Historical legacies of spatial and temporal climate exposure on thermal physiology shape butterfly vulnerability to recent climate change

Sarah E. Diamond[1*], Carmen R. B. da Silva[2]

1 Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA
2 School of Natural Sciences, Macquarie University, North Ryde, New South Wales, Australia

*address for correspondence: sarah.diamond@case.edu

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Few observations are more indelible in ecology than widespread variation in the spatial and temporal occurrence of species. Although the mechanistic underpinnings of such variation are likely multifarious, temperature is argued to be a key driver (Ashe-Jepson et al. 2024). Understanding how temperature shapes species ranges and seasonal activity not only provides insights into historical biogeographic patterns, but also how legacies of historical adaptation to climate impact responses to recent climate change (Bennett et al. 2021). Butterflies serve as a model taxon for both areas of research. For example, climatic niche attributes are associated with range size, phenology, and shifts in these responses under climate change (Diamond et al. 2011, Hausharter et al. 2023, Hällfors et al. 2024). Here, we expand on this work to explicitly consider how thermal adaptation in physiological tolerance traits might set the range limits and seasonal activity of butterflies. At a global scale, greater cold tolerance was significantly associated with higher latitude of the cold range edge and cooler climatic niche extremes. Within a temperate butterfly community, greater cold tolerance was also significantly associated with earlier seasonal emergence timing and the cold climatic niche extreme during the adult flight period. By contrast, heat tolerance was not associated with the latitude of the warm range edge. However, greater heat tolerance was weakly associated with warmer climatic niche extremes during the adult flight period. These warm-season butterflies were exposed to more high temperature events. Overall, a greater number of high temperature events during the adult flight season was associated with butterfly population declines over the last two decades. Climate exposure therefore appears to strongly mediate butterfly vulnerability to recent climate change.

The significant relationship between cold tolerance and latitude of the cold range edge (Figure 1a; Table S1) is consistent with historical expansion of butterflies from the tropics to higher latitude environments (Kawahara et al. 2023). The explanation for maintenance of high heat tolerance at high latitudes (Figure 1c) is less clear, but consistent with results from other ectothermic species (Sunday et al. 2019). The ability to inhabit high latitudes while maintaining high heat tolerance enables greater thermal buffering through larger warming tolerance, or the difference between heat tolerance and environmental temperature. By contrast, microclimatic temperatures already encroach upon butterfly heat tolerances in tropical habitats (Figure 1b). As a consequence, butterflies, like many ectotherms, could be at relatively greater risk in the tropics owing to elevated climate exposure (Figure 1d) (Huey et al. 2012).

In parallel with the results for range limits, seasonal timing of emergence and the cold climatic niche extreme during the adult flight period were both significantly associated with cold tolerance (Figure 2a; Table S1) among species within a temperate butterfly community in North America (extent: 39 to 42 °N latitude). However, while the results for range limits showed no evidence of association with heat tolerance, we did find a weak, marginally non-significant association between the warm climatic niche extreme during the adult flight period and heat tolerance (Figure 2c; Table S1). Species that were active during the warmest part of the season were exposed to a greater number of high temperature events (in excess of 36 °C). Greater frequency of exposure to high temperature events was in turn associated with population declines over the last two decades of climatic warming (Figure 2d; Table S1). Effectively, historical legacies of temperature effects on seasonal timing and heat tolerance appear to render heat tolerant butterflies vulnerable to increases in the frequency and severity of high temperature extremes under climate change (Buckley and Huey 2016). Despite relatively high phenological warming tolerance–the difference between heat tolerance and environmental temperature across the adult flight period (range of species minimums: 9.92 - 15.6 °C; Figure 2b)–climate exposure to high temperature events significantly affected population trends. This result suggests an important role for sub-lethal physiological effects of heat stress (Huey et al. 2012). Alternatively, these patterns could also reflect thermal effects on butterfly host plant timing or viability (Diamond et al. 2011).

Overall, butterflies have high heat tolerance compared to other taxa (Sunday et al. 2019), yet are likely still vulnerable to climate change. Concordance between cold tolerance and high latitude range edges and seasonal emergence that we observed are consistent with species rapidly expanding their leading range edges and shifting their emergence timing earlier in response to climatic warming and relaxation of constraints imposed by cold temperatures (Diamond et al. 2011, Ittonen et al. 2023, Hällfors et al. 2024). By contrast, at lower latitudes, and at higher latitudes among species that inhabit warm climatic niches during their flight periods, we found that butterflies already exhibit vulnerability to the negative effects of climate exposure. This result suggests the critical importance of preserving habitat to maximize microclimatic buffering capacities (Laird-Hopkins et al. 2023). It also suggests that understanding butterfly capacities for plastic and evolved shifts in heat tolerance and range and seasonal timing shifts (Ashe-Jepson et al. 2024) should likewise remain a key priority.

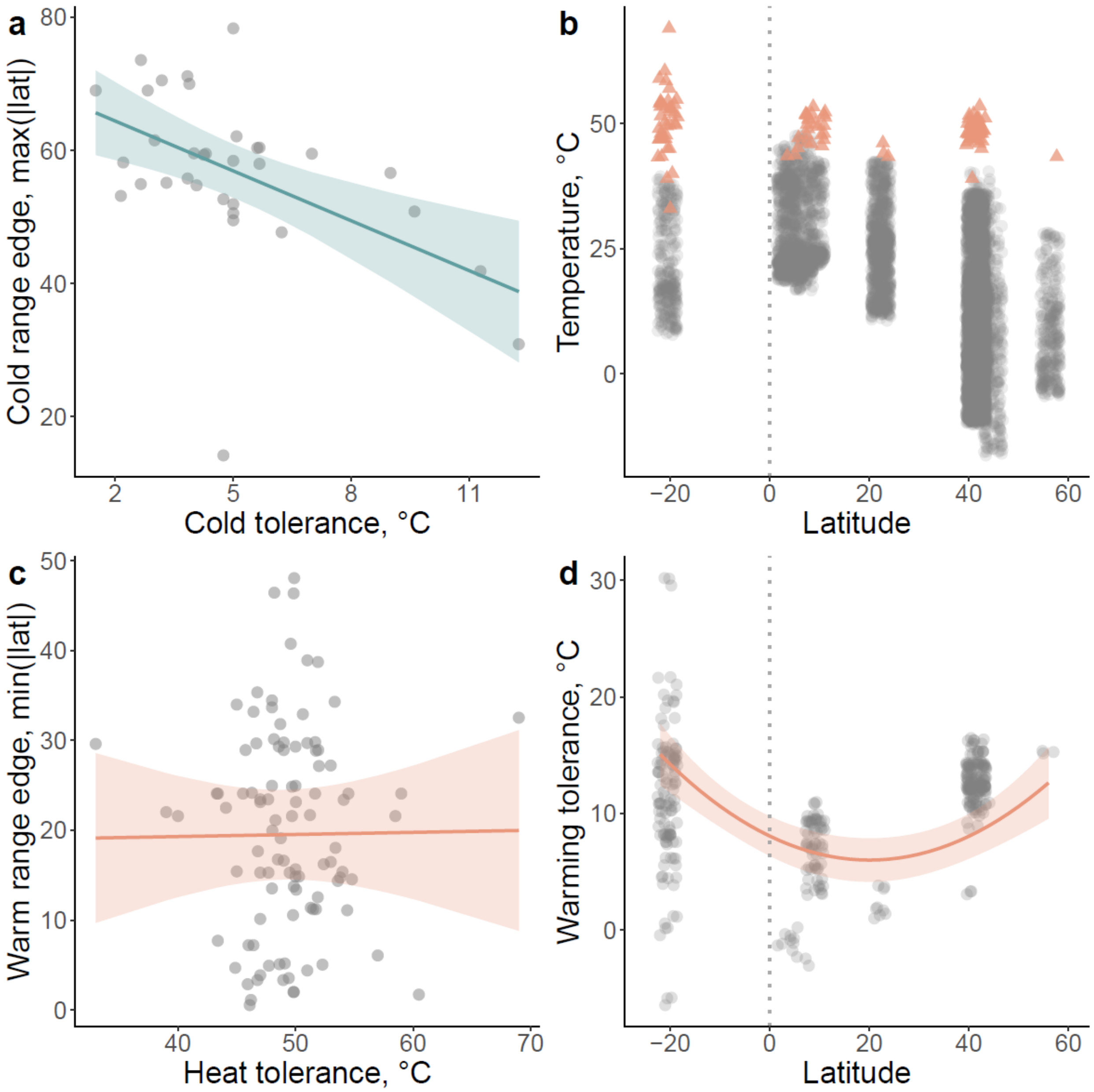

Figure 1. Relationships between range limits, thermal tolerance, and environmental temperature. a) Latitude of the cold range edge as a function of cold tolerance; b) Microclimatic temperature (circles) and heat tolerance (triangles) as a function of latitude; c) Latitude of the warm range edge as a function of heat tolerance; d) Warming tolerance (difference between heat tolerance and microclimatic temperature; 0.99 quantile) as a function of latitude. In panels a,c,d, solid lines represent regression coefficients (including the second-order polynomial in panel d) and polygons represent 95% confidence intervals.

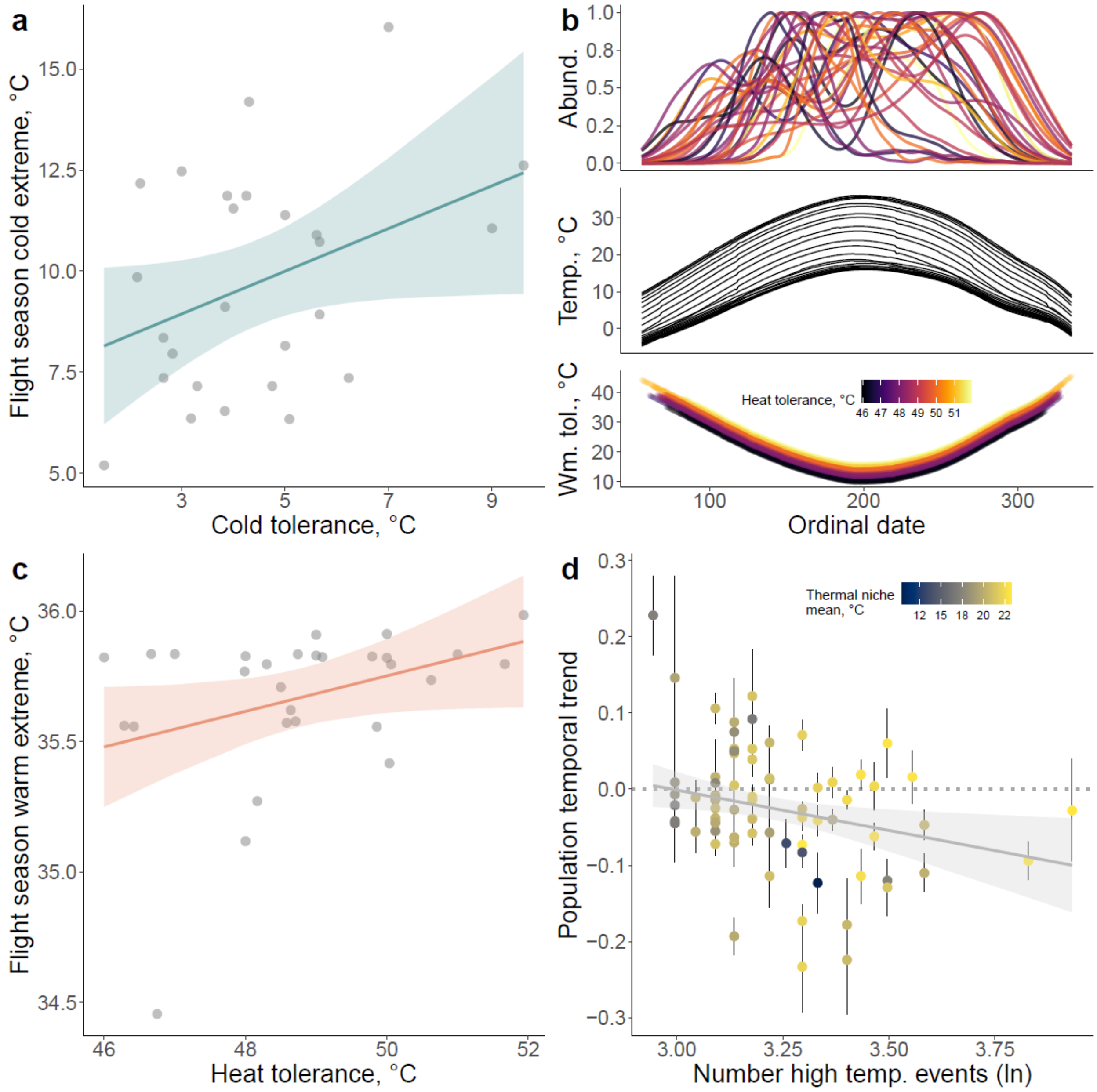

Figure 2. Relationships between seasonal thermal niches, thermal tolerance, and population temporal trends. a) Cold niche extreme as a function of cold tolerance; b) Normalized phenology for each species, color coded by heat tolerance; microclimatic temperature profiles across the butterfly flight season, where lines represent different time points throughout the day; phenological warming tolerances, estimated at the warmest daily time interval (minute 780); c) Warm niche extreme as a function of heat tolerance; d) Population temporal abundance trend

as a function of the number of high temperature events during the flight period (natural-log transformed), with the mean climatic niche color-coding the points. In panels a,c,d, solid lines represent regression coefficients and polygons represent 95% confidence intervals.

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Supporting Information

Methods

Range limits

We produced range maps for each species for which we had thermal tolerance data using the *gbif.range* package (Chauvier et al. 2022) in R (R Core Team 2024). We used the custom ecoregions from this package to estimate species ranges. These maps formed the basis for our estimation of range limits and thermal niches at range limits. We also checked the robustness of our results using range maps from ButterflyMaps (Daru 2025). Our results were qualitatively similar using range maps estimated by gbif.range as those from ButterflyMaps despite seventeen species in the thermal tolerance data not having corresponding range maps from ButterflyMaps. We elected to use the maps from gbif.range as this covered all species in the thermal tolerance dataset with the exception of three species. For these species (*Memphis appias*, *Moneuptychia giffordi*, and *Taygetis drogoni*), there was an insufficient number of occurrences with appropriate georeferencing. We determined the farthest poleward range edge position using the maximum of the absolute value of the latitudes of range limits. Similarly, we determined the most equatorward range edge position using the minimum of the absolute value of the latitudes of range limits.

Flight season activity

We estimated the timing of flight season activity for a community of butterflies in Ohio, USA, a relatively high-latitude location (latitudinal extent of observations: 38.70 °N to 41.81 °N) with strong seasonality. These estimates are derived from citizen science monitoring by the Ohio Lepidopterists, who use a weekly, fixed-transect scheme at multiple sites across the state (Diamond et al. 2014). We estimated a mean phenological profile of adult flight season for each species in the monitoring scheme with a minimum of 100 observations. These estimates were based on the kernel density distribution of ordinal date, weighted by abundance.

We used these phenological profiles in multiple ways. We used them to estimate emergence timing, which we based on the date at the cumulative sum of 10% of the weights in the kernel density distribution of abundance-weighted ordinal dates. This burn-in period minimized detection of extreme early emergers that did not reflect the overall population trend in emergence timing. We also used the phenological profiles to develop weighted estimates of climatic niches and climate exposure.

Thermal tolerance

We used estimates of heat and cold tolerance, the critical thermal maximum (CT_{max}) and minimum (CT_{min}), from PapilioTherm version 2 (Diamond 2024, Diamond et al. 2024). These values define the upper and lower temperatures (in °C) at which normal activity ceases (Terblanche et al. 2011). Most estimates are from individuals at the adult life stage and were recorded using a dynamic temperature ramping protocol. However, like all such databases, methodological variation that can influence tolerance estimation, such as in the rate of temperature change and initial acclimation temperatures, is present, at least among the species considered in our global analysis of range limits and thermal tolerance. This is unlikely to be problematic owing to the large scale over which tolerances are being compared in our analyses of range limits and the fact that the tolerances come from a limited number of studies with many species being assessed using comparable methods. Further, the tolerance data used in our seasonal activity analyses all used the same estimation protocols. We excluded any records without georeferencing, and for which individuals could not be identified to the species level. The CT_{min} values used in our analyses were recorded from warm-season acclimated individuals, and are best interpreted as a low temperature threshold permissive to activity during the growing season.

For our analyses on the relationship between the timing of the flight activity season and thermal tolerance, we excluded the five migratory species for which we had at least an upper and/or lower thermal tolerance estimate (*Danaus plexippus*, *Hylephila phyleus*, *Junonia coenia*, *Vanessa atalanta*, and *Vanessa virginiensis*). Migratory species are subject to seasonal cues in their overwintering locations and thus might have little expectation of an association between thermal tolerance and seasonal activity in their summer breeding grounds. For all other analyses not focused on examining the relationship between thermal tolerance and range limits or seasonal activity, we allowed seasonally migrating species to remain. Specifically, these species were retained in the analyses of warming tolerance and population temporal trends.

Climate exposure

To estimate microclimates, we used NicheMapR (Kearney and Porter 2020). We included estimates throughout the day (60-minute intervals) and across the year. We also allowed the model to run twice to calculate microclimate estimates for both sun and shade (90% and 0% cover, respectively). We used the default estimate of the organism height for which microclimates should be estimated (0.01 m), as this would likely capture near-surface conditions to which butterflies are exposed to temperature while feeding on their larval host plants.

We used microclimates in two ways. First, we used these data to estimate warming tolerance, or the difference between CT_{max} and environmental temperature across latitude. Here, we computed a full set of microclimate estimates (time of day and sun/shade) at the middle of each month for each location in our georeferenced dataset of heat tolerance. Second, we used microclimates in our analyses of seasonal activity. Here, we computed a full set of microclimate estimates (time of day and sun/shade) for each day of the year at a single location, the Squire Valleevue Farm (41.50 °N, -81.42 °W), where the large majority of the thermal tolerance data are from for this specific butterfly community. Cold niche extremes were calculated as the 0.01 quantile of temperatures at emergence, and warm niche extremes were calculated as the 0.99 quantile of temperatures throughout the flight period. We relied primarily on seasonal climatic niches for comparison with heat and cold tolerance traits owing to the fact that temperatures are relatively cooler at emergence, rise to a maximum, and then decline again at the end of the season prior to entry into seasonal diapause. Further, species can shift their timing to avoid high temperature exposure, so temperature exposure weighted by phenological changes in abundance are the most direct test of our question regarding thermal tolerance and climate exposure. However, we did also examine emergence timing, as this metric provided a straightforward interpretation of exposure to cold temperature extremes.

For range-wide climatic niche estimation, we used Worldclim 2.1 (Fick and Hijmans 2017) obtained via the *geodata* package (Hijmans et al. 2024). We did so using 10 km grid cells to cover broad climatic exposure across multiple generations. We extracted the long-term average bioclimate variables within each species range, focusing on bio5 (maximum temperature) and bio6 (minimum temperature). We used a quantile approach to estimate extreme warm and extreme cold niches at range limits, using the 0.99 quantile for the warm niche and the 0.01 quantile for the cold niche.

Models

We constructed linear mixed effects models for our primary analyses using *lme4* (Bates et al. 2015). We used the *car* package to assess statistical significance of predictors (Fox and Weisberg 2019). In all models, we included a random effect of nested taxonomy, genus within family. We obtained qualitatively similar results using a phylogenetically-informed approach with a phylogeny based on the NCBI taxonomy. However, because no currently available time-calibrated butterfly phylogenies captured the range of species in our analyses coupled with our desire to avoid making assumptions about evolutionary rates, we elected to use the nested random effects approach.

For analyses of range limits, we examined, in separate models, the farthest poleward range edge position and the thermal niche cold extreme, each as a function of species mean CT_{min} (per location). Likewise, we examined, in separate models, the minimum equatorward range edge position and the thermal niche warm extreme, each as a function of species mean CT_{max} (per location).

For each combination of site and species, we computed the geographic warming tolerance, or the difference between CT_{max} and environmental temperature, and modeled this index as a function of latitude. Our model also included the second-order polynomial for latitude to account for curvature in the pattern of response. We included only the 0.99 quantile of warming tolerance values in this model, as these are the most relevant for assessing how buffers against exposure to climatic extremes change across latitude. Because the geographic warming tolerance computation resulted in multiple estimates per location, we included location as an additional random intercept in this model.

For analyses of seasonal timing, we examined, in separate models, emergence timing and the cold niche extreme, each as a function of species mean CT_{min} (for observations within the Ohio Lepidopterists monitoring scheme extent). Similarly, we examined the warm niche extreme as a function of species mean CT_{max} (for observations within the Ohio Lepidopterists monitoring scheme extent).

For each species, we computed the phenological warming tolerance, again as the difference between CT_{max} and environmental temperature, but this time across each day within a given species flight period, weighted by their abundance. Here we were most interested in the minimum phenological warming tolerance for each species, so we simply report summary statistics (range, mean, variance) for this variable.

To explore the consequences of historical forces shaping thermal tolerance traits and seasonal activity for responding to recent climate change, we constructed a model of population temporal abundance trend from a previously published analysis (Wepprich et al. 2019) as a function of the number of high temperature events (microclimates estimated at or above 36 °C) across the season. We included the standard error of the population trend as a model weight (1/SE).

Supporting results

Table S1. Model results including parameter estimates, standard errors, test statistics, and P-values. Number of species (season, population temporal trend), species * site combinations (latitude), or species * site * environmental temperature combinations (latitude-based warming tolerance) are also provided (n).

Scope	Model	n	Estimate	SE	Chi	P
Latitude	High latitude range limit ~ CT_{min}	33	-2.50	0.722	11.9	0.000549
	Cold extreme ~ CT_{min}	33	1.30	0.357	13.2	0.000283
	Low latitude range limit ~ CT_{max}	100	0.0234	0.252	0.00860	0.926
	Warm extreme ~ CT_{max}	100	-0.00805	0.0484	0.0277	0.868
	Warming tolerance ~ latitude + latitude^2	366	-58.9 45.7	11.8 7.93	45.3	<0.0001
Season*	Emergence date ~ CT_{min}	26	3.54	1.72	4.21	0.0401
	Cold extreme ~ CT_{min}	26	0.528	0.262	4.05	0.0441
	Warm extreme ~ CT_{max}	29	0.0681	0.0349	3.81	0.0511
Population temporal trend	Trend ~ number high temperature events	74	-0.106	0.0423	6.25	0.0124
	Number high temperature events ~ mean thermal niche	74	0.0193	0.00894	4.67	0.0310

* Minimum phenological warming tolerance for each species ranged from 9.92 to 15.6 °C with a mean of 12.8 °C and standard deviation of 1.53 °C.

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