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Niche width predicts extinction from climate change and vulnerability of tropical species

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Abstract

Climate change may be a major threat to global biodiversity, especially to tropical species. Yet, why tropical species are more vulnerable to climate change remains unclear. Tropical species are thought to have narrower physiological tolerances to temperature, and they have already experienced a higher estimated frequency of climate-related local extinctions. These two patterns suggest that tropical species are more vulnerable to climate change because they have narrower thermal niche widths. However, no studies have tested whether species with narrower climatic niche widths for temperature have experienced more local extinctions, and if these narrower niche widths can explain the higher frequency of tropical local extinctions. Here, we test these ideas using resurvey data from 538 plant and animal species from 10 studies. We found that mean niche widths among species and the extent of climate change (increase in maximum annual temperatures) together explained most variation (>75%) in the frequency of local extinction among studies. Surprisingly, neither latitude nor occurrence in the tropics alone significantly predicted local extinction among studies, but latitude and niche widths were strongly inversely related. Niche width also significantly predicted local extinction among species, as well as among and (sometimes) within studies. Overall, niche width may offer a relatively simple and accessible predictor of the vulnerability of populations to climate change. Intriguingly, niche width has the best predictive power to explain extinction from global warming when it incorporates coldest yearly temperatures.

KEYWORDS
animals, climate change, climatic niche, extinction, global warming, latitude, niche width, plants

1 | INTRODUCTION

Global warming may pose a major threat to global biodiversity (Urban, 2015), and the risk of extinction from climate change may be far greater for tropical species. For example, projected extinction rates have been predicted to be highest among species from low-latitude biodiversity hotspots (Malcom et al., 2006). Recent projections based on extinctions that have already occurred suggest that future species-level extinctions may be twice as high in frequency among tropical species than among temperate species (Román-Palacios & Wiens, 2020). While many authors have postulated that tropical species may be more vulnerable to climate change (e.g., Deutsch et al., 2008; Huey et al., 2009; Linck et al., 2021; Rohr et al., 2018; Sunday et al., 2011; Tewksbury et al., 2008; Vinagre et al., 2016), the reasons for this greater vulnerability remain unresolved.

Many explanations have been proposed for why tropical species may be more sensitive to climate change. First, lower-latitude species may have less ability to adjust their upper thermal tolerances following long-term exposure to high temperatures (i.e., limited acclimation

TABLE 1 Summary information for the 10 studies included here

Study	Species	Taxonomic group	Historical	Modern	Location
Brusca et al. (2013)	27	Plant	1963	2011	Tucson, Arizona
Chen et al. (2011)	208	Insect	1965	2007	Mount Kinabalu; Sabah, Borneo; Malaysia
Felde et al. (2012)	105	Plant	1900	2008	Geovekst & Norwegian municipalities, Norway
Forero-Medina et al. (2011)	55	Bird	1969	2012	Huanuco, Peru
Freeman and Class Freeman (2014)	54	Bird	1965	2012	Mt. Karimui northwestern ridge, New Guinea
Menendez et al. (2014)	39	Insect	1982	2007	Sierra Nevada, Spain; south-western Alps, France
Ploquin et al. (2013)	16	Insect	1988	2009	Asturias, Spain
Raxworthy et al. (2008)	30	Amphibia/Squamata	1993	2003	Tsaratanana Massif, Madagascar
Sheldon (2012)	2	Insect	1977	2006	Smoky Mountains National Park, Tennessee
Warren and Chick (2013)	2	Insect	1973	2012	Appalachian Mountains, north Georgia

Note: For each study, the total number of species, taxonomic group (major clade to which the species belong), dates of historical and modern surveys, and approximate geographic region (location) are reported.

capacity: Rohr et al., 2018; Stillman & Somero, 2000; Stillman, 2003; Vinagre et al., 2016; but see Gunderson & Stillman, 2015; Sørensen et al., 2016). This pattern has been attributed to reduced temperature seasonality in the tropics, which may select for narrower physiological tolerances (Ghalambor et al., 2006; Janzen, 1967). However, evidence that seasonal temperature variation predicts acclimation capacity is mixed (Rohr et al., 2018; Seebacher et al., 2014). Second, species' warming tolerances (the difference between their critical thermal maxima and mean annual surface air temperatures where they occur) seem to decrease at lower latitudes (Deutsch et al., 2008). Third, critical thermal tolerance breadths (maxima minus minima) seem to decrease at lower latitudes (Addo-Bediako et al., 2000; Huey et al., 2009; Sunday et al., 2011). Realized climatic niche widths for temperature, or the range of climatic temperatures where a species occurs, are potentially constrained by these thermal tolerance breadths. Because of this, studies have predicted that species with narrower climate niche widths are more vulnerable to warming (Herrera et al., 2018; Thuiller et al., 2005; Williams et al., 2007) but have not tested this across temperate and tropical regions. Overall, these studies suggest that the narrower range of climatic temperatures experienced by tropical species may make them more vulnerable to climate change. However, they have not linked narrower niche widths to tropical extinctions that have occurred so far. For example, the studies of physiological tolerances have not shown that these limited tolerances actually lead to local or species-level extinctions as climate warms.

Conversely, research has shown that climate-related local extinctions appear to be more frequent in the tropics than in the temperate zone (Wiens, 2016), but has not addressed why this happens. "Local extinction" means that a species no longer occurs at a given site where it once occurred (regardless of the underlying cause). The populations of a species at the warmest edge of its geographic range (i.e., lowest elevation or latitude) are those predicted to go extinct first as climate warms (Chen et al., 2011; Hickling et al., 2006; Walther et al., 2002). In a meta-analysis including 976 species that had been surveyed and resurveyed over time, warm-edge local extinctions were significantly more frequent among tropical species

than temperate species (Wiens, 2016). Most species surveyed were terrestrial plants and animals along elevational gradients. Among these species ($n = 805$), there were warm-edge local extinctions in 55% of the tropical species and only 28% of the temperate species. These results suggest that tropical species have already experienced more climate-related local extinctions than temperate species. However, they do not address the underlying causes of this pattern.

These two types of studies (physiological, resurvey) together suggest that tropical species may be more vulnerable to extinction from climate change, and that narrower climatic niche widths for temperature might help explain this pattern. However, to our knowledge, no study has shown that species with narrower climatic niche widths actually experience a greater frequency of climate-related local extinctions.

Here, we attempt to fill this crucial gap in the literature by directly analyzing the relationship between climatic niche width and climate-related local extinctions that have already occurred. We utilize data from 10 resurvey studies (Table 1) to quantify the frequency of warm-edge local extinction among 538 terrestrial plant and animal species along elevational gradients. These studies documented the presence and absence of these 538 species at 581 sites over time based on an initial historical survey and a more recent resurvey of the same sites. A total of 44% of these 538 species experienced local extinctions at their warmest site on their elevational transect. Furthermore, climatic data are available for each site, both from the general time of the initial survey and that of the more recent resurvey (Román-Palacios & Wiens, 2020). These climatic data are necessary to assess the potential influence of both climatic niche width and the extent of climate change on local extinction.

These climatic data also allowed us to generate different measures of temperature niche width to test their relationship to local extinction. It is unclear which measure of temperature niche width should best predict local extinction from climate change. The realized climatic niche width for temperature can be calculated based on the range of climatic temperatures that a species is exposed to over the course of a year (i.e., hottest annual temperature minus coldest annual temperature). This measure can be calculated both for each

sampled locality and for the overall species range (e.g., Quintero & Wiens, 2013) and is potentially consistent with the physiology-based predictions described above. Local extinction might be best predicted by climatic niche widths at species' warmest-edge localities, where climate change is most likely to drive extinction. Alternatively, niche widths based on the species' overall temperature range might be a better predictor. Both measures of niche width incorporate the coldest temperatures a population or species experiences. But it is unclear if these coldest temperatures are the most relevant. Indeed, the increase in hottest annual temperatures was found to best predict local extinctions among these 538 species (Román-Palacios & Wiens, 2020). Therefore, a measure of niche width based on species-level variability in exposure to hottest temperatures might be a more relevant and accurate predictor of local extinctions from climate change among species. To our knowledge, no previous studies have compared how these different measures of temperature niche width might be related to local extinctions.

It is also crucial to include the extent of climate change. Species may be more likely to have warm-edge local extinctions because they were exposed to a greater increase in temperature, regardless of their climatic niche width. It is especially important to include the increase in hottest annual temperatures over time (Román-Palacios & Wiens, 2020). Other measures, such as the change in mean annual temperatures, may be positively misleading about local extinctions from climate change (Román-Palacios & Wiens, 2020).

In this study, we test the relationship between climatic temperature niche width and local extinction. First, we calculate three different measures of niche width (Figure 1): two based on the difference between maximum and minimum annual temperatures (either for the warmest-edge locality of a species' range, or for all sampled localities across the species' range), and a third based on variability in maximum annual temperatures across all sampled localities. We also incorporate the amount of climate change at the warmest-edge site (Figure 1). Second, we test the relationships between temperature niche width, climate change, and local extinction, to see if species with narrower climatic niche widths are more likely to have warm-edge local extinctions (for a given amount of climate change). We perform three levels of analyses. Our main analysis (using linear regression) treats each study as a unit using mean values of niche width and climate change among species and the overall frequency of warm-edge local extinction among species in each study. This accounts for the greater variation in latitude and niche width among studies (relative to variation among species within a study of a single region). We also conduct logistic regression analyses treating each species as a unit across all species and studies, as well as separate analyses across species within each individual study. Overall, our results show that climatic niche width (based on the range of hottest to coldest temperatures at the warmest-edge locality) can be an important predictor of the frequency of warm-edge local extinctions, especially when combined
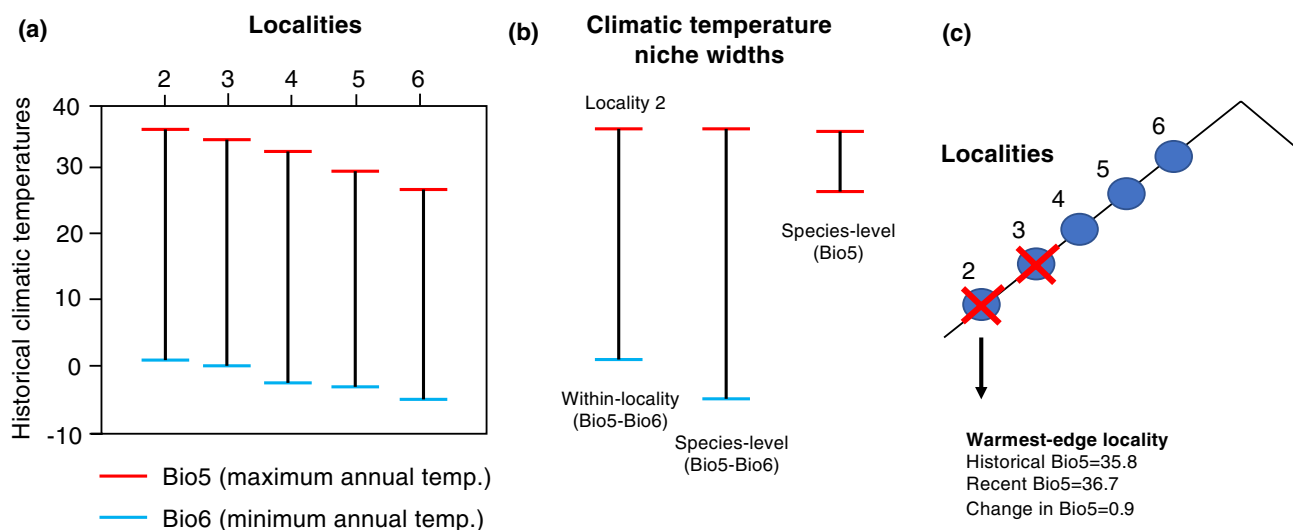

FIGURE 1 Example illustrating how temperature niche widths and climate change are measured for each species in this study. Data are from a succulent plant species (sotol; *Dasylirion wheeleri*) near Tucson, Arizona, with distributional data from Brusca et al. (2013) and climatic data from Román-Palacios and Wiens (2020). The species was surveyed repeatedly at eight localities along an elevational transect and occurred at sites 2 to 6 in the initial survey (1963) and sites 4 to 6 in the subsequent resurvey (2011). In (a), the range of climatic temperatures that the species experienced at each locality (in °C) is given for the time of the historical survey (1963), based on the maximum temperature of the warmest month (Bio5; red horizontal line) and minimum temperature of the coldest month (Bio6; light blue horizontal line). In (b), the three measures of climatic niche width for this species are shown, all based on the range of historical temperatures in (a), and the same y-axis. These are the within-locality niche width (Bio5 minus Bio6) for the warmest-edge locality (locality 2, with the highest historical Bio5), the species-level niche width (based on the maximum Bio5 and minimum Bio6 across all five localities), and the species-level niche width for Bio5 (maximum minus minimum Bio5 across all five localities). In (c), the calculation of the extent of climate change is shown, based on the difference between the value of Bio5 (in °C) for the warmest-edge locality (locality 2) at the time of the initial survey (1963; 10-year window) and the Bio5 value for this locality at the time of the resurvey (2011; 10-year window). The species had local extinction at the two lowest-elevation sites after the initial survey (sites 2 and 3, indicated with red Xs). [Colour figure can be viewed at wileyonlinelibrary.com]

with the extent of climate change. Moreover, even though niche width is strongly related to latitude, niche width seems to be a better predictor of local extinction than latitude or occurrence in tropical regions.

2 | METHODS

2.1 | Data

We started with the distributional and climatic data set generated by Román-Palacios and Wiens (2020). This data set compiled distributional information from 10 studies for 538 species across 581 sites along elevational transects (Table 1; Figure 2). Each study documented the presence and absence of each species at each site based on both historical surveys and modern resurveys of each site. The time between surveys was at least 10 years (Table 1), with historical surveys from 1900 to 1993 (mean = 1968) and recent resurveys from 2003 to 2012 (mean = 2009). These 538 species included 132 plant species and 406 animal species. The majority of animals were insects ($n = 267$), whereas the others were vertebrates ($n = 139$; mostly birds). This sampling generally reflects broad-scale patterns of plant and animal diversity (i.e., more animals than plants, more insects than vertebrates; Ower & Roskov, 2019). The frequency of warm-edge local extinction seems to be broadly similar among taxonomic groups and habitats (present in ~40%–60% of species;

Wiens, 2016), but with higher frequencies in fish and freshwater (not included here). Four studies were from tropical locations (Figure 2) and six were from temperate locations (with the three studies from the southern US considered temperate or subtropical rather than tropical). Most species were tropical ($n = 347$). Again, this reflects broad-scale patterns of plant and animal diversity. Each sampled species was present in only one study. Note that those authors (Román-Palacios & Wiens, 2020) also ruled out habitat modification and other non-climatic human impacts as the primary explanation for the observed warm-edge extinctions in their study.

Román-Palacios and Wiens (2020) also generated fine-scale climatic data for each site at the time of each initial survey and the resurvey. Data spanned the years 1901 to 2013 and used the CRU TS 3.22 data set (Harris et al., 2013), using 1901 in place of 1900 (Table 1). To account for interannual variation in climatic variables, they used empirical mode decomposition (Wu et al., 2007), a widely used method that incorporates variability over the entire period between the sampling dates to estimate climate values for each date. Their results were generally similar using climatic values averaged from 5 to 10 years before each survey (when possible). Values for each of the 19 WorldClim variables (as defined by O'Donnell & Ignizio, 2012) were calculated for each site for the time window of the historical survey and recent resurvey.

We used these data to generate our own data set on niche width, temperature change between surveys, and local extinction. We focused on these variables at the warmest sampled locality for each
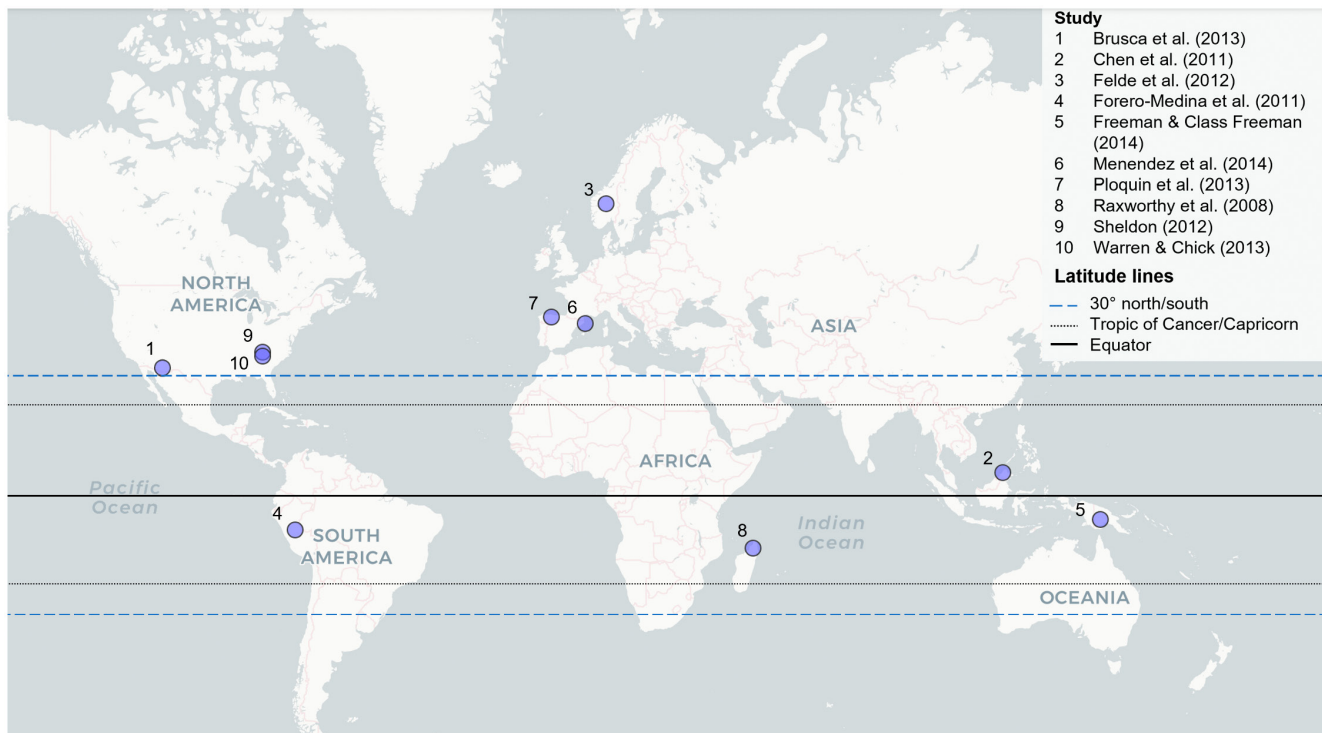

FIGURE 2 World map indicating the location of each study. Latitude and longitude values of each point were calculated as the mean values among localities within each study. The equator, Tropic of Cancer, and Tropic of Capricorn are shown. The dashed blue lines at 30° north and south latitude indicate the demarcation used between tropical and temperate regions. Map was created with the MAPVIEW package in R (Appelhans et al., 2022). Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

species (that with the highest value for maximum annual temperature, Bio5). Local extinctions caused by rising temperatures are expected to occur first at the warmest locality within a species' range, such as the lowest-elevation site on an elevational transect (Chen et al., 2011; Hickling et al., 2006; Walther et al., 2002). The amount of warming experienced by a given species was calculated as the difference in Bio5 between historical and modern surveys at the species' warmest historical locality (i.e., locality with highest Bio5 value at the time of the historical survey) on the transect. We used Bio5 because increases in Bio5 were found to be the best predictor of which sites had local extinctions for these 538 species (Román-Palacios & Wiens, 2020).

Data for each sampling location are given in Datafile S1. Data for each species are given in Datafile S2. Data for each study are given in Datafile S3. All R code used is in Datafile S4. All data files are available on Dryad (Grinder & Wiens, 2022).

2.2 | Niche-width calculations

We calculated three measures of niche width for each species (Figure 1), based on their realized climatic niche for temperature. These were within-locality (WL) niche width, species-level (SP) niche width, and Bio5 (B5) niche width. We calculated niche widths based on historical climate data (those from the time of the initial survey) because niche widths based on the time of the resurveys would potentially be influenced by the local extinction events that we are trying to predict (e.g., loss of the warmest-edge populations could make the climatic niche narrower) and by climate change (e.g., rising temperatures could make climatic niches wider).

First, we calculated each species' WL niche width for its warmest locality (i.e., locality with the highest Bio5). Thus, we subtracted the minimum temperature of the coldest month (Bio6) from the maximum temperature of the warmest month (Bio5) of the warmest historical locality (Bio5 minus Bio6; Quintero & Wiens, 2013).

Second, we calculated SP niche width as the overall annual range of temperatures experienced by each species across all sampled localities. SP niche width was calculated as the difference between the maximum Bio5 and the minimum Bio6 across all localities occupied by a species along the transect at the time of the historical survey (Quintero & Wiens, 2013). This measure assumes that a species' overall temperature niche width is influenced by variation in climatic conditions among localities. Some species ($n = 44$) were found at only one locality, making SP and WL niche widths identical in these species.

Finally, we calculated the B5 niche width for each species by subtracting the minimum Bio5 value from the maximum Bio5 value across all sampled localities at the time of the historical survey. We used this measure because of the demonstrated importance of Bio5 to local extinctions in these species (Román-Palacios & Wiens, 2020). Therefore, within-species variability in Bio5 might be most relevant to the species' vulnerability or resilience to climate change in Bio5.

An important caveat about these measures of species-level niche width is that they are only based on the localities along the elevational transects that were the focus of these studies. Many species have much wider geographic ranges outside of these transects. However, we think that this is unlikely to be problematic for our study, for several reasons. First, we show that WL niche widths are strongly related to transect-wide niche widths (see below). Second, we show that WL niche widths are better predictors of local extinction than these transect-wide variables (which suggests that the WL niche widths will be better predictors than species-wide niche widths as well). Third, more generally, within-locality and species-wide temperature niche widths are generally strongly related, in both plants and animals (Liu et al., 2020). Fourth, the WL and SP niche widths that are based only on these transects may be the most relevant to predicting local extinction along these same transects. If our estimates of local extinction were based on the entire species' range instead, then species-wide niche widths might be more relevant.

2.3 | Statistical analyses

2.3.1 | Overview

Our primary question is whether climatic niche width is a significant predictor of climate-related local extinction. Across all the data points (species, sites, and studies), we expected most variation in niche width, climate change, and extinction to be among studies rather than among sites and species within each study. That is because studies were conducted at diverse locations across the globe (from subarctic to tropical) and focused on different groups of organisms (Table 1). By contrast, each study focused on an elevational transect at one geographic location and one group of organisms (e.g., insects vs. plants vs. birds). We therefore primarily focused on comparisons among studies, with the 10 studies as the units of analyses. For each study, extinction frequency was calculated as the number of species that had local extinction at their warmest locality, divided by the total number of species in the study. Species that occurred lower in elevation in the resurvey (downward shift) were not counted as having a warm-edge local extinction, regardless of other changes in their distributions (Datafile S2). Latitude for each study was calculated as the mean absolute value of latitude values across all sites surveyed in that study (this variation was very limited). One disadvantage of this approach is that it treats all studies as equivalent, regardless of the number of species sampled, and there is potential for error caused by studies with few species (Table 1). We also conducted analyses across all 538 species (using species as units). Finally, we conducted some analyses among species within a given study. All statistical analyses were conducted in R version 4.11 (R Development Core Team, 2020).

2.3.2 | Extinction, latitude, and niche width

In addition to our primary question (see next section), we first addressed several related questions that provide essential background.

Most importantly, we needed to know whether local extinction was indeed greater in tropical regions and/or lower latitudes in general. First, we asked whether local extinctions were more frequent among tropical species, as predicted above. We performed an unpaired *t*-test (in R) comparing extinction frequencies between studies conducted in tropical versus temperate zones. Studies located below 30° absolute latitude north and south were classified as tropical, and studies above 30° absolute atitude north and south were classified as temperate (Henry, 2005). Using an alternative threshold (23.4° latitude) yields an identical set of studies being classified as tropical versus temperate (Figure 2). We accounted for the boundedness of extinction frequencies using a non-parametric Wilcoxon test in the R package RSTATIX 0.70 (Kassambara, 2021). Second, we performed a linear regression (with the function *lm* in R) to test if there was a negative relationship between the latitudinal location of a study (independent variable) and the frequency of local extinction among the species surveyed (dependent). We predicted more frequent local extinction in tropical regions and at lower latitudes in general. We also tested the relationship between absolute values of latitude and niche width among studies as well as among species. We predicted narrower niche widths at lower absolute latitudes. For our species-level analyses, we used the absolute value of latitude of the warmest sampled locality occupied by a species and the species' value for each niche width variable, and we used mean absolute values of latitude across localities for our study-level analysis. Finally, we tested how our three measures of niche width were related to each other among species using linear regression. For species found at only one historical locality ($n = 44$), the SP and WL niche widths were necessarily identical, and so we confirmed that the relationship between them was similar after removing these species. We acknowledge that our analyses at the species-level did not correct for phylogeny. This is partly why our main analyses were based on the comparison among studies (which do not require a phylogenetic correction). Unfortunately, we do not know of a phylogeny that spans all these species, especially the many Asian moth species in Chen et al. (2011).

2.3.3 | Comparison among studies

For our primary question, our focus was on testing whether variation in the frequency of warm-edge local extinction among studies was predicted by narrower temperature niche widths and by larger increases in Bio5. Specifically, we used linear regression models to test if the frequency of local extinctions among species within each study (dependent variable) was negatively related to the mean climatic niche width among species in each study (independent variable) and positively related to the mean change in Bio5 at each species' warmest locality (independent variable). We first calculated mean values of niche width (WL, SP, B5) among the species in each study. We then calculated the change in Bio5 between surveys at the warmest historical locality for each species within each study, and then averaged these values among species in each study. Four

regression models were created to test niche width and change in Bio5 as predictors of local extinction frequency: (1) one testing only change in Bio5, (2) another testing only the effect of a niche-width variable, (3) a third including both niche width and change in Bio5, and (4) a fourth model including niche width, change in Bio5, and an interaction effect between niche width and change in Bio5. A separate set of four models was run for each of the three measures of niche width. To compare model fit, we calculated Akaike (1974) information criterion (AIC) values for each model using the *lm* function in R. Models with lower AIC values were considered to have better fit.

2.3.4 | Comparison among species across studies

To further test the effects of niche width and Bio5 change on local extinction, we ran logistic regression analyses treating each species as a unit, including all 538 species across all studies. Local extinction was represented as a binary dependent variable indicating whether a species had local extinction at its warmest historical locality or not. For the SP analyses, we created single and multiple logistic regression models with different combinations of niche width and change in Bio5 as independent variables (and local extinction as the dependent variable). Models were: (1) change in Bio5; (2) a niche-width variable alone; (3) a niche-width variable and change in Bio5; and (4) a niche-width variable, change in Bio5, and their interaction effect. The latter three models were generated for each niche-width variable (WL, SP, or B5), for a total of 10 models overall. Analyses were run using the *glm* function in R. We compared the AIC of each model to determine the best-fit model. We used the PERFORMANCE package in R to calculate a pseudo-r^2, known as Tjur R^2 (Lüdecke et al., 2021). Tjur R^2 is used to determine how well independent variables predict the dependent variable within a model. It is calculated as the difference between the average fitted probability of the two categorical dependent outcomes (in this case, local extinction or persistence; Tjur, 2009). Higher values of Tjur R^2 indicate models with greater predictive power. To account for the potential confounding effects of taxonomic group, we ran separate multiple logistic regression models (matching those listed above) among all plants, all animals, vertebrates, and insects.

2.3.5 | Comparison among species within studies

We also performed similar analyses among species within each study. For studies with fewer species, logistic regression models fit using *glm* resulted in complete separation as a result of model covariates more-or-less perfectly predicting the binary response (Abrahantes & Aerts, 2012). We therefore used Bayesian logistic regression models for all the within-study analyses. We used the *bayesglm* function in the R package ARM (Gelman & Su, 2020). Bayesian logistic models determine model parameter weights by drawing from a binomial distribution of the probable values for each

predictor variable. We fit models using Cauchy priors with a scale of 2.5 (the default using *bayesglm*), as recommended in the presence of complete separation (Gelman et al., 2008). The *bayesglm* function runs iterations until convergence is reached: the number of generations is not set in advance, and burnin is eliminated automatically. We fit 10 Bayesian logistic models matching the logistic regression models described above for our species-level analyses. We then compared AIC values from the *bayesglm* output to determine the best-fit models. We excluded Sheldon (2012) and Warren and Chick (2013) from these within-study analyses because both studies had only two species each. All other studies had 16 or more species. We could not perform within-study analyses for studies with only two species, but we could still include their data in our among-study and species-level analyses.

3 | RESULTS

Data on local extinction, niche width, and climate change for each study are summarized in Table 2. The frequency of warm-edge local extinction was higher in studies in tropical regions than in temperate regions (mean among studies: temperate = 0.33, $n = 6$; tropical = 0.50; $n = 4$). However, this difference was not significant based on a *t*-test ($n = 10$; $p = .335$) or Wilcoxon test ($p = .454$). Similarly, there was no significant relationship across studies between the absolute value of latitude and local extinction frequency ($n = 10$; $r^2 = .130$; $p = .306$). However, there was a significant positive relationship across studies between the absolute value of latitude and both WL niche width and SP niche width ($n = 10$; WL: $r^2 = .663$; $p = .004$; SP: $r^2 = .650$; $p = .005$; Figure 3; Table S1).

Among species, SP niche width and WL niche width (Table S2) were both significantly and positively related to the absolute value

of the latitude of a species' warmest locality ($n = 538$; SP: $r^2 = .733$, $p < .001$; WL: $r^2 = .841$, $p < .001$). Hottest-temperature (B5) niche width was not significantly related to latitude ($n = 538$; $r^2 < .001$, $p = .455$).

Different measures of niche width showed different degrees of covariation among species (Table S3). SP and WL niche widths were strongly related to each other ($n = 538$; $r^2 = .911$, $p < .001$). Excluding the 44 species found at a single locality (which must have identical SP and WL niche widths) had little effect on this relationship ($n = 494$; $r^2 = .915$, $p < .001$). SP and WL niche widths were each more weakly related to B5 niche width (Table S3; $n = 538$; SP: $r^2 = .139$, $p < .001$; WL: $r^2 = .013$, $p = .007$). We found that WL niche width was the best predictor of local extinctions compared with other measures of niche width (Table 3 vs. Tables S4 and S5), and we present results based on this measure first.

Among studies (Table 3), mean WL niche width and mean change in Bio5 explained similar amounts of variation in the frequency of local extinction among species within studies (Figure 4; $n = 10$; WL: $r^2 = .300$, $p = .101$; Bio5 change: $r^2 = .340$, $p = .077$). However, neither relationship was significant. Narrower niche widths combined with greater change in Bio5 were associated with higher frequencies of local extinction than change in Bio5 alone ($n = 10$; $r^2 = .683$, $p = .011$). The best-fitting model included an interaction between these variables. This model explained most of the variance in the frequencies of local extinction among studies ($n = 10$; $r^2 = .768$, $p = .018$).

Results were broadly similar when analyzing all 538 species separately using logistic regression (Table 4). However, WL niche width more strongly predicted local extinction than change in Bio5 alone ($n = 538$; WL niche width: R^2 Tjur = .077, $p < .001$; change in Bio5: R^2 Tjur = .030, $p < .001$). The best-fitting model included an interaction between these two variables and seemed to explain much more variance in local extinction among species (R^2 Tjur = .135; Table 4).

TABLE 2 Data used for analyses among studies

Study	Local extinction frequency	Mean SP niche width	Mean WL niche width	Mean Bio5 niche width	Mean Bio5 change	Region
Brusca et al. (2013)	0.58	38.06	34.02	7.64	0.78	Temperate
Chen et al. (2011)	0.56	13.16	8.93	3.67	0.49	Tropical
Felde et al. (2012)	0.09	32.20	32.20	2.56	0.18	Temperate
Forero-Medina et al. (2011)	0.30	18.63	16.70	1.21	−0.10	Tropical
Freeman and Class Freeman (2014)	0.75	14.72	12.48	2.16	0.09	Tropical
Menendez et al. (2014)	0.55	33.03	29.25	5.25	0.64	Temperate
Ploquin et al. (2013)	0.73	30.69	24.90	3.95	0.39	Temperate
Raxworthy et al. (2008)	0.38	19.02	18.05	1.27	0.28	Tropical
Sheldon (2012)	0.00	37.92	35.81	3.92	−0.03	Temperate
Warren and Chick (2013)	0.00	36.15	34.18	2.91	0.00	Temperate

Note: For each study, the local extinction frequency was calculated as the number of species that had local extinction at their historical warmest site (i.e., locality with the highest Bio5 value at the time of the historical survey), divided by the total number of species in the study. All niche width variables were calculated as averages across species within each study, including within-locality (WL), species-level (SP) niche width, and Bio5 (B5) niche width (all in °C). Mean Bio5 change was the change in Bio5 between historical and modern surveys at the warmest historical locality for each species, averaged across all species within a study. Region indicates whether a study was conducted in the tropics or the temperate zone (Figure 2).
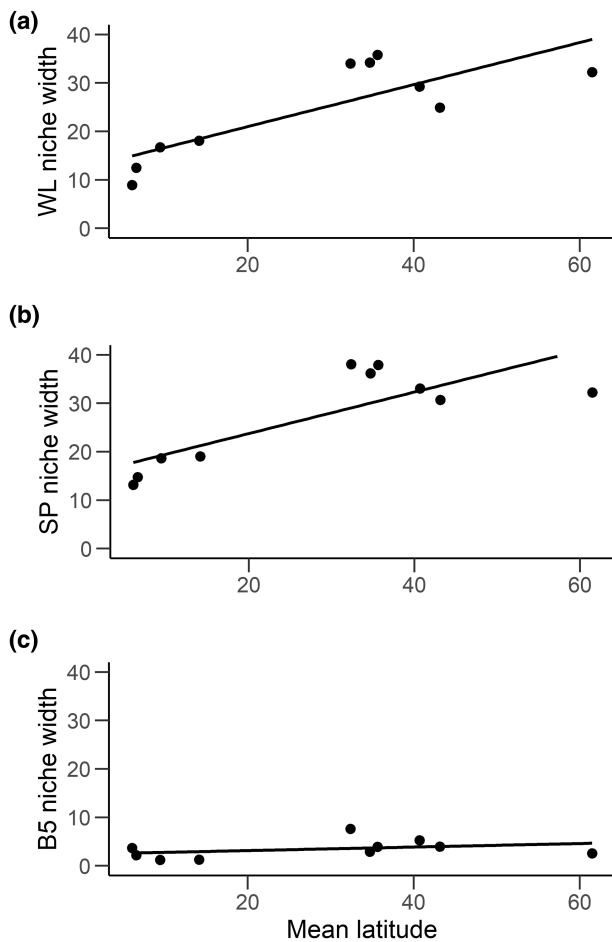
FIGURE 3 Relationships between latitude and different measures of niche width among studies. (a) Linear regression between latitude (absolute value, mean among warm-edge localities for each species in the study) and the mean value of within-locality (WL) niche width among species in each study ($r^2 = .664$; $p = .004$; $n = 10$). (b) Linear regression between latitude and mean species-level (SP) niche width ($r^2 = .649$; $p = .005$; $n = 10$). (c) Linear regression between latitude and mean Bio5 (B5) niche width ($r^2 = .122$; $p = .321$; $n = 10$). Each data point is from one study. Niche widths are in °C.

Results were similar (but weaker) using SP and B5 niche widths (Tables S6 and S7).

We ran similar species-level logistic regression analyses among all plants, all animals, vertebrates, and insects (Tables S8–S13). WL niche width significantly predicted local extinction among plants (Table S8; $n = 132$ species; R^2 Tjur $= .158$; $p < .001$; Figure S1), but the relationship was positive, seemingly because of more extinction and greater variability in niche widths in Brusca et al. (2013), relative to Felde et al. (2012). Species in both of these temperate studies had similar niche widths overall (Table 1). When we analyzed all animals together, narrower WL alone did not significantly predict local extinction (Table S9; $n = 406$; R^2 Tjur $= .006$, $p = .071$; Figure S1), but it did in the multiple regression model ($p = .025$). We predicted that this non-significant result occurred because of large differences in niche width between temperate and tropical insects. Therefore, we first analyzed vertebrates and insects separately. Among vertebrates, narrower WL niche width significantly predicted local extinction (Table S10; $n = 124$; R^2 Tjur $= .091$, $p < .001$; Figure S2). However, WL did not significantly predict local extinction across all insects, as expected (Table S11; $n = 267$; R^2 Tjur $= .002$, $p = .419$; Figure S3a). We next analyzed tropical and temperate insects separately. As expected, narrower WL niche width was a significant predictor of local extinction among both tropical insects (Table S12; $n = 207$; R^2 Tjur $= .087$, $p < .001$; Figure S3b) and temperate insects (Table S13; $n = 59$; R^2 Tjur $= .068$, $p = .024$; Figure S3c). Despite some variability within these groups, all four groups seemed to contribute to the overall pattern of wider niche widths and lower extinction frequencies at higher latitudes and narrower niche widths and higher extinction frequencies at lower latitudes (Tables 1 and 2).

We also analyzed relationships between WL niche width, change in Bio5, and local extinction among species within each study using Bayesian logistic regression models. Two studies were excluded from these within-study analyses because of low sample sizes (see Methods). Among the other eight studies, most showed no significant relationships between local extinction and niche width or change in Bio5 (Tables S14–S21). However, there were significant relationships
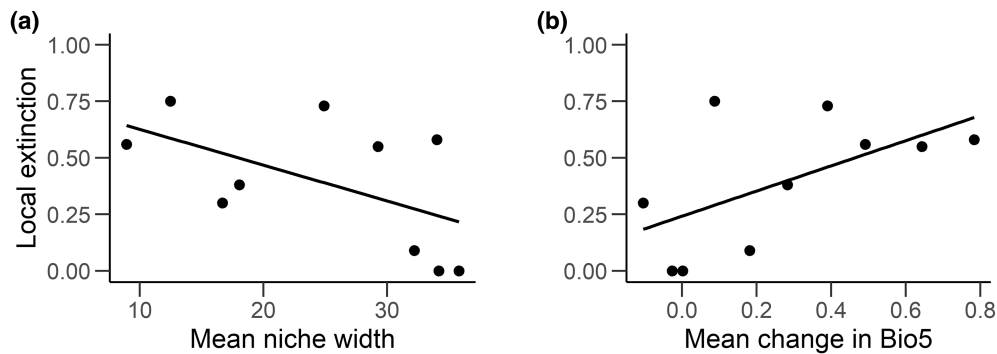

FIGURE 4 Relationships between niche width, climate change, and local extinction among studies. (a) Linear regression ($r^2 = .300$; $p = .101$; $n = 10$) between the frequency of warm-edge local extinction among species in the study and mean within-locality (WL) niche width (difference between Bio5 and Bio6 at the warmest historical locality for each species, averaged among all species in the study, in °C). (b) Linear regression ($r^2 = .340$; $p = .077$; $n = 10$) between local extinction frequency and the mean change in Bio5 (difference in Bio5 between historical and modern surveys at a species' warmest locality, averaged across all species in the study, in °C). The frequency of local extinction was the number of species that went locally extinct at their warmest historically sampled locality divided by the total number of species in the study. Each data point is from one study. Data are in Table 2, and full statistical results are in Table 3.

TABLE 3 Testing the predictors of climate-related local extinctions among studies

Model	Variables	Coefficient	p	r^2	AIC	Model p
(1) Mean change in Bio5	Mean change in Bio5	0.56	.077	.340	4.2	0.077
(2) Mean WL niche width	Mean WL niche width	−0.02	.101	.300	4.7	0.101
(3) Mean WL niche width + change in Bio5	Mean WL niche width	−0.02	.028	.683	−1.2	0.018
	Mean change in Bio5	0.59	.023			
(4) Mean WL niche width * change in Bio5	Mean WL niche width	−0.03	.019	.768	**−2.3**	0.025
	Mean change in Bio5	−0.30	.652			
	mean WL niche width: change in Bio5	0.03	.188			

Note: Results are from linear regression analyses with the frequency of local extinction among species in each study as the dependent variable and mean change in Bio5 and mean WL niche width (separately and together) as the independent variables. The fourth model includes an interaction between niche width and change in Bio5. The AIC of the best-fitting model is boldfaced. Results using alternative measures of niche width are in Tables S4 and S5. Models are numbered and the top row for each model indicates the r^2, AIC, and model p for the model overall. Coefficients and p-values for each row correspond to each variable included in the model.

TABLE 4 Results of logistic regression models predicting local extinction among all 538 species

Model	Variables	Coefficient	p	R^2 Tjur	AIC
(1) Change in Bio5	Change in Bio5	1.26	<.001	.030	727.2
(2) WL niche width	WL niche width	−0.06	<.001	.078	699.9
(3) Change in Bio5 + WL niche width	Change in Bio5	1.14	<.001	.097	689.4
	WL niche width	−0.06	<.001		
(4) Change in Bio5 * WL niche width	Change in Bio5	−2.70	.001	.135	**665.4**
	WL niche width	−0.14	<.001		
	niche width: change in Bio5	0.19	<.001		

Note: Local extinction was the dependent variable, and the independent variables were (1) the change in Bio5, (2) within-locality (WL) niche width, (3) both variables, and (4) both variables and their interaction. Local extinction was a binary variable summarizing whether a species went locally extinct at its warmest historical locality. The best-fitting model (lowest AIC) is boldfaced. Results using two alternative measures of niche width are in Tables S6 and S7. Models are numbered and the top row for each model indicates the R^2 Tjur, AIC, and p for the model overall. Coefficients and p-values for each row correspond to each variable included in the model.

in three studies (all of which were in the tropics). In the study with the largest sample size of species ($n = 208$; Chen et al., 2011), WL niche width was significantly, negatively related to local extinction (Table S15; R^2 Tjur = .103, $p<.001$) but change in Bio5 was not (R^2 Tjur<.001, $p = .833$). For the study by Freeman and Class Freeman (2014), WL niche width was significantly, negatively related to local extinction (Table S18; $n = 54$; R^2 Tjur = .108, $p = .021$) and change in Bio5 was not (R^2 Tjur = .003, $p = .680$). By contrast, in the study of Raxworthy et al. (2008), WL niche width was significantly but positively related to local extinction (Table S21; $n = 30$; R^2 Tjur = .299, $p = .024$) and Bio5 change was not (R^2 Tjur = .096, $p = .127$).

For all three of these studies, elevation had a significant relationship with WL niche width. However, this relationship could be positive (R^2 Tjur = .880, $p<.001$; for the data from Chen et al., 2011; R^2 Tjur = .333, $p<.001$; for Freeman & Class Freeman, 2014) or negative (R^2 Tjur = .991; $p<.001$; for Raxworthy et al., 2008). All three studies also showed a significant, negative relationship between elevation and local extinction among species using logistic regression (R^2 Tjur = .085, $p<.001$: Chen et al., 2011; R^2 Tjur = .237, $p<.001$: Freeman & Class Freeman, 2014; R^2 Tjur = .281, $p = .003$: Raxworthy et al., 2008). Thus, in the study of Raxworthy et al. (2008), species at lower elevations were more likely to experience local extinction

(as in the other two studies), but these lower-elevation species had wider niche widths (in contrast to the other two studies).

Across all analyses, we found that models using WL niche width were generally the best predictors of local extinction. More specifically, models with WL niche width generally had lower p-values and higher r^2 values (Tables 3 and 4, Tables S14–S21) compared with models with SP niche width and B5 niche width (Tables S4–S7 and S22–S37). The within-study analyses using B5 and SP niche widths (Tables S22–S37) generally gave non-significant results, except with the data set of Chen et al. (2011), which showed significant relationships between local extinction and B5 niche width (Table S23) and SP niche width (Table S35).

4 | DISCUSSION

Rising temperatures are a major threat to global biodiversity (Malcom et al., 2006; Urban, 2015). Tropical species are predicted to be the most vulnerable to warming (Deutsch et al., 2008; Huey et al., 2009), but the reasons why have remained unclear. Past studies have speculated that narrower climatic niche widths and thermal tolerance breadths in tropical species may make these species more vulnerable to global

warming (Deutsch et al., 2008; Thuiller et al., 2005). Additionally, warm-edge local extinctions already appear to be more widespread among tropical species (Wiens, 2016). However, no previous study has shown a relationship between narrower climatic niche widths and climate-related local extinctions at the global scale. Here, we found that narrower temperature niche widths are associated with higher frequencies of local extinction across 538 plant and animal species. We found this pattern among studies, among species across studies, and even among species within some studies (i.e., two tropical studies that together include 49% of the sampled species). Moreover, we also found that latitude was significantly related to temperature niche width, but that latitude was not itself significantly related to local extinction. These results suggest that narrower temperature niche widths may primarily explain why tropical species have experienced more local extinction, and not some other factor that is related to latitude. In the sections that follow, we address the causes of these patterns, their implications for conservation, weaknesses of our study, and areas for future research.

4.1 | Why do these patterns occur?

Our results show that narrower climatic niche widths at lower latitudes are associated with higher frequencies of local extinctions. This pattern may be related to latitudinal trends in thermal tolerance breadths and acclimation capacity. First, previous studies have suggested that tropical organisms are more vulnerable to warming because they have narrower thermal tolerance breadths (Addo-Bediako et al., 2000; Sunday et al., 2011). Additionally, Deutsch et al. (2008) and Huey et al. (2009) proposed that tropical organisms are more vulnerable because their mean annual environmental temperatures are already close to their thermal physiological limits. Furthermore, there is evidence of a positive relationship between acclimation capacity and latitude among fungi, invertebrates, and vertebrates, from freshwater, marine, and terrestrial habitats (Rohr et al., 2018; but see Gunderson & Stillman, 2015). This latter pattern suggests that the short-term acclimation capacity of temperate species may allow them to better survive long-term climate warming. All three of these observations may help explain the patterns that we observe here. However, additional studies are needed to link variation in physiological tolerances and acclimation capacity to the patterns of climate-related local extinction that are already occurring.

Our results suggest a very counterintuitive explanation for why tropical species are more vulnerable to climate change: a lack of exposure to cold temperatures. Several lines of evidence suggest this pattern. First, WL niche width based on the yearly range from hottest to coldest temperatures (Bio5-Bio6) was a much better predictor of local extinction than niche width based on the range of hottest annual temperatures (Bio5) across localities. Second, upper thermal tolerance shows little variation with latitude in terrestrial organisms, whereas lower thermal tolerance declines with latitude (e.g., Addo-Bediako et al., 2000; Ghalambor et al., 2006; Sunday et al., 2011). Thus, latitudinal trends in thermal tolerance breadth are primarily

driven by variation in lower thermal tolerance. Similarly, our data show that latitudinal trends in temperature niche width are primarily driven by variation in cold temperatures. We performed supplementary regression analyses among studies and found that Bio6 varied negatively with latitude (n=10; r^2 = .878, $p < .001$) and WL niche width (r^2 = .735, $p = .002$, using the warmest-locality Bio6 and WL niche width). By contrast, Bio5 was not significantly related to either latitude (n=10; r^2 = .047, $p = .546$) or WL niche width (r^2 = .061, $p = .493$). Therefore, the narrower temperature niche widths in tropical species are primarily related to low temperatures in temperate species. Furthermore, temperate species had a greater acclimation capacity to high temperatures than tropical species in an extensive study (Rohr et al., 2018). Given that tropical and temperate species differ primarily in their exposure to low temperatures, the increased acclimation capacity of temperate species may be driven by exposure to cold temperatures rather than high temperatures. One (very speculative) explanation involves heat-shock proteins (*hsps*), molecular chaperones that increase heat tolerance (Feder & Hoffman, 1999). The induction of *hsps* significantly increases following exposure to cold temperatures in insects (e.g., Burton et al., 1988; Huang et al., 2009; Sejerkilde et al., 2003). However, it is unclear if increased synthesis of *hsps* in winter helps protect organisms from heat in later months.

Our within-study comparisons among species also suggest the importance of cold temperatures to withstanding global warming. More specifically, in the studies of Chen et al. (2011) and Freeman and Class Freeman (2014), tropical species at higher elevations had larger temperature niche widths and lower frequencies of local extinction. These larger niche widths seem to occur because there is greater variation in daily temperatures at higher elevations (Pepin et al., 2016). These two studies showed that tropical species exposed to cooler temperatures at higher elevations experienced fewer local extinctions than species at lower elevations. However, while the frequency of local extinction in the study of Raxworthy et al. (2008) also showed a negative relationship with elevation, there was a positive relationship between local extinction and niche width (with wider niche widths and more local extinctions at lower elevations). That study was also unusual in that species were surveyed at only three locations, all at relatively high elevations (1600–2500 m).

In summary, our results suggest that species with wider climatic niche widths (e.g., temperate and high-elevation tropical species) are more resistant to local extinction from climate change. Nevertheless, the counterintuitive relationship suggested between exposure to lower temperatures and surviving higher temperatures will require explicit testing. Perhaps most importantly, a mechanistic explanation for the patterns found here should encompass all the relevant groups, including plants. Therefore, animal-specific mechanisms (e.g., behavior) may not be adequate.

4.2 | Conservation implications

Through this study, we have identified a predictor of climate-related local extinction that is relatively easy to calculate. Previous studies

have predicted species' vulnerability to warming based on latitudinal trends in acclimation capacity (Stillman, 2003), warming tolerance windows (Deutsch et al., 2008; Huey et al., 2009), and thermal tolerance breadths (Addo-Bediako et al., 2000; Sunday et al., 2011). However, these studies did not show a direct link between these variables and climate-related local extinctions. Furthermore, we found that the best predictor of local extinction was a measure of niche width based on historical climate data from a single locality. Therefore, it was not necessary to obtain climatic data from throughout the species' geographic range or from different time windows. Moreover, it can be relatively straightforward to obtain historical climatic data for specific sites (e.g., using the WorldClim data set; Hijmans et al., 2005), far more so than physiological data. Biotic factors may contribute to declines and local extinctions from climate change (e.g., disease, reduced food resources; Cahill et al., 2013; Ockendon et al., 2014). However, it remains unresolved as to whether climate-related extinctions are predominantly caused by changing biotic interactions, limited acclimation or physiological tolerances, or other mechanisms. Yet, our results suggest that climatic niche width may have considerable predictive power without knowing the details of these mechanisms. Importantly, the realized climatic niche widths used here potentially reflect the impact of both biotic and abiotic factors on where species occur (as opposed to measures based on physiological tolerances alone).

4.3 | Limitations of the study and areas for future research

There are some key limitations of our study. First, these 538 species are not a comprehensive set of plant and animal species. We did not include marine or freshwater groups, and this should be a high priority for future studies. Even among terrestrial species, future studies should incorporate tropical plants (for example), more vertebrate groups from more regions (beyond birds), additional insects, and other invertebrate groups (e.g., mollusks). A major limiting factor for including additional species may be the lack of detailed survey and resurvey data (and climatic data for the times of the historical survey and modern resurvey). Nevertheless, analyses of diverse plants and vertebrates suggest that climatic niches follow similar patterns (and relationships with latitude) across plants and animals (Liu et al., 2020). Inclusion of surveys from latitudinal gradients (not just elevational gradients) would also be valuable. Second, more research is needed on the mechanisms underlying these patterns. For example, data on species' acclimation capacity could provide insights into why species exposed to cold temperatures each year seem more resilient to warming. Third, incorporating short-term extreme weather events and climatic variability (in addition to long-term trends) could also be valuable. Fourth, our inferences about local extinctions and species distributions on transects depend on the data from surveys and resurveys over time. These data doubtless contain some errors (e.g., a species missed at a site was inferred to be absent and locally extinct). Nevertheless, we do not know of a mechanism by which

such errors could explain our findings. For example, our results show that these local extinctions are often significantly related to climate change and are not simply random (see also Román-Palacios & Wiens, 2020). Furthermore, the resurvey data show that species that apparently went extinct at lower elevations were still present at higher elevations (i.e., not that the resurveys simply failed to detect the species). Even if some species simply became too rare to be detected at a site rather than being truly extinct, such declines are an obvious precursor to local extinction. Fifth, the susceptibility of warm-edge populations to extinction is only one factor that might help predict species-level extinctions from climate change. Species-level extinction may depend on many other factors, especially dispersal. However, our results are relevant to whether local populations can shift their niches in response to climate change, and this may be far more important than dispersal in determining species survival (Román-Palacios & Wiens, 2020). Finally, there may be synergy among threats to species (e.g., climate change and habitat destruction and overharvesting; Guo et al., 2018).

5 | CONCLUSIONS

Many studies have predicted that tropical species are more vulnerable to extinction from climate change, but the reasons why remain unresolved. Using data from 538 species, we found that species with narrower realized temperature niche widths are more likely to have experienced local extinctions, and that these niche widths are narrower in tropical species. Thus, our results help explain why tropical species are more vulnerable to global warming. We found that climatic niche width and the extent of temperature change together explain most of the variation in the frequency of local extinction among studies. Our results suggest the intriguing possibility that temperate and high-elevation tropical species have a greater ability to survive rising temperatures because of their exposure to cold temperatures. Overall, we suggest that climatic temperature niche width may be a relatively accessible and accurate predictor of the vulnerability of populations to climate change, without the need for data on physiological tolerances or biotic interactions.

AUTHOR CONTRIBUTIONS
Rollie M. Grinder and John J. Wiens designed the study and wrote the paper. R.M.G. performed analyses.

CONFLICT OF INTEREST
The authors declare no competing interests.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Dryad at http://doi.org/doi:10.5061/dryad.pk0p2ngrp.

CODE AVAILABILITY
The code used are available in Dataset S4, which is available on Dryad (https://doi.org/10.5061/dryad.pk0p2ngrp).

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