



Shifting precipitation regimes alter the phenology and population dynamics of low latitude ectotherms

Erica H. Henry^{a,*}, Adam J. Terando^{a,b}, William F. Morris^c, Jaret C. Daniels^d, Nick M. Haddad^e

^a Department of Applied Ecology, North Carolina State University, Box 7617, Raleigh, NC 27695, USA

^b U.S. Geological Survey, Southeast Climate Adaptation Science Center, North Carolina State University, Raleigh, NC, USA

^c Biology Department, Duke University, Durham, NC, USA

^d Department of Entomology and Nematology, University of Florida, Gainesville, FL, USA

^e Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, MI, USA

ARTICLE INFO

Keywords:

Butterfly
Tropical
Climate change
Drought
Climate model
Population dynamics

ABSTRACT

Predicting how species respond to changes in climate is critical to conserving biodiversity. Modeling efforts to date have largely centered on predicting the effects of warming temperatures on temperate species phenology. In and near the tropics, the effects of a warming planet on species phenology are more likely to be driven by changes in the seasonal precipitation cycle rather than temperature. To demonstrate the importance of considering precipitation-driven phenology in ecological studies, we present a case study wherein we construct a mechanistic population model for a rare subtropical butterfly (Miami blue butterfly, *Cyclargus thomasi bethunebakeri*) and use a suite of global climate models to project butterfly populations into the future. Across all iterations of the model, the trajectory of Miami blue populations is uncertain. We identify both biological uncertainty (unknown diapause survival rate) and climate uncertainty (ambiguity in the sign of precipitation change across climate models), and their interaction as key factors that determine persistence vs. extinction. Despite uncertainty, the most optimistic iteration of the model predicts that Miami blue butterfly populations will decline under the higher emissions scenario (RCP 8.5). The lack of climate model agreement across the projection ensemble suggests that investigations into the effect of climate change on precipitation-driven phenology require a higher level of rigor in the uncertainty analysis compared to analogous studies of temperature. For tropical species, a mechanistic approach that incorporates both biological and climate uncertainty is the best path forward to understand the effect shifting precipitation regimes have on phenology and population dynamics.

Introduction

Climate change is shifting the timing of life history events (phenology) across a wide variety of taxa [1,2]. The timing of these events evolved to maximize species' ability to exploit seasonal resources. As underlying seasonality changes, there are consequences, both positive and negative, that ultimately determine which species persist and which go extinct [3,4]. Nearly all of our knowledge of climate-driven phenological shifts come from studies of temperate species for which temperature and photoperiod are critical drivers of phenology [1,5]. At low-latitudes, seasons are more likely to be defined by the arrival and departure of periods of intense rainfall rather than seasonal temperature variations (Fig. 1) (for simplicity, in this paper we use the term tropical to refer to these environments and the species that inhabit them). The highest seasonal variation between wet and dry seasons peaks in both hemispheres between approximately 10- and 25-degrees latitude. It is in this loca-

tion where changes in seasonal precipitation cycles are likely to drive temporal changes in behavior and abundance of species [6,7], as we investigate here.

Climate-driven shifts in phenology affect individual fitness by changing species interactions, environmental conditions, and resource availability, which can lead to changes in population dynamics [8,9]. In temperate regions, species that track changing climate and match their phenology accordingly generally incur fitness benefits [10–12]. For example, earlier snowmelt triggers earlier marmot emergence from hibernation, which leads to earlier weaning of young, larger adult body mass and increased adult survival, which ultimately results in population increases [13], but see [14]. For butterflies, increasing spring temperature leads to earlier emergence. Multivoltine species capitalize on earlier emergence, and a longer activity period, by adding generations, which leads to population growth [15,16]. What remains unknown is whether these same patterns hold true in precipitation-driven systems. Under-

* Corresponding author.

E-mail address: ehenry@ncsu.edu (E.H. Henry).

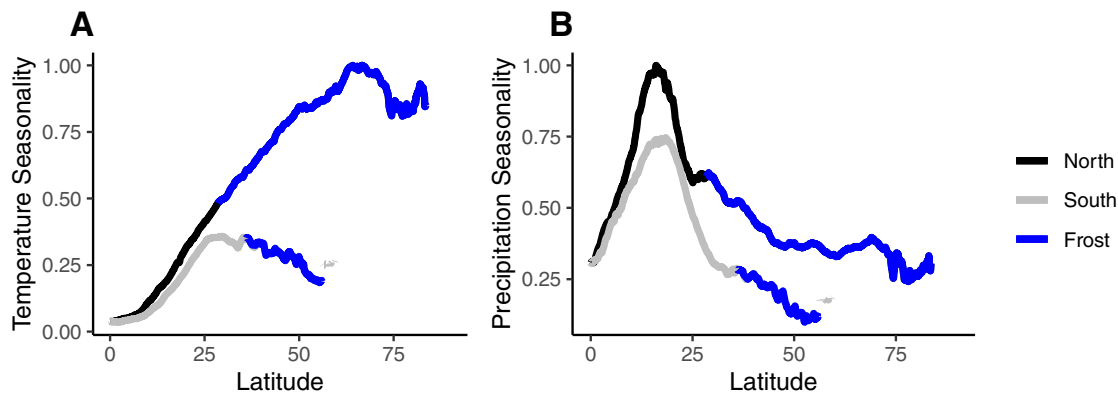


Fig. 1. Differences between observed (and standardized) seasonality for temperature and precipitation, by latitude. Black and gray lines represent latitudinal averages for the Northern and Southern Hemispheres, respectively (1970–2000; WorldClim <https://www.worldclim.org/> [19]). Blue lines represent latitudinal bands that commonly experience seasonal freezing periods where the mean temperature of the coldest quarter is below 2 °C. Temperature seasonality is defined as the difference between the warmest and coldest quarters and is normalized relative to the latitude band with the maximum value. Precipitation seasonality is derived from the calculated coefficient of variation and normalized in the same way as temperature.

standing these mechanisms is central to being able to make predictions about how sensitive a species might be under future environmental conditions or to identify management actions that may increase a species resilience to changes in climate [17,18].

Even though the majority of earth's biodiversity is found at low latitude, very few studies have examined how changing precipitation patterns are affecting the phenology and population dynamics of tropical species [1,5,20]. One major challenge is that, unlike temperature, the effects of increasing atmospheric CO₂ on precipitation are more indirect (mainly arising from increasing temperatures) and variable [21]. In general, temperatures are increasing globally. Temperature increases lead to longer growing seasons and shorter dormancy periods, both of which can increase population growth, especially for insects [11,22]. The direction of precipitation change, however, is not uniform across the globe. Some regions are projected to experience increases in precipitation and others decreases [23]. In addition to changes in the total amount of precipitation, seasonal precipitation is projected to shift [21]. In subtropical regions, more frequent precipitation may elongate the growing season and decrease the length of dry season dormancy. Less frequent precipitation may shorten growing seasons and increase dormancy. If populations respond to precipitation change as they do to warming temperature, more frequent rains would result in population growth, and less frequent rains in population decline (Fig. 2).

The challenge to uncovering these patterns in tropical systems is that, compared to temperate regions, long-term monitoring data and *in situ* meteorological observations are less widely available [6,24, but see 25]. This makes it difficult to conduct empirical phenological studies commonly applied to high latitude species such as pairing meteorological observations with long-term species monitoring and/or herbarium specimens [22]. Mechanistic models offer another way to test hypotheses about how changing climate will affect population dynamics [26]. The discrete, stochastic nature of precipitation events favor mechanistic models over correlative approaches [27,28]. Models that explicitly link vital rates (birth and death rates) to precipitation events and project precipitation-driven population dynamics are powerful tools for understanding what the future may hold for many tropical species [29].

Key to building informative global change projections of biological systems is incorporating multiple sources of uncertainty [30]. This is especially important in the context of precipitation change, the projections of which are much “noisier” than temperature projections (Fig. 3). This inherent uncertainty in our analyzes of how species with precipitation-driven phenology are likely to be affected by future warming must be acknowledged in model results. Additionally, the knowledge we have about how behavior, physiology, genes, and species interact to shape adaptive (or non-adaptive) responses to climate change is highly un-

certain, especially in the context of precipitation change and tropical species [18,31,32]. Neglecting either climate model-driven or biological uncertainty in our projections of future conditions increases the risk that decision makers will be misinformed about the actual range of possible outcomes that may result from conservation actions (or inactions).

Butterflies provide a model system in which we can mechanistically explore how changes in precipitation patterns are affecting tropical insect phenology and population dynamics [11,33,34]. The phenology of temperate butterfly species is generally driven by temperature and photoperiod; spring time emergence depends on heat accumulation and fall diapause by photoperiod [35]. Although small changes in temperature and photoperiod also cue periods of dormancy in the tropics, tropical butterfly phenology fluctuates more closely with precipitation patterns than temperature [36–38]. Peak abundance of many tropical insects occurs during the wet season [39–41] and many insects spend the dry season in a state of diapause [42,43], the end of which is triggered by rainfall [44].

To better understand how a changing climate will alter these seasonal patterns and resulting population dynamics, we focus on an endangered tropical butterfly (Miami blue, *Cyclargus thomasi bethunebakeri*); a multivoltine species whose abundance is sensitive to seasonal precipitation cycles [37]. In parallel with other terrestrial insects, Miami blue range and abundance have declined considerably in the last 40 years [45–47]. We explore what role future changes in precipitation may have in controlling population trends for Miami blues by mechanistically linking butterfly emergence from diapause with accumulated precipitation [7] and predict future population dynamics using daily rainfall projections. Our modeling approach provides a framework for understanding the effects of changing precipitation regimes on tropical insects across the globe. With this model we ask two questions: 1) How sensitive are population size and growth rate to projected changes in precipitation and the uncertainty in those projections? 2) How sensitive are our predictions of persistence vs. extinction to uncertainty in vital rates? By describing Miami blue butterfly lifecycles in which growth and reproduction are triggered by rainfall, our approach provides a model to represent a common and critically important life history strategy among many tropical organisms.

Methods

Study species

We use the Miami blue butterfly (*Cyclargus thomasi bethunebakeri*) as a model organism to demonstrate the importance of precipitation in

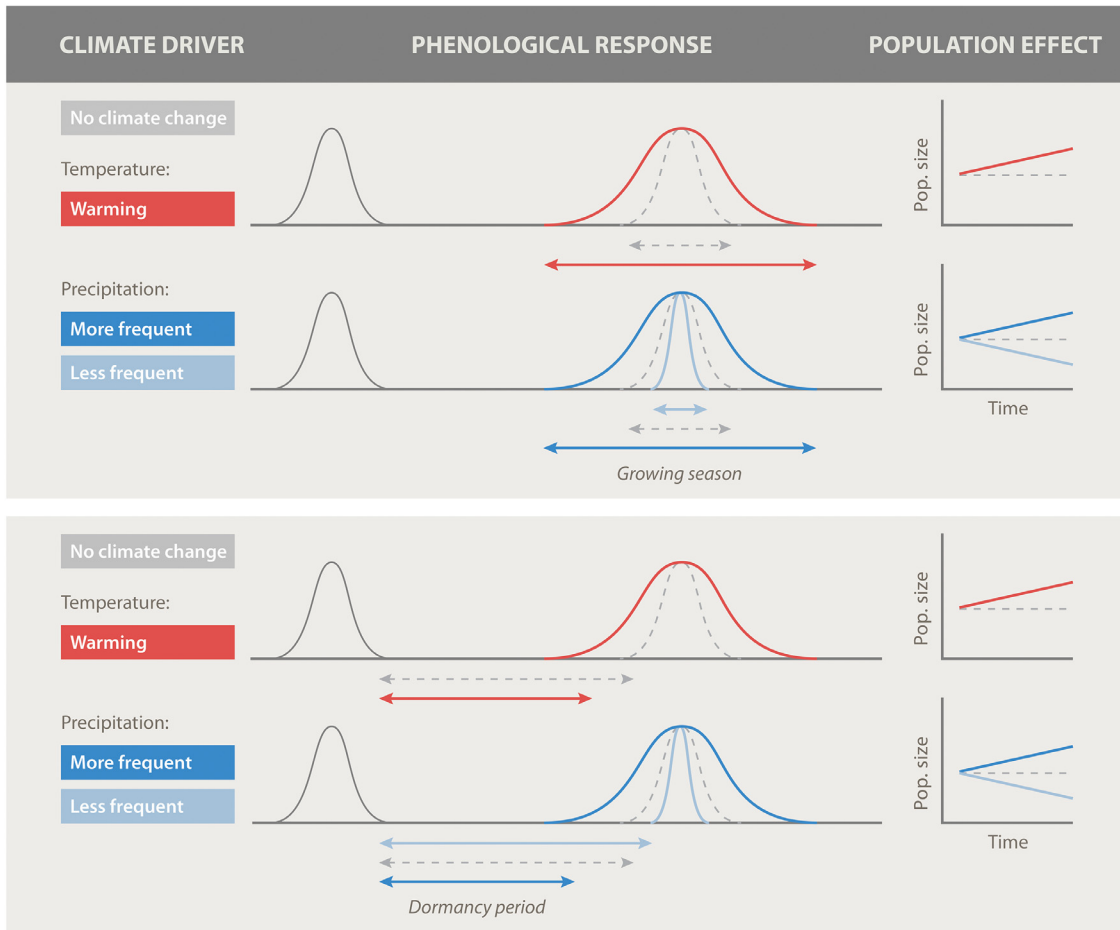


Fig. 2. Conceptual model of population responses to temperature and precipitation change. Top panel highlights that increasing temperature lengthens growing season, which allows for population growth, whereas rainy seasons may become more frequent OR less frequent which could cause growing seasons to lengthen and populations to increase OR growing seasons to shorten and populations to decrease. As growing seasons change, so does the interval between them, the dormancy period, depicted in the bottom panel. As temperatures rise, the dormancy period becomes shorter and populations increase, more frequent rainy seasons also shorten dormancy periods and cause population increases, and less frequent rainy seasons lengthen the dormancy period and populations decline.

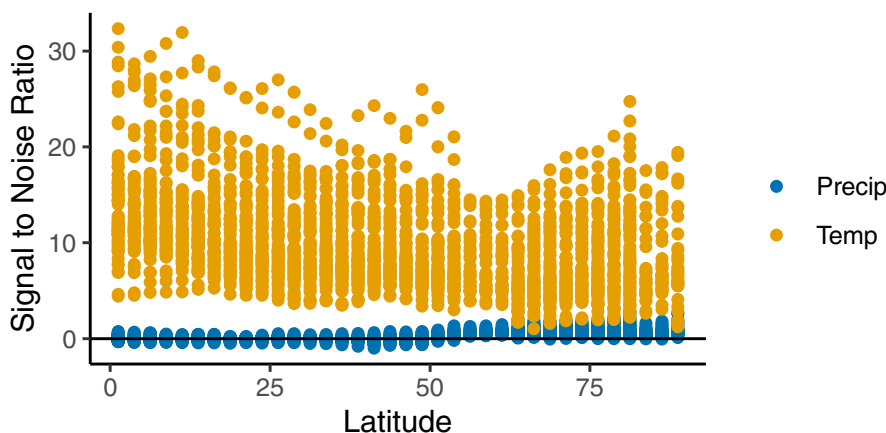


Fig. 3. Signal-to-noise ratios (SNRs) of projected changes for annual temperature and precipitation, by latitude. SNR is calculated as the ratio of the mean projected change for a given latitudinal band for the end of the 21st century (2080–2099) relative to the period 1980–1999 compared to the standard deviation calculated over the same historical period. Temperature (orange) and precipitation (blue) SNRs for 39 GCMs from the CMIP5 project under the higher emissions scenario, RCP8.5, are shown. CMIP5 output were obtained from the KNMI Climate Explorer Tool (<http://climexp.knmi.nl/>).

driving low-latitude species phenological responses to climate change. Miami blues are near extinction; their global distribution is 18 ha comprised of seven beaches on six islands located 30 km west of Key West (Florida, USA, 24.5551° N, 81.7800° W). The Florida Keys climate is subtropical, with seasonality driven by precipitation. The annual precipitation regime is characterized by a dry season (December–April) that

receives 25% of annual precipitation, and a wet season (June–October) that receives 60% of annual precipitation. Mean monthly temperatures are warm and variation is low (high: 23–32 °C, low: 18–26 °C). Climate models project a decrease in precipitation in this region, particularly in the historical “rainy season” [48]. This drying pattern is predicted across the Caribbean and much of the neotropics [23]. Therefore, many

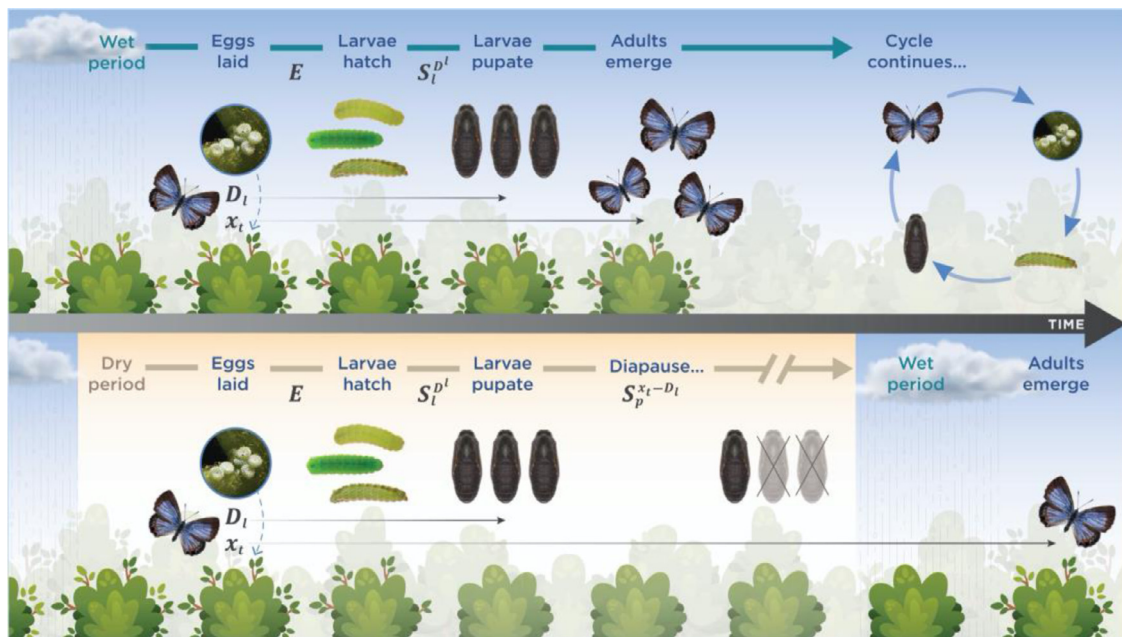


Fig. 4. Conceptual figure of the population model. In the model, female butterflies lay eggs (E) on new growth of hostplants. Those eggs hatch and caterpillars feed on the tender new plant growth until they pupate ($S_p^{D_l}$). If it has rained a sufficient amount prior to the day the egg was laid (wet period), we assume there is still new growth on the plants, and that butterflies will emerge from pupae $x_t - D_l$ days later, continuing the cycle. If it has not rained a sufficient amount prior to egg laying (dry period), we assume the host plants have dried out and are no longer palatable, therefore pupae will diapause ($S_p^{x_t - D_l}$) waiting for rain. Once a sufficient amount of rain falls, the host plants start producing new leaves, and butterflies emerge from pupae $x_t - D_l$ days later. x_t represents the days it takes for an egg to become a butterfly and varies based on precipitation patterns. Because survival rates are daily, diapause mortality increases as x_t increases. (Infographic credit: Neil McCoy).

precipitation-driven species may experience similar effects to those we predict for Miami blues.

Henry et al. [37] found that periods of high adult Miami blue abundance are followed by periods of low, or no, adult butterflies. Phenology of adult emergence and abundance is fine-tuned to precipitation patterns: high adult abundances occur five weeks after total rainfall in a five-week period exceeds 130 mm (see “Precipitation and butterflies” in supplement, Fig. S2). It is likely that this pattern of precipitation-triggered emergence stems from response of Miami blue host plants to precipitation. Miami blue butterflies can use at least three larval hosts including, Florida Keys blackbead (*Pithecellobium keyense*), gray nickerbean (*Caesalpinia bonduc*), and ballonvine (*Cardiospermum corindum*). In the current occupied range of the Florida Keys, Florida Keys blackbead is the only host that is present. Female butterflies lay eggs on newly emerged leaves and flower buds of their hosts. The phenology of flowering and leaf production of this species is not well understood, but appears to be sporadic, happening in pulses, the timing of which varies from year to year [49].

We hypothesize that moisture modulates host plant quality, which affects larval development [7]. We assume that during rainy periods, butterfly host plants produce sufficient new growth to sustain continuous growth and reproduction of Miami blue butterflies; larvae develop directly into adults without entering diapause (Fig. 4, top panel). Lack of sufficient rain, however, will cause host plants to stop producing new growth, which cues immature butterflies to enter diapause, either as late-instar larvae or pupae. Diapause termination is then triggered once a sufficient amount of precipitation has fallen for host plants to again produce new plant growth suitable for larval development (Fig. 4, bottom panel). The specific environmental cue that triggers diapause termination for Miami blue butterflies is unknown. This relationship between abundance and precipitation reveals a clear mechanism through which future changes in precipitation patterns could impact Miami blue butterfly populations. If diapause periods become longer and/or more frequent (i.e. less accumulated precipitation), butterfly populations could

decline. During diapause, other factors, such as increased exposure to predation and parasitism or decreased resources [50], could interact with climate change to reduce population sizes.

Butterfly model

We built a model of Miami blue butterfly population dynamics based on the above assumed relationship between precipitation and butterfly abundance. To capture these dynamics, we use a variable, x_t , to explicitly link butterfly phenology and population dynamics to precipitation patterns. In our model, x_t represents the total immature development time, partitioned into life stage lengths for larvae (D_l), pupae (D_p), and diapause (D_d): $x_t = D_l + D_p + D_d$. The sum of the first two terms is the active development time required to reach adulthood and thus always takes on a positive value. The third term, the diapause stage length, depends on daily precipitation and can, therefore, have lengths greater than or equal to zero. Borrowing from models that use growing degree days to predict butterfly emergence [11,27], we estimated a threshold amount of precipitation P that must accumulate over a time window, w , to trigger butterfly emergence. If the precipitation threshold (P) has already been reached at the time of oviposition then diapause length (D_d) will be zero. If the threshold has not been reached, then diapause length is the number of subsequent days required to reach the precipitation threshold: $D_d = \min f(t)$ subject to $\sum_{i=t-w}^t p_i \geq P$ where p_i is the precipitation occurring on day i .

We derived empirical estimates of ($D_l + D_p$), P , and w , from two years of survey data (see “Precipitation and Butterflies” in supplement). From these data, the values that resulted in the best set of predictors of butterfly abundance were $P = 130\text{mm}$ and (coincidentally) 35 days for both w and ($D_l + D_p$) (Figs. S1 and S2). Our estimate for ($D_l + D_p$) is in good agreement with laboratory-based estimates of 24–31 days under ideal conditions (S. Steele Cabrera, University of Florida, personal communication). We interpret this threshold (130 mm, Fig. 3) to be the

Table 1

Parameter definitions and data sources. Development time and daily larval survival data are for larvae in a captive colony raised on Florida keys blackbead (*Pithecellobium keyense*). See “Vital Rates” in supplement for detailed methods on estimating vital rates.

Parameter	Estimate	Data source
Daily adult survival	0.53	Captive individuals in flight cage (S. Steele Cabrera, University of Florida, unpublished data)
Egg laying rate (E) (eggs/day)	14 ± 7	Captive individuals in the laboratory (E. Heffernan, New College of Florida, unpublished data)
Larval development time (D_l) (days)	22 ± 3	Captive individuals in laboratory (J. Daniels et al. unpublished data)
Daily larval survival (S_l)	$0.96 \pm 0.023^*$	Captive individuals in the absence of predation (J. Daniels et al. unpublished data)
Daily diapause survival (S_d)	0.980–0.995	This is the range across which model predictions flip from extinction to persistence

*daily survival of 0.96 equates to total larval survival of 0.42.

minimum amount of cumulative precipitation that must fall within the 35-day window, w , to stimulate or maintain new plant growth which in turn triggers both the end of diapause (if it was initiated because $t > 1$), and the ensuing 35-day active development period (the ‘lag’) required before butterfly emergence. Although we model this as the same ($D_l + D_p$) period, we note that it is currently unknown if individuals are already within D_p at the end of diapause, or if they are actually in larval diapause state.

We connected butterfly abundance to precipitation patterns using x_t with the following equation:

$$N_{\bar{t}} = \frac{N_{(t-x_t)}}{2} E S_l^{D_l} S_d^{x_t - D_l} \quad (1)$$

This equation predicts the number of butterflies with mean emergence on day \bar{t} . This is the product of the number of female butterflies that were present x_t days prior, $N_{t-x_t}/2$ (division by 2 assumes an equal sex ratio in the population), the eggs laid per day, E (eggs hatch in three days or less and their daily mortality is negligible so we assume 100% survival), the fraction of larvae that survived for D_l days at a daily rate of S_l , and the fraction of those that survived in the diapause and pupation stages for $x_t - D_l$ days at a daily rate of S_d . Because any cohort of butterflies does not all emerge on one day, we used Zonneveld’s [51] model of insect abundance over time to distribute butterfly emergence across a flight period with mean emergence day \bar{t} . The Zonneveld model predicts butterfly emergence based on the following four parameters: population size, mean and standard deviation of the emergence day, and daily death rate [51]. With this approach, we both distribute each cohort of butterflies over multiple days and allow each adult to live for multiple days post-emergence based on the daily death rate in the model (see “Emergence Curve” in supplement). Finally, we imposed a maximum population size of 100,000 butterflies in our model – this is the maximum abundance we estimate for the wild population using peak abundance estimates from Henry et al. [37] and the emergence curve described above.

All vital rates used in this model were estimated with captive individuals at the Florida Museum of Natural History (Table 1 – see “Vital Rates” in supplement), except for diapause survival. Miami Blue diapause is the one life stage about which we know almost nothing. For this reason, we ran the model with a range of diapause survival values and report results across that range. The range of diapause survival values was tuned to capture the values where the model predictions flip from extinction to persistence. We used vital rates from captive individuals because we have yet to estimate vital rates in the wild.

Predicting future population dynamics

To evaluate how projected changes in precipitation patterns affect the persistence or extinction of Miami blue butterflies, we used down-scaled projections of daily rainfall. We used downscaled data for two

reasons: (1) the two-degree resolution of global climate models is larger than the entire range of Miami blue butterflies, and (2) precipitation patterns in south Florida are largely driven by local climate forcings of convective thunderstorms and island cloudlines, phenomena that occur on a scale much smaller than two degrees. The daily precipitation data we used are part of the MACAv2-METDATA dataset. Climate forcings in this dataset were drawn from a statistical downscaling of 20 global climate models from the Coupled Model Intercomparison Project 5 CMIP5 [52] using the Multivariate Adaptive Constructed Analogs (MACA) method. This method statistically downscales the two-degree resolution of the global climate model data to four-kilometer resolution. Like all statistical downscaling techniques, this method relies on a training dataset that is based on historical meteorological observations from weather stations. The training dataset used to produce MACAv2-METDATA projections is METDATA [53]. The southern extent of METDATA, and therefore MACAv2-METDATA projections, is 25°N, which includes the southernmost tip of mainland Florida and part of Key Largo, but excludes the lower Florida Keys and the range of Miami blue butterflies. Since we could not select model output directly from the lower Florida keys for our projections, we instead chose the location in the data set that was closest to Key West while still in the Florida Keys, which was in Key Largo (–80.4939E, 25.2764 N).

We used the projected daily precipitation values to drive the butterfly population dynamics of our model (Eq. (1)). We simulated population dynamics from 2018 to 2100 under two greenhouse gas emissions scenarios, RCP 4.5 (stable emissions rate followed by a decline in emissions by mid-century) and RCP 8.5 (near status quo emissions). For each climate change scenario, we simulated butterfly populations using each of the 20 models in the MACA ensemble. At the end of each simulation, we extracted the last date on which at least one adult butterfly was predicted to occur as a measure of population persistence or extinction. To understand how sensitive our results were to daily diapause survival, the parameter for which we have no prior information, we ran the model across a range of daily diapause survival values from 0.980 to 0.995 in increments of 0.001. Additionally, we evaluated the effect of population size on the potential for future extinction by varying the initial population size over three orders of magnitude, specifically 100, 1000, and 10,000 adult female butterflies. This resulted in a total of 1920 simulations of Miami blue populations (2 GHG scenarios x 20 GCMs x 16 values of S_d x 3 values of N_0).

In addition to examining whether butterfly populations persisted or went extinct, we analyzed the trend in population size across the most optimistic simulation, starting population size 10,000, daily diapause survival 0.995. To do this, we first calculated annual population size by summing the total number of adult butterflies that emerge each year for each of the 20 climate models. Because populations fluctuate widely from year to year, we then calculated mean annual population size for the first and last decade of the simulation. We used these decadal av-

erages to approximate a per-decade geometric growth rate for each climate model using Eq. (2).

$$\lambda = \left(\frac{N_d}{N_0} \right)^{\frac{1}{d}} \quad (2)$$

For N_0 , we used mean annual abundance from 2020–2029, for N_d , mean annual abundance from 2090–2099, and 7 as d , the number of decades represented in our approximation. We calculated a per-decade lambda for each of the 20 global climate models. With this proxy for geometric growth, we compared population trajectories by summarizing ensemble medians and 95% confidence intervals for both greenhouse gas scenarios. To evaluate the sensitivity of these population growth rates to each vital rate in the model, we performed proportional one-at-a-time decreases in each vital rate, an analysis analogous to LTRE sensitivity analyses [54]. For each iteration, we decreased one vital rate by 0.01 and calculated the percent change in λ relative to the baseline scenario described above.

Results

Across all iterations of the model, the future of Miami blue butterflies is highly uncertain. Sources of uncertainty were biological or climatological. Biological uncertainty arose as butterfly persistence is highly sensitive to diapause survival. At both high and low values of daily diapause survival, the variation across climate models is irrelevant; all models predict persistence or extinction, respectively. Climatological uncertainty arose at mid-range values of daily diapause survival when the predictions of each climate model vary widely. For the same value of diapause survival some models predicted persistence and others early-century extinction. This is true regardless of greenhouse gas scenario or initial population size.

Regardless of starting population size or greenhouse gas scenario, there was a narrow range of values of daily diapause survival over which the model prediction flipped from extinction to persistence (Fig. 5). As expected, there was an inverse relationship between population size and the daily diapause survival rate for which half the global climate models predicted persistence ($S_{d_{min}}$); at higher population sizes, models predicted population persistence with lower values of diapause survival. For example, in the RCP 8.5 scenario, for a starting population of 100, 1000, and 10,000 butterflies, $S_{d_{min}} = 0.989, 0.987, \text{ and } 0.986$, respectively.

Greenhouse gas scenario had little effect on $S_{d_{min}}$, but had a pronounced effect on the overall population trend. In the best-case simulation (daily diapause survival = 0.995 and initial population size 10,000 butterflies), Miami blue population dynamics across the century are stable under RCP 4.5 (median per-decade $\lambda = 1.002$, 95%CI: 0.928–1.061) and declining under RCP 8.5 populations (median $\lambda = 0.916$, 95%CI: 0.810–1.031) (Fig. 6). The variability across GCMs in these projections is much higher under RCP 8.5 than RCP 4.5. Under RCP 8.5, only five climate models result in per-decade population growth rates >1 and one climate model results in a per-decade population growth rate as low as 0.791.

Sensitivity analyses reveal that per-decade population growth rates are more sensitive to diapause survival than any of the other vital rates. A 1% reduction in daily diapause survival is the difference between all 20 GCMs predicting persistence and only 8 GCMs predicting persistence (Fig. 5). The same 1% reduction in the remaining vital rates resulted in all 20 GCMs still predicting persistence, and overall changes in lambda of less than 0.1% (Supplemental Table 1).

Discussion

By mechanistically linking butterfly population dynamics to precipitation patterns, we demonstrate that precipitation driven shifts in butterfly phenology can cause populations to decline, and are nearly certain to

do so under the higher emissions scenario (RCP 8.5). In this scenario, under the most optimistic iteration of the model ($S_d = 0.995$, $N_0 = 10,000$), fifteen of the twenty (15/20 = 75%) global climate models predicted Miami blues will decline throughout the century. Projected declines are due to shifts in precipitation patterns and a corresponding increase in the average time a butterfly spends in diapause (Fig. S2).

Consistent with global trends of declines of 0.9–2.6% per year across all terrestrial insects [47,55], our model projects a decline of 8% per-decade (with a range from +3% per-decade to –21% per-decade). This result is alarming because dry season diapause, the termination of which is triggered by rainfall, is common across tropical insects [42,43]. Despite this being a common life history strategy, we know very little about the mechanisms that control diapause decisions for these taxa [7,43]. Since studies of global insect population trends rarely include tropical species, we also know very little about population trends for these species, [55]. Given our results, future work to uncover mechanisms that mechanistically link diapause and climate is key to predicting future population dynamics for tropical insects. Analyses of insect declines invoke climate change as a possible cause of decline, but, in general, they lack the data necessary to determine mechanisms of decline [45].

Drought affects population dynamics across trophic levels in ways that could interact synergistically or antagonistically with the effects of drought-driven phenological shifts we documented. In addition to reducing population growth rates by extending diapause length, which we demonstrated, drought can also reduce herbivore survival directly through reductions in water balance [56] and indirectly by lowering host quality [56,57]. However, drought also has the potential to increase herbivore fitness by decreasing host defenses and reducing predator and parasitoid populations [58,59]. These are just a few examples of additional mechanisms through which changing precipitation regimes, particularly in water-limited, as opposed to heat-limited areas [60], have the potential to control future fluctuations in insect population dynamics.

We did not take into account the effects that changes in temperature will have on insect populations. It is widely recognized that small increases in temperature are likely to push low-latitude insects beyond their critical thermal maximum temperatures [61–63], with the potential to cause widespread declines. If Miami blue daily diapause survival is currently close to the daily diapause survival rate for which half the global climate models predicted extinction, further temperature or drought-driven reductions in this parameter [64], would likely accelerate Miami blue extinction. We also acknowledge that by using vital rates estimated from near-ideal conditions in captivity, we are likely modeling an overly optimistic future trajectory of Miami blue butterflies under the selected climate scenarios. Understanding the mechanisms through which vital rates of tropical insects are controlled by climate parameters throughout the life cycle is crucial to building robust projections of population dynamics. Filling these knowledge gaps will increase our ability to understand and model potential threats and adaptive capacity of these species to a changing climate [65–68].

The future of Miami blue butterflies is highly uncertain. The location of Miami blue habitat, just above sea level on coastal berms, makes the butterflies extremely vulnerable to sea level rise. Their limited distribution also leaves them exposed to extinction via one major disturbance event such as a catastrophic hurricane. In this context, reintroductions are paramount to expanding the butterfly's range and increasing the species' resilience to these threats. Our model is one tool that can help managers identify actions to promote the butterfly's persistence, such as selecting reintroduction sites that will be viable under future climate scenarios. Incorporating multiple sources of uncertainty in our projections of future population dynamics is critical to making informed conservation decisions. There are clear places where further study has the potential to reduce uncertainty, such as measuring diapause survival in the field. Our modeling effort is the first step in an iterative adaptive management process [69–71]. More broadly, including both biological

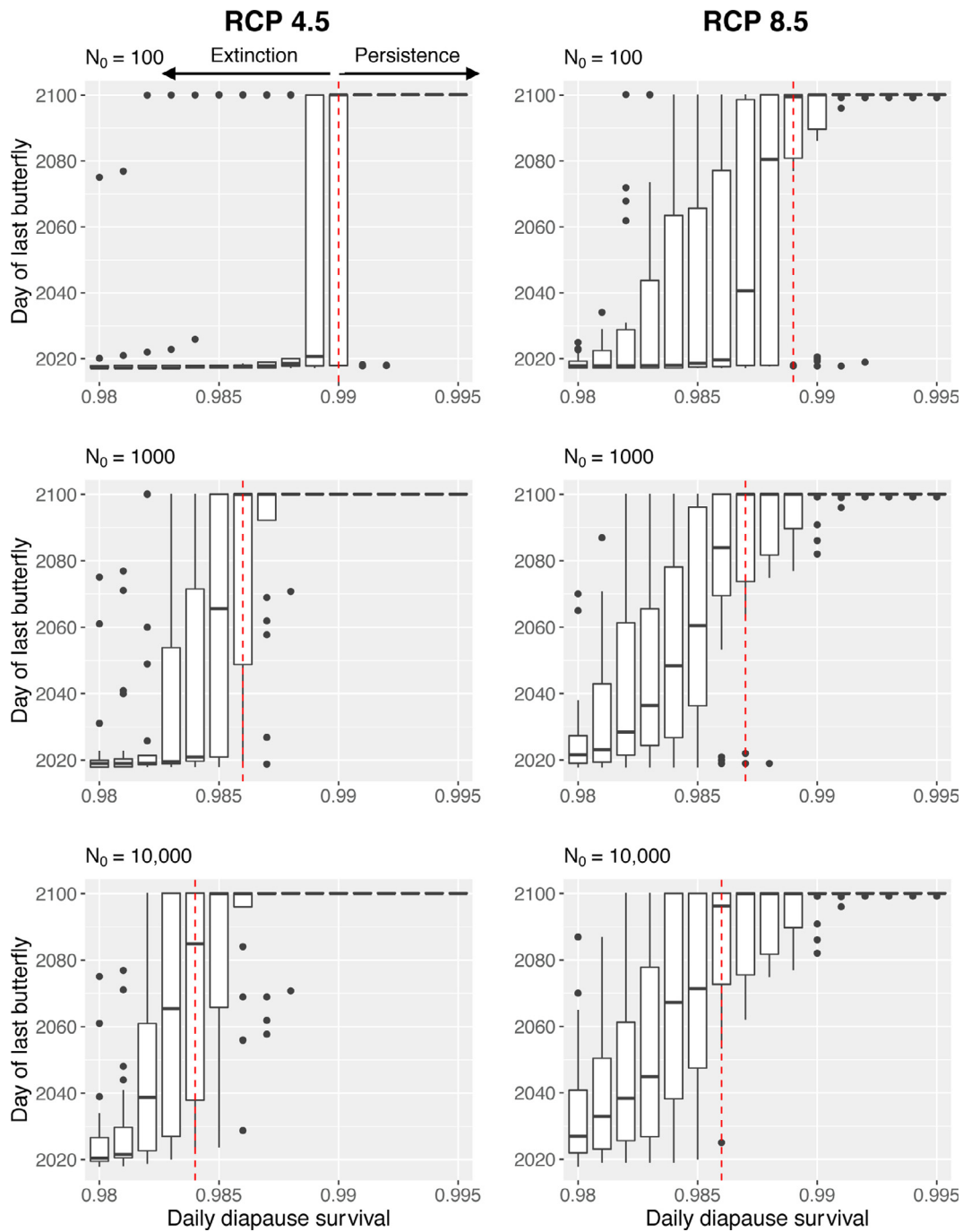


Fig. 5. The day of last butterfly predicted by the model for each combination of diapause survival and initial population size. Box plots summarize results from 20 global climate models in each simulation. Boxplots summarize median, 1st and 3rd quartiles (shoulders), 1.5 times the IQR (whiskers), and results that fall outside that range (outliers). Red lines represent $S_{d_{min}}$, the diapause survival value for which at least half of GCMs predict persistence to 2100, for each simulation.

and climate uncertainty in an adaptive management framework provides land managers with the information necessary to broadly assess the risk that climate change poses to key resources or populations and to efficiently allocate resources to develop responsive management actions. Without this context, land managers risk making decisions that at best are sub-optimal, and at worst, potentially catastrophic for the species whose survival they are entrusted with.

Maintaining persistent populations of threatened species in a warming world requires knowledge of how climate interacts with species biology. We demonstrate the critical importance of seasonal precipitation accumulation in driving species persistence of a tropical butter-

fly, something that has been overlooked. We accomplished this despite knowledge gaps that are common in temperature- and precipitation-driven systems over the period of detectable anthropogenic climate warming [72]. We were able to achieve this by combining monitoring data with global climate observing systems, and small-scale demographic experiments to reveal mechanistic effects of climate and climate change on phenology and population dynamics. Our methods for modeling precipitation-driven phenology and its effects on population dynamics could be applied to economically important species, such as those that provide both ecosystem services, including pollinators and decomposers, and disservices, such as agricultural pests and invasive

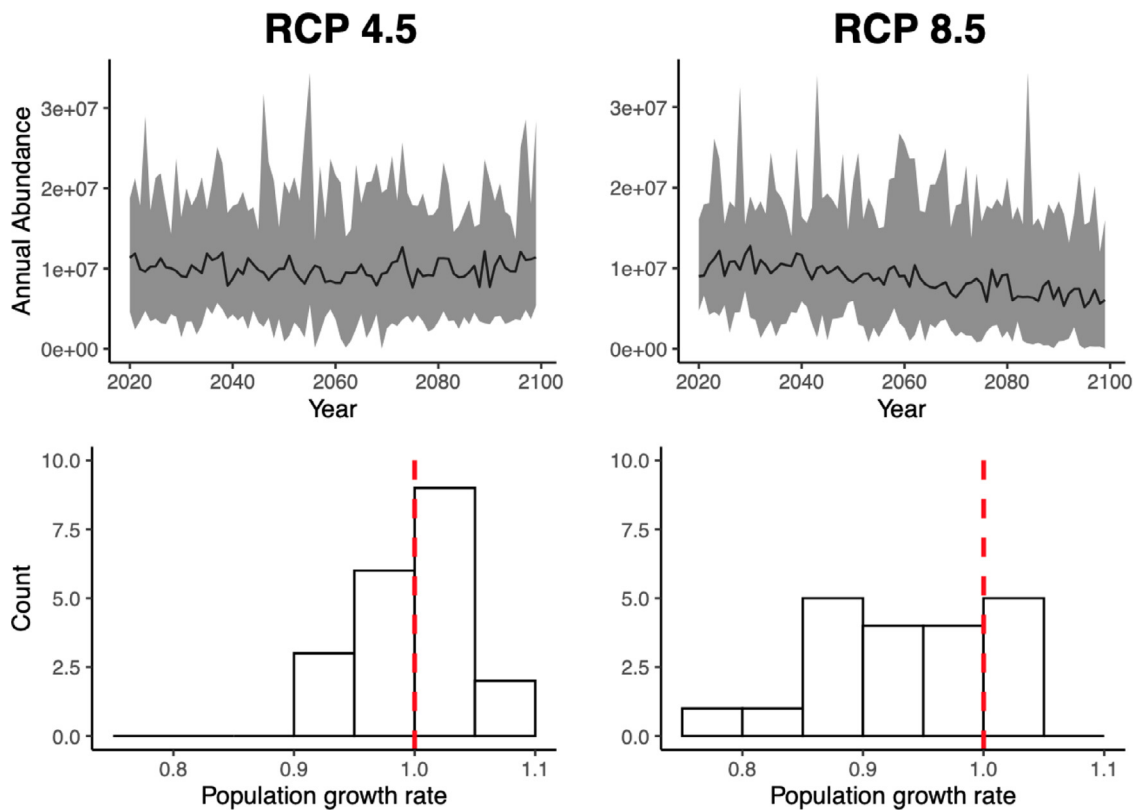


Fig. 6. Top panels: Annual abundance for each year from 2017–2099 under the best-case simulation (starting population of 10,000 butterflies and diapause survival = 0.995). Solid line represents the annual multi-model median from all 20 global climate models. Shading represents annual maximum and minimum values from the climate model ensemble. Bottom panels: histograms of per-decade population growth rates from 20 GCMs. Dotted red line at 1.0, growth rates above the line represent models that project growing populations and those below, models that project shrinking populations.

species. The focus on temperature in studies of phenology shifts has so far restricted the ability to predict the consequences of climate change for species of interest to those at high latitude. We identified prolonged drought as a compelling mechanism that may explain past, and will likely be responsible for future, tropical insect population declines.

Funding

Southeast Climate Adaptation Science Center Global Change Fellowship awarded to E. Henry, Disney Conservation Fund, Florida Keys National Wildlife Refuges.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank E. Saarinen and S. Steele Cabrera for sharing unpublished data with us. We also thank N. McCoy for creating graphics for this paper. This work would not have been possible without numerous volunteers who assisted on Miami blue butterfly surveys.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2022.100051.

References

- [1] J.M. Cohen, M.J. Lajeunesse, J.R. Rohr, A global synthesis of animal phenological responses to climate change, *Nat. Clim. Chang.* 8 (2018) 224–228, doi:10.1038/s41558-018-0067-3.
- [2] T.L. Root, J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, J.A. Pounds, Fingerprints of global warming on wild animals and plants, *Nature* 421 (2003) 57–60, doi:10.1038/nature01333.
- [3] S.S. Renner, C.M. Zohner, Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates, *Annu. Rev. Ecol. Syst.* 49 (2018) 165–182, doi:10.1146/annurev-ecolsys-110617-062535.
- [4] M. Zimova, L.S. Mills, J.J. Nowak, High fitness costs of climate change-induced camouflage mismatch, *Ecol. Lett.* 19 (2016) 299–307, doi:10.1111/ele.12568.
- [5] L.E. Chambers, R. Altwegg, C. Barbraud, P. Barnard, L.J. Beaumont, R.J.M. Crawford, J.M. Durant, L. Hughes, M.R. Keatley, M. Low, P.C. Morellato, E.S. Poloczanska, V. Ruoppolo, R.E.T. Vanstreels, E.J. Woehler, A.C. Wolfaardt, Phenological changes in the southern hemisphere, *PLoS One* 8 (2013) e75514, doi:10.1371/journal.pone.0075514.
- [6] K. Abernethy, E.R. Bush, P.M. Forget, I. Mendoza, L.P.C. Morellato, Current issues in tropical phenology: a synthesis, *Biotropica* 50 (2018) 477–482, doi:10.1111/btp.12558.
- [7] M.J. Tauber, C.A. Tauber, J.P. Nyrop, M.G. Villani, Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms, *Environ. Entomol.* 27 (1998) 523–530, doi:10.1093/ee/27.3.523.
- [8] N.E. Miller-Struttman, J.C. Geib, J.D. Franklin, P.G. Kevan, R.M. Holdo, D. Ebert-May, A.M. Lynn, J.A. Kettenbach, E. Hedrick, C. Galen, Functional mismatch in a bumble bee pollination mutualism under climate change, *Science* 349 (2015) 1541–1544, doi:10.1126/science.aab0868.
- [9] G.L. Pardee, D.W. Inouye, R.E. Irwin, Direct and indirect effects of episodic frost on plant growth and reproduction in subalpine wildflowers, *Glob. Chang. Biol.* 24 (2018) 848–857, doi:10.1111/gcb.13865.
- [10] E.E. Cleland, J.M. Allen, T.M. Crimmins, J.A. Dunne, S. Pau, S.E. Travers, E.S. Zavaleta, E.M. Wolkovich, Phenological tracking enables positive species responses to climate change, *Ecology* 93 (2012) 1765–1771, doi:10.1890/11-1912.1.
- [11] N.Z. Kerr, T. Wepprich, F.S. Grevstad, E.B. Dopman, F.S. Chew, E.E. Crone, Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly, *Glob. Chang. Biol.* (2019) n/a, doi:10.1111/gcb.14959.
- [12] V. Radchuk, T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P. Adamik, F. Adriaenssen, M.P. Ahola, P. Arcese, J.M. Avilés, J. Balbontin,

- K.S. Berg, A. Borras, S. Burthe, J. Clobert, N. Dehnhard, F. de Lope, A.A. Dhondt, N.J. Dingemans, H. Doi, T. Eeva, J. Fickel, I. Filella, F. Fossøy, A.E. Goodenough, S.J.G. Hall, B. Hansson, M. Harris, D. Hasselquist, T. Hickler, J. Joshi, H. Kharouba, J.G. Martínez, J.B. Mihoub, J.A. Mills, M. Molina-Morales, A. Moksnes, A. Ozgul, D. Parejo, P. Pilard, M. Poibleau, F. Rousset, M.O. Rödel, D. Scott, J.C. Senar, C. Stefanescu, B.G. Stokke, T. Kusano, M. Tarka, C.E. Tarwater, K. Thonicke, J. Thorley, A. Wilting, P. Tryjanowski, J. Merilä, B.C. Sheldon, A.P. Møller, E. Matthysen, F. Janzen, F.S. Dobson, M.E. Visser, S.R. Beissinger, A. Courtiol, S. Kramer-Schadt, Adaptive responses of animals to climate change are most likely insufficient, *Nat. Commun.* 10 (2019) 1–14, doi:10.1038/s41467-019-10924-4.
- [13] A. Ozgul, D.Z. Childs, M.K. Oli, K.B. Armitage, D.T. Blumstein, L.E. Olson, S. Tuljapurkar, T. Coulson, Coupled dynamics of body mass and population growth in response to environmental change, *Nature* 466 (2010) 482–485, doi:10.1038/nature09210.
- [14] J.E. Lane, L.E.B. Kruuk, A. Charmantier, J.O. Murie, F.S. Dobson, Delayed phenology and reduced fitness associated with climate change in a wild hibernator, *Nature* 489 (2012) 554–557, doi:10.1038/nature11335.
- [15] J.P. Michielini, E.B. Dopman, E.E. Crone, Changes in flight period predict trends in abundance of Massachusetts butterflies, *Ecol. Lett.* 24 (2021) 249–257, doi:10.1111/ele.13637.
- [16] T. Wepprich, *Effects of Climatic Variability On a Statewide Butterfly Community, Dissertation, North Carolina State University, 2017.*
- [17] N. McLean, C.R. Lawson, D.I. Leech, M. van de Pol, Predicting when climate-driven phenotypic change affects population dynamics, *Ecol. Lett.* 19 (2016) 595–608, doi:10.1111/ele.12599.
- [18] M.C. Urban, G. Bocedi, A.P. Hendry, J.B. Mihoub, G. Pe'er, A. Singer, J.R. Bridle, L.G. Crozier, L. De Meester, P.W. Godsoe, A. Gonzalez, J.J. Hellmann, R.D. Holt, A. Huth, K. Johst, C.B. Krug, P.W. Leadley, S.C.F. Palmer, J.H. Pantel, A. Schmitz, P.A. Zollner, J.M.J. Travis, Improving the forecast for biodiversity under climate change, *Science* 353 (2016) aad8466, doi:10.1126/science.aad8466.
- [19] S.E. Fick, R.J. Hijmans, *WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas, Int. J. Climatol.* 37 (2017) 4302–4315.
- [20] C.J. Brown, M.I. O'Connor, E.S. Poloczanska, D.S. Schoeman, L.B. Buckley, M.T. Burrows, C.M. Duarte, B.S. Halpern, J.M. Pandolfi, C. Parmesan, A.J. Richardson, Ecological and methodological drivers of species' distribution and phenology responses to climate change, *Glob. Chang. Biol.* 22 (2016) 1548–1560, doi:10.1111/gcb.13184.
- [21] A.G. Pendergrass, R. Knutti, F. Lehner, C. Deser, B.M. Sanderson, Precipitation variability increases in a warmer climate, *Sci Rep.* 7 (2017) 17966, doi:10.1038/s41598-017-17966-y.
- [22] E.K. Meineke, C.C. Davis, T.J. Davies, Phenological sensitivity to temperature mediates herbivory, *Glob. Chang. Biol.* 27 (2021) 2315–2327, doi:10.1111/gcb.15600.
- [23] IPCC, *Climate Change Synthesis Report. Contribution of Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Geneva, Switzerland, 2014 2014.*
- [24] L.P.C. Morellato, B. Alberton, S.T. Alvarado, B. Borges, E. Buisson, M.G.G. Camargo, L.F. Cancian, D.W. Carstensen, D.F.E. Escobar, P.T.P. Leite, I. Mendoza, N.M.W.B. Rocha, N.C. Soares, T.S.F. Silva, V.G. Staggemeier, A.S. Streher, B.C. Vargas, C.A. Peres, Linking plant phenology to conservation biology, *Biol. Conserv.* 195 (2016) 60–72, doi:10.1016/j.biocon.2015.12.033.
- [25] Y.Y. Chen, A. Satake, I.F. Sun, Y. Kosugi, M. Tani, S. Numata, S.P. Hubbell, C. Fletcher, M.N.N. Supardi, S.J. Wright, Species-specific flowering cues among general flowering Shorea species at the Pasoh research forest, Malaysia, *J. Ecol.* 106 (2018) 586–598, doi:10.1111/1365-2745.12836.
- [26] V. Radchuk, K. Johst, J. Groeneveld, V. Grimm, Behind the scenes of population viability modeling: predicting butterfly metapopulation dynamics under climate change, *Ecol. Model.* 259 (2013) 62–73, doi:10.1016/j.ecolmodel.2013.03.014.
- [27] H.L. Cayton, N.M. Haddad, K. Gross, S.E. Diamond, L. Ries, Do growing degree days predict phenology across butterfly species? *Ecology* 96 (2015) 1473–1479, doi:10.1890/15-0131.1.
- [28] S.J. Wright, O. Calderón, H.C. Muller-Landau, A phenology model for tropical species that flower multiple times each year, *Ecol. Res.* 34 (2019) 20–29, doi:10.1111/1440-1703.1017.
- [29] J.L. Maino, J.D. Kong, A.A. Hoffmann, M.G. Barton, M.R. Kearney, Mechanistic models for predicting insect responses to climate change, *Curr. Opin. Insect Sci.* 17 (2016) 81–86, doi:10.1016/j.cois.2016.07.006.
- [30] A.J. Terando, B. Reich, K. Pacifici, J. Costanza, A. McKerron, J.A. Collazo, K. Riley, P. Webley, M. Thompson, Uncertainty quantification and propagation for projections of extremes in monthly area burned under climate change, *Natural Hazard Uncertainty Assessment: Modeling and Decision Support, Geophysical Monograph 223, American Geophysical Union, 2017 (accessed April 6, 2020).*
- [31] T.C. Bonebrake, L.C. Ponisio, C.L. Boggs, P. Ehrlich, More than just indicators: a review of tropical butterfly ecology and conservation, *Biol. Conserv.* 143 (2010) 1831–1841.
- [32] T.C. Bonebrake, M.D. Mastrandrea, Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts, *Proc. Natl. Acad. Sci.* 107 (2010) 12581–12586, doi:10.1073/pnas.0911841107.
- [33] D.D. Murphy, K.E. Freas, S.B. Weiss, An environment-metapopulation approach to population viability analysis for a threatened invertebrate, *Conserv. Biol.* 4 (1990) 41–51.
- [34] V. Radchuk, C. Turlure, N. Schtickzelle, Each life stage matters: the importance of the response to climate change over the complete life cycle in butterflies, *J. Anim. Ecol.* 82 (2013) 275–285, doi:10.1111/j.1365-2656.2012.02029.x.
- [35] E. Kieckbusch, *Effects of Temperature, Phenology, and Geography on Butterfly Population Dynamics under Climate Change, Dissertation, North Carolina State University, 2020.*
- [36] V. Grøtan, R. Lande, S. Engen, B.E. Sæther, P.J. DeVries, Seasonal cycles of species diversity and similarity in a tropical butterfly community, *J. Anim. Ecol.* 81 (2012) 714–723, doi:10.1111/j.1365-2656.2011.01950.x.
- [37] E.H. Henry, N.M. Haddad, J. Wilson, P. Hughes, Point-count methods to monitor butterfly populations when traditional methods fail: a case study with Miami blue butterfly, *J. Insect Conserv.* 19 (2015) 519–529.
- [38] A. Valtonen, F. Molleman, C.A. Chapman, J.R. Carey, M.P. Ayres, H. Roininen, Tropical phenology: bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage, *Ecosphere* 4 (2013) art36, doi:10.1890/ES12-00338.1.
- [39] D.L. Denlinger, Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya, *Biotropica* 12 (1980) 100, doi:10.2307/2387725.
- [40] P.S. Grimbacher, N.E. Stork, Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in Australia, *Biotropica* 41 (2009) 328–337, doi:10.1111/j.1744-7429.2008.00477.x.
- [41] D.J. Kemp, Reproductive seasonality in the tropical butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae) in northern Australia, *J. Trop. Ecol.* 17 (2001) 483–494, doi:10.1017/S0266467401001365.
- [42] D.L. Denlinger, Dormancy in tropical insects, *Annu. Rev. Entomol.* 31 (1986) 239–264.
- [43] K. Kishimoto-Yamada, T. Itoika, How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomol. Sci.* 18 (2015) 407–419, doi:10.1111/ens.12134.
- [44] H. Wolda, Insect seasonality: why? *Annu. Rev. Ecol. Syst.* 19 (1988) 1–18, doi:10.1146/annurev.es.19.110188.000245.
- [45] M.L. Forister, C.A. Halsch, C.C. Nice, J.A. Fordyce, T.E. Dilts, J.C. Oliver, K.L. Prudic, A.M. Shapiro, J.K. Wilson, J. Glassberg, Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West, *Science* 371 (2021) 1042–1045, doi:10.1126/science.abe5585.
- [46] E.V. Saarinen, J.C. Daniels, Using museum specimens to assess historical distribution and genetic diversity in an endangered butterfly, *Anim. Biol.* 62 (2012) 337–350, doi:10.1163/157075612X624176.
- [47] T. Wepprich, J.R. Adrion, L. Ries, J. Wiedmann, N.M. Haddad, Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA, *PLoS One* 14 (2019) e0216270, doi:10.1371/journal.pone.0216270.
- [48] K. Hayhoe, D.J. Wuebbles, D.R. Easterling, D.W. Fahey, S. Doherty, J. Kossin, W. Sweet, R. Vose, M. Wehner, D.R. Reidmiller, C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, B.C. Stewart, Our changing climate, in: *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II, U.S. Global Change Research Program, Washington, DC, USA, 2018, pp. 72–144.*
- [49] J.R. Redwine, Leaf Morphology Scales Multi-Annual Trends in Nutrient Cycling and leaf, flower, and fruiting phenology among species in the Sub-Tropical Hardwood Forests of the Northern Florida Keys, Florida International University, 2007.
- [50] D.A. Hahn, D.L. Denlinger, Meeting the energetic demands of insect diapause: nutrient storage and utilization, *J. Insect Physiol.* 53 (2007) 760–773, doi:10.1016/j.jinsphys.2007.03.018.
- [51] C. Zonneveld, Estimating death rates from transect counts, *Ecol. Entomol.* 16 (1991) 115–121.
- [52] K.E. Taylor, R.J. Stouffer, G.A. Meehl, An overview of CMIP5 and the experiment design, *Bull. Am. Meteorol. Soc.* 93 (2012) 485–498, doi:10.1175/BAMSD-11-00094.1.
- [53] J.T. Abatzoglou, Development of gridded surface meteorological data for ecological applications and modeling, *Int. J. Climatol.* 33 (2013) 121–131, doi:10.1002/joc.3413.
- [54] H.E. Johnson, L.S. Mills, T.R. Stephenson, J.D. Wehausen, Population-specific vital rate contributions influence management of an endangered ungulate, *Ecol. Appl.* 20 (2010) 1753–1765.
- [55] R. van Klink, D.E. Bowler, K.B. Gongalsky, A.B. Swengel, A. Gentile, J.M. Chase, Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances, *Science* 368 (2020) 417–420, doi:10.1126/science.aax9931.
- [56] J.D. Burdine, K.E. McCluney, Differential sensitivity of bees to urbanization-driven changes in body temperature and water content, *Sci. Rep.* 9 (2019) 1–10, doi:10.1038/s41598-018-38338-0.
- [57] M.D. Hunter, J.N. McNeil, Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore, *Ecology* 78 (1997) 977–986, doi:10.1890/0012-9658(1997)078[0977:HPQIDA]2.0.CO;2.
- [58] A.G. Dale, S.D. Frank, Warming and drought combine to increase pest insect fitness on urban trees, *PLoS One* 12 (2017) e0173844, doi:10.1371/journal.pone.0173844.
- [59] C. Gely, S.G.W. Laurance, N.E. Stork, How do herbivorous insects respond to drought stress in trees? *Biol. Rev.* (2019) n/a, doi:10.1111/brv.12571.
- [60] B.A. Hawkins, R. Field, H.V. Cornell, D.J. Currie, J.F. Guégan, D.M. Kaufman, J.T. Kerr, G.G. Mittelbach, T. Oberdorff, E.M. O'Brien, E.E. Porter, J.R.G. Turner, Energy, water, and broad-scale geographic patterns of species richness, *Ecology* 84 (2003) 3105–3117, doi:10.1890/03-8006.
- [61] P.A. Deutsch, J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalambor, D.C. Haak, R.R. Martin, Impacts of climate warming on terrestrial ectotherms across latitude, *Proc. Natl. Acad. Sci.* 105 (2008) 6668–6672, doi:10.1073/pnas.0709472105.
- [62] K. Scranton, P. Amarasekare, Predicting phenological shifts in a changing climate, *Proc. Natl. Acad. Sci.* 114 (2017) 13212–13217, doi:10.1073/pnas.1711221114.
- [63] J.M. Sunday, A.E. Bates, N.K. Dulvy, Global analysis of thermal tolerance and latitude in ectotherms, *Proc. R. Soc. B* 278 (2011) 1823–1830, doi:10.1098/rspb.2010.1295.
- [64] J.A. Thomas, D.J. Simcox, R.T. Clarke, Successful conservation of a threatened maculinea butterfly, *Science* 325 (2009) 80–83, doi:10.1126/science.1175726.

- [65] J.G. Kingsolver, H.Arthur Woods, L.B. Buckley, K.A. Potter, H.J. MacLean, J.K. Higgins, Complex life cycles and the responses of insects to climate change, *Integr. Comp. Biol.* 51 (2011) 719–732, doi:[10.1093/icb/ucr015](https://doi.org/10.1093/icb/ucr015).
- [66] O. Levy, L.B. Buckley, T.H. Keitt, C.D. Smith, K.O. Boateng, D.S. Kumar, M.J. Angilletta, Resolving the life cycle alters expected impacts of climate change, *Proc. R. Soc. B* 282 (2015) 20150837, doi:[10.1098/rspb.2015.0837](https://doi.org/10.1098/rspb.2015.0837).
- [67] C.B. Schultz, N.M. Haddad, E.H. Henry, E.E. Crone, Movement and demography of At-risk butterflies: building blocks for conservation, *Annu. Rev. Entomol.* 64 (2019) 167–184.
- [68] C.M. Sgrò, J.S. Terblanche, A.A. Hoffmann, What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* 61 (2016) 433–451, doi:[10.1146/annurev-ento-010715-023859](https://doi.org/10.1146/annurev-ento-010715-023859).
- [69] B. Abrahms, D. DiPietro, A. Graffis, A. Hollander, Managing biodiversity under climate change: challenges, frameworks, and tools for adaptation, *Biodivers. Conserv.* 26 (2017) 2277–2293, doi:[10.1007/s10531-017-1362-4](https://doi.org/10.1007/s10531-017-1362-4).
- [70] S. Canessa, G. Guillera Arroita, J.J. Lahoz Monfort, D.M. Southwell, D.P. Armstrong, I. Chadès, R.C. Lacy, S.J. Converse, Adaptive management for improving species conservation across the captive-wild spectrum, *Biol. Conserv.* 199 (2016) 123–131, doi:[10.1016/j.biocon.2016.04.026](https://doi.org/10.1016/j.biocon.2016.04.026).
- [71] R. Serrouya, D.R. Seip, D. Hervieux, B.N. McLellan, R.S. McNay, R. Steenweg, D.C. Heard, M. Hebblewhite, M. Gillingham, S. Boutin, Saving endangered species using adaptive management, *Proc. Natl. Acad. Sci. U. S. A.* 116 (2019) 6181–6186, doi:[10.1073/pnas.1816923116](https://doi.org/10.1073/pnas.1816923116).
- [72] C.L. Boggs, The fingerprints of global climate change on insect populations, *Curr. Opin. Insect Sci.* 17 (2016) 69–73, doi:[10.1016/j.cois.2016.07.004](https://doi.org/10.1016/j.cois.2016.07.004).