RESEARCH ARTICLE

Substantial urbanization-driven declines of larval and adult moths in a subtropical environment

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Abstract

Recent work has shown the decline of insect abundance, diversity and biomass, with potential implications for ecosystem services. These declines are especially pronounced in regions with high human activity, and urbanization is emerging as a significant contributing factor. However, the scale of these declines and the traits that determine variation in species-specific responses remain less well understood, especially in subtropical and tropical regions, where insect diversity is high and urban footprints are rapidly expanding. Here, we surveyed moths across an entire year in protected forested sites across an urbanization gradient to test how caterpillar and adult life stages of subtropical moths (Lepidoptera) are impacted by urbanization. Specifically, we assess how urban development affects the total biomass of caterpillars, abundance of adult moths and quantify how richness and phylogenetic diversity of macro-moths are impacted by urban development. Additionally, we explore how life-history traits condition species' responses to urban development. At the community level, we find that urban development decreases caterpillar biomass and adult moth abundance. We also find sharp declines of adult macro-moths in response to urban development across the phylogeny, leading to a decrease in species richness and phylogenetic diversity in more urban sites. Finally, our study found that smaller macro-moths are less impacted by urban development than larger macro-moths in subtropical environments, perhaps highlighting the tradeoffs of metabolic costs of urban heat favoring smaller moths over the relative benefits of dispersal for larger moths. In summary, our research underscores the far-reaching consequences of urbanization on moths and provides compelling evidence that urban forests alone may not be sufficient to safeguard biodiversity in cities.

KEYWORDS
caterpillars, frass, insect conservation, lepidoptera, subtropical ecology

1 | INTRODUCTION

Insect declines have been documented across many taxa and regions (reviewed in (Wagner, 2020; Wagner, Fox, et al., 2021)), with studies showing steep losses in insect richness (Forister et al., 2021), abundance (van Klink et al., 2023) and biomass (Hallmann et al., 2017). Although not all species and locations are experiencing such losses (e.g. Schowalter et al., 2021; Wagner, Grames, et al., 2021; Yazdanian et al., 2023), reported decreases are alarming given the key role insects play in providing ecosystem services, such as pollination, decomposition and pest control (Kawahara et al., 2021; Losey & Vaughan, 2006). Insect declines are greatest in areas with high human activity (Wagner, Fox, et al., 2021) and among the many interacting stressors, urbanization—a multifaceted form of disturbance—is increasingly recognized as contributing to declines (Fenoglio et al., 2020). The release of local and regional pollutants (air, pesticide, light and noise pollution), change of ambient temperature due to heat accumulation, and the loss and fragmentation of habitats (Grimm et al., 2008) are all results of urbanization. These are all likely to affect insect populations (Fenoglio et al., 2021), but the magnitude of declines in urban areas (Egerer et al., 2017, Piano et al., 2020), and consistency of urbanization responses across climatic gradients is still being debated (Secondi et al., 2020).

Urban stressors that influence insect population dynamics also likely interact with species-specific life-history traits, modulating how susceptible populations and species are to urbanization. While some species have shown dramatic declines in the face of urbanization (Merckx & Van Dyck, 2019), others have seen population increases (Raupp et al., 2012). Traits such as body size, mobility, thermophily and dietary generalism are thought to be critical in determining the success of an insect species in an urban environment (Callaghan et al., 2021; Piano et al., 2017; Schmitt & Burghardt, 2021). Larger species with greater mobility may allow species to better cope with fragmented urban landscapes (Merckx & Van Dyck, 2019). Species with strong heat tolerance and generalist feeding may also survive under urban stressors in hot cities with low native plant diversity (Callaghan et al., 2021; Merckx & Van Dyck, 2019). However, predicting which life history traits impact urban affinity is challenging, as our knowledge is predominantly based on temperate insect species (but see Gaona et al., 2021), which often possess unique characteristics for surviving harsh winters (Theodorou, 2022; Wenzel et al., 2020). Therefore, expanding the geographic focus of studies to the subtropics and tropics is critical for better understanding the impact of urbanization on insect populations and community dynamics.

Equally important as expanding geographic foci is extending our understanding of urbanization impacts across insect life-stages. While the effect of urbanization on the abundance and diversity of adult insects has been assessed (Fenoglio et al., 2020; Piano et al., 2020; Vaz et al., 2023), larval life-stages have received much less attention, and we are unaware of studies that have simultaneously collected larval and adult data to examine trends across urbanization gradients. In contrast to the growing evidence documenting overall declines of adult moth abundance in response to urbanization (Merckx & Van Dyck, 2019; Straka et al., 2021), the few studies focusing on caterpillar abundance or biomass have documented increases (Isaksson & Andersson, 2007), decreases (Marciniak et al., 2007; Seress et al., 2018), or no evidence of significant trends (Solonen, 2001) in urbanized environments. Understanding how insects respond to urbanization across life stages is crucial to conservation planning of insect populations (Merckx et al., 2024; Radchuk et al., 2013).

Taken as a whole, determining impacts of urbanization on both larval and adult life-stages in subtropical and tropical regions is of pressing priority since these regions host the greatest insect diversity and are areas where urbanization is predicted to expand quickly (Seto et al., 2012). A working hypothesis is that lower latitude insect communities will be more negatively impacted by urbanization in part because they are more sensitive to increases in temperature (Diamond et al., 2015). Two meta-analyses examining if urbanization impacts insects at greater levels in tropical climate regions found contradictory results, highlighting the need for additional evidence. Fenoglio et al. (2020) found that the climate region of cities was unimportant in conditioning the effects of urbanization on arthropod diversity and abundance, whereas Vaz et al. (2023) reported that tropical zones exhibit a more pronounced negative impact compared to temperate zones. Insect communities in subtropical regions can comprise a mix of species with core ranges occurring in both tropical and temperate zones (Thang et al., 2020), likely making thermal tolerance traits important in predicting species-specific responses to urbanization in subtropical communities.

Here, we sampled both larval and adult moths across an urban-to-rural gradient for an entire year to test the effect of urban development on total caterpillar biomass and adult abundance in a subtropical environment. For adult macro-moths, we also examine the effect of urbanization on richness and phylogenetic diversity. Finally, we test if responses to urbanization differed depending on life history traits for adult macro-moths. We expected increased levels of urbanization to decrease both biomass of caterpillars and abundance of macro- and micro-moths. We also expected adult macro-moth abundance and richness to decrease in response to urbanization and for species that are warm-adapted, larger and less specialized (i.e. caterpillars feeding on a greater variety of host plants) to be less impacted by urban development.

2 | METHODS

2.1 | Study sites and sampling

We collected adult moths and caterpillar frass approximately once per week at nine study sites along an urbanization gradient in Alachua County, Florida, USA from March 10, 2019, to February 28, 2020. In total, sampling occurred for 51 distinct weeks over this sampling period. The most urban sites were in the city of Gainesville, a small municipality in North Central Florida, USA with a population of 141,085 (density of 860/km^2) as of the 2020 census (U.S. Census Bureau, 2020). Our rural sites in eastern Alachua County occur in

a matrix of intermittent agriculture, semi-natural landscapes, and small towns (<2000 residents).

We selected sites by mapping the proportion of impervious surface using the 2016 National Land Cover Database, which provides land cover information at a 30-m resolution (Homer et al., 2020). We included areas classified as developed open space, low intensity, medium intensity, and high intensity development as "developed areas". Based on the percentage of land classified as developed surrounding each pixel at a 1-km and 10-km scale, we selected three sites each to represent three distinct urbanization classes: urban, suburban, and rural urbanization (Figure 1). Urban sites had at least 60% of the area within 1-km and at least 50% of the area within 10-km classified as developed. Suburban sites had 10–50% of the surrounding land within 1-km and 25–50% of the land within 10-km classified as developed. Rural sites were defined as those where less than 10% of the area around the site was classified as developed at both the 1- and 10-km spatial scales. All nine sites were located within forested conservation areas managed either by the University of Florida, City of Gainesville, Florida Department of Environmental Protection, or local conservation-focused non-profit organizations. Permitting was secured at each site in consultation with the land agency administering each site.

Sites were selected to ensure light and frass traps were in compositionally similar hardwood forests where oaks (*Quercus*) were the dominant tree species. Other abundant canopy species included *Celtis laevigata*, *Liquidambar styraciflua*, and *Pinus taeda*. According to classifications of the Florida Land Cover Classification System (Kawula & Redner, 2018), for both our suburban and urban sites, we sampled at one site in a mixed wetland hardwood forest, another site in a mesic flatwood forest, and the third in a mixed coniferous forest. One rural site was classified as mixed wetland hardwood, while the other two were mesic flatwoods. The two closet sites are 1.2-km apart, and the second closest sites are 2.7-km apart.

Adult moths were sampled using a single LED funnel light trap per site and caterpillar frass was sampled using six frass traps per site as a proxy for caterpillar biomass (Tinbergen & Dietz, 1994). Light traps were built by adapting the low-cost LED funnel trap design described by White et al. (2016) and adding a light sensor to turn on the LED light at dusk and turn off the light at dawn. These are funnel traps that consist of a plastic funnel, plastic collecting container, plastic vanes, and two 15-cm strips of low-wavelength (395–405 nm) LED blacklights that were powered by a 12-volt battery. This trap is known to trap fewer moths than mercury vapor traps but offers a safe, small-battery powered alternative that can facilitate automated trapping in more diverse settings (White et al., 2016). Frass traps were built to sustain sampling throughout the entire year, including the wet season. To do so, we built funnels with a radius of 11.66 inches out of wire mesh and attached a plastic collection jar with the bottom of the jar replaced with wire mesh (Figure S1). Mesh funnels were attached to a 20″ X 20″ wooden frame that was on 24″ stilts, allowing the traps to be off the forest floor and above seasonal flooding. We strung a 9″ pie tin over the collection jar to serve as a rainfly. Light traps were set by connecting the traps to a 12-volt

battery and adding a collecting jar to the trap that was filled with ca. 4″ of 70% isopropyl alcohol. We note that although isopropyl alcohol was effective at preserving specimens until they were collected, it did remove scales of some organisms making subsequent taxonomic identification challenging for certain specimens.

Our sampling protocol consisted of visiting each of the nine sites twice per week. On the first visit, we collected the frass samples from the six traps per site (54 total frass traps) and set the light traps (nine total light traps). Any material on the frass trap but not in the collection jar was brushed into the collection jar using a large paintbrush. The collecting jar was then removed and replaced with a new one. The following day, the light tracollection jar with insect specimens and the battery were collected. Light trap samples were sorted into groups of lepidopterans and non-lepidopterans, and these samples were stored in 50 mL conical tubes in 70% ethanol (EtOH). Frass samples were dried at room temperature for at least 3 days in the collecting jars before being sorted, during which non-frass debris, such as plant material and mammal feces, were removed. In instances where we were unsure if sampled frass pellets were from a caterpillar or another arthropod (e.g., a sawfly), we included the sample as frass. Once sorted, frass samples were transferred to microcentrifuge tubes where they were stored at room temperature in an HVAC controlled room. After at least 3 months in microcentrifuge tubes, each frass sample was weighed using a scale with 0.001 precision in grams and the amount of frass over the sampling period (mg/day) was calculated.

The total number of micro-moths (defined in this study as moths having a total length of ≤10 mm from head, excluding antennae, to abdominal tip) and macro-moths (total length >10 mm for the same region) were counted for each light trap sampling day. Additionally, each macro-moth was identified to its lowest taxonomic unit, which was often the species-level. Species-level identification was not always possible (e.g., due to adult moths losing scales necessary for identification or genera like *Datana* where species identification is known to be challenging (Miller, Wagner, et al., 2018)). In such cases, specimens were identified to the finest taxonomic rank possible and were excluded from species-specific analyses. We identified all *Halysidota* specimens as *Halysidota tessellaris* even though differentiating between *H. tessellaris* and *H. harrissii* cannot be done without genitalia dissection. We did so because American Sycamore (*Plantanus occidentalis*), the host plant of *H. harrissii* (Miller, Wagner, et al., 2018), was not found at study sites.

2.2 | Measure of urbanization

We included one urbanization variable as a predictor variable in analyses described below: proportion of developed land within 1-km of a light trap. Proportion of developed land reflected the proportion of 30-m resolution pixels classified as developed (open space and low, medium and high intensity) within a 1-km neighborhood of the light trap based on the 2016 National Land Cover Database (Homer et al., 2020). We measured our urban development variable at 1-km
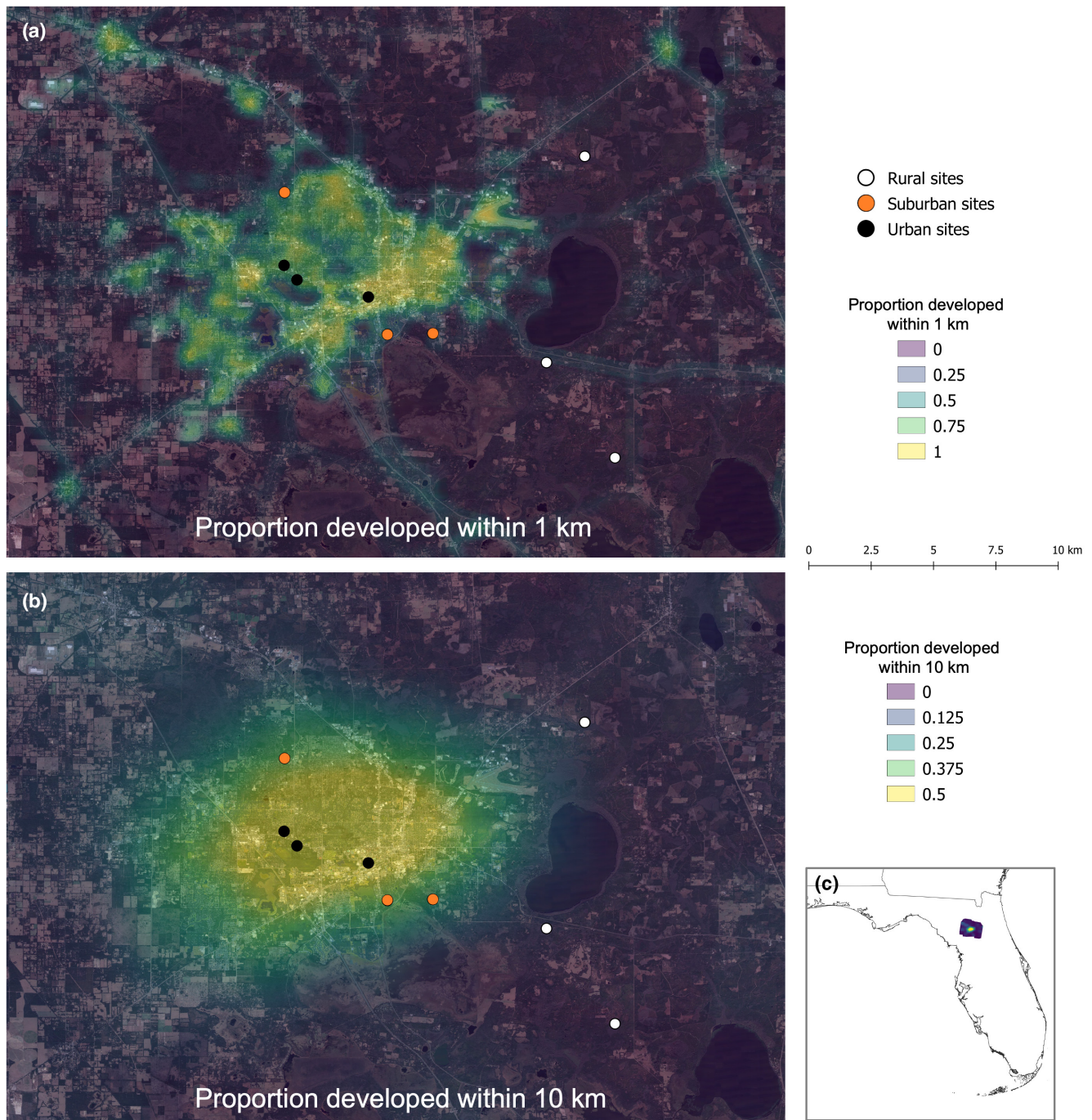
FIGURE 1 Location of study sites in relation to the urbanization density of Gainesville, FL. The proportion of developed land cover within a 1-km (a) and 10-km (b) buffer is represented by a color gradient. Panel (c) shows the location of the county in which the study took place within the state of Florida, USA. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

because urbanization effects strongly influence insects at this scale (González-Césped et al., 2021).

2.3 | Life history traits

We included life history traits as predictor variables in the species-specific adult macro-moth analysis described below. For each identified macro-moth species, we collected the following traits: (1)

body size, (2) host plant specificity (HPS), and (3) temperature niche. Information on body size and host plant specificity were gathered from Leckie and Beadle (2018). Body size measurements were extracted as the upper total length range listed in Leckie and Beadle (2018). In cases where only wingspan was listed instead of total length, body size was calculated as half the upper value of wingspan (García-Barros, 2015). Host plant specificity was a categorical variable where species with caterpillars that feed on multiple families or detritus were classified as "generalist", species that feed on a single family

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were classified as "intermediate", and species that feed on a single genus or single species were classified as "specialist" (Futuyma, 1976). Following approaches to calculate a species temperature niche indices based on open data (Sparrius et al., 2018), average temperature niche values were calculated as follows. First, we downloaded occurrence records for each species from the Global Biodiversity Information Facility (GBIF, 2023). 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 30s resolution; Fick & Hijmans, 2017) for each occurrence point. Average temperature niche was calculated as the mean value among all annual temperature values.

2.4 | Statistical analyses

2.4.1 | Caterpillar biomass and pooled abundance of adult macro- and micro-moths

We used a hierarchical Bayesian framework using a zero-inflated negative binomial distribution to test the effect of urban development on the total pooled abundance of adult macro-moths and adult micro-moths per sampling event. The non-zero part of the model estimated abundance of adult moths as a function of the proportion of development at a site. To control for environmental variation in sampling nights, we also included the lunar illumination of the sampling night, total precipitation of the day of sampling, and minimum temperature of a sampling night. These control variables were not correlated ($r < |0.2|$) with each other or the urban development variable. Lunar illumination data was gathered using the R package lunar (Lazaridis, 2022), and daily weather variables were downloaded from daymet (Thornton et al., 2016). Site was included as a random intercept. The zero-inflated part of the model estimated the probability that a sampling event collected zero moths as a function of the proportion of development at a site, lunar illumination, precipitation, and minimum temperature. Site was again included as a random intercept.

The caterpillar biomass model predicted $\log(x_i + 0.001)$, where x = frass mass per site i/number of days between sampling events (Seress et al., 2018). Frass mass per day was modeled using a gaussian distribution as a function of the proportion of development at the site, the average lunar illumination over the collection week, the average minimum temperature over the collection week, and the average precipitation over the collection week. Average minimum temperature and average precipitation were weakly correlated $r = 0.47$ with each other. Site was included as a random intercept.

For these models and all models described below, we fit models in STAN, a probabilistic programming model that fits Bayesian models through Markov chain Monte Carlo methods (Carpenter et al., 2017) using the R package brms (Bürkner, 2017) with minimally informed priors. We chose a Bayesian modeling framework in part because Bayesian models have clear and valid interpretation even with limited sample size (McElrath, 2020), and because we were able to fit

phylogenetically informed zero-inflated negative binomial models. For models with multiple predictor variables, continuous predictor variables were scaled to have a mean of zero and a standard deviation of one to allow for easily interpretable model effect sizes across variables. For each model, we ran 2400 iterations each with a warmup of 1000 iterations. No models had divergent transitions (Carpenter et al., 2017) or Rhat values ≥1.1. Data simulated from posterior predictive distributions were similar to observed data. Since our most urban site had by far the lowest abundance in macro-moths, we tested if our results are robust to the inclusion of this site. We ran all models both with the entire dataset intact and without this site. Code and associated data to replicate all analyses are archived on Zenodo (Belitz, 2024).

2.4.2 | Adult macro-moth richness and phylogenetic diversity

For adult macro-moths identified to the species-level, we calculated species richness at each sampling site. We also quantified phylogenetic diversity using Faith's PD (Faith, 1992) and mean pairwise distance (Webb et al., 2008). Species richness was measured as the number of distinct macro-moth species, using a morphospecies approach. If a macro-moth was identified to a genus that was not included as a distinct macro-moth species, then those moths were also included as a new "species".

We calculated community phylogenetic diversity metrics by first generating a synthesis phylogeny for the macro-moth species in our analysis from the Open Tree of Life (Michonneau et al., 2016). Synthesis phylogenies are demonstrated to yield reliable results in community phylogenetic analyses that are similar to purpose-built phylogenies (Li et al., 2019). The database TimeTree of Life (Kumar et al., 2017) was queried to estimate the divergence time of the internal nodes and the branch lengths were scaled from these times using the R package phylocomr (Ooms & Chamberlain, 2019). For each site, we calculated proportional phylogenetic diversity as the percentage of overall branch lengths for species found in a site compared to branch lengths of all species in the total phylogeny (Miller, Jolley-Rogers, et al., 2018). Abundance-weighted mean pairwise distance was calculated between all species in each site to compare how closely related the average pair of individuals are in a community. Proportional phylogenetic diversity and mean pairwise distance values were calculated using the R package picante (Kembel et al., 2010). We fit a Bayesian univariate linear model using the gaussian distribution to estimate the effect of the proportion of development within 1-km on taxonomic richness, phylogenetic diversity, and mean pairwise distance.

2.4.3 | Species-specific adult macro-moth abundance

We used a hierarchical Bayesian framework using a zero-inflated negative binomial distribution to quantify the effect of urban

development, life history traits, and the interactions among these variables on the abundance of individual moth species at a site. For the positive count data, total abundance of a species collected across the entire year at each site was the response variable. Predictor variables for the non-zero part of the model were the proportion of developed area at a 1-km scale around the sample site, moth body size, moth temperature niche, and moth host plant specificity. We also included interaction effects between urban development and the three trait variables. A random intercept was included for each species. We first fit this model to 253 species, after dropping species with missing trait data. Next, we fit a model to 226 species that included a covariance matrix containing the phylogenetic distances between the species as a random intercept term, since ignoring phylogenetic relationships in multi-species models examining trait-environment relationships can lead to overly precise coefficient estimates (Li & Ives, 2017). We dropped 27 species from this analysis because they were not available on Open Tree of Life. The zero-inflated part of the model estimated the probability that a species was not observed at a site as a function of the proportion of urban development, host plant specificity, and body size. We present results based on the model that includes the phylogenetic term. The model without this term that includes 27 more species can be found in Supporting Information S1 (Table S4).

3 | RESULTS

In total, we collected and sorted 30,497 micro-moths and 5505 macro-moths from 15 families (Supporting Information S2). Macro-moths of the following five families had the greatest number of individuals captured across all sites and represent most of the macro-moth data: Erebidae (1230 individuals), Geometridae (1064 individuals), Notodontidae (1046 individuals), Megalopygidae (316 individuals), and Noctuidae (236 individuals). At least 317 distinct macro-moth morphospecies were sampled across our sites. The five species that were collected in the highest abundances across all sites were *Heterocampa obliqua* (324 individuals), *Halisidota tessellaris* (175 individuals), *Megalopyge opercularis* (174 individuals), *Nadata gibbosa* (158 individuals), and *Apantesis vittata* (104 individuals). Many moths were rare with 68 species being sampled a single time (Supporting Information S2).

3.1 | Caterpillar biomass and pooled abundance of adult macro- and micro-moths

At the community level, urban development negatively impacted pooled abundance of macro-moths and micro-moths, and caterpillar biomass (proxied by frass mass; Figure 2). Adult moths were more abundant during warmer sampling nights, and less abundant during more lunar illuminated nights (Table 1). Caterpillar mass was also higher during warmer weeks, but lower during wetter weeks (Table 2). Precipitation did not have a large effect on adult moth abundance (Table 1).
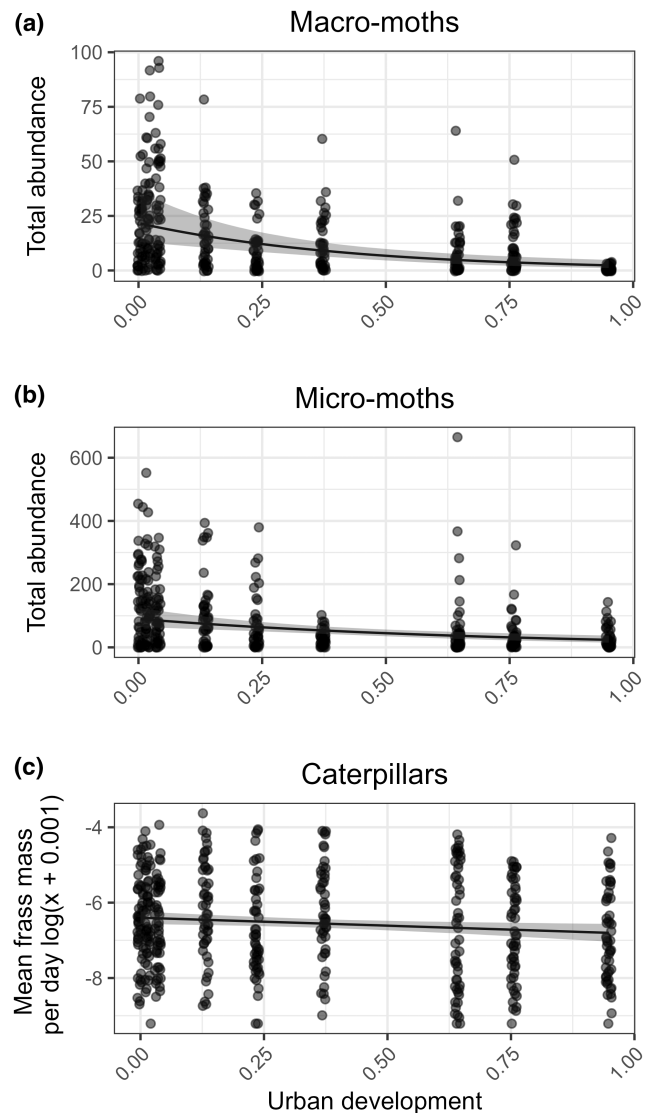

FIGURE 2 Mean coefficient estimate and 89% credible interval of urban development on non-zero abundance of macro-moths (a), micro-moths (b), and biomass of caterpillars (as proxied by frass mass) (c). Points represent abundance and biomass collected at individual weeks of sampling for each site.

The zero parts of our pooled adult abundance models showed that temperature and lunar illumination, but not urban development influenced the probability of occurrence of macro-moths being sampled (Table 1). Sampling events were more likely to capture zero macro- and micro-moths on nights that were cooler and had less lunar illumination; precipitation during the sampling night did not influence probability of capturing zero adult moths (Table 1).

Effect sizes and credible intervals were similar for models predicting total community abundance of macro-moths and micro-moths whether the most urban site was included (Table S1). However, in the caterpillar model, the effect size of urban development predicting frass mass was slightly smaller with larger credible intervals that overlapped zero (urban development slope coefficient

Fixed effect	Macro moth			Micro moth		
	Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI
Intercept	2.26	1.89	2.60	4.01	3.79	4.22
Urban development	−0.80	−1.18	−0.45	−0.47	−0.69	−0.25
Lunar illumination	−0.21	−0.29	−0.13	−0.19	−0.28	−0.10
Precipitation	0.06	−0.05	0.17	−0.06	−0.15	0.04
Temperature	0.51	0.41	0.61	0.77	0.66	0.88
ZI Intercept	−8.25	−12.11	−5.19	−8.80	−12.25	−6.17
ZI Urban development	0.95	−0.16	2.15	−0.01	−0.93	0.86
ZI Lunar illumination	−1.50	−2.68	−0.58	−1.08	−2.19	−0.29
ZI Precipitation	0.76	−0.60	1.88	−3.01	−8.91	0.22
ZI Temperature	−4.17	−6.27	−2.48	−3.84	−5.42	−2.58

Note: ZI represents coefficient estimates for the part of the model predicting the probability of zero adult moths sampled. Estimates are displayed on the log scale, and predictor variables were mean centered and rescaled to have a standard deviation of one.

TABLE 2 Coefficient estimates and 89% credible intervals for the model predicting pooled caterpillar biomass.

Fixed effect	Estimate	Lower 89% CI	Upper 89% CI
Intercept	−6.55	−6.66	−6.43
Urban development	−0.14	−0.26	−0.03
Lunar illumination	−0.05	−0.13	0.04
Temperature	0.68	0.58	0.77
Precipitation	−0.24	−0.34	−0.14

Note: Predictor variables were mean centered and rescaled to have a standard deviation of one.

−0.13 [−0.30–0.04 89% CI]) in the model that removed the most urban site (Table S2).

3.2 | Richness and phylogenetic diversity

Richness and phylogenetic diversity decreased in response to increased levels of urban development (Figure 3). However, the effect size of urban development on phylogenetic diversity is smaller and uncertainty higher when the most urban site is removed from the model (Table S3). We did not find evidence, given our sampling regime, that mean pairwise distance is negatively associated with urban development (urban development slope coefficient estimate −10.29 [89% CI: −25.82 to 5.68]).

3.3 | Species-specific adult macro-moth abundance

The zero-part of our model provides evidence that species were more likely to not be detected (zero abundance) at more urban sites (zero-inflated urban development slope coefficient=6.13 [89% CI: 4.03–8.42]). The non-zero part of our model showed that urban development decreases moth abundance, but the body size and host
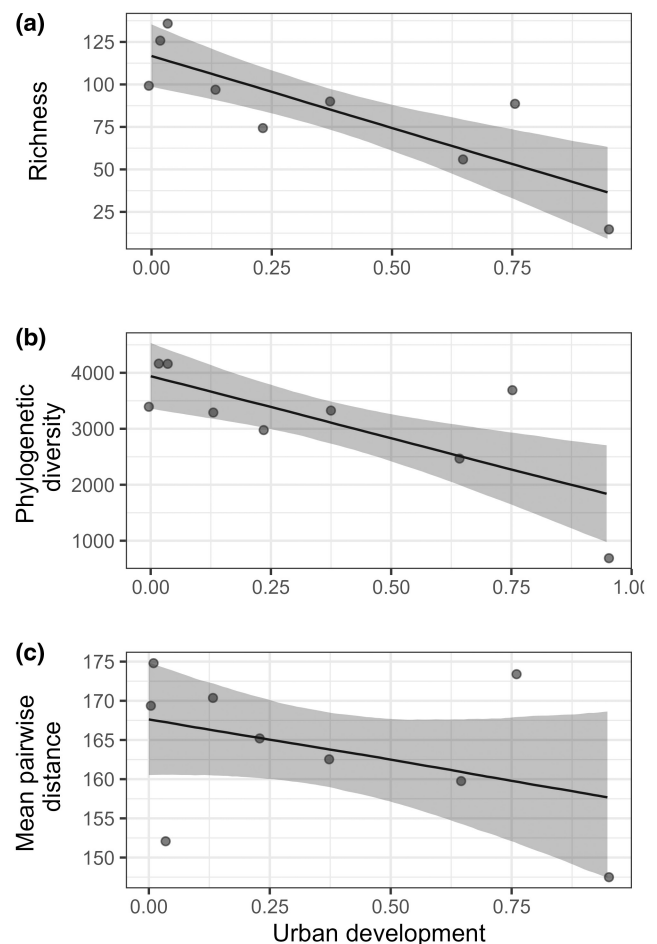

FIGURE 3 Mean effect and 89% credible interval of urban development on macro-moth species richness (a), phylogenetic diversity (b) and mean pairwise phylogenetic distance (c).

plant specificity of the species mediates this response (Table 3). Specifically, we found larger macro-moths decrease in abundance in response to urban development, while smaller macro-moths had

TABLE 3 Coefficient estimates and 89% credible intervals for the model predicting species-specific macro-moth abundance.

Coefficients	Estimate	Lower 89% CI	Upper 89% CI
Intercept	−0.68	−1.16	−0.24
Urban development	−0.33	−0.46	−0.20
Body size	−0.19	−0.39	−0.01
Temperature niche	0.09	−0.06	0.24
Host plant specificity (HSP) [2]	−0.29	−0.76	0.19
Host plant specificity (HSP) [3]	−0.76	−1.11	−0.39
Urban development:Body size	−0.25	−0.39	−0.12
Urban development: Temperature niche	0.07	−0.03	0.17
Urban development:HSP[2]	−0.59	−0.91	−0.27
Urban development:HSP[3]	−0.44	−0.68	−0.21
ZI Intercept	−10.07	−13.95	−6.68
ZI Urban development	6.13	4.03	8.42
ZI HSP [2]	−6.52	−22.16	0.39
ZI HSP [3]	−0.62	−3.26	1.23
ZI Body size	−0.50	−1.64	0.52
sd(Intercept) of phylogenetic relatedness	0.08	0.04	0.11
sd(Intercept) of species name	0.89	0.65	1.10

Note: ZI represents coefficient estimates for the part of the model predicting the probability of zero adult moths sampled. HSP [2] represent macro-moths that feed on a single family and HSP [3] represent macro-moths that feed on a single genus or species. Estimates are displayed on the log scale, and continuous predictor variables were mean centered and rescaled to have a standard deviation of one.

relatively consistent abundance across the urbanization gradient until the most urban sites (Figure 4a). Species that feed on multiple plant families displayed the least negative response to urban development, while those that feed on a single plant genus or family displayed greater decreases in abundance in response to urban development (Figure 4b). We did not find evidence that a species' temperature niche was important in mediating the effects of urban development (Figure 4c). Phylogenetic relatedness explained little variation in abundance, and results were largely similar for the model that did not include a phylogenetic relatedness term (Table S4). Species random intercept was important in explaining variation (Table 3). Results of the species-specific zero-inflated abundance model remained similar when the most urban site was removed from the dataset (Table S5).

4 | DISCUSSION

Urbanization can substantially impact community assemblages by transforming landscapes, including through habitat destruction, fragmentation, increased levels of pollution, and disrupted hydrology (Grimm et al., 2008). In response to urbanization stressors, reductions
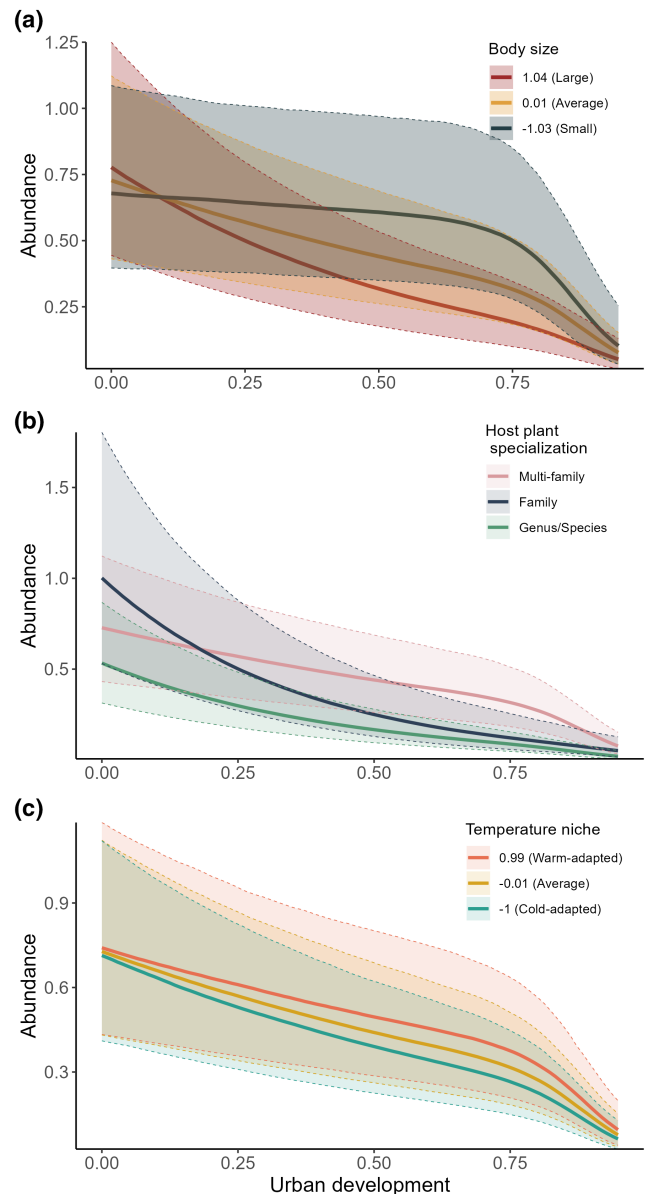

FIGURE 4 Effect of urban development on species-specific abundance is conditioned by body size (a) and host plant specificity (b), but not temperature niche (c). Numbers in body size and temperature niche legend denotes standard deviations away from mean moth species. Shading represents 89% credible interval of coefficient estimate.

in both species richness and abundance have been observed across various insect taxa (Fenoglio et al., 2020; Piano et al., 2020), particularly in temperate regions. However, the assessment of urbanization impacts in subtropical regions and their consistency across different life stages and assemblages, such as macro-moths and micro-moths, are far less well known. We conducted repeated sampling of larval and adult moths along an urban-to-rural gradient within a subtropical environment to quantify the effects of urban development on larval and adult moth communities. Our study highlights the far-reaching consequences of urban development on moth species and communities, with urbanization negatively impacting the overall

abundance of caterpillars, micro-moths, and macro-moths. All sites included in our study were within protected forests, emphasizing that action beyond preserving urban parks will be needed to conserve insect biodiversity in cities. Furthermore, our study identifies key life history traits that mediate the impact of urbanization on the abundance of individual moth species.

4.1 | Adult moth response to urbanization

Adult moths were strongly impacted by urban development with the pooled community abundance of both macro- and micro-moths decreasing along the urbanization gradient. This aligns with the consistent findings in temperate regions, where urbanization has been linked to declines in moth abundance (Bates et al., 2014; Merckx & Van Dyck, 2019; Straka et al., 2021). However, far fewer studies have quantified the consequences of urbanization on insects in subtropical and tropical regions (Wenzel et al., 2020). One of the few studies examining the impacts of urbanization on tropical moths observed that abundance and diversity of geometrid moths was far lower in urban sites than forest sites (Gaona et al., 2021). The implications of urbanization-driven declines in insect biodiversity in subtropical and tropical environments are particularly disconcerting given the exceptional diversity of arthropods in these regions (Basset et al., 2012; Merckx et al., 2013) and the projections of expanding urban populations in the subtropics and tropics over the coming decades (United Nations, 2018).

In general, our results demonstrate the prominence of micro-moth diversity in the collected samples, yet identification bottlenecks mean that we cannot test phylogenetic, and trait driven species-level variation in response to urbanization. We also note that even within macro-moths, smaller and cryptic species are less likely to be identified to species using our sampling protocol. This challenge with identification is not unique to the work presented here, limiting more general predictions of the winners and losers under environmental change and making insect meta-analyses and direct cross-study comparisons more difficult. Efficiently identifying micro-moths remains a major bottleneck for ecological studies encompassing entire moth communities. Promising avenues for addressing this issue include automated light traps with computer vision technology and DNA metabarcoding, although the power of these solutions are limited by incomplete DNA and photo libraries (Montgomery et al., 2021).

4.2 | The importance of adult life-history traits

Our results indicate that two life history traits are pivotal in identifying the responses of macro-moths at a species-specific level. Notably, larger bodied moths exhibited more negative responses to urban development, while smaller macro-moths showed almost no change in abundances across urban development gradients. These results are contrary to our prediction and a previous study conducted in high-latitude sites within Belgium that found larger

macro-moths were relatively more prevalent in urban sites, which was interpreted as a shift towards increased mobility shaped by habitat fragmentation (Merckx, Souffreau, et al., 2018; Merckx & Van Dyck, 2019). Our results may instead suggest that in subtropical climate contexts, urban heat favors smaller species due to elevated metabolic costs at warmer sites, a pattern observed at the same Belgium-based study sites in non-moth terrestrial arthropods such as ground spiders, ground beetles, weevils, and cladocerans (Merckx, Kaiser, & Van Dyck, 2018). Urbanization may impact biodiversity differently in low-latitude locations, such that in warmer contexts where there is increased heat stress, the metabolic costs of urban heat may favor small moths over the relative benefits of dispersal for larger moths. An alternative explanation is that larger and more mobile moths require larger intact forest patches to sustain populations of forest specialists (Slade et al., 2013).

As expected, we found that species with a more general larval feeding strategy fared relatively better in urban environments. Such a strategy has been identified as an important trait for predicting urban-avoiding Lepidoptera species (Callaghan et al., 2021) and in animals more generally (Callaghan et al., 2019; Geslin et al., 2016). Urban development can lead to decreases in plant diversity, specifically through reduction of endemic species and increased proportions of exotics (Yan et al., 2019), which will limit opportunities for caterpillars with narrow diets. However, the dominance of oak species in all of our forested sites may have allowed species with specialized larval diets to respond similarly to those with intermediate host plant specificity, since oaks serve as a host plant for many moth species including specialists (Narango et al., 2020). This phenomenon has also been reported in Western Europe, where abundance of butterflies that feed on one host plant (*Urtica dioca*) that has become common in urban areas show similar responses to urbanization as more polyphagous species (Merckx & Van Dyck, 2019).

We do not find evidence that a third trait, species' temperature niche, interacts with urban warming to impact species-specific abundances. This result contradicts the findings of previous studies in higher latitudes that found urbanization to favor thermophilic moth species in temperate regions (Franzén et al., 2020; Merckx & Van Dyck, 2019). Our results again suggest key differences in how individual species will respond across regional climate gradients. We also cannot discount that our temperature niche trait is too coarse a proxy for a mechanistic thermal niche (Sparrius et al., 2018). In particular, there may be a tendency for values to skew colder and with increased uncertainty in southern species due to more limited occurrence point sampling in southern compared to northern regions (Rocha-Ortega et al., 2021).

4.3 | Species level losses but lack of phylogenetically clustered filtering

Our results also showcase negative consequences of urban development on macro-moth taxonomic richness and phylogenetic diversity. Our results corroborate results of Merckx and Van Dyck (2019)

indicating that urban development can negatively affect moth species richness on a landscape scale. Light pollution, which is strongly associated with urbanization, is one mechanism that may explain the observed declines of moth richness and diversity across urbanization gradients (Straka et al., 2021). Light pollution can potentially lead to population declines and local extirpation by disrupting reproduction (Boyes et al., 2020), larval development (Boyes et al., 2021), and preventing pupal diapause (Merckx et al., 2023). Recent work also indicates that streetlamps with UV emission negatively affect moth species richness on a landscape scale (Straka et al., 2021). Although richness declined across our urban gradient, we did not find strong evidence of lower mean pairwise distance (MPD) in sites with higher levels of urban development, although the trends are in the same direction. Taken together, these results suggest there is broad filtering of species across all clades rather than clade-specific losses. Still we might expect MPD to decrease over urbanization gradients if the entire order of Lepidoptera were examined given the fact that diurnal groups of Lepidoptera (i.e., butterflies) may be less impacted by urbanization compared to nocturnal moths (Merckx & Van Dyck, 2019).

4.4 | Larval moth response to urbanization

The impact of urbanization on larval insects, such as caterpillars, remains poorly understood, despite their critical roles as herbivores and prey in ecosystems. Our results show a reduction in caterpillar biomass, as indicated by frass fall, across an urban development gradient. Our caterpillar results further strengthen our adult moth findings, since caterpillar sampling avoids the use of light traps which can be susceptible to biases because insects in urban areas may have reduced flight-to-light response (Altermatt & Ebert, 2016).

Despite the clear evidence of declines across urbanization gradients, the effect of urban development was less severe for caterpillars than adult moths. One plausible explanation is that moths face high mortality in cities during the transition from late-stage caterpillars to adulthood. Many caterpillars stop feeding near the end of their final instar and wander from their host plant to find a location to pupate (Kingsolver et al., 2011; Lee & Roh, 2010). Wandering caterpillars are at greater risk in urban environments, including hazards like road mortality (Ciolan et al., 2017). Moreover, urban soils are often compacted, and topsoil disturbance is common, potentially impeding caterpillars seeking subterranean or leaf litter pupation sites (Schmitt & Burghardt, 2021). Those that successfully pupate may still face higher mortality in urban sites due to desiccation, since urban areas are likely to increase dehydration stress (Kaiser et al., 2016) and pupal stages are particularly sensitive to such stresses (Benoit et al., 2023).

We also note that caterpillar and adult abundance proxies, and resolution to taxonomic units, are not the same in this study. Effectively measuring caterpillar abundance or biomass remains challenging as sampling techniques are less developed and field-tested compared to those used for adult moths. Our study takes an important first step at pairing larval and adult datasets, but we recognize that determining the processes underlying differential responses for caterpillars and adults to urbanization are likely complex and continued effort is needed. The ongoing development of environmental metabarcoding techniques offers promising opportunities for using frass traps to determine at least operational taxonomic unit richness and community compositions of forest caterpillars across disturbance gradients (Rytkönen et al., 2019).

4.5 | Enormous impact of urbanization on adult moth abundance: Conclusions, limitations, and next steps

Our study reveals a striking pattern where the site surrounded by the most extensive urban development at a 1-km resolution exhibited an order of magnitude lower macro-moth abundance and richness compared to rural sites. The primary conclusions of this study remain robust even when the most urban site was removed from our analysis, reinforcing our finding that urban development has far-reaching ecological consequences on moth communities. The lack of macro-moths at the most urban site suggests the potential existence of ecological thresholds in urban landscapes (Andersen et al., 2009), where abrupt declines in abundance and richness are observed once a certain degree of urbanization occurs. For example, the response of all macro-moths, regardless of body size, decreased in abundance precipitously at the extreme end of our urbanization gradient. Identifying these tipping points and the relative contributions of various urban stressors in reaching them hold crucial implications for urban planning aimed at creating biodiverse cities (Peng et al., 2017).

Although we find strong evidence that areas with higher urban development are associated with lower moth abundance and diversity, our study is not able to identify the mechanisms driving these trends. Urbanization can directly cause loss of insect biodiversity through a variety of drivers such as habitat destruction, habitat fragmentation, urban warming, pollution, and due to exotic plant species replacing native species (Fenoglio et al., 2021). Urbanization can also indirectly lead to population declines through disrupting species interactions or changing the availability, quality, and composition of local resources (Fenoglio et al., 2021). We argue that additional research, including experimental approaches, will be necessary to gain a deeper understanding of the causal mechanisms of urbanization-driven declines in subtropical and tropical moths (Weisser et al., 2023).

In conclusion, we find extensive consequences of urbanization on nocturnal Lepidopteran communities in a subtropical region, further substantiating that urbanization-induced stressors act at the landscape scale and dramatically alter insect populations and communities across life-stages. Comparing the rural site with the greatest total abundance and the urban site with the lowest total abundance across the entire year, we documented a 68% reduction in caterpillar frass mass, an 80% reduction in pooled micro-moth abundance, and a staggering 97% reduction in pooled macro-moth abundance. These findings are of particular concern considering that our urban

sites were situated within a relatively small city (approximately 150,000 total residents and 860 residents/km^2) and were located within forested protected parks, highlighting that urban parks alone will not maintain insect biodiversity at comparable numbers to rural areas. Insights from a global meta-analysis suggest that urbanization has a more pronounced impact on insect abundance and richness in tropical areas compared to temperate regions (Vaz et al., 2023). This phenomenon may in part be attributed to the higher baseline abundance and richness found in these areas but much more work is needed to understand the magnitude of losses in the most urbanized areas and mechanistic basis for those losses.

AUTHOR CONTRIBUTIONS

Michael W. Belitz: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; writing – original draft. **Asia Sawyer:** Data curation; methodology; project administration; resources; software; writing – review and editing. **Lillian Hendrick:** Data curation; funding acquisition; project administration; writing – review and editing. **Akito Y. Kawahara:** Conceptualization; methodology; resources; writing – review and editing. **Robert P. Guralnick:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available on Zenodo at https://doi.org/10.5281/zenodo.10525136. The code to fully reproduce the results and figures presented in this paper can be also be found on Github at https://github.com/mbelitz/Urban-Moth-Abundance. This repository also includes trait information and raw survey data for all species included in our analysis.

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REFERENCES

Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, *12*, 20160111.

Andersen, T., Carstensen, J., Hernández-García, E., & Duarte, C. M. (2009). Ecological thresholds and regime shifts: Approaches to identification. *Trends in Ecology & Evolution*, *24*, 49–57.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A. K., Winchester, N. N., Roubik, D. W., Aberlenc, H.-P., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., ... Leponce, M. (2012). Arthropod diversity in a tropical forest. *Science*, *338*, 1481–1484.

Bates, A. J., Sadler, J. P., Grundy, D., Lowe, N., Davis, G., Baker, D., Bridge, M., Freestone, R., Gardner, D., Gibson, C., Hemming, R., Howarth, S., Orridge, S., Shaw, M., Tams, T., & Young, H. (2014). Garden and landscape-scale correlates of moths of differing conservation status: Significant effects of urbanization and habitat diversity. *PLoS One*, *9*, e86925.

Belitz, M. W. (2024). Urban-Moth-Abundance: Code for manuscript submission (0.1.2). *Zenodo*. https://doi.org/10.5281/zenodo.10525136

Benoit, J. B., McCluney, K. E., DeGennaro, M. J., & Dow, J. A. T. (2023). Dehydration dynamics in terrestrial arthropods: From water sensing to trophic interactions. *Annual Review of Entomology*, *68*, 129–149.

Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2020). Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conservation and Diversity*, *14*, 167–187.

Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2021). Street lighting has detrimental impacts on local insect populations. *Science Advances*, *7*, eabi8322.

Bürkner, P. C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28.

Callaghan, C. T., Bowler, D. E., & Pereira, H. M. (2021). Thermal flexibility and a generalist life history promote urban affinity in butterflies. *Global Change Biology*, *27*, 3532–3546.

Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T., & Cornwell, W. K. (2019). Generalists are the most urban-tolerant of birds: A phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, *128*, 845–858.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, 1-32.

Ciolan, E., Cicort-Lucaciu, A.-Ş., Sas-Kovács, I., Ferenţi, S., & Covaciu-Marcov, S.-D. (2017). Wooded area, forest road-killed animals: Intensity and seasonal differences of road mortality on a small, newly upgraded road in western Romania. *Transportation Research Part D: Transport and Environment*, *55*, 12–20.

Diamond, S. E., Dunn, R. R., Frank, S. D., Haddad, N. M., & Martin, R. A. (2015). Shared and unique responses of insects to the interaction of urbanization and background climate. *Current Opinion in Insect Science*, *11*, 71–77.

Egerer, M. H., Arel, C., Otoshi, M. D., Quistberg, R. D., Bichier, P., & Philpott, S. M. (2017). Urban arthropods respond variably to changes in landscape context and spatial scale. *Journal of Urban Ecology*, *3*, jux001.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.

Fenoglio, M. S., Calviño, A., González, E., Salvo, A., & Videla, M. (2021). Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecological Entomology*, 46, 757–771.

Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, 29, 1412–1429.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Forister, M. L., Halsch, C. A., Nice, C. C., Fordyce, J. A., Dilts, T. E., Oliver, J. C., Prudic, K. L., Shapiro, A. M., Wilson, J. K., & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American west. *Science*, 371, 1042–1045.

Franzén, M., Betzholtz, P.-E., Pettersson, L. B., & Forsman, A. (2020). Urban moth communities suggest that life in the city favours thermophilic multi-dimensional generalists. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20193014.

Futuyma, D. J. (1976). Food plant specialization and environmental predictability in lepidoptera. *The American Naturalist*, 110, 285–292.

Gaona, F. P., Iñiguez-Armijos, C., Brehm, G., Fiedler, K., & Espinosa, C. I. (2021). Drastic loss of insects (lepidoptera: Geometridae) in urban landscapes in a tropical biodiversity hotspot. *Journal of Insect Conservation*, 25, 395–405.

García-Barros, E. (2015). Multivariate indices as estimates of dry body weight for comparative study of body size in lepidoptera. *Nota Lepidopterologica*, 38, 59–74.

GBIF.org. (2023). *GBIF Occurrence Download*. https://doi.org/10.15468/dl.va2v37

Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S., & Dajoz, I. (2016). The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecology and Evolution*, 6, 6599–6615.

González-Césped, C., Alaniz, A. J., Vergara, P. M., Chiappa, E., Zamorano, J., & Mandujano, V. (2021). Effects of urban environmental conditions and landscape structure on taxonomic and functional groups of insects. *Urban Forestry & Urban Greening*, 58, 126902.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, 319, 756–760.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809.

Homer, C., Dewitz, J., Jin, S., Xian, G., Costello, C., Danielson, P., Gass, L., Funk, M., Wickham, J., Stehman, S., Auch, R., & Riitters, K. (2020). Conterminous United States land cover change patterns 2001–2016 from the 2016 National Land Cover Database. *ISPRS Journal of Photogrammetry and Remote Sensing*, 162, 184–199.

Isaksson, C., & Andersson, S. (2007). Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. *Journal of Avian Biology*, 38, 564–572.

Kaiser, A., Merckx, T., & Van Dyck, H. (2016). The urban heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity. *Ecology and Evolution*, 6, 4129–4140.

Kawahara, A. Y., Reeves, L. E., Barber, J. R., & Black, S. H. (2021). Eight simple actions that individuals can take to save insects from global declines. *Proceedings of the National Academy of Sciences*, 118, e2002547117.

Kawula, R., & Redner, J. (2018). Florida land cover classification system. Center for spatial analysis. In *Fish and wildlife research institute. Florida Fish and Wildlife Conservation Commission*. https://myfwc.com/media/20455/land-cover-classification-revision-2018.pdf

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante:

R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Kingsolver, J. G., Arthur Woods, H., Buckley, L. B., Potter, K. A., MacLean, H. J., & Higgins, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integrative and Comparative Biology*, 51, 719–732.

Kumar, S., Stecher, G., Suleski, M., & Hedges, S. B. (2017). TimeTree: A resource for timelines, timetrees, and divergence times. *Molecular Biology and Evolution*, 34, 1812–1819.

Lazaridis, E. (2022). *Lunar: Lunar phase & distance, seasons and other environmental factors*.

Leckie, S., & Beadle, D. (2018). *Peterson field guide to moths of southeastern North America*. HarperCollins.

Lee, K. P., & Roh, C. (2010). Temperature-by-nutrient interactions affecting growth rate in an insect ectotherm. *Entomologia Experimentalis et Applicata*, 136, 151–163.

Li, D., & Ives, A. R. (2017). The statistical need to include phylogeny in trait-based analyses of community composition. *Methods in Ecology and Evolution*, 8, 1192–1199.

Li, D., Trotta, L., Marx, H. E., Allen, J. M., Sun, M., Soltis, D. E., Soltis, P. S., Guralnick, R. P., & Baiser, B. (2019). For common community phylogenetic analyses, go ahead and use synthesis phylogenies. *Ecology*, 100, e02788.

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, 56, 311–323.

Marciniak, B., Nadolski, J., Nowakowska, M., Loga, B., & Bańbura, J. (2007). Habitat and annual variation in arthropod abundance affects blue tit Cyanistes caeruleus reproduction. *Acta Ornithologica*, 42, 53–62.

McElrath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and STAN* (Second ed.). Chapman and Hall.

Merckx, T., Huertas, B., Basset, Y., & Thomas, J. (2013). A global perspective on conserving butterflies and moths and their habitats. *Key Topics in Conservation Biology*, 2, 237–257.

Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Global Change Biology*, 24, 3837–3848.

Merckx, T., Nielsen, M., Kankaanpää, T., Kadlec, T., Yazdanian, M., & Kivelä, S. (2024). Continent-wide parallel urban evolution of increased heat stress in a moth species. *Evolutionary Applications*, 17, e13636.

Merckx, T., Nielsen, M. E., Kankaanpää, T., Kladec, T., Yazdanian, M., & Kivelä, S. M. (2023). Dim light pollution prevents diapause induction in urban and rural moths. *Journal of Applied Ecology*, 60, 1022–1031.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hendrickx, F., Higuti, J., Lens, L., Martens, K., … Van Dyck, H. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*, 558, 113–116.

Merckx, T., & Van Dyck, H. (2019). Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography*, 28, 1440–1455.

Michonneau, F., Brown, J. W., & Winter, D. J. (2016). Rotl: An R package to interact with the open tree of life data. *Methods in Ecology and Evolution*, 7, 1476–1481.

Miller, J. S., Wagner, D. L., Opler, P. A., & Lafontaine, J. D. (2018). *Drepanoidea, Doidae; Noctuoidea, Notodontidae (Part): Pygaerinae, Notodontinae, Cerurinae, Phalerinae, Periergosinae, Dudusinae, Hemiceratinae. The Moths of America North of Mexico, Fascicle 22.1A*: 146; pl. A-5, figs. 18-21.

Miller, J. T., Jolley-Rogers, G., Mishler, B. D., & Thornhill, A. H. (2018). Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution*, 56, 663–667.

Montgomery, G. A., Belitz, M. W., Guralnick, R. P., & Tingley, M. W. (2021). Standards and best practices for monitoring and benchmarking insects. *Frontiers in Ecology and Evolution*, 8, 513.

Narango, D. L., Tallamy, D. W., & Shropshire, K. J. (2020). Few keystone plant genera support the majority of lepidoptera species. *Nature Communications*, 11, 5751.

Ooms, J., & Chamberlain, S. (2019). *phylocomr: Interface to "Phylocom.".*

Peng, J., Tian, L., Liu, Y., Zhao, M., Hu, Y., & Wu, J. (2017). Ecosystem services response to urbanization in metropolitan areas: Thresholds identification. *Science of the Total Environment*, 607–608, 706–714.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., Lens, L., Merckx, T., Mertens, D., van Kerckvoorde, M., De Meester, L., & Hendrickx, F. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, 23, 2554–2564.

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., Decaestecker, E., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hanashiro, F. T. T., Higuti, J., Lens, L., ... Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 26, 1196–1211.

Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82, 275–285.

Raupp, M. J., Shrewsbury, P. M., & Herms, D. A. (2012). Disasters by design: Outbreaks along urban gradients. In *Pages 311–340 Insect Outbreaks Revisited*. John Wiley & Sons, Ltd.

Rocha-Ortega, M., Rodriguez, P., & Córdoba-Aguilar, A. (2021). Geographical, temporal and taxonomic biases in insect GBIF data on biodiversity and extinction. *Ecological Entomology*, 46, 718–728.

Rytkönen, S., Vesterinen, E. J., Westerduin, C., Leviäkangas, T., Vatka, E., Mutanen, M., Välimäki, P., Hukkanen, M., Suokas, M., & Orell, M. (2019). From feces to data: A metabarcoding method for analyzing consumed and available prey in a bird-insect food web. *Ecology and Evolution*, 9, 631–639.

Schmitt, L., & Burghardt, K. T. (2021). Urbanization as a disrupter and facilitator of insect herbivore behaviors and life cycles. *Current Opinion in Insect Science*, 45, 97–105.

Schowalter, T. D., Pandey, M., Presley, S. J., Willig, M. R., & Zimmermann, J. K. (2021). Arthropods are not declining but are responsive to disturbance in the Luquillo experimental Forest, Puerto Rico. *Proceedings of the National Academy of Sciences*, 118, e2002556117.

Secondi, J., Davranche, A., Théry, M., Mondy, N., & Lengagne, T. (2020). Assessing the effects of artificial light at night on biodiversity across latitude—Current knowledge gaps. *Global Ecology and Biogeography*, 29, 404–419.

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., Sinkovics, C., Evans, K. L., & Liker, A. (2018). Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecological Applications*, 28, 1143–1156.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109, 16083–16088.

Slade, E. M., Merckx, T., Riutta, T., Bebber, D. P., Redhead, D., Riordan, P., & Macdonald, D. W. (2013). Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, 94, 1519–1530.

Solonen, T. (2001). Breeding of the great tit and blue tit in urban and rural habitats in southern Finland. *Ornis Fennica*, 78, 49–60.

Sparrius, L. B., van den Top, G. G., & van Swaay, C. A. M. (2018). An approach to calculate a species temperature index for flora based on open data. *Groteria*, 40, 73–78.

Straka, T. M., von der Lippe, M., Voigt, C. C., Gandy, M., Kowarik, I., & Buchholz, S. (2021). Light pollution impairs urban nocturnal pollinators but less so in areas with high tree cover. *Science of the Total Environment*, 778, 146244.

Thang, T. H., Thu, A. M., & Chen, J. (2020). Tree species of tropical and temperate lineages in a tropical Asian montane forest show different range dynamics in response to climate change. *Global Ecology and Conservation*, 22, e00973.

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

Thornton, P. E., Thornton, M. M., Mayer, B. W., Wei, Y., Devarakonda, R., Vose, R. S., & Cook, R. B. (2016). *Daymet: Daily surface weather data on a 1-km grid for North America, Version 3*. ORNL DAAC.

Tinbergen, J. M., & Dietz, M. W. (1994). Parental energy expenditure during brood rearing in the great tit (Parus major) in relation to body mass, temperature, food availability and clutch size. *Functional Ecology*, 8, 563–572.

U.S. Census Bureau. (2020). *2020 Decennial Census*.

United Nations. (2018). *World economic situation and prospects 2018*. United Nations.

van Klink, R., Bowler, D. E., Gongalsky, K. B., Shen, M., Swengel, S. R., & Chase, J. M. (2023). Disproportionate declines of formerly abundant species underlie insect loss. *Nature*, 1–6. https://doi.org/10.1038/s41586-023-06861-4

Vaz, S., Manes, S., Khattar, G., Mendes, M., Silveira, L., Mendes, E., de Morais Rodrigues, E., Gama-Maia, D., Lorini, M. L., Macedo, M., & Paiva, P. C. (2023). Global meta-analysis of urbanization stressors on insect abundance, richness, and traits. *Science of the Total Environment*, 903, 165967.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480.

Wagner, D. L., Fox, R., Salcido, D. M., & Dyer, L. A. (2021). A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proceedings of the National Academy of Sciences*, 118, e2002549117.

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*, 118, e2023989118.

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24, 2098–2100.

Weisser, W., Blüthgen, N., Staab, M., Achury, R., & Müller, J. (2023). Experiments are needed to quantify the main causes of insect decline. *Biology Letters*, 19, 20220500.

Wenzel, A., Grass, I., Belavadi, V. V., & Tscharntke, T. (2020). How urbanization is driving pollinator diversity and pollination—A systematic review. *Biological Conservation*, 241, 108321.

White, P. J. T., Glover, K., Stewart, J., & Rice, A. (2016). The technical and performance characteristics of a low-cost, simply constructed, black light moth trap. *Journal of Insect Science*, 16, 25.

Yan, Z., Teng, M., He, W., Liu, A., Li, Y., & Wang, P. (2019). Impervious surface area is a key predictor for urban plant diversity in a city undergone rapid urbanization. *Science of the Total Environment*, 650, 335–342.

Yazdanian, M., Kankaanpää, T., Itämies, J., Leinonen, R., Merckx, T., Pöyry, J., Sihvonen, P., Suuronen, A., Välimäki, P., & Kivelä, S. M. (2023). Ecological and life-history traits predict temporal trends in biomass of boreal moths. *Insect Conservation and Diversity*, 16, 600–615.

SUPPORTING INFORMATION

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