

REPORT

Temperature niche and body size condition phenological responses of moths to urbanization in a subtropical city

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Abstract

Urbanization in temperate climates often advances the beginning and peak of biological events due to multiple factors, especially urban heat islands. However, the effect of urbanization on insect phenology remains understudied in more tropical areas, where temperature may be a weaker phenological cue. We surveyed moths across an urban gradient in a subtropical city weekly for a year to test how impervious surface and canopy cover impact phenology at the caterpillar and adult life stages. For macro-moths, we also examine how these effects vary with life history traits. When pooling all individuals, we found no effect of urbanization proxy variables on timing of caterpillar or adult phenology. At the species-specific level, we found timing of peak adult macro-moths is influenced by canopy cover, which also interacts with two traits: temperature niche and body size. Cold-adapted species delay timing of peak abundance in more shaded sites, while warm-adapted species were not affected. Smaller species, associated with lower dispersal ability, were more phenologically sensitive to canopy cover than larger bodied species. These results highlight the importance of canopy cover within cities and its interaction with species' traits in mediating impact of urbanization on moth phenology in subtropical systems.

KEYWORDS

canopy cover, caterpillars, insects, phenology, subtropical ecology, urban heat

INTRODUCTION

Urbanization is a major driver of habitat and biodiversity loss as cities are rapidly expanding worldwide (Simkin et al., 2022). Cities may also disrupt ecological dynamics in more subtle ways such as altering the timing of life history events (i.e., phenology) (Neil & Wu, 2006; Villalobos-Jiménez & Hassall, 2017). In temperate regions, urbanization most often leads to earlier

phenological events, a phenomenon best documented in plants (Jochner & Menzel, 2015; Neil & Wu, 2006). The cause of urbanization-driven shifts in phenology is often attributed to the urban heat island effect, a process which leads to warmer urban environments than surrounding natural environments (Jochner & Menzel, 2015). Many factors influence urban climates, and variability in air temperature within cities can vary dramatically (up to 5.7°C in a mid-sized Midwestern US city), with the

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greatest cooling occurring in areas with canopy cover exceeding 40% (Ziter et al., 2019). Urbanization likely also affects phenology through other mechanisms (Li et al., 2019), such as lower moisture availability shortening plant growing season in cities (Kabano et al., 2021), changes in source-sink dynamics leading to observed butterflies immigrating from surrounding habitat thus appearing later in cities (Altermatt, 2012), or artificial light at night disrupting the induction of diapause (Merckx et al., 2021).

Urban footprints are expanding most rapidly in subtropical and tropical regions (Seto et al., 2012; United Nations, 2018). However, far fewer studies exist in these regions, and methods for low latitude phenological research are still being developed (Davis et al., 2022). Studies testing the impact of urbanization on subtropical and tropical phenology have most often focused on plants, finding stark differences compared with urbanization studies in temperate regions where the magnitude of the urban heat island effect is larger (Manoli et al., 2019). For example, urban budburst often occurs earlier in temperate cities, but is delayed in most tropical cities (Gazal et al., 2008). Likewise, the growing season of plants was found to be reduced in cities compared with surrounding rural areas since temperature is likely a less important phenological cue in tropical ecosystems, but urban warming can lead to greater water stress (Kabano et al., 2021). These results have also been demonstrated in macroscale studies that found the onset of plant phenology to be earlier in more urbanized areas in temperate regions, but later in warmer, subtropical regions (Li et al., 2019).

The potential interaction between regional climate context and the effect of urbanization is far less known in insects. A study across a temperature gradient in Ohio, United States, suggests a similar pattern as found in plants, where urbanization led to earlier first appearances and peak abundance of butterflies in cooler areas (Diamond et al., 2014). Conversely, the phenology of several butterfly species was delayed in areas that were urbanized and relatively warm (Diamond et al., 2014). Existing work suggests that low-latitude insect phenology is more likely to be driven by changes in seasonal precipitation rather than by temperature or day length (Henry et al., 2022). Still, understanding of insect phenology is particularly limited in subtropical and tropical areas due in part to the challenges of year-round sampling (Slade & Ong, 2023). Surprisingly, we are not aware of a study that tests the impacts of urbanization on insect phenology in a subtropical or tropical climate. Given the disproportionate amount of biodiversity harbored in subtropical and tropical locales, combined with the

projected urban development in these areas (United Nations, 2018), it is timely to quantify the effect of urbanization on ecological dynamics in these areas.

Here, we use repeated structured surveys at sites along an urbanization gradient to test how the peak abundance timing of a subtropical moth (Lepidoptera) community across both caterpillar and adult life stages is influenced by the proportion of impervious surface and canopy cover. We first examine how the timing of abundance peaks is influenced by land cover variables at the overall macro-moth, micro-moth, and caterpillar community level. We then examine how land cover responses are mediated across species-specific life history traits for macro-moths. We hypothesize that canopy cover will have a greater influence on moth phenology since tree canopies provide important cooling in urban environments (Ziter et al., 2019), and we expect sites with greater canopy cover will have later peak dates of both caterpillars and adults. We further predict a strong interaction between canopy cover and life history traits, and in particular, we expect smaller and more cold-adapted species to shift their phenology more in response to variation in canopy cover. We expect smaller species will have lower dispersal ability and thus are worse at tracking microclimatic conditions and more dependent on tracking the phenology of their host plants (Diamond et al., 2011). Warm-adapted species are expected to shift their adult activity period less since phenology of these species is likely less strongly cued by temperature (Buckley, 2022).

METHODS

Study sites and sampling protocol

The data used in this study come from the same dataset used to examine the effect of urban development on the biomass of caterpillars and the abundance of adult moths (Belitz et al., 2024). The sample sites and sampling protocol are described in detail in Belitz et al. (2024), which we briefly summarize below. We repeatedly sampled nine study sites along an urbanization gradient in Alachua County, located in North Central Florida, United States (Figure 1A,B). We collected caterpillar frass (i.e., feces) and adult moth samples approximately once per week between March 10, 2019, and Feb. 28, 2020. The most urban sites were located in the center of Alachua County, which occupies the city-center of the county's largest city—Gainesville—with a population of 141,085 as of the 2020 census (U.S. Census Bureau, 2020). All nine sites were located

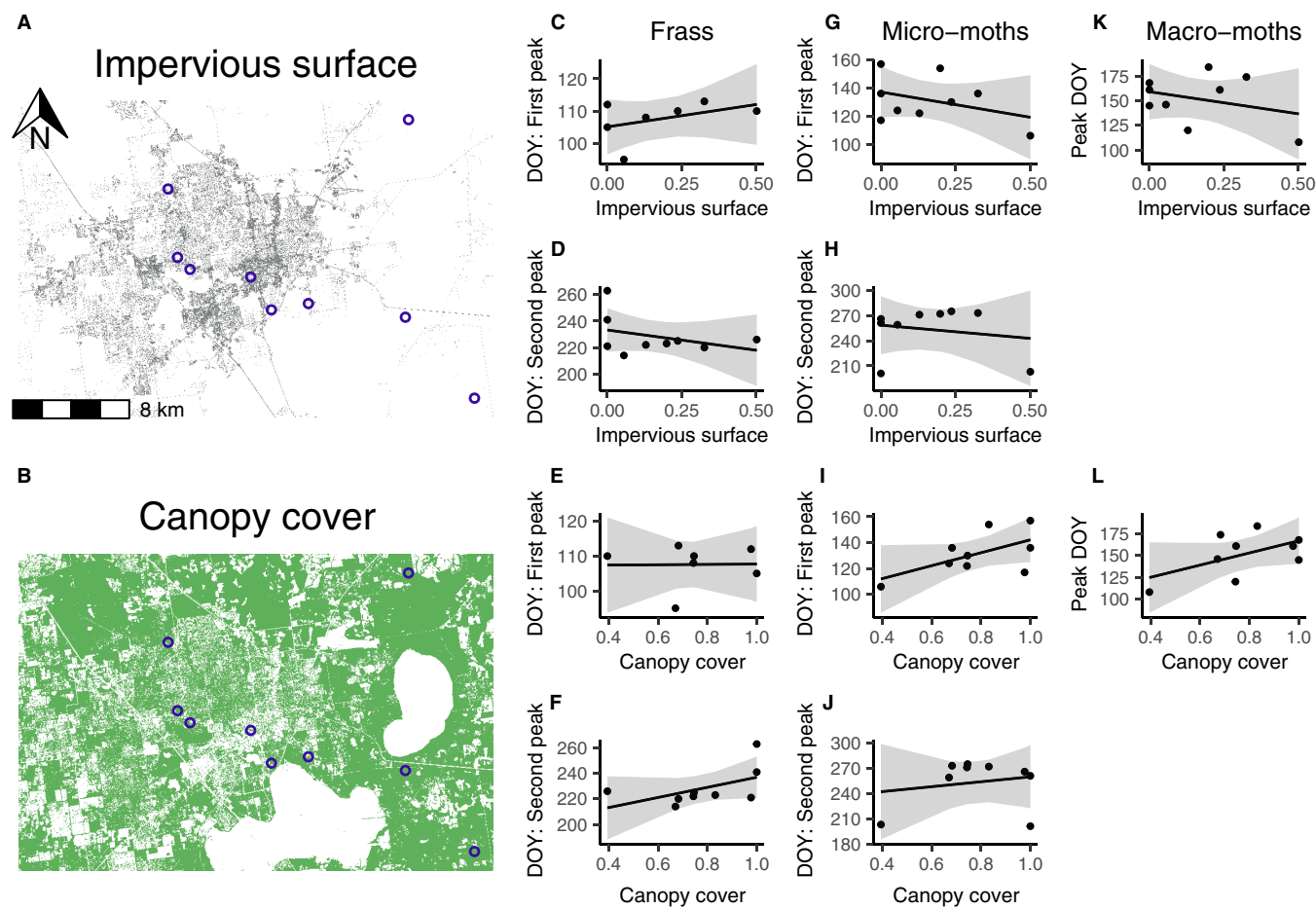


FIGURE 1 Study area and effect plots of pooled community response to the two land cover variables: proportion of impervious surface and canopy cover within 300 m radius of the light trap. Map of impervious surface (A) and canopy cover (B) within study area is shown at a 1-m resolution. Fixed-effect plots predicting the effect of impervious surface on pooled frass (C, D), micro-moth (G, H), and macro-moth peak (K) phenology. Fixed-effect plots also display the effect of canopy cover on pooled frass (E, F), micro-moth (I, J), and macro-moth peak (L) phenology. Our results provide no evidence that these urbanization variables affect the timing of the pooled abundance of moths, as the 95% CIs of all estimated slope coefficients included a slope of zero. DOY, day of year.

within forested conservation areas, and sites were selected to ensure light and frass traps were in compositionally similar forests where oaks (*Quercus*) were the dominant tree species.

Within each site, we selected six locations for frass traps and one location for a light trap for capture of adult moths. Frass biomass is commonly used as an index of caterpillar biomass (Seress et al., 2018). Our frass traps were positioned below the canopy of oaks and were custom-made to allow frass sampling to occur throughout the wet season (Appendix S2: Figure S1), and although frass was indeed collected year-round, less frass mass was collected during rainier weeks (Belitz et al., 2024). We processed frass by first removing non-frass debris from the samples. Frass samples were dried at room temperature before being weighed using a scale with 0.001 precision in grams, and the amount of frass over the sampling period (mg/day) was calculated.

Light traps were positioned in approximately the centroid location among the six frass traps. All macro-moths, defined here as individuals with a length from head to abdomen greater than 10 mm, were identified to the finest taxonomic resolution possible (see supplemental materials for further details on identification protocol). The total number of micro-moths collected at each site on each sampling night was recorded, but samples were left unidentified because doing so is extremely difficult and time consuming. In total, we collected and sorted 30,497 micro-moths and 5505 macro-moths.

Phenology estimates

We estimated the day of year (DOY) with the peak amount of cumulative micro-moths, macro-moths, and

frass at each site. To do so, we fit generalized additive models for each site (GAMS) using a cubic spline smoothing basis where the response variables were the total of micro-moths, macro-moths, or frass mass (measured in mg per day between sample collection) collected at each site and the predictor variable was DOY. For the adult moths, we fit the GAMs using the negative binomial distribution since this distribution family better fit our over-dispersed count data (see Appendix S1 for residual diagnostics of GAMs). The frass data were fit using the gaussian family. Since our sampling wrapped around the calendar year, 365 days were added to the 2020 DOY dates. Illuminated fraction of the moon was gathered from the R package *suncalc* (Thieurmel & Elmarhraoui, 2022) and included as a predictor variable in the adult moth models to account for lunar phase, since this is known to influence effectiveness of light traps (Bowden & Church, 1973). Similar to Stemkovski et al. (2020), we set the dimension of the DOY smoothing basis to six, and the dimension of the lunar illumination smoothing to three. The frass mass model included trap number as a random effect to account for trap-specific variation.

We made predictions using our fitted GAMs to estimate the timing of peaks in abundance during our study duration. Fitted GAMs were predicted across DOY, while holding lunar phase at its mean value. Because our caterpillar frass (Appendix S2: Figure S2) and micro-moth (Appendix S2: Figure S3) GAMs showed bimodality, we opted to estimate the dates of the first and second peaks of frass and micro-moth abundance. First peak dates correspond to a spring peak and were estimated as the DOY with the highest peak abundance before the start of summer (June 21; DOY 172). We could not predict an unambiguous first peak of frass in two sites (Appendix S2: Figure S3) and thus these sites are not included in downstream analysis. Second peak dates correspond to a fall peak and were estimated as the DOY with the highest predicted peak after the start of summer. Macro-moth counts only had one peak across sites (Appendix S2: Figure S4) and therefore we only extracted the DOY when the abundance peaked for each site.

We used the same approach described above to estimate the peak of activity for macro-moths at the species-specific level if the species was sampled on at least three unique days within the same site. We examined the output of all GAMs, and instances where our model did not predict an unambiguous abundance peak were removed from further analyses (as in Stemkovski et al., 2020). Species needed phenology estimates for at least two sites to be included for downstream analyses. In total, 120 combinations of species and sites had estimates

of peak abundance, representing 33 species with varying life history traits.

Land cover variables

We included two land cover variables as predictors in analyses described below: (1) proportion of man-made impervious land surface and (2) proportion of forest canopy cover. Proportion of impervious surface reflects the proportion of 1-m-resolution pixels classified as impervious within a 300-m-buffer around a light trap based on the 2022 Coastal Change Analysis Program (C-CAP) High-Resolution Land Cover (NOAA, 2023). The proportion of canopy cover was calculated in the same way but for the land classification forest canopy cover. We measured our land cover variables at 300 m as there is evidence that this is an ecologically relevant scale to study urban heat islands (Morabito et al., 2021).

Trait data

For the 33 species with phenology estimates, we collected trait information thought to be relevant to subtropical insect phenology. These traits were body size and temperature niche. Information on body size was gathered from Leckie and Beadle (2018). Temperature niche for each species was calculated as an average of range-wide annual temperature values using occurrence records. Detailed methods on how traits were gathered and summarized can be found in Appendix S2.

Statistical analyses

We used linear models to examine the effects of urbanization on the timing of peak moths at the overall community levels. Estimates of the timing of peak micro-moth, macro-moth, and frass abundance were the response variables. For each response variable, we fit two univariate models to estimate the effect of our land cover variables on our phenological metric. The two land cover variables, proportion of impervious surface and proportion of canopy cover, were strongly correlated ($r = -0.87$) and therefore were never included in the same models.

At the species-specific level, we used linear mixed models to examine whether the effect of land cover on the phenology of macro-moth species differs across life history traits. We fit two models with the response variables being a species' date of peak abundance, which was treated as a gaussian process. Predictor variables were

either proportion of impervious surface or proportion of canopy cover, and the life history traits. We also included two two-way interactions between the land cover variable and the two life history traits. Predictor variables were scaled to have a mean of zero and a SD of 1 to allow for easily interpretable model effect sizes across variables. We accounted for species-level variation by modeling each species with a random intercept. We used a likelihood ratio test to quantify whether these full models fit the data better than a model with only an intercept fixed effect and random intercepts for species. We also checked the robustness of our top linear mixed model result by building a phylogenetic linear mixed model that accounts for phylogenetic relationships among species (see Appendix S2 for detailed methods). The phylogenetic linear mixed model showed that results were largely the same (Appendix S2: Table S1). In the main text, we report results of our linear mixed model that does not include the phylogenetic term.

RESULTS

At the community level, we did not find evidence that the phenology of the pooled abundance of caterpillars, micro-moths, or macro-moths was influenced by either the proportion of impervious surface or the proportion of canopy cover surrounding the sites, as the 95% CIs around our slope coefficient estimates always encompassed a slope of zero (Appendix S2: Table S2). The steepest slope estimates were the effects of canopy cover on the first peak of macro- and micro-moths, which showed later dates of first peaks in sites with greater canopy cover (Figure 11,L). However, the coefficient estimates of these slopes had high uncertainty and wide CIs that encompass a line of zero slope (slope coefficient estimate for micro-moth model = 49.98, 95% CI -10.66, 110.62; slope coefficient estimate for macro-moth model = 70.02, 95% CI -24.15, 164.18).

At the species-specific level, we found evidence that the proportion of canopy cover, but not the proportion of impervious surface, affects the timing of a macro-moth species' peak abundance (Table 1). Holding other variables constant, a 1 SD increase in the proportion of canopy cover (0.13) delays species-specific peak abundance by about 11 days (slope coefficient estimate = 11.19, 95% CI 1.74, 20.73). We also found an important interaction between canopy cover and species' temperature niche (slope coefficient estimate = -12.26, 95% CI -22.57, -1.97) and between canopy cover and body size (slope coefficient estimate = -16.73, 95% CI -16.73, -1.38). Specifically, we found that species with colder temperature niches had later peaks in sites with greater canopy

TABLE 1 Mean fixed effect coefficient estimates and 95% CIs for models predicting the species-specific timing of peak macro-moth abundance.

Predictor variables	Impervious surface model	Canopy cover model
(Intercept)	182.26 (164.03, 200.65)	184.55 (167.23, 202.04)
Proportion land cover (300 m)	-3.30 (-12.97, 6.23)	11.19 (1.74, 20.73)
Body size	10.61 (-13.21, 34.46)	11.44 (-10.97, 33.90)
Temperature niche	-13.59 (-32.84, 5.18)	-14.64 (-32.73, 3.04)
Prop land cover: body size	9.57 (-8.10, 27.32)	-16.73 (-32.14, -1.38)
Prop land cover: temperature niche	1.90 (-9.15, 12.99)	-12.26 (-22.57, -1.97)
Marginal R^2	0.07	0.14
Conditional R^2	0.48	0.61
χ^2	5.10	16.98
Degrees of freedom	5	5
<i>p</i> value	0.40	0.004

Note: CIs that exclude 0 are shown in bold. Proportion land cover in the predictor variables column reflects either impervious surface or canopy cover which is indicated by column headers. The χ^2 values represent test statistics and associated degrees of freedom and *p* values for a likelihood ratio test quantifying whether the full models fit the data better than a model with only an intercept fixed effect and random intercept for species. The canopy cover model, but not the impervious surface model, demonstrated a better fit than the intercepts-only model. Predictor variables are scaled to have a mean of zero and SD of 1.

cover, while species with warmer temperature niches did not vary the timing of peak abundance across a canopy cover gradient (Figure 2C). The body size interaction estimates indicate that smaller macro-moths had later peak abundances, while the timing of peak abundance was unaffected for larger macro-moths (Figure 2D).

DISCUSSION

We repeatedly sampled larval and adult moths across an urbanization gradient in a subtropical environment to better understand the impacts of urbanization-driven changes in land cover on the timing of peak abundance for larval and adult moths. At an overall, pooled community level, we did not find evidence that changes in the amount of impervious surface or canopy cover impacts the timing of peak phenology. However, our species-specific models provide evidence that certain species had delayed peak abundances in sites with greater

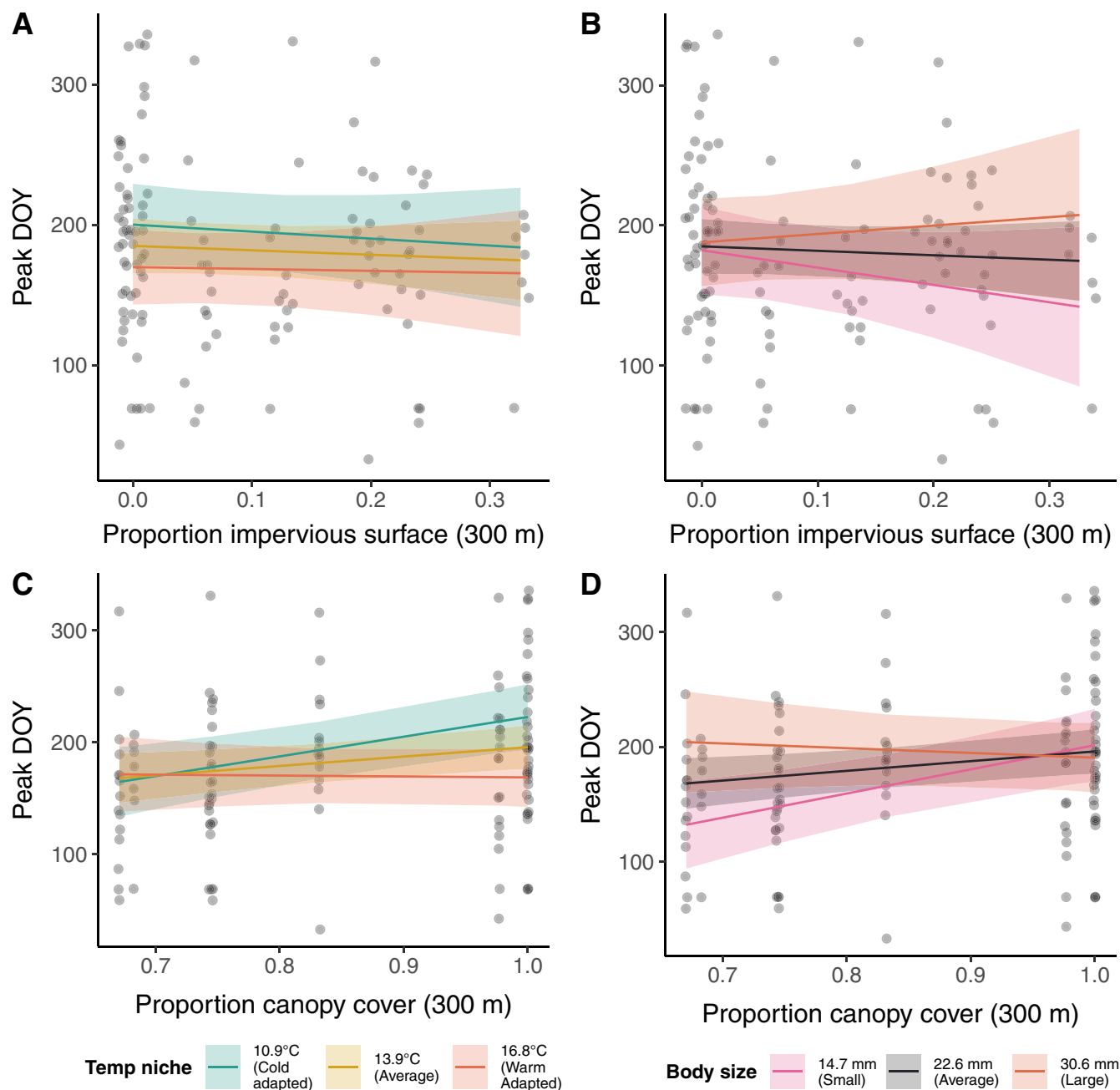


FIGURE 2 Predicted values of the interaction between the two land cover variables and the two life history traits, while keeping all other variables constant. The date of peak abundance for macro-moth species did not change across an impervious surface gradient regardless of trait values (A, B). Species with cooler temperature niches are predicted to have later peak abundance in sites that are surrounded by more canopy cover, while species with warmer temperature niches are predicted to have consistent peak abundance dates (C). Smaller species were most phenologically responsive to increases in canopy cover, while larger species have consistent dates of peak abundance regardless of the amount of canopy cover (D). Niche and body mass traits are continuous and values in the legend for those traits denote mean and 1 SD for those values. Values in the legend are then used for displaying predicted interactions. Points are jittered to better display data density. DOY, day of year.

canopy cover. Specifically, species with a cooler temperature niche and smaller body size had later peak abundances in sites that were surrounded by more canopy trees.

While results were not significant at the community level, proportion of canopy cover did explain over 25% of

the variation in the timing of the second frass peak and the first peak of pooled micro- and macro-moths, with more canopy cover corresponding to later dates. Our sampling design focused on strong temporal replication over a more limited number of sites, a choice which may have limited our power to detect differences across the

urbanization gradient. Further, documenting phenological effects at the community level might be particularly challenging in subtropical climates because the moth community comprises both temperate and tropical species. While temperate species might respond phenologically to the cooling provided by canopy cover, overall signal may be weak since the phenology of more tropical species is not strongly driven by temperature (Henry et al., 2022).

At the species-specific level, we found the timing of species' peak abundance to be later in sites with more extensive forest canopy cover within a 300 m radius of the site. The proportion of impervious surface surrounding a site however did not influence the timing of a species' peak abundance. Although canopy and impervious surface cover are both known to influence air temperature in urban areas, the relative benefit of increased canopy cover in the surrounding landscape likely exceeds that of reducing impervious surface cover (Ziter et al., 2019). Planting native trees in urban environments may offer several benefits such as mitigating negative effects of light pollution on moths (Straka et al., 2021), supporting higher abundance of caterpillars (Narango et al., 2017), and cooling the local area.

Not all macro-moth species had peak phenology that was influenced by the amount of canopy cover surrounding a site. We found that temperature niche and body size determine which species were sensitive to different amounts of canopy cover. The delayed phenology of cold-adapted species as compared with the lack of response of warm-adapted species may enable cold-adapted species to maintain trophic synchrony with host and nectar plants across much of their range, as urbanization otherwise leads to earlier plant leaf-out and flowering phenology in temperate regions (Li et al., 2019). The different responses between warm- and cold-adapted species may also relate to adapted differences in the degree to which temperature is a phenological cue (Henry et al., 2022), with species adapted to colder environments relying more heavily on temperature cues to synchronize phenology with favorable environmental conditions to maximize fitness (Forrest & Miller-Rushing, 2010).

We also found that smaller moth species were more sensitive to the amount of canopy cover than larger moth species, supporting our hypothesis that moths with greater dispersal ability (as proxied by body size) are less sensitive to urban warming since they can more easily track suitable microclimatic conditions and are also less dependent on tracking the local phenology of their host plants (Diamond et al., 2011). Our result also supports a previous study that found the phenological sensitivity of butterfly species in Canada to be greater in less mobile

species compared with more mobile species (Kharouba et al., 2014), expanding the relevancy of dispersal ability to predict phenological sensitivity in Lepidoptera in both high latitude and subtropical environments. Unfortunately, direct measures of dispersal ability are poorly quantified for most moth species (Nieminen et al., 1999, but see Ovaskainen et al., 2019), leading us to use body size as our proxy variable (Sekar, 2012), and our conclusions would be strengthened with greater species-specific knowledge of moth dispersal ecology.

The literature presents mixed findings on how insects respond to urbanization: some studies report phenological advancements (Chick et al., 2019; Diamond et al., 2014), including studies examining date of peak frass fall (Hajdasz et al., 2019), while others have found no phenological differences across urban gradients (Fisogni et al., 2020; Seress et al., 2018). One challenge in this area of research is that urbanization often leads to reduced insect abundance (Belitz et al., 2024; Seress et al., 2018), which can skew phenological estimates toward later dates (Eddowes, 2023). Our approach of using GAMs to estimate peak abundance is likely more robust to variation in population size (Moussus et al., 2010), but careful thought must be taken to address abundance-driven bias when testing how urbanization influences the beginning or end of phenological events.

Our study is constrained by limited replication, both spatially (nine sites within one county) and temporally (1 year), which restricts our statistical power and heightens the risk that our findings might be influenced by unmeasured aspects of our study environment or peculiarities of the sampling year. We note that our study occurs in a subtropical environment with a distinct wet and dry season, and the impacts of urbanization on moth phenology in dry subtropical areas remain unknown. Additionally, our most urbanized sites were situated in a relatively small city that has an impressive network of forested city parks. Cities with greater densification and fewer trees would have a greater urban heat island effect, potentially generating different results. Larger urban areas may also have greater nonthermal environmental changes, such as shifts in relative humidity and increased water stress (Kabano et al., 2021), which could also influence moth phenology.

We are unaware of other studies estimating the effect of urbanization on insect phenology in a subtropical or tropical climate. Here, we get a first glimpse into how urbanization impacts caterpillars and adult moth phenology in a region that is less seasonal but not fully tropical. While our findings provide a basis for understanding how insects will respond to environmental change in subtropical environments, pressing questions remain unanswered. An essential next question is determining if temperature niche remains an important trait in

predicting phenological sensitivity in other taxonomic groups, such as plants, in subtropical areas. Phenological studies of insects in low-latitude environments have been nascent in large part because the continuous sampling necessary is extremely time-consuming and costly. However, monitoring networks of camera traps that use image processing to monitor insects are under rapid development, providing opportunities to decrease the time spent processing samples and expanding the gradients at which urban phenology questions can be asked.

AUTHOR CONTRIBUTIONS

Michael W. Belitz and Robert P. Guralnick conceived the idea of the study design and manuscript. Michael W. Belitz, Asia Sawyer, Lillian Hendrick, and Robert P. Guralnick conducted the fieldwork, led by Michael W. Belitz. Michael W. Belitz, Asia Sawyer, and Lillian Hendrick processed and identified field specimens, led by Asia Sawyer. Michael W. Belitz conducted the analyses. Michael W. Belitz and Robert P. Guralnick led the writing of the manuscript. All authors contributed critically to manuscript drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Belitz, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.13905288>.

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SUPPORTING INFORMATION

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

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