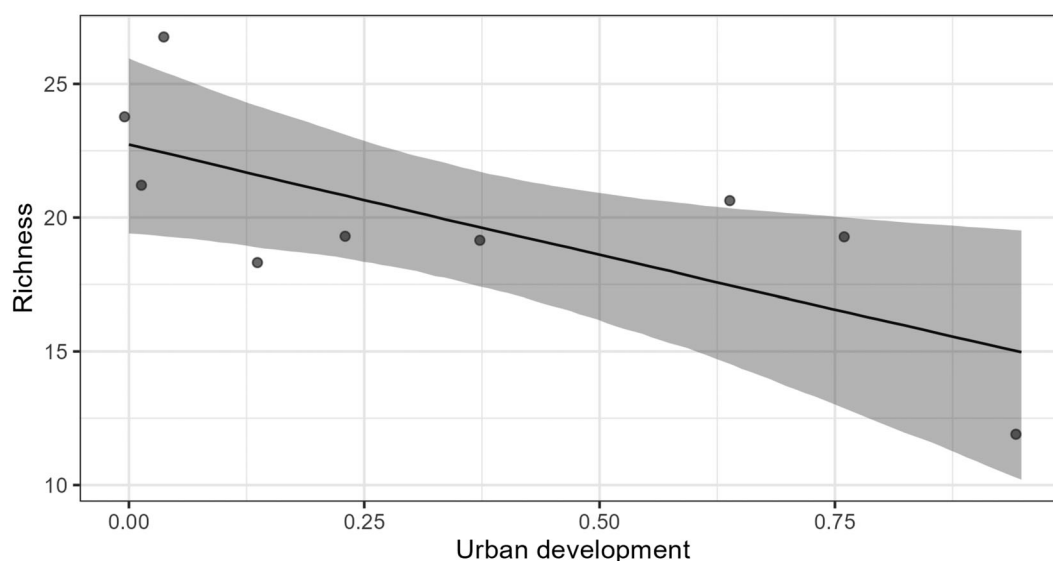
The number of species from our species list sampled at each site decreased in response to increased levels of development within 1 km of the site (Figure 2). Approximately eight species from our list were expected to be lost at a site with 100% urban development surrounding it compared with a site with no urban development within 1 km (urban development slope coefficient estimate  $-8.24$  [95% Bayesian credible interval {BCI}:  $-15.12$  to  $-1.42$ ]; Table S2.1).

### Response of insects to urban development by order

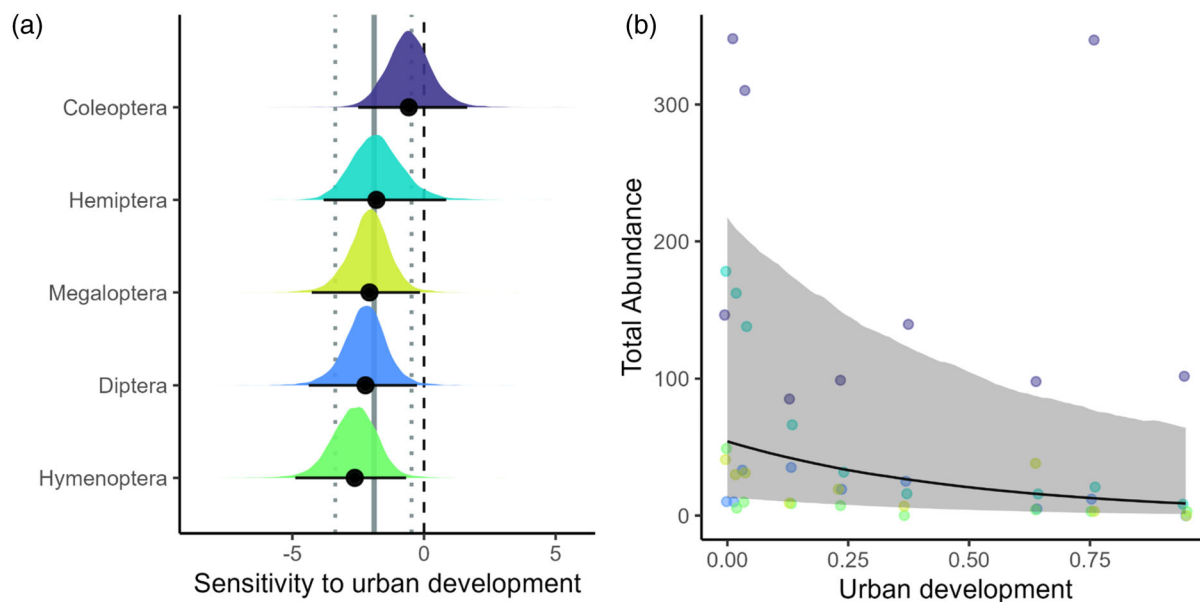
On average, the number of individual insects per order per site decreased as urban development increased (community-level urban development slope coefficient estimate  $-1.90$  [95% CI:  $-3.37$  to  $-0.47$ ]; Figure 3b; Table S2.2). The order-specific slope coefficient estimates show that the pooled abundance of Hymenoptera, Diptera and Megaloptera decreases at the sharpest rate in response to urban development (Figure 3a). Conversely, the pooled abundance of Coleoptera was least negatively impacted by urban development, followed by Hemiptera, with the 95% BCI of these orders encompassing zero (Figure 3a). These results were robust to removing the most abundant species, *H. bimarginatus*, from the dataset (Figure S5). The mean coefficient estimates were very similar to the model fit to the full dataset, but precision increased in the community-level slope estimate (Figure S5B).

### Species-specific abundance model

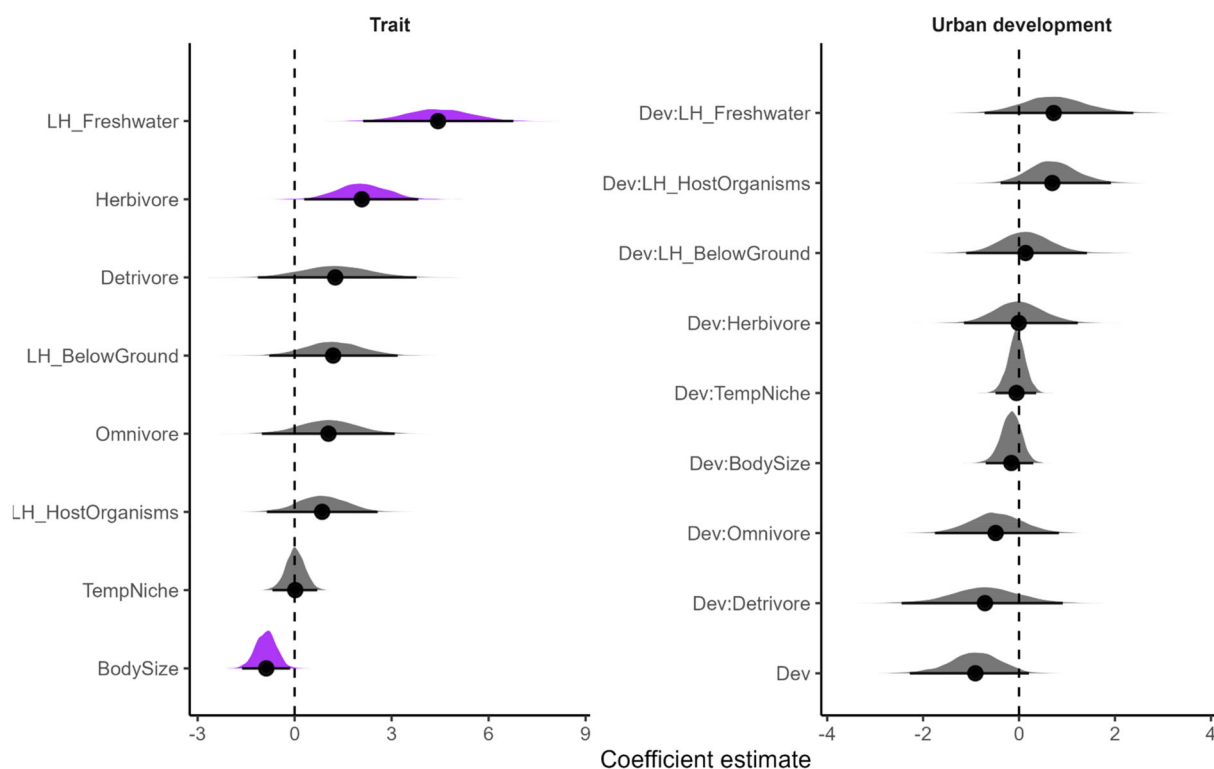
When estimating the abundance of specific species at each site, the slope estimate of urban development and interactions between urban development and life history traits had coefficient estimates with 95%



**FIGURE 2** Richness of selected species list along an urban development gradient. Line shows mean coefficient estimate of model fit and shading represents 95% credible intervals.



**FIGURE 3** Community and order-level effects of urban development on abundance per order. (a) The community-level effect of urban development on abundance per order is shown by the grey vertical line with grey dotted lines showing 95% BCI. The posterior distribution of order-specific responses to urban development is shown with the dot representing the mean estimate and the error bars displaying 95% BCI. (b) Community response of pooled abundance per order to urban development with 95% BCI. Each coloured point represents the abundance of an order at a site.



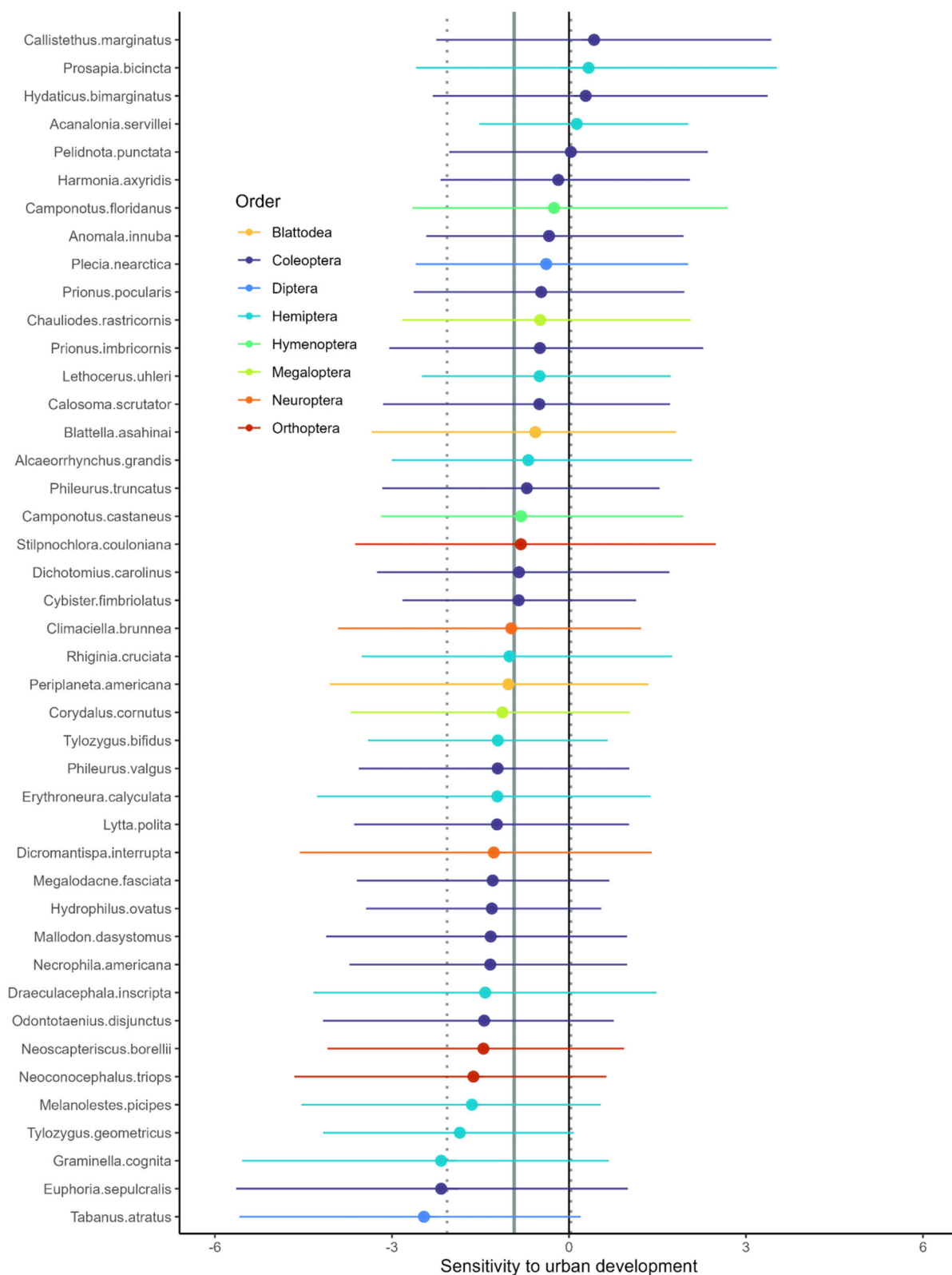
**FIGURE 4** Posterior distributions of the Bayesian hierarchical model estimating species-specific abundance per site. The left panel of the figure shows the response of insect abundance to life-history traits. The right panel of the figure shows the response of insect abundance to urban development (last row) and the interactions between development and traits. Coefficient estimates with 95% Bayesian credible intervals that encompass zero are shaded in grey, while those with 95% BCI that do not encompass zero are purple.

Bayesian credible intervals that overlapped zero (Figure 4, right panel; Table S2.3). Three traits did have posterior distributions with 95% BCI that did not encompass zeros. Species that spent their larval life cycle

in freshwater, herbivores, and are smaller were overall more abundant (Figure 4, left panel). Although the BCI of the urban development coefficient encompassed zero, the mass of the probability distribution

showed a negative impact of urban development on species abundance, and almost all species had mean slope estimates to urban development that were negative (Figure 5). Again, these results were

similar when the most abundant species, *H. bimarginatus*, was removed from the dataset (Figure S6). Without the highly abundant and relatively small species in the dataset, the fixed effect of body size



**FIGURE 5** Species-specific slope estimates in response to urban development. The points are mean values of the posterior distribution and whiskers are 95% BCI. Colour corresponds to insect order of each species. The community-level sensitivity of species-specific abundance to urban development is shown by the grey vertical line with grey dotted lines showing 95% BCI.

now had 95% BCI that encompassed zero, but the estimates of trait by development interactions were consistent (Figure S6).

## DISCUSSION

Urban areas are rapidly expanding, and this growth is projected to be especially rapid in the subtropics and tropics over the coming decades (United Nations, 2018). It is, therefore, critical to expand our understanding of how insects respond to urban development in subtropical environments to better understand the magnitude of impacts and best design biodiverse cities (Diamond et al., 2023). Here, we examine the impact of urban development on insects across eight orders in a subtropical environment, revealing a general decline in species richness and abundance. The response to urbanisation varied widely among species, and although certain traits were important in determining if a species was generally more abundant, we were unable to find trait by development interactions that reliably predicted species' sensitivity to development.

### Urbanisation-driven declines in insect species richness

In line with our hypothesis, we found that species richness was negatively impacted by urban development. This result confirms the findings of several other studies that report a decline in species richness due to urbanisation (Camacho et al., 2021; Faeth et al., 2011; Fenoglio et al., 2020; Merckx & Van Dyck, 2019; Montgomery et al., 2020). However, few studies have examined community effects of urbanisation on nocturnal insects outside of nocturnal moths, which have been found to decrease in richness at higher rates than other invertebrates (Piano et al., 2020), including diurnal butterflies (Merckx & Van Dyck, 2019). Light pollution is one urban stressor that is proposed as an explanation of why nocturnal taxon appears to be more sensitive to urbanisation (Merckx & Van Dyck, 2019). Since over 60% of insect species are nocturnal (Hölker et al., 2010), our results suggest that urban development might have wide-reaching impacts on nocturnal insect communities, and in turn, ecosystem function. Continued effort is needed to determine the ultimate drivers of such species filtering, and determine if artificial light at night is as impactful in low-latitude regions as temperate regions (Secondi et al., 2020). Although the population- and community-level effects of specific urbanisation stressors such as artificial light are increasingly being tied to declines in moth diversity (Grenis et al., 2023; Straka et al., 2021), quantifying mechanistic explanations of urban insect dynamics more generally will likely require experimental approaches (Weisser et al., 2023).

### Insect orders' differential responses to urbanisation

Our study revealed differential impacts of urbanisation on total abundance per insect order. For example, Coleoptera abundance showed resilience to urban development. This finding contrasts a meta-

analysis that reported higher sensitivity of Coleoptera to urbanisation compared to Diptera and Hymenoptera (Fenoglio et al., 2020). Our Coleoptera response is in part attributed to one highly abundant pre-daceous diving beetle within Coleoptera, *H. bimarginatus*. This species was by far the most abundant species in our study and also showed the third lowest sensitivity to urban development among all studied insects. The abundance of *H. bimarginatus* was likely unaffected by urban development due to its affinity for densely vegetated eutrophic water (Larson et al., 2001), a habitat found near all three urban sites. Still, a different Coleoptera species, *Callistethus marginatus*, was the least negatively impacted by urban development, and even when *H. bimarginatus* was removed from the dataset, Coleoptera remained the order least impacted by urban development. Hemiptera also showed minimal impact, aligning with prior research that found their abundance was unaltered by the amount of impervious surface surrounding a site (Lagucki et al., 2017).

Conversely, Hymenoptera was the order most affected by urban development in our study. The outcome contrasts a previous finding that Hymenoptera, especially bees, show higher species richness and flower visitation rates in cities (Theodorou et al., 2020). Since the Hymenoptera included in our studies were all light-attracted ants and did not include bee species, discrepancies are not entirely unexpected. Our contrasting results emphasises the important influence that sampling methods and taxon filtering have on studies examining urban insect dynamics. To draw broader, more accurate generalisations about how insect orders respond to urbanisation, it will be essential to sample using multiple techniques that capture broadly within and across larger taxonomic groups.

### The challenge of finding generalizable traits leading to urban-sensitivity

Our results suggest that most insect species are less abundant in urban sites compared with rural sites, although species vary widely in their response to urban development and these estimates have wide uncertainty. However, we did not identify traits that determine a species' response to urbanisation. Insects are extremely diverse, both functionally and taxonomically, and have complex life histories (Schmitt & Burghardt, 2021), making it difficult to discover which traits determine if an insect species will be an urban exploiter or avoider. Determining the scale at which insect species and populations respond to urbanisation is a fundamental pursuit of the landscape ecology of insects (Betts et al. 2019), and previous studies have demonstrated the spatial scale at which insects respond to urbanisation differs across taxonomic and functional groups (Chust et al., 2004; González-Céspedes et al., 2021; Liao & Lin, 2024). Our approach, which tested urbanisation effects on multiple insect orders at a uniform spatial scale, may have missed crucial interactions between traits and urbanisation operating at either smaller or larger spatial scales than examined. For example, larger species with greater dispersal ability may respond to urbanisation at larger spatial scales than smaller species with limited dispersal capabilities (Jackson & Fahrig, 2012).



Another complicating factor is that trait-environment responses may differ in different climate contexts. For example, urbanisation appears to favour larger moths in colder environments (Merckx & Van Dyck, 2019) but may select for smaller moths in warmer environments (Belitz et al., 2023). One trait that might be expected to generalise across all taxonomic groups and environments is diet generalism, since this has been demonstrated to be an important strategy for insect success in urban areas (Callaghan et al., 2021; Geslin et al., 2016; Lizée et al., 2011). The species whose abundance was second least impacted by urbanisation, *Prospiza bicincta*, is a generalist who feeds on a variety of warm-season turf grasses in both adult and nymph stages and can also feed on many ornamental plants as adults (Cranshaw & Shetlar, 2017). Unfortunately, we were not able to assess the effect of diet generalism in this study due to limited information on the diet breadth of many insect species.

## Importance of community delineation in community-abundance analyses

Our study design, where we pre-determined the species included in our community analysis, may have favoured those with urban affinity. This approach potentially underestimates the negative impacts of urban development on insect abundance and richness. For example, comprehensive sampling of Lepidoptera communities at the same sites revealed significant declines in overall abundance, species-specific abundance and species richness due to urban development (Belitz et al., 2023). Consequently, our study suggests that the selection criteria constraining which species are included in a community abundance analysis can influence outcomes. This insight is crucial for designing local studies, which should aim to include a random array of species across varying levels of urban affinity if abundance of all species within an ecological community is not attainable. It also impacts macroecological studies that rely on data from citizen science platforms like iNaturalist, which contribute to aggregators such as GBIF. These platforms tend to be more heavily sampled in urban areas and thus likely include more urban tolerant and widespread species (Di Cecco et al., 2021), potentially influencing macroecological insights.

## Conclusions and next steps

Insect biodiversity peaks in subtropical and tropical regions, yet the impact of urbanisation in these regions is underexplored (Slade & Ong, 2023). Our study in a subtropical region has revealed that urban development adversely affects insect abundance and richness. However, our sampling method might have biased our results towards species that are more adapted to urban environments, potentially leading to a conservative estimate of the true impact of urbanisation on insect diversity.

This conservative estimate might be reinforced by two other aspects of our study design. First, our urban study sites were in a relatively small city (about 150,000 residents, with a density of 860 residents/km<sup>2</sup>). Second, our sites were located within protected forested parks. We anticipate more pronounced declines in insect diversity in larger urban areas and those with fewer green spaces. Our method of using light traps may have influenced our results in the opposite direction, since long-term exposure to urban light pollution can reduce an insects' attraction to light (Altermatt & Ebert, 2016). However, this effect was likely minimal in our study, as all sites were within conservation areas with no detectable artificial light at the light trap location.

Better understanding urbanisation's impacts on insect biodiversity in subtropical and tropical areas will require a multifaceted approach. This approach should integrate traditional taxonomic methods, contemporary molecular approaches and advanced automated monitoring and identification tools (Slade & Ong, 2023). Despite current limitations in taxonomic, geographic and life history knowledge, the ongoing development of methods like metabarcoding (e.g., Theodorou et al., 2020) and automated insect sensors (e.g., Möglich et al., 2023), coupled with comprehensive trait assembly (e.g., Coleman et al., 2023; Shirey et al., 2021), presents promising avenues for expanding and scaling future research.

## AUTHOR CONTRIBUTIONS

**Nicholas A. Federico:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; project administration; resources; data curation. **Robert P. Guralnick:** Writing – review and editing; resources; supervision; conceptualization. **Michael W. Belitz:** Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; project administration; supervision; data curation.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in InsectUrbanization: Code for Manuscript Re-Submission at <https://doi.org/10.5281/zenodo.10419482>.

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## SUPPORTING INFORMATION

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

**Table S1.** Order abundance, species abundance, urbanization levels, and traits.

**Figure S1.** Graphical posterior predictive checks of species richness model.

**Figure S2.** Graphical posterior predictive checks of mode estimating order-specific abundance.

**Figure S3.** Graphical posterior predictive checks of model estimating species-specific abundance.

**Figure S4.** Estimated response of total abundance across an urban development gradient.

**Figure S5.** Community and order-level effects of urban development on abundance per order after removing the most abundant species from the dataset. A) The community-level effect of urban development on abundance per order is shown by the grey vertical line with grey dotted lines showing 95% BCI. The posterior distribution of order-specific responses to urban development are shown with the dot representing the mean estimate and the error bars displaying 95% BCI. B) Community response of pooled abundance per order to urban development with 95% BCI. Each coloured point represents the abundance of an order at a site.

**Figure S6.** Posterior distributions of Bayesian hierarchical model estimating species-specific abundance per site when the most abundant species is removed from the dataset. The left panel of the figure shows response of insect abundance to life-history traits. The right panel of the figure shows the response of insect abundance to urban development (last row) and the interactions between development and traits. Coefficient estimates with 95% Bayesian credible intervals

that encompass zero are shaded in grey, while those with 95% BCI that do not encompass zero are purple.

**Table S2.1.** Richness model coefficient estimates.

**Table S2.2.** Fixed effect coefficient estimates of model estimating order-specific abundance.

**Table S2.3.** Fixed effect coefficient estimates of model estimating species-specific abundance.

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