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LETTER

# Climate drivers of adult insect activity are conditioned by life history traits

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## Abstract

Insect phenological lability is key for determining which species will adapt under environmental change. However, little is known about when adult insect activity terminates and overall activity duration. We used community-science and museum specimen data to investigate the effects of climate and urbanisation on timing of adult insect activity for 101 species varying in life history traits. We found detritivores and species with aquatic larval stages extend activity periods most rapidly in response to increasing regional temperature. Conversely, species with subterranean larval stages have relatively constant durations regardless of regional temperature. Species extended their period of adult activity similarly in warmer conditions regardless of voltinism classification. Longer adult durations may represent a general response to warming, but voltinism data in subtropical environments are likely underreported. This effort provides a framework to address the drivers of adult insect phenology at continental scales and a basis for predicting species response to environmental change.

**KEYWORDS**
citizen-science, duration, emergence, insect seasonality, interactive effects, phenology, termination, voltinism

## INTRODUCTION

Shifts in phenology, that is, the timing of seasonal biological events, are among the most noticeable impacts of human-caused global change (Cleland et al., 2007; Parmesan, 2007). Numerous studies have shown that recent climate warming advances the timing of spring events, for example, budburst, breeding of amphibians and arrival of migrating birds (Cohen et al., 2018; Parmesan, 2007; While & Uller, 2014). Beyond global climate change, large-scale landscape modification can also impact phenology. For example, urbanisation has been shown to advance the timing of seasonal events such as plant flowering, in part through the urban heat island effect (reviewed in Neil & Wu, 2006). However, more recent work has revealed that urbanisation can also delay phenological events, especially in warmer regional climates (Li et al., 2019), although the mechanisms driving these delays have yet to be determined. Overall, there is considerable variation in phenological responses to global change both within and among species (Edwards

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Robert P. Guralnick and Brian J. Stucky these authors contributed equally to this work.

& Richardson, 2004; Park et al., 2019; Thompson & Clark, 2006). If interdependent species differentially respond to human-mediated changes, phenological mismatches may occur with potentially significant, negative demographic consequences (Miller-Rushing et al., 2010; Renner & Zohner, 2018).

Better understanding insect phenological responses is critical given their vast diversity, temperature-dependent developmental timing and critical role in ecosystems and the services they provide. These services include dung burial, pest control, pollination and wildlife nutrition and are valued at over $57 billion annually in the United States (Losey & Vaughan, 2006). Further, several recent papers have reported dramatic declines in insect populations (Hallmann et al., 2020; Wagner, 2020), potentially due to human-caused land-use change, climate change, introduced species and pollution (Wagner et al., 2021). Phenological shifts may exacerbate losses due to mismatches, but might provide a means to adapt to warmer temperatures and could even lead to overall population growth rates, particularly in species that can successfully add a generation due to extended growing seasons (Kerr et al., 2020).

Most insect phenological studies focus on how climate drives the *emergence* of insects. In general, warmer-than-average years cause adult insects to emerge earlier (Bartomeus et al., 2011; Roy et al., 2015; Villalobos-Jiménez & Hassall, 2017). Much less is known about what determines termination or total duration of insect activity (Forrest, 2016). Given extended growing seasons for many plant species (Steltzer & Post, 2009), it might be expected that insects also delay termination of adult insect activities in warmer regions. Longer growing seasons are increasing the number of generations per year (voltinism) of some insects (Altermatt, 2010a; Pöyry et al., 2011), but many species are obligate univoltine across their entire range, including warm regions (Forrest, 2016). For these reasons, life history traits, known to be important in determining insect activity (Diamond et al., 2011; Zografou et al., 2021), may strongly determine adult insect termination. For example, Stemkovski et al. (2020) found that timing of bee emergence was most influenced by climatic variation, but termination of adult bee foraging was better explained by life history traits. Specifically, bee species that nest below ground ended foraging earlier than species nesting above, but bee species that overwinter as prepupae ended foraging later than those that overwinter as pupae (Stemkovski et al., 2020).

Interannual regional climate variation is not the only driver of insect phenology. Urbanisation is in general leading to earlier flowering in many plant species due to the urban heat island effect, although these responses may be complex and context dependent (Jochner & Menzel, 2015). Less is known about insects' phenological response to urbanisation. The emergence of some insect species appears to be advancing in urbanised areas (Chick et al., 2019; Diamond et al., 2015), but other studies have found no change in phenology across urbanisation gradients, despite phenological advances in co-occurring plant species (Fisogni et al., 2020; Seress et al., 2018). The interaction between urbanisation and regional temperature can be an important driver of spatial phenology patterns, as urbanisation appears to advance plant phenology in cold areas but causes delays in warm areas (Li et al., 2019). Diamond et al. (2014) also demonstrated that the urbanisation effect on phenological responses of butterflies depends on regional temperature. This expected interaction between urbanisation and temperature remains untested at larger spatial scales and across a broader range of insect groups.

Establishing generalities about determinants of emergence, termination and duration of adult insect activity is challenging because most phenological research relies on surveys that provide much needed information on species' population abundance but are limited spatially and taxonomically. Recent enormous growth in open and freely accessible and curated community science photographs, such as those available via the iNaturalist platform, are allowing researchers to ask novel phenological questions at greater spatial and taxonomic scales (Li et al., 2021). However, careful data curation and specialised analytical methods must be used to generate biologically meaningful results (Larsen & Shirey, 2021).

Here, we use community-science-generated digital vouchers and digitised museum specimens to investigate how the emergence, termination and total duration of adult insects varies spatially in response to climate and urbanisation. We also examine how such responses differ across species-specific life history traits. We predict strong interactions between traits and key climate predictors. For example, we expect the seasonal activity of insects with thermally buffered larval stages to be less sensitive to variation in temperature than species without thermally buffered larval stages, aligning with a recent study on bees (Stemkovski et al., 2020). We further predict adult duration to vary based on voltinism, with multivoltine species showing stronger responses to temperature than univoltine species. Lastly, we predict adult insect termination to be later and adult duration longer in warmer and urbanised areas, consistent with recent studies in plants (Li et al., 2021).

## MATERIALS AND METHODS

### Insect species selection and data acquisition

Our study focused on the phenology of adult insects because they are often more active and easier to observe and identify, leading to more incidental records on biodiversity discovery platforms. We focused on the five most speciose orders with highly distinct adult forms: Coleoptera (beetles), Diptera (flies), Hymenoptera (bees, wasps, ants and sawflies), Lepidoptera (butterflies and moths) and Trichoptera (caddisflies). We also include the order Odonata (dragonflies and damselflies) and Cicadidae (cicadas), for which nymphs or larvae are visually distinct from adults and occupy infrequently surveyed habitats (aquatic and subterranean, respectively). A detailed explanation on the species selection protocol can be found in the Supporting Information.

Within these seven higher-level taxonomic groups, we used overall record counts in iNaturalist to select an initial set of candidate species. We limited searching to research-grade observations (verifiable observations with at least two independent species identifications) and included all insect species in focal groups that had at least 1000 observations within Canada, the United States and Mexico as of 8 April 2020. A total of 470 insect species met our search criteria, representing all our focal higher taxonomic groups except for Trichoptera.

We then further filtered to species primarily observed as adults and maintained those for which at least 99.5% of annotated observations had the life stage annotated as 'Adult' by iNaturalist users. Because Lepidoptera are commonly observed as juveniles, we only kept records annotated as adults in our final data set. Using our final species list, we collected data from GBIF (GBIF 2020a, 2020b, 2020c, 2020d, 2020e) and iDigBio, which aggregate iNaturalist records along with other biological collections. In total, we collected records for 435 species across six insect orders. We limited the temporal scope of our study to the recent years of 2015–2019.

## Phenology estimates

We gridded our study area into 25 × 25-km equal area cells using the North America Albers Equal Area Conic projection. Community science observations can be biased by organised, public observation events (e.g. iNaturalist's City Nature Challenge) generating an unusually high number of observations that do not reflect the actual seasonality of a species. We, therefore, filtered our data set to include only one observation per day of each species in a year, given each cell. Next, the number of observations for each cell-by-year-by-species combination was counted and deemed usable if at least 10 observations were documented. For each unique cell-year-species combination, we estimated the 0.05 and 0.95 sample quantiles using the quantile() function within the *stats* R package (R Core Team, 2020) to represent the emergence (first appearance) and termination (last evidence) of adult insect activity. These quantiles are demonstrated to be more robust estimates of phenology than estimating the absolute bounds of a phenophase (Belitz et al., 2020). We calculated the duration of adult insect activity as the difference between the termination and emergence. In total, we used 228,423 records to generate 5469 emergence, termination and duration estimates across 626 unique grid cells for 284 species. Over 97% had a basis of record listed as human observation, indicating the vast majority of the data were generated by community scientists.

## Trait data

We collected trait information from literature and web sources for the 284 species. We focused on traits thought to be relevant to insect phenology, including the following: (1) voltinism, (2) development type, (3) habitat of immature life stage, (4) diapause stage and (5) larval diet. We also estimated a categorical trait for the season of adult emergence. The seasonal categorisation of a species' emergence depends on its geographic location. Therefore, we use Hopkins' law, which states that phenology delays 4 days for every degree poleward, five degrees eastward, every 400 feet in elevation (Hopkins, 1920) to calculate a standardised emergence value for each species (see Supporting Information for more details). Species that on average emerge as adults in the first quartile among our study species were categorised as spring species, those between the first and third quartile were categorised as summer species, and the remaining insects were categorised as fall species. Voltinism (broods per year) was categorised as either obligate univoltine or not (including species that are only univoltine in part of their range and semi-, parti- and merovoltine species). Development type was categorised as either hemimetabolous or holometabolous. Habitat of immature life stage was categorised as above ground, freshwater, or underground. Diapause stage was categorised as egg, larva, pupa, adult, none or migratory. The larval diet was categorised as carnivorous, detritivorous or herbivorous.

Fifty-three species that passed initial filters for numbers of observations were missing trait data and were excluded from further analyses (Figure 1). We also removed species that do not diapause or are migratory, as these species likely have different physiological responses to temperature and urbanisation than the other species. Additionally, eusocial insects were removed because many can thermoregulate in unique ways (Heinrich, 1972; Jones & Oldroyd, 2006; Menzel & Feldmeyer, 2021). Finally, we removed species that had less than five unique year-by-grid cell combinations. In total, we were left with 2643 estimates of emergence, termination and duration from 101 species across 412 unique grid cells (Figure 2).

## Climate and urbanisation data

We included four climate and one urbanisation variable in our modelling framework. The climate variables were year-specific and included mean annual temperature, annual precipitation, temperature seasonality and precipitation seasonality. We obtained annual mean values

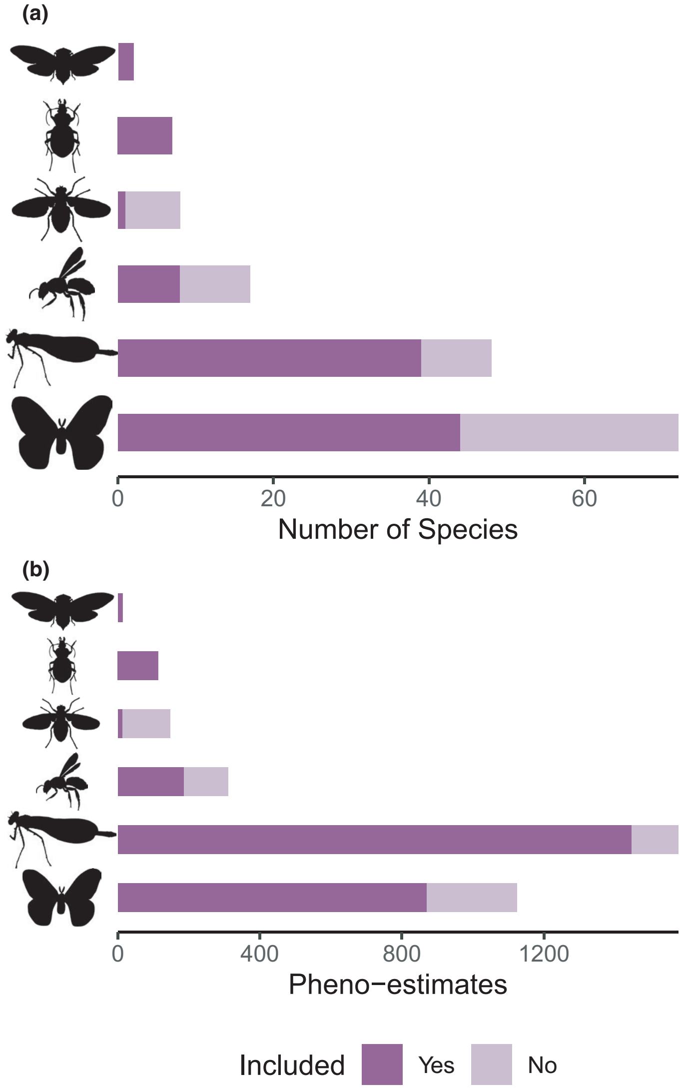

**FIGURE 1** Number of study species (a) and number of phenology estimates (b) included in or excluded from our modelling framework per taxonomic group (Cicadidae, Coleoptera, Diptera, Hymenoptera, Odonata and Lepidoptera in top to bottom order shown above). The same species could contribute multiple phenology estimates to the model by having enough records to generate estimates across multiple cells and years. Dark purple indicates the number of species or phenology estimates included in the modelling framework. Light purple indicates species or phenology estimates with enough phenology observations (>1000 iNaturalist observations and available in at least five year-by-cell combinations) that were removed from the analyses because of missing trait data. Counts do not include species that were eusocial, migratory, or do not diapause, as these were not included in our analyses. Silhouettes of Coleoptera (vectorisation by T. Michael Keesey; photography by Thorsten Assmann, Jörn Buse, Claudia Drees, Ariel-Leib-Leonid Friedman, Tal Levanony, Andrea Matern, Anika Timm and David W. Wrase), Hymenoptera (vectorisation by Melissa Broussard), Odonata (vectorisation by Maxime Dahirel) and Lepidoptera (vectorisation by Mali'o Kodis, photograph by Jim Vargo) were downloaded from www.phylopic.org. NS generated the Diptera and cicada silhouettes

of the maximum temperature and annual precipitation values for North America at a 1-km spatial resolution for the 5 years of our study from Daymet (Thornton et al., 2016a). We generated annual temperature and precipitation seasonality using the monthly maximum temperature and precipitation summaries provided by Daymet (Thornton et al., 2016b). Temperature seasonality was calculated as the standard deviation of the monthly maximum temperature values for the corresponding year, and precipitation seasonality was the coefficient of variation of the monthly precipitation values for the corresponding year.

We used estimated human population density for the year 2020 as a proxy for urbanisation and obtained these data from the Center for International Earth Science Information Network, which provides global estimates of population density at a 0.25-degree resolution (~27-km; CIESIN, 2017). Global estimates of human population density are only available on 5-year intervals, so we choose to only use the 2020 estimates as a proxy for urbanisation given our temporal extent. Year-specific changes in human population density are minimal compared with the variation across space and, therefore, should have little impact on statistical models.

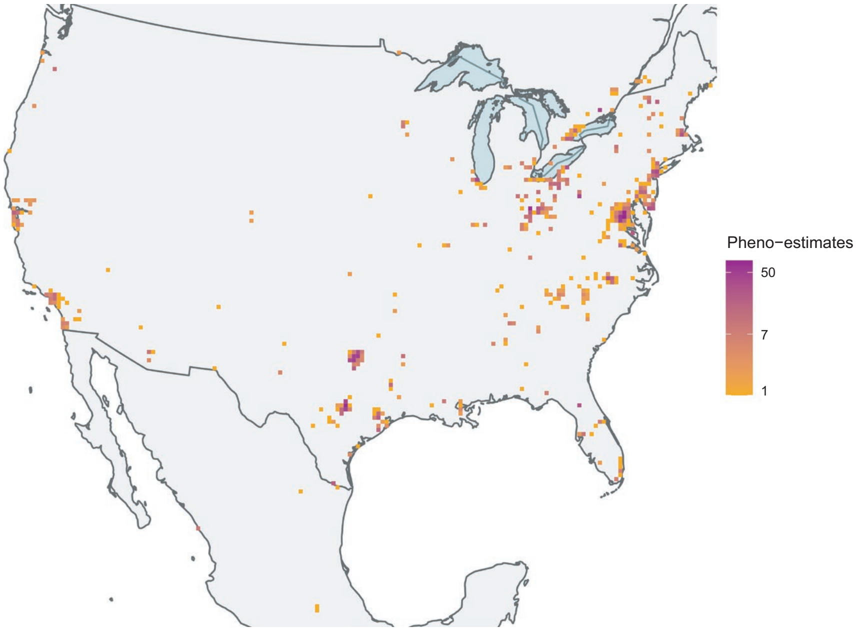

**FIGURE 2** Locations of 25 × 25-km cells with at least one species-by-year combination with enough data to produce phenology estimates of emergence, termination and duration. Number of species-year combinations are represented by the colour of the cell

## Statistical analysis

We used linear-mixed models (LMMs) to examine the effects of climate, urbanisation and life history traits on the emergence, termination and duration of adult insect activity across North America. Estimates of emergence, termination and duration were the response variables, and we included human population density, mean annual temperature, annual precipitation, temperature seasonality, precipitation seasonality as predictor variables along with two, two-way interactions based on previous biological knowledge. The two-way interaction terms tested were as follows: (1) whether the effects of annual temperature changed along a precipitation gradient and (2) whether the impacts of human population density changed along a temperature gradient. Areas with higher human population densities may have more incidental data records, biasing phenological metrics, and we controlled for this by including the number of observations as a fixed effect in our initial model. We scaled variables to have a mean of zero and standard deviation of one to ensure comparable model effect sizes across variables. Cell identity and insect species were included as random terms for intercepts, and insect species were included as a random term for the slope of each predictor variable. Next, we used backward model selection using the step function from the R package *lmerTest* (Kuznetsova et al., 2017). If any variance inflation factor (VIF) was greater than five for a variable in the best model, we removed the correlated variable with the lower absolute coefficient value and reran our backward selection process. We choose to remove correlated variables with VIFs greater than five, as it has been suggested for detecting potentially harmful multicollinearity (Kutner et al., 2004).

After selecting the best model with only climate, human population density and number of observation variables, we added insect traits to our models. We added two-way interaction terms between each trait variable with the climate and human population density variables to examine if adult insect phenology along climate and population density gradients changed for each trait. Backward model selection was performed as described above to reduce model variables and select a best model.

LMM can lead to false conclusions and inflated Type I error rates if phylogenetic relationships are ignored (Li & Ives, 2017). We, therefore, generated a subtree from the Open Tree of Life for the 101 insects in our analysis using the R package *rotl* (Michonneau et al., 2016). Branch lengths were generated by searching the TimeTree of Life database (Kumar et al., 2017) to get the estimated divergence time of each internal node. The branch lengths were then scaled from these ages using the ph_bladj() function from the R package *phylocomr* (Ooms & Chamberlain, 2019). We used this synthesis phylogeny to fit phylogenetic linear-mixed models (PLMMs) using a Bayesian framework with the default uninformative INLA priors (Rue et al., 2009). We used the R package *phyr* (Li et al., 2020) to fit our top LMM as PLMM. Our results differed slightly between the PLMM and LMM, and therefore, we present the results based on PLMM. Results of non-PLLMs are included in the supporting information (Table S1–S3).

We also examined spatial autocorrelation and the degree of autocorrelation of our top PLMM model residuals was calculated using Moran's *I* across different spatial lags starting at 25-km using the correlog() function from the R package ncf (Bjornstad, 2020). If significant Moran's *I* was detected at the nearest spatial distance, a spatial correlation covariance matrix was constructed for the cells in our study and included as a random term in top model. We found significant negative spatial autocorrelation in the residuals of the top termination and duration models at the two nearest distance classes (Figure S1), and, therefore, a spatial correlation covariance random term was for these models. We checked residuals of the top models to ensure models did not have any obvious deviation from model assumptions (See Supporting Information for more details and Figure S2 for residuals of the top models). We measured the goodness of fit of our PLMM using the package *rr2* (Ives & Li, 2018) to generate partial $R^2$ values (see supporting information for additional details).

## RESULTS

The emergence of adult insect activity is impacted by temperature, precipitation, temperature seasonality, life history traits, and the interactions among these variables (Table 1). Species that diapause as an egg have later emergence dates (approximately 43.5 days) than species that overwinter as adults (Table 1). A one standard deviation (SD) increase in temperature (4.77°C) led to earlier emergence of approximately 11.4 days (95% Bayesian credible intervals (CI) 2.4–20.5, but the effects of temperature varied with respect to regional precipitation and human population density values. Emergence values are later in cool areas with high human population density and earlier in warm areas with high human population density compared with corresponding rural areas (Figure 3a). Insects in warmer areas emerge earlier than in cool areas, and these shifts are more extreme in wet areas compared with drier areas (Figure 3b). The interaction between temperature and diapause stage, and the interaction between precipitation and voltinism also impacted the emergence of adult insect activity. The emergence of species that diapause as larva or pupa were more sensitive to temperature than species that diapause as adults or eggs (Figure 3c). Univoltine species had earlier emergence in areas with more precipitation, whereas species that are not univoltine had later emergence in areas with more precipitation (Figure 3d), although this interacting effect had credible intervals that encompassed zero. There was phylogenetic signal of the random species-specific intercept and the random species-specific slopes of precipitation (Figure S3). The partial $R^2$ of our best emergence model was 0.75 (Figure S4).

The top termination model consisted of a set of predictors that included precipitation, temperature seasonality, life-history traits and the interaction between temperature seasonality and immature habitat (Table 1). A one SD increase in precipitation (324 mm) led to a delay in termination of approximately 4 days (95% CI 2.4–6.3). Termination of activity was earlier for species that are first observed in spring or summer compared with species that are first observed as adults in fall (Table 1). Additionally, insect species that diapause as larvae terminate adult activity earlier than insects that diapause in other life stages (−20.4, 95% CI −38.3 to −2.4; Table 1). The termination of species whose immature habitat is underground remained relatively consistent across the temperature seasonality gradient, whereas species whose immature habitat is above ground or freshwater had earlier terminations at similar rates across the temperature seasonality gradient (Figure 4). Species that spend their immature life stage underground had earlier termination than species that spend their immature life stage in freshwater or aboveground. Detritivores had later terminations than herbivores or carnivores. Phylogenetic signal was again apparent for the species-specific random intercept and species-specific random slope of temperature seasonality and precipitation (Figure S3). The partial $R^2$ of our best termination model was 0.58 (Figure S4).

The top model of adult insect duration was predicted by climate, life history traits and the interaction between temperature and these other variables. Areas with greater temperature seasonality had shorter durations (Table 1). Wet regions had durations more sensitive to temperature than arid regions (Figure 5a). In contrast to species whose immature habitat is above ground or in freshwater, species whose immature habitat is underground were found to have consistent durations, regardless of whether they were in a warm or cool region (Figure 5b). Diapause stage was again an important trait, with insects that diapause as adults having the longest durations. Conversely, the durations of species that diapause as larvae were the shortest, 44.7 days shorter than species that diapause as adults (95% CI 25.9–62.9; Table 1). The duration of detritivores was strongly tied to regional temperature, with duration being much longer in warm regions compared with cool regions (Figure 5c). In addition to there being a phylogenetic signal in species-specific intercept and the species-specific slope of temperature, variation in duration was also partially explained by the phylogenetic signal in the species-specific precipitation slope (Figure S3). The partial $R^2$ of our best duration model was 0.75 (Figure S4). The number of observations used to estimate the phenometrics was included as a predictor variable in the top duration model, as well as in the top emergence and termination model.

## DISCUSSION

Most studies of insect phenology have focused on regional scales, and the few studies at larger spatial scales have been constrained to species easily identified by trained volunteers such as butterflies in the United Kingdom (e.g. Hodgson et al., 2011; Roy et al., 2015).

**TABLE 1** Fixed effects coefficients for top emergence, termination and duration models

| Term | Emergence | Termination | Duration |
|---|---|---|---|
| (Intercept) | **109.4 (93.5–125.3)** | **276.8 (246.8–306.6)** | **149.3 (120.7–177.2)** |
| Temperature | **−11.4 (−20.5 to −2.4)** | | 11.5 (−7.9 to 30.9) |
| Population density (human) | −0.98 (−3.3 to 1.4) | | |
| Precipitation | **3.2 (0.8–5.6)** | **4.3 (2.4–6.3)** | 1.1 (−1.6 to 3.9) |
| Temperature seasonality | **6.1 (2.7–9.6)** | **−12.6 (−17.5 to −7.8)** | **−13.9 (−18.4 to −9.5)** |
| Diapause stage (egg) | **43.5 (20.6–66.1)** | −16.6 (−38.3 to 5.2) | **−43.8 (−65.1 to 21.7)** |
| Diapause stage (larvae) | **31.2 (12.6–49.5)** | **−20.4 (−38.3 to −2.4)** | **−44.7 (−62.9 to 25.9)** |
| Diapause stage (pupae) | **40.0 (20.1–59.7)** | −1.4 (−20.5 to 17.8) | **−33.1 (−51.8 to −13.7)** |
| Flights (univoltine) | 4.6 (−6.1 to 16.2) | | |
| Season (spring) | | **−33.5 (−47.1 to −19.9)** | |
| Season (summer) | | **−21.2 (−31.4 to −10.9)** | |
| Immature habitat (freshwater) | | 12.7 (−23.4 to 48.8) | 4.7 (−30.3 to 40.4) |
| Immature habitat (underground) | | **−31.0 (−51.5 to −10.2)** | **−31.0 (−52.2 to −9.2)** |
| Larval diet (detritivorous) | | **36.1 (4.1–67.9)** | **34.6 (0.8–67.6)** |
| Larval diet (herbivorous) | | 10.3 (−13.3 to 33.9) | −1.4 (−25.9 to 22.9) |
| Temperature: precipitation | **−2.6 (−4.5 to −0.7)** | | **4.2 (1.5–7.0)** |
| Temperature: population density | **−2.2 (−4.3 to −0.1)** | | |
| Temperature: diapause stage (Egg) | −6.9 (−18.4 to 4.5) | | |
| Temperature: diapause stage (Larvae) | **−11.4 (−20.7 to −1.9)** | | |
| Temperature: diapause stage (Pupae) | **−12.8 (−22.7 to −2.7)** | | |
| Precipitation: flights (Univoltine) | −4.6 (−9.5 to 0.2) | | |
| Temperature seasonality: diapause stage (egg) | | | |
| Temperature seasonality: immature habitat (freshwater) | | −2.8 (−8.5 to 2.7) | |
| Temperature seasonality: immature habitat (underground) | | **12.2 (0.7–23.6)** | |
| Temperature: larval diet (detritivorous) | | | **29.1 (6.5–51.6)** |
| Temperature: larval diet (herbivorous) | | | 7.0 (−10.0 to 23.9) |
| Temperature: immature habitat (freshwater) | | | 10.7 (−11.0 to 33.1) |
| Temperature: immature habitat (underground) | | | −13.9 (−27.4 to 0.3) |
| Number of observations | **−3.6 (−4.5 to −2.8)** | **4.5 (3.5–5.4)** | **8.2 (7.1–9.4)** |

Bolding denotes coefficients whose 95% Bayesian credible interval does not include zero.

Here, we leverage rapidly increasing, openly available observation records to achieve the broad phylogenetic sampling necessary for finding commonalities in phenological sensitivity related to climate and life history traits, both important predictors of insect phenology. Our key finding is that timing of adult insect activity is temperature-driven but strongly conditioned by species traits. As we discuss below, these findings provide a basis for prediction of phenological responses in the face of environmental change.

## Drivers of adult insect emergence, termination and duration

In comparison with other aspects of insect phenology, the drivers of adult emergence are relatively well understood. The emergence of many insect species is controlled by temperature because the growth rate of immature stages increases at warmer temperatures (Gilbert & Raworth, 1996; Hodgson et al., 2011). Life history traits, particularly diapause stage, are also known to be an important predictor of when insects emerge (Altermatt, 2010b; Scott & Epstein, 1987). Our results confirm earlier emergence in warmer areas and in species that diapause as adults.

Less is known about drivers of termination and duration of adult insects. For many insects, photoperiod is likely predictive of activity termination because it is a primary cue in many insects to initiate diapause (Denlinger, 2002; Tauber & Tauber, 1976). Although photoperiod is often the main driver, diapause induction has also been related to temperature, food availability, moisture and chemical cues (Danks, 2007). Our results also suggest that many factors contribute to the termination of adult

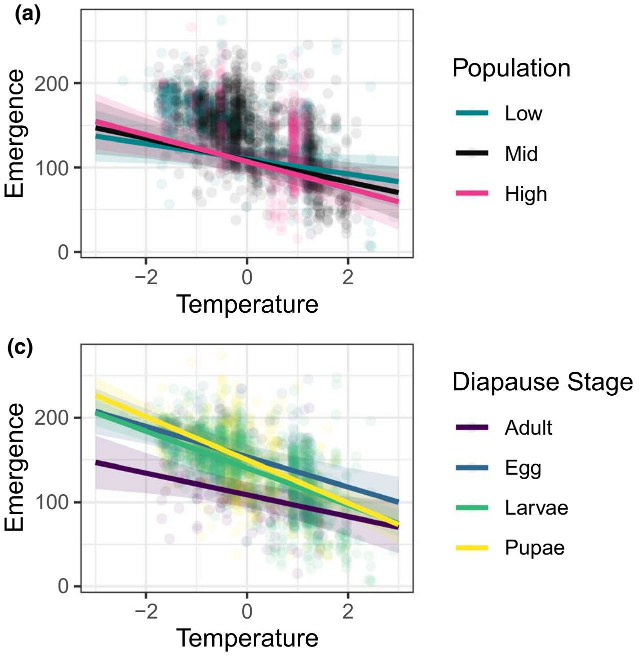

**FIGURE 3** Two-way interactions included in the top model predicting emergence of adult insect activity. Overall, adult emergence of adult insect activity was earlier in warmer areas and was even earlier in warm areas with high human population densities (a). High precipitation led to earlier emergence in warm areas, but delayed emergence in cool areas (b). The sensitivity of insect emergence to temperature differs depending on what life stage an insect enters diapauses (c). Emergence was earlier for univoltine species in areas with high precipitation compared with species that are not univoltine (d). Low, mid and high population density and precipitation values represent values that are one SD above the mean, at the mean, or one SD below the mean

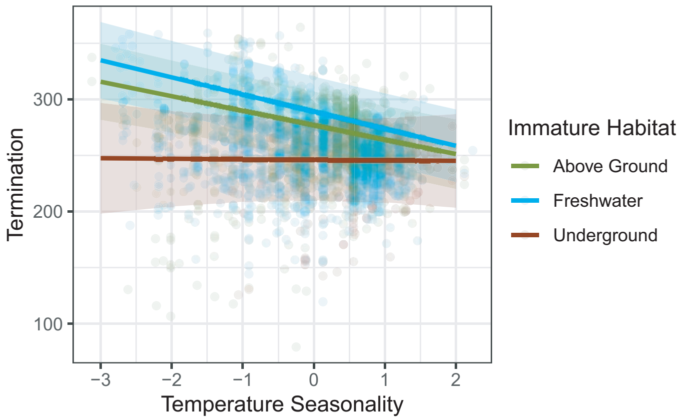

**FIGURE 4** Two-way interaction included in the top model predicting termination of adult insect activity. Termination of adult insect activity was earlier in areas with greater temperature seasonality for species that spend their larval stage above ground or in freshwater but was consistent for species that spend their larval stage underground

activity and indicate that these processes may be linked to temperature seasonality, timing of the first fall freezes, or resource depletion caused for example by drought. In multivoltine insects, we expected longer activity durations in warmer regions, due to the production of additional adult generations in areas with longer growing seasons (Altermatt, 2010a; Zeuss et al., 2017). It is less clear how temperature influences the duration of univoltine insects. Because obligate univoltine species cannot produce additional generations in warmer regions, we expected more consistent activity durations across temperature gradients, regardless of emergence dates. However, we did not find an interaction between temperature and voltinism, suggesting similar temperature-driven increases in duration regardless of voltinism. This surprising result could be explained by multiple mechanisms for extending adult activity, including lengthening timing of activity of cohorts of adults, more generations per season and reduced adult synchrony of univoltine populations in warm areas. However, this result may be due to our simplistic trait coding system labelling semi-, parti- and merovoltine species as 'not univoltine'.

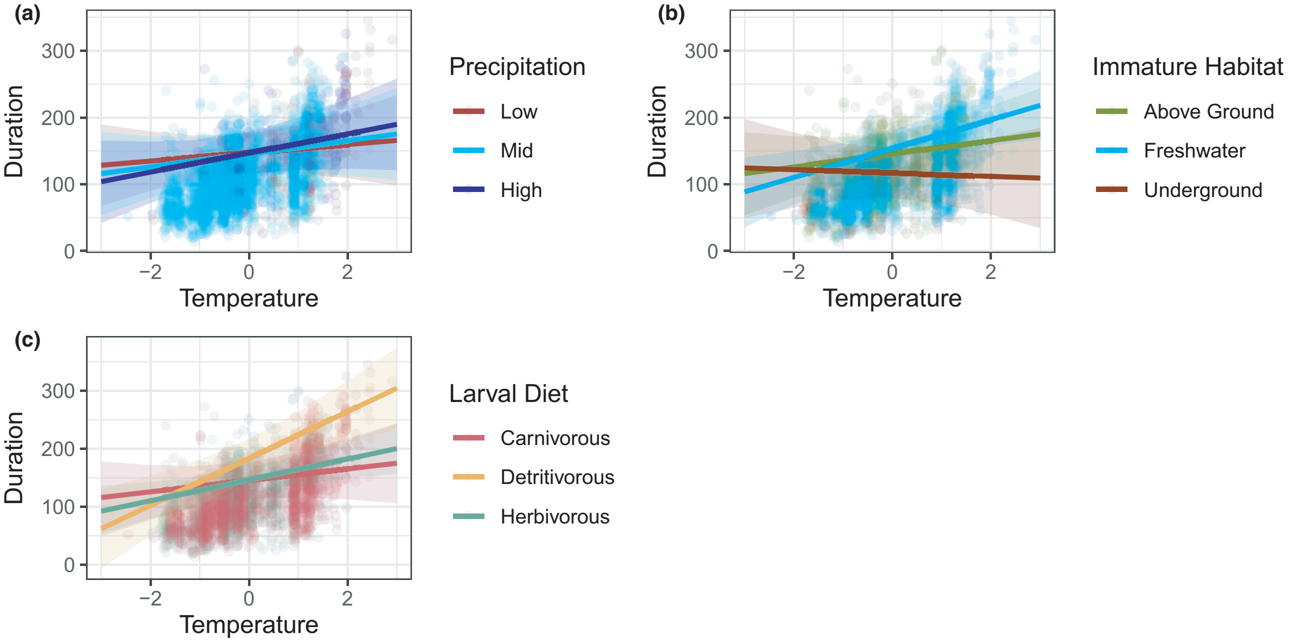

**FIGURE 5** Two-way interactions included in the top model predicting duration of adult insect activity. Insects were active longer in warm areas, especially warm areas with high (one SD above the mean) precipitation (a). Species with immature habitats that are underground had relatively constant durations regardless of the regional temperature (b). Detritivores had durations that were most sensitive to temperature (c)

Although this does not impact our finding of longer activity periods for univoltine (and multivoltine) species in warmer regions, more finely scored voltinism states may help elucidate trait-mediated phenology responses to temperature. We also note that our understanding of life history traits, particularly voltinism and migratory behaviour, is incomplete across broad temperature gradients. Species that are documented in the literature as non-migratory and univoltine may in fact have undescribed migratory patterns (Robinson et al., 2009) or potentially multiple generations in warmer regions that remain unreported.

One of the challenges with understanding phenological sensitivities is that regional contexts may impact not only the strength of sensitivity but also its direction. Li et al. (2019) showed, for example, that urbanisation shifts from advancing flowering in cold regions to delaying in warmer ones. Here we also find strong evidence of these region-specific contextual effects. One of the clearest examples is that the influence of precipitation and life history traits on insect duration varies with regional temperature. Warm, wet areas demonstrated longer adult insect duration than cooler, wetter regions. This interaction is expected, considering that snow contributes to annual precipitation in cool regions and snowmelt date delays the beginning of activity more than the end (Stemkovski et al., 2020). These regional effects also included life history interactions with temperature. We found that detritivores terminated activity later and had longer durations than carnivores, potentially due to detritus being more available later into the fall compared with green leaf materials or prey items. This effect is especially strong in warm environments, where detritus can accumulate year round.

We also expected a complex interaction between temperature and urbanisation, similar to the results of Diamond et al. (2014) for butterflies in Ohio, which documented earlier emergence in cold areas with high human population density and delayed emergence in warmer, more urbanised areas. Although we found such an interaction, it was in the opposite direction than expected: insects generally emerged later in cool, urbanised areas and earlier in warm, urbanised areas, in comparison with corresponding rural areas. Due to our species selection protocol, our species list likely overrepresented exploitative species because these are commonly observed. Exploitative butterflies showed smaller delays in first appearance in warm and urbanised areas (Diamond et al., 2014), potentially, in part, explaining our differing results. We encourage future work exploring how urbanisation impacts insect phenology and at what spatial scales urbanisation influences are most apparent.

## Ecological implications

Our results suggest that adult insects will emerge earlier under climate change scenarios due to warming temperatures, but the termination of insect activity will be less sensitive to changing climates. This may lead to an overall lengthening of insect duration in response to global warming, particularly in areas with high precipitation. Longer insect activity periods may buffer against phenological mismatch of insects interacting with other trophic levels, as long as insect abundance is sufficiently high. However, mounting evidence suggests widespread terrestrial insect declines (van Klink et al., 2020; Wagner et al., 2021; Warren et al., 2021), which raises the threat of reduced ecological services regardless of how much synchrony occurs between interacting species.

One of the fundamental unanswered questions in understanding insect response to global change is which species will thrive – the winners – and which will be most negatively impacted – the losers. Phenology may be a key indicator of winners versus losers given recent work demonstrating that changes in insect population sizes correlate with phenological lability. Some insects may be able to adjust and thrive in warmer environments if additional land use changes are not occurring (Michielini et al., 2021). For example, multivoltine Lepidoptera with early adult emergence in warm years showed increased within- and between-year population growth in Britain (Macgregor et al., 2019). Elongated adult activity periods were also the best predictor of increases in relative abundance of Massachusetts butterflies (Michielini et al., 2021).

Our results point to two life history traits that may predict winners and losers in the face of future climate change. Detritivores and insects with larval habitats in freshwater exhibit a stronger response of activity period to temperature than do other insects, indicating these species may be relatively better suited to persist in novel climate scenarios. Conversely, species that have underground larval habitats may be more at risk, as duration for these species remains relatively fixed across temperature gradients. We note that these conclusions must be interpreted with care, as our models are primarily fit across a spatial gradient. Space-for-time models of ecological change are controversial because ecological processes are often nonstationary (Damgaard, 2019). Still, some empirical studies support these inferences. A recent meta-analysis found broad declines in terrestrial insects but increases in freshwater insect populations (van Klink et al., 2020). No net declines in detritivores were detected across five long-term ecological research sites (Crossley et al., 2020), although these results have been questioned (Welti et al., 2021).

## Future work and caveats

Our study is unique in its spatial and taxonomic extent, yet the majority of the species used are in Odonata and Lepidoptera. This is not surprising because these clades have relatively large body sizes and are easy to see and photograph. In addition to the taxonomic biases in our data set, the 25 × 25-km grid cells that were included in our analyses were biased geographically, with most cells occurring in metropolitan areas in the Eastern Temperate Forests ecoregion and along the California Coast. There are noticeable sampling gaps in the Great Plains, North American deserts and the complex and diverse ecoregions of southern Mexico. Finally, we note that increasing observer effort, measured as the number of observations, did show a significant, albeit relatively weak effect on phenology estimates. Although our modelling framework attempted to control for these effects both in our data filtering and modelling framework, care must be taken when fitting estimations using community science data sets. As the amount of available incidental data continues to grow, we expect better spatial, and phylogenetic resolution, but biases are still likely, unless concerted efforts are made to survey more rural locations (Shirey et al., 2021).

Even if more species-specific phenology estimates can be generated for insects, our full ability to understand drivers of insect phenology will be hampered by the lack of available trait data. We had enough incidental observations to generate phenological estimates for 154 species with at least five year-by-cell combinations but could only use 101 species because of missing trait data. This is particularly problematic because our results highlight the importance of life history traits in predicting all aspects of adult insect phenology. Therefore, to better understand how insects will respond to climate change and urbanisation, it is imperative that continued effort goes into generating, compiling and archiving openly available insect life history information (e.g. Middleton-Welling et al., 2020). Improving insect trait knowledge and access will allow researchers to better understand ecological processes using the accelerating accumulation of occurrence and other natural history records.

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## AUTHORSHIP

All authors collectively conceived the idea for the manuscript and contributed to study design. VB, BJS and MWB collected and curated the occurrence data. MWB, VB, JRD, MMH, DL, JAO, NS, MW and BJS gathered trait data. MWB and DL conducted the analyses. MWB and RPG led the writing of the manuscript. All authors discussed the results and contributed critically to manuscript drafts.

## PEER REVIEW

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## OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://doi.org/10.5281/zenodo.5137739.

## DATA AVAILABILITY STATEMENT

The data and code to fully reproduce the results and figures presented in this paper can be found on GitHub (https://github.com/mbelitz/InsectDuration) and is archived on Zenodo (https://doi.org/10.5281/zenodo.5137739) (Belitz, 2021). These repositories also host the cleaned occurrence records used to estimate phenology metrics. The raw GBIF records used in this paper can be found via the DOIs listed in the following references (GBIF 2020a, 2020b, 2020c, 2020d, 2020e).

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## SUPPORTING INFORMATION

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