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RESEARCH ARTICLE

The multidimensional (and contrasting) effects of environmental warming on a group of montane tropical lizards

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Abstract

1. Mountains are cradles for biodiversity and crucibles for climate-driven species loss, particularly for tropical ectotherms. Constriction on activity and amplified heat stress are two key sources of warming-driven vulnerability in tropical montane ectotherms. These threats, however, might be counterbalanced if rising temperatures also release organisms from limits on activity induced by cold stress.
2. We used biophysical modelling to estimate activity patterns and thermal stress under warming in a group of summit-dwelling *Anolis* lizards (*A. armouri* and *A. shrevei*) endemic to the Caribbean island of Hispaniola. Activity is currently constrained by the prevalence of temperatures too cold for activity. Under warming, our models predict expanded hours of potential activity and reduced cold stress, especially under a high emission scenario. Crucially, release from cold stress does not come at the expense of heightened exposure to heat stress. This result arises from a steep mismatch between these species' warm-adapted ecology and the surprisingly cold environments they occupy.
3. Yet, resilience in some dimensions belies vulnerability along others, particularly with regard to critical macrohabitat. We capitalized on a long-term monitoring dataset to predict forest distributions under warming. Our models predict upslope shifts in montane cloud forests that may constrict the high-elevation pine forests to which these lizards are inexorably linked. Warming-driven macrohabitat loss can 'pin' the montane endemics into progressively shrinking ranges, especially since a rising cloud forest also facilitates upslope transport of a close relative, *A. cybotes* (a species associated with broadleaf forests).
4. Many tropical ectotherms (including these anoles) are adapted to forest edges, a feature often associated with a relatively warm-adapted ecophysiology. When such species are also found in cool environments, such as those found on mountaintops, warming-amplified thermal stress is surprisingly limited. Therefore, the direct effects of warming on tropical ectotherms are quite broad, and can even include potential benefits to fitness-based activities.
5. Rising temperatures may often present a dual-edged sword: warming simultaneously releases these organisms from constraints on activity while exposing them to other threats. Whether due to the direct or indirect effects of climate warming, exceptional vulnerability may indeed reside where biodiversity is highest.

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KEYWORDS
Anolis lizards, behavioural thermoregulation, Caribbean, climate warming, ecophysiology, heat stress

1 | INTRODUCTION

Rising temperatures are a global threat to biodiversity, but not all organisms are at equal risk. Mountains harbour disproportionately high species richness (Myers et al., 2000; Rahbeck et al., 2019), and climate change is altering mountaintop environments more rapidly than many other landscapes (Dobrowski & Parks, 2016). The pernicious effects of warming might be magnified in tropical ectotherms, as these organisms currently experience conditions approaching (or exceeding) their physiological limits (Huey et al., 2009). Yet, empirical support for warming-induced extirpations of montane species is relatively scant, even in the tropics (Freeman et al., 2018; Sheldon et al., 2011). While cool-edge range expansions (and warm-edge contractions) are common, they are far from universal: many montane species' ranges remained stable or even shifted downslope over the past century (Lenoir & Svenning, 2015; Moritz et al., 2008; Muñoz & Moritz, 2016). Furthermore, recent studies have documented that warming can benefit organisms, particularly if their physiological preferences are substantially higher than their thermal environment (Clarke & Zani, 2012; Ljungström et al., 2015; Shine et al., 2002). More generally, relatively little is known about the behaviour and ecophysiology of tropical organisms, limiting our understanding of their vulnerability to ongoing global change. Such varied responses urge a deeper exploration of how environmental variation and physiological performance interact under rapidly changing conditions (Huey et al., 2012; Moritz & Agudo, 2013).

Environmental warming can destabilize energy balance by constraining activity time for resource acquisition (Adolph & Porter, 1993; Grant & Dunham, 1988). Thermal stress may be accentuated in montane species, which can be substantially less heat tolerant than their low-elevation counterparts (Garcia-Robledo et al., 2016; von May et al., 2017). Yet, the local thermal environment can often be a surprisingly poor proxy for upper physiological limits (Bodensteiner et al., 2021; Diamond & Chick, 2018). Instead, many montane species are highly heat tolerant and exhibit behavioural preferences for relatively warm temperatures (Huey et al., 2009; Shah et al., 2017; Sunday et al., 2011). In such cases, warming might benefit organisms via reduced cold stress. Nonetheless, depending on a species' physiology and its corresponding environment, release from cold stress might come at the expense of increased heat stress. And, even if activity patterns are unaltered, montane species may nonetheless be vulnerable to warming along many other ecological axes. For example, the indirect effects of warming, such as the reshuffling of species assemblages, changes in biotic pressures, and/or the loss of critical macrohabitat, are key features associated with range loss (Alexander et al., 2015; Diamond et al., 2016; Jankowski et al., 2010; Urban et al., 2012). Predicting vulnerability, therefore, presents a multi-pronged challenge encompassing direct and indirect effects. Nonetheless, whether patterns of vulnerability should align or differ among ecological axes remains uncertain.

The adaptive radiation of Caribbean anoles (150+ species) is a lineage of concern under warming, as most species from this ecologically diverse radiation are endemic to individual islands, and many of those are further restricted to one or a few nearby summits (Losos, 2009). Here, we examine the effects of warming on two summit-dwelling anole species (*Anolis armouri* and *A. shrevei*) that are endemic to the island of Hispaniola (Figure S1). These species independently diversified into cool, high-elevation habitats on different mountain ranges, where they are found exclusively in pine forests and nearby rocky savannas (Glor et al., 2003; Hertz & Huey, 1981; Schwartz, 1989). Due to their narrow ranges and restriction to summit habitats, these species are of particular conservation concern (de Queiroz & Mayer, 2011).

Here, our goal was to test whether (and how) patterns of vulnerability to warming vary among several ecological axes for *Anolis armouri* and *A. shrevei*. To this end, we test three different, non-mutually exclusive hypotheses regarding several potential impacts of warming on *Anolis armouri* and *A. shrevei*. The first hypothesis is that rising temperatures accentuate physiological stress and limit activity. To address this 'thermal constraint on activity' hypothesis, we built a series of biophysical models to determine whether rising temperatures will reduce potential activity and enhance thermal stress in the montane anoles. Both anole species have broad thermal tolerances and behaviourally prefer relatively high temperatures (Muñoz & Losos, 2018; Muñoz et al., 2014), suggesting that warming will benefit surface activity by reducing cold stress. However, such may come at the expense of enhanced heat stress. Therefore, biophysical models can help address whether (and by how much) surface activity is eroded or enhanced under warming.

Our other two hypotheses centre around two potential indirect effects of warming on the montane anoles. Historically, frost and fire have limited the altitudinal extent of the cloud forest–pine forest ecotone (Martin et al., 2011; Sherman et al., 2005). Environmental change might reduce the availability of the pine forest that supports these montane lizards by making high-elevation environments more climatically suitable to cloud forest (as has historically occurred on Hispaniola; Crausbay et al., 2015). To test this 'macrohabitat loss' hypothesis, we infused a long-term monitoring dataset of Hispaniolan cloud forest plant species into a series of distribution models to predict whether warming should shift the ranges of cloud forest tree species upslope. The lower elevational limit for these montane anoles coincides with the ecotone separating high-elevation pine forest from cloud forests, where *A. armouri* and *A. shrevei* are parapatrically replaced by

Anolis cybotes, a closely related species found along the edges of broadleaf forest (Glor et al., 2003; Schwartz, 1989). Rising cloud forest may also permit the upslope transport of the close relative, *A. cybotes*, if warming also renders high-elevation habitats more climatically suitable, and allow this species to track the upper limit of broadleaf forest. The presence of *A. cybotes* at higher elevations can preclude expansion of *A. armouri* and *A. shrevei* through space occupancy effects, which can limit the montane endemics into progressively narrower ranges (Urban et al., 2012). To test this 'competitor benefits' hypothesis, we used biophysical models to determine whether warming makes high-elevation habitats more thermally hospitable to *A. cybotes*, specifically by reducing cold stress and enhancing opportunities for behavioural thermoregulation. Lastly, we discuss how the direct and indirect effects of warming can attenuate or accentuate vulnerability in montane organisms and offer insight on the general biological features that predict such patterns.

2 | MATERIALS AND METHODS

2.1 | Study system

The cybotoids are a clade of nine anole species belonging to the 'trunk-ground' ecomorph of the *Anolis* adaptive radiation (Losos, 2009; Schwartz, 1989). This diverse anole group is distributed across an elevational range exceeding 3,000 m (Glor et al., 2003; Schwartz, 1989; Wollenberg et al., 2013). This study focuses on three closely related species in this radiation. One species, *A. cybotes*, is found nearly island-wide along the edges of broadleaf forests (Hertz & Huey, 1981; Muñoz & Losos, 2018; Schwartz, 1989). The other two species, *A. armouri* and *A. shrevei*, occur exclusively at high elevations, where they are found in open habitat dominated by the bunchgrass *Danthonia domingensis* and along the edges of pine forest dominated by *Pinus occidentalis*. The montane anoles are nimble thermoregulators: they retreat under boulders and logs under inclement weather and are highly active when conditions favour basking (Boronow et al., 2018; Conover et al., 2015; Hertz & Huey, 1981; Muñoz & Losos, 2018). *Anolis cybotes* is also an effective thermoregulator, but is less cold tolerant (mean critical thermal minimum, CT_{min} = 10.6°C) than *A. armouri* (mean CT_{min} = 7.6°C) and *A. shrevei* (mean CT_{min} = 8.1°C; Muñoz et al., 2014).

Two large mountain chains, the Sierra de Baoruco and the Cordillera Central, dissect Hispaniola and provide the majority of high-elevation habitat on the island (Figure S1). Cloud forest occurs from ~1,600 to 2,200 m a.s.l. on the mountains' windward slopes (Sherman et al., 2005) and reaches its structural and floristic peak at ~2,100 m (Martin et al., 2007). At a discrete ecotone at ~2,200 m a.s.l., the cloud forest cedes to pine forest and savannah. Cloud forest tree species can tolerate climates above the ecotone and colonize the understory of monodominant pine stands up to ~2,500 m, but wildfires maintain the dominance of pine above the ecotone (Crausbay & Martin, 2016; Martin & Fahey, 2006; Martin et al., 2007, 2011). At the elevational ecotone separating forest types, *A. cybotes* is replaced by *A. armouri* in the Sierra de Baoruco and by *A. shrevei* in the Cordillera Central (Schwartz, 1989). A pronounced climate discontinuity occurs at ~2,500 m created by the Trade Wind inversion by which warm, rising trade wind air collides with cool, sinking Hadley circulation air (Shubert et al., 1995). Conditions above the inversion are drier and colder (Martin & Fahey, 2014), favouring pine forest over cloud forest (Martin et al., 2011; Sherman et al., 2005). At lower elevations, by contrast, greater humidity and cloud immersion allow cloud forest to dominate (Foster, 2001; Martin et al., 2011). The upper elevational limit of the cloud forest has fluctuated in response to historical changes in the prevailing climatic conditions. During a warm period ~5,500 years ago, for example, cloud forest occupied high-elevation areas currently characterized by monodominant pine forest (Crausbay et al., 2015).

2.2 | Modelling hourly thermal conditions

To model the thermal microhabitat, we used the 'microclimate' function in the R package NicheMapR (vers. 1.0.0; Kearney & Porter, 2017), which integrates ~15-km^2 global climate data (New et al., 1999, 2002) with terrain data to enhance the spatial resolution of our models. Specifically, we used a 1 km^2 digital elevation model to calculate slope, aspect and 24 horizon angles, which we used to model thermal conditions. The model can provide hourly estimates of thermal conditions at a variety of perch heights (e.g. below ground, on the surface, 1.2 m above the surface) and under different shade conditions (e.g. 90% shade vs. 100% sun) for each 1 km^2 grid cell (Kearney & Porter, 2017, 2020). These anoles are 'trunk-ground' species and previous work has shown that they are most commonly observed perching within 1.5 m of the ground (Schwartz, 1989; Wollenberg et al., 2013); correspondingly, we gathered estimated temperatures at ground level and at 1.2 m above ground. These lizards are also nimble at capitalizing on sun/shade structure to seek appropriate body temperatures (Hertz & Huey, 1981; Muñoz & Losos, 2018; Muñoz et al., 2014). Correspondingly, we used the microclimate model to estimate thermal conditions in both full sun (0% shade) and high shade (90% shade) for ground level and 1.2 m perch heights.

2.3 | Biophysical models of lizard activity

Mechanistic niche models (MNMs) use energy balance theory to predict the distribution of microhabitat suitability across space and time (Kearney, Isaac, et al., 2014; Kearney & Porter, 2017; Kearney, Shamakhy, et al., 2014; Urban et al., 2016). We were interested in modelling potential activity time for each lizard species based on the available microclimates (described above) combined with thermal physiological data measured from each species (described below). In

particular, we used the 'ectotherm' function in NicheMapR (Kearney & Porter, 2017), which uses the microclimate model in conjunction with physiological parameters to compute body temperature and estimate hourly activity. We parameterized our biophysical models using behavioural and physiological traits (defined in Table S1) for each species, which we gathered from re-analysis of previously published data (Muñoz & Bodensteiner, 2019; Muñoz et al., 2014). Briefly, field body temperatures (T_b) were measured during daylight hours (06:00–19:00) at 10 localities across Hispaniola, corresponding to 19 days of sampling effort for *A. cybotes*, 8 days for *A. shrevei* and 7 days for *A. armouri* (Table S2). For each lizard captured, the 'basking status' (i.e. whether the lizard was perching in the sun or in the shade) was recorded, from which T_{bask} (the lowest observed basking temperature) was extracted for each species (Table S3). Using a laboratory heat gradient, the preferred temperature (T_{pref}) was measured (Table S2). From these experiments, the voluntary thermal maximum (VT_{max}) and minimum (VT_{min}) were extracted; these variables describe the hottest and coldest temperatures that lizards will voluntarily tolerate, respectively (Table S3). We measured the critical thermal minimum (CT_{min}) and the critical thermal maximum (CT_{max}) as the lower and upper thermal limits, respectively, of locomotion (Spellerberg, 1972). We estimated critical thermal limits by estimating the lower and upper temperatures at which a lizard failed to right itself after being flipped onto its back (Spellerberg, 1972). Briefly, cooling was performed by submerging a plastic container (Tupperware brand) that held the lizard into an ice bucket, and warming was performed by exposure to a 100 W light bulb suspended ~30 cm above the plastic container with the lizard (Muñoz et al., 2014). In both experiments, the rate of body temperature change was 1°C/min (Muñoz et al., 2014).

Based on the thermal preferences and limits of lizards, the biophysical model determines whether the thermal environment is suitable for activity. Given that anoles are diurnal, we also constrained activity to daylight hours. The biophysical model allows the lizard to utilize different perch heights and shade conditions as needed to track their preferred thermal conditions and avoid conditions that exceed their thermal tolerances. The body temperature (T_b) for the lizard is calculated based on conductance from the substrate, solar radiation and air temperature (see Kearney and Porter, 2020). The model assumes that lizards are active if thermal conditions permit and that, if possible, lizards will thermoregulate to maintain body temperatures within their preferred range (Kearney & Porter, 2004), which is consistent with the observed thermoregulatory behaviours of these species (Hertz & Huey, 1981; Muñoz & Losos, 2018; Muñoz et al., 2014). The model was run at hourly time steps for 1 year across the entire island of Hispaniola under current thermal conditions. We then modelled future microclimate for 2070 as predicted by the HadGEM2-ES Global Climate Model (GCM) under two emission scenarios: RCP 4.5 (mid-level emissions) and RCP 8.5 (high-level emissions). RCP 4.5 is a moderate model that assumes greenhouse gas emissions will peak around 2040 and then decline. The RCP 8.5 model assumes that emissions will continue well into the future.

2.4 | Thermal safety margins

We also calculated the thermal safety margins (TSM), which describe how closely environmental (operative) temperatures (T_e) encroach on (or exceed) the species' thermal limits (Deutsch et al., 2008; Sunday et al., 2014). We used the estimated body temperatures from our NicheMapR ectotherm models and critical thermal limits for each species to calculate thermal safety margins under current conditions and the more extreme climate change scenario (RCP 8.5). The minimum thermal safety margin was calculated as $T_e - CT_{min}$ and the maximum thermal safety margin was calculated as $CT_{max} - T_e$. Since we used the minimum and maximum T_e for a given location to make these calculations, our measures of thermal safety margins represent the extreme conditions that the lizards are expected to experience. TSMs do not describe the absolute margins for species presence or absence; rather, they describe the acceptable thermal boundaries for activity. Some lizard species, for example, are capable of surviving for extended periods below their CT_{min} (Huang & Tu, 2008).

2.5 | Distribution models of forest macrohabitats

We obtained presence records of cloud forest tree species by combining the forest plot data from previous work (Martin et al., 2007; Sherman et al., 2005, 2012). The vegetation data were collected in the Cordillera Central mountain range of Hispaniola in 262 permanent plots (0.1 or 0.05 ha in size) sampled over a 2,000 m elevational range, from 1,000 m a.s.l. to the summit of Pico Duarte, the highest point in the Caribbean. In each plot, all trees (≥10 cm DBH) were tagged, measured and identified to species with the assistance of the herbarium in the Jardín Botánico Nacional, Santo Domingo. Plots were sampled multiple times over the course of 16 years to increase representation and confirm species identities (Sherman et al., 2012).

We created presence-based distribution models for the 14 dominant cloud forest and single pine forest tree species (scientific names are listed in Figure 3 below; see Martin et al., 2007 for more details) using MAXENT (Phillips et al., 2006). Cloud forest tree species are the modelling focus as prior increases in temperature during the Holocene thermal maximum (9,000–5,000 years before present) pushed cloud forest taxa into higher elevations at the expense of high-elevation monodominant pine forest (Crausbay et al., 2015). We used the occurrence locations and a set of seven bioclimatic variables chosen a priori based on their recognized importance in determining the performances and distributions of plants (Kreft & Jetz, 2007). The climate variables used in the models were Mean Annual Temperature (BIO1), Temperature Seasonality (BIO4), Maximum Temperature of Warmest Month (BIO5), Minimum Temperature of Coldest Month (BIO6), Annual Precipitation (BIO12), Precipitation of Driest Month (BIO14) and Precipitation Seasonality (BIO15). Rasters of the climate variables (mean climatologies for 1970–2000) were downloaded from

WorldClim at a spatial resolution of 30 arc seconds. MAXENT models were constructed using the DISMO package (Hijmans et al., 2015) with 20% of species records withheld for model evaluation. MAXENT models were created for all species with ≥10 unique occurrence records after filtering and cleaning. Any species with insufficient records were excluded from the subsequent analyses with the exceptions of *Cyathea* sp. and *Alsophila* sp.; for these two treeferns, we created MAXENT models and range maps at the genus level using all available congeneric occurrence records from the study area.

Using the MAXENT models, we predicted each taxon's probability of occurrence based on the distribution of the climate variables. The probabilities of each species were thresholded at the values providing the maximum sum of the True Positive Rate (TPR) and the True Negative Rate (TNR). TPR and TNR were determined through model evaluation to estimate the current elevation distribution of each species. We used the same procedure to predict the future ranges of each species using the climate variables predicted under the same GCM and emissions scenarios as used above.

3 | RESULTS AND DISCUSSION

3.1 | Rising temperatures enhance potential activity at high elevation

To minimize physiological stress due to rising temperatures, organisms can reduce activity and increase their use of thermal refugia (Deutsch et al., 2008; Kearney et al., 2009; Sunday et al., 2014). Far from amplifying thermal stress, however, our biophysical models predicted that both montane lizard species, *Anolis armouri* and *A. shrevei*, will experience expanded hours of potential activity as their environments warm (Figure 1). Montane habitats will become more thermally hospitable for activity for both anole species under climate change, especially if warming is severe. Under current conditions, *A. armouri* and *A. shrevei* can be active during 59% and 53% of available daytime hours, respectively (Table 1). Potential hours of activity grow by 12%–14% under the moderate-emission (RCP 4.5) scenario and by 17%–20% under high-emission (RCP 8.5) warming.

Expanded hours of potential activity do not come at the expense of heightened exposure to lethally hot temperatures. Even under

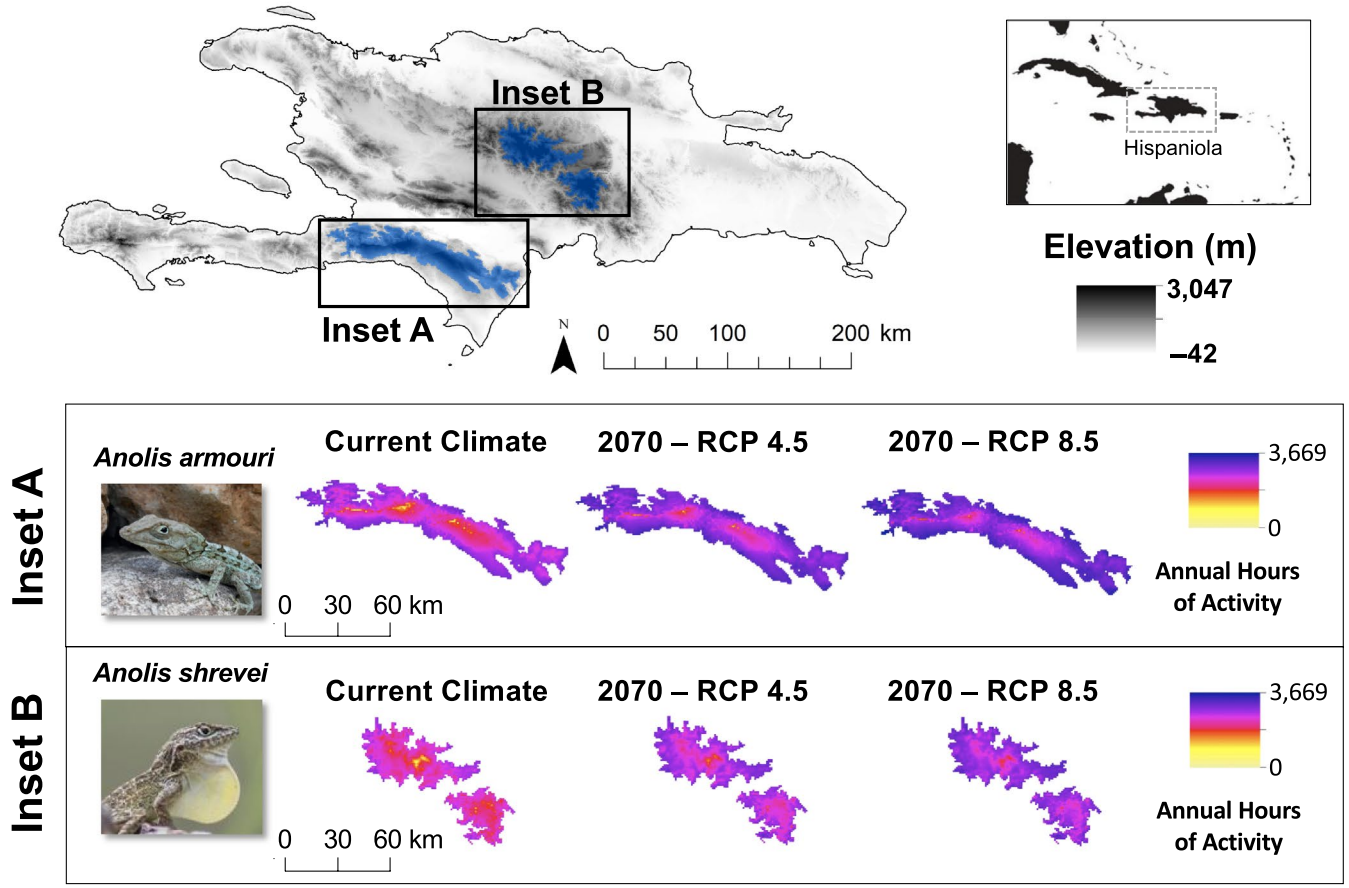


FIGURE 1 Predicted hours of activity increase for mountaintop anoles as environments warm. The topographic map of Hispaniola shown at the top illustrates the geographical ranges for *Anolis armouri* (Inset A) and *Anolis shrevei* (Inset B) in blue. Inset A illustrates predicted annual hours of potential activity for *A. armouri* under current conditions, in 2070 under a mid-level emission scenario (RCP 4.5), and in 2070 under a high-level emission scenario (RCP 8.5). Inset B shows predicted hours of potential activity under current and future climate for *A. shrevei*. Rising temperatures render montane environments more thermally hospitable for surface activity, which is reflected in the greater potential hours of activity for both lizard species (see also Table 1). Photo of *A. shrevei* provided by D. L. Mahler

TABLE 1 Mean annual activity time ±1 *SD* (in hours) are given for the two montane endemics, *Anolis armouri* and *Anolis shrevei*, and for the more lowland species, *Anolis cybotes*, under current and future environmental conditions. The top three rows describe hours of activity for each species within its current range. The bottom two rows describe hours of activity for *A. cybotes* in the ranges currently occupied by *A. armouri* and *A. shrevei*. For current conditions, the percentage of annual daytime hours available for activity under current conditions is included (±1 *SD*). For future climate scenarios, the relative increase or decrease in hours of activity relative to current conditions are given

	Current climate		2070 – RCP 4.5		2070 – RCP 8.5	
Species	Annual hours of activity	Percent of daytime hours	Annual hours of activity	Activity shift relative to present	Annual hours of activity	Activity shift relative to present
A. armouri	2,571 ± 347 hr	58.6%	2,872 ± 301 hr	+11.7%	3,012 ± 285 hr	+17.1%
A. shrevei	2,324 ± 287 hr	53.0%	2,647 ± 241 hr	+13.9%	2,796 ± 227 hr	+20.3%
A. cybotes	2,941 ± 443 hr	67.1%	2,833 ± 356 hr	−3.6%	2,680 ± 377 hr	−8.8%
A. cybotes in *A. armouri* range	2,193 ± 434 hr	50.0%	2,539 ± 352 hr	+15.8%	2,695 ± 327 hr	+22.9%
A. cybotes in *A. shrevei* range	1,369 ± 472 hr	31.2%	1,857 ± 375 hr	+35.7%	2,056 ± 339 hr	+50.2%

a high-emission scenario, rising temperatures are unlikely to push the montane lizards beyond their upper thermal safety margins because the high-elevation habitats they occupy are simply too cold (Figure 2; Table S4). Instead, warming reduces cold stress by limiting the frequency of temperatures below the species' lower safety margins (Figure 2; Table S5). As active thermoregulators, *A. armouri* and *A. shrevei* precisely target microsites to maintain body temperatures within their preferred range (Hertz & Huey, 1981; Muñoz & Losos, 2018). Nonetheless, activity at high elevation is constrained by the prevalence of stressfully cold temperatures (Figure 2). Consistent with this prediction, our field data indicate that the montane anoles are less active during the cooler times of day, even in the summer when environments are warmest (Figure S2). In other words, staying sufficiently warm appears to be the thermoregulatory priority for these montane lizards, and environmental warming releases them from some thermal constraints on activity (Figure 2; Tables S4 and S5). Together, our results reject the notion that climate warming will thermally constrain the potential surface activity of these montane lizards.

3.2 | Macrohabitat reshuffling impacts montane anoles

In response to warmer and wetter conditions, our models predict that habitats near the Cordilleran summit will become more climatically suitable (and lowland habitats less suitable) for nearly all the cloud forest tree species examined (Figure 3). Our models also predict attrition near the forests' lower elevational limits (Figure 3; Figures S3 and S4). These changes result in substantial upslope range shifts (mean shift = +49 and +163 m/decade under RCP 4.5 and RCP 8.5, respectively; Figure 3). For most cloud forest tree taxa, modest warming is predicted to expand the total area of potentially suitable habitat in the Cordillera Central (Table S6) and increase cloud forest tree species richness at higher elevations (Figure S3). Under high emissions and severe warming, however, suitable climate erodes (Figure 3; Figures S3 and S4; Table S6). If climate change causes cloud forest tree species to shift upslope as predicted by the model, then the extent of monodominant pine forests on Hispaniolan summits will be progressively constricted. Our results therefore support the hypothesis that warming will reconfigure macrohabitat distributions, which may substantially reduce the amount of suitable environment to *A. armouri* and *A. shrevei*, even as the hotter environmental temperatures would allow for their increased potential activity.

Rising temperatures also render montane habitats more thermally hospitable for *A. armouri* and *A. shrevei*'s lowland congener, *A. cybotes* (Figure S5). Currently, hours of potential activity for *A. cybotes* in the habitat occupied by *A. armouri* is 25% lower than within its core range, and is 53% lower in the habitat occupied by *A. shrevei* (Table 1). Under moderate emissions, potential activity for *A. cybotes* increases by 16% in *A. armouri*'s habitat and by 36% in *A. shrevei*'s habitat. Under severe warming, the increase in *A. cybotes*' activity time swells to 23% and 50%, respectively, and transforms

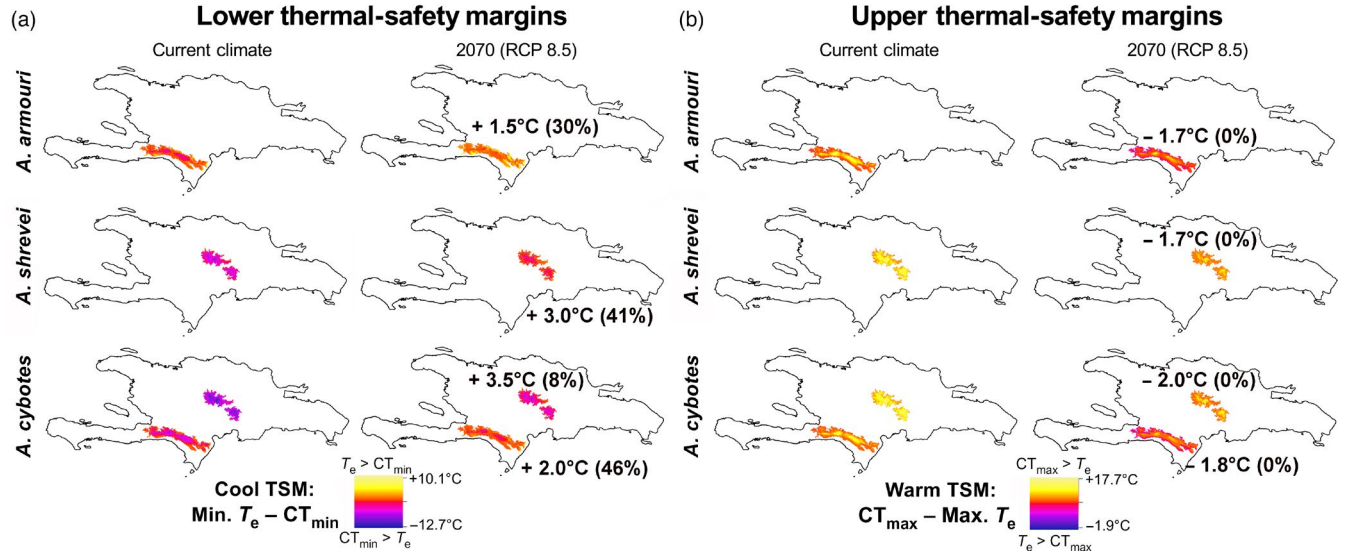


FIGURE 2 Cold stress decreases, whereas heat stress is mostly unchanged under environmental warming. (a) Maps illustrating the lower thermal safety margin (TSM), which describes the difference between minimum operative body temperature (Min. T_e) and the critical thermal minimum (CT_{min}). Positive values (warmer colours) indicate regions where minimum temperatures do not drop below CT_{min}, whereas negative values (cooler colours) indicate regions where lizards experience minimum temperatures below their CT_{min}. The lower TSM for *Anolis armouri* and *Anolis shrevei* are given in the top two panels. The predicted lower TSM for *A. cybotes* in the current range of *A. armouri* and *A. shrevei* are given in the bottom panel. (b) Maps illustrating the upper TSM are given for the two montane species, *A. armouri* and *A. shrevei*, in the top two panels. The predicted upper TSM for *Anolis cybotes* in the current ranges for *A. armouri* and *A. shrevei* are given in the bottom panel. The bold values in each panel denote the difference in TSM under the future climate scenario compared to current conditions ($TSM_{future} - TSM_{current}$). The value in parentheses is the difference between future and current percent areas where the TSM never drops below zero (indicating the critical thermal limit was never reached at that location)

many high-elevation sites into areas thermally comparable to regions within its current range (Table 1; Figures S5 and S6). In its current range, by contrast, potential hours of activity for *A. cybotes* remain largely stable (with some attrition in activity near sea level; Figure S6). We do not posit that warming and upslope movement will bring *A. cybotes* into more-frequent direct contact with the montane endemics, as they are parapatrically separated by the forest ecotone. Rather, the upslope presence of *A. cybotes* along the edges of broadleaf forests can create space-occupancy effects that prevent the expansion of *A. armouri* and *A. shrevei* out of pine forests (Brooker et al., 2007; Urban et al., 2012). Co-occurrence of closely related, morphologically similar species (like this species complex of trunk-ground anoles) is generally low, limiting the likelihood of stable sympatry (Losos & Glor, 2003). Indeed, among closely related and morphologically similar species of Hispaniolan anoles (including the species examined here), incumbency effects strongly predict species' range limits (Algar et al., 2013), meaning that these species rarely co-occur (a result that aligns with our observations over the several years of fieldwork). Together, these observations suggest that a rising cloud forest and upslope shifts of *A. cybotes* have the potential to pin *A. armouri* and *A. shrevei* into progressively shrinking macrohabitat ranges.

Since the Last Glacial Maximum, Neotropical forests have responded to climatic fluctuations by shifting up- and downslope (Bush et al., 2004). Based on climate suitability, our models agree that the cloud forest is poised to shift upslope and constrict the extent of monodominant pine forest. The future of the cloud forest, however, also hinges on other factors, such as soil composition (Whitaker et al., 2014), the presence of key pollinators (Potts et al., 2010) and cloud immersion (Foster, 2001). The forest is also linked to the climate of the broader Caribbean basin (Martin & Bellingham, 2016). The projected increase in tropical temperatures and CO_2 concentrations is expected to raise the elevational optima of cloud forest tree species by several hundred metres (Foster, 2001; Hotchkiss & Juvik, 1999), as supported by our models. Other climate change scenarios, however, project a high-elevation drought on tropical mountains (Loope & Giambelluca, 1998) owing to a general reduction in the cloudiness that envelopes tropical cloud forests (Foster, 2001), a lower elevation of the Trade Wind Inversion and an increased frequency of the El Niño–Southern Oscillation (Timmermann et al., 1999). Likewise, a deeper understanding of the competitive dynamics among plant species (and how competition and climate interact; Armitage & Jones, 2020) and their underlying physiological processes (e.g. plant growth rates; Schouten et al., 2020) stand to improve our predictions of the cloud forest range under warming.

3.3 | Predicting vulnerability (still) poses multivariate challenges

More hours of *potential* activity need not translate into greater hours of *realized* activity. Increased activity, for example, imposes higher

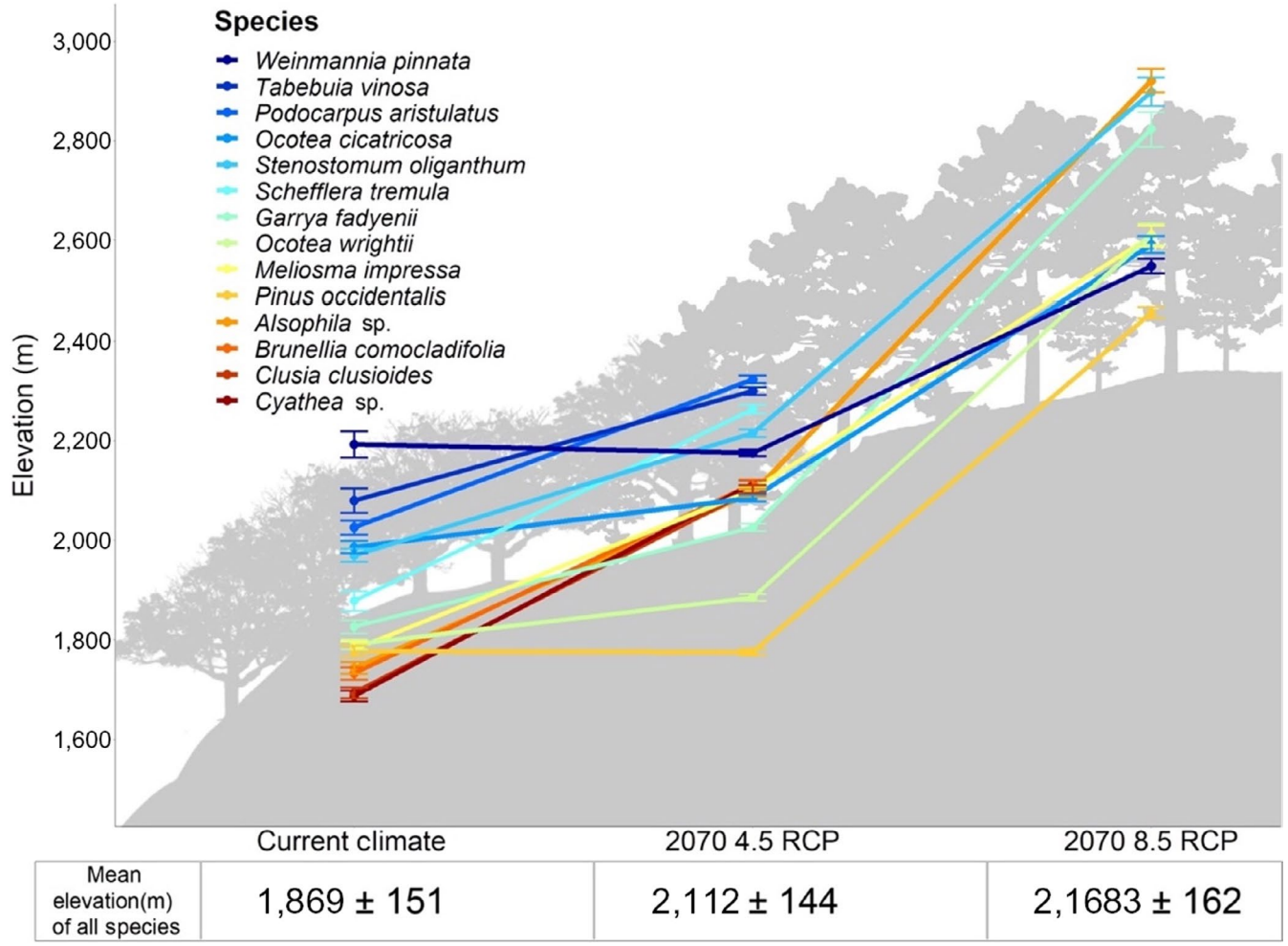


FIGURE 3 Climate change pushes cloud forest plant species upslope. The background silhouette depicts the ecotone between cloud forest at lower elevations and pine-dominated high-elevation forests under current environmental conditions in the Cordillera Central, Dominican Republic. The coloured points show the mean predicted elevation (±1 *SD*) of the 14 most important cloud forest tree taxa under current conditions and in 2070 under two emission scenarios (RCP 4.5 and RCP 8.5). Under the mid-level emissions (RCP 4.5), the mean elevation for cloud forest species is predicted to shift upslope (mean shift = 49 m per decade). Under high-emission warming (RCP 8.5), all tree species shift their mean elevations upslope (mean = 163 m per decade) but six dominant tree species (*Tabebuia vinosa*, *Podocarpus aristulatus*, *Schefflera tremula*, *Brunellia comocladifolia*, *Clusia clusioides* and *Cyathea* sp.), constituting ~43% of the total, lose access to climatically suitable habitat. Note that *Pinus occidentalis* is found nearly island-wide, but its mean elevations shown in this plot are based exclusively on its occurrences in the cloud forest

metabolic demands. Assuming that lizards are active during all potential hours, energy expenditure should increase by 12%–14% under mid-level emissions warming and by 17%–20% under high-emission warming. To metabolically accommodate greater activity, lizards should consume more prey (Congdon et al., 1982). Arthropod biomass on Puerto Rico, however, has declined more than 10-fold since 1970, resulting in parallel declines of the island's insectivores, including anoles (Lister & Garcia, 2018). Comparable data are not available for Hispaniolan anoles due to historically haphazard sampling, but bird capture rates have declined on the island over the past two decades (Lloyd et al., 2016). Prey decline may also precipitate a negative feedback loop with the thermal sensitivity of metabolism: reduced food intake slows growth rates, which triggers lower temperature preferences to offset metabolic costs, in turn constricting activity time (Huey & Kingsolver, 2019). Likewise, deforestation through logging is a major biodiversity threat in Hispaniola, particularly in Haiti (Hedges et al., 2018), although several parks do protect high-elevation habitats on the island (including the area where our forest plots took place). Cleared habitats typically impose hotter microclimates, which can increase warming threats (Mollinari et al., 2019). Previous work found that *A. cybotes* fares well in both natural and highly modified environments on Hispaniola (Frishkoff et al., 2019), but comparable data are not available for *A. armouri* and *A. shrevei*; further research, therefore, is needed to address how habitat modification interacts with warming to influence vulnerability in this anole lineage.

We further emphasize that the proximate effects of warming on these montane anoles extend beyond the thermal limits on activity. Thermal constraints on egg development, for example, contribute to elevational range limits in lizards (Monasterio et al., 2011, 2016), and thermal stress during embryogenesis induces phenotypic

malformations and/or reduces offspring survivorship (Gunderson et al., 2020; Sanger et al., 2018). Incubation temperature and thermal stress can also influence the development of fitness-relevant traits in anoles, like sprint performance (Hall & Warner, 2019; Pearson & Warner, 2016). Although all anoles are oviparous, some species (including *A. shrevei*) retain eggs in the maternal oviduct to protect embryos from severe environmental conditions (Huey, 1977; Stamps, 1976). Egg retention can be plastic in reptiles (Telemeco et al., 2010; Olsson et al., 2018) but remains poorly understood in Hispaniolan anoles (Huey, 1977). Previous experiments with the montane cybotoids failed to induce shorter inter-clutch intervals under laboratory conditions that mirrored adult lizards' preferred temperature (mean = 29.4°C; Muñoz & Losos, 2018). In *Anolis sagrei* (a species with similar T_b and CT_{max}), the incubation temperatures necessary for embryonic malformation are higher than the average ambient conditions on Hispaniolan summits (Sanger et al., 2018). Female *A. sagrei* prefer cool nesting sites that minimize thermal stress on embryos, suggesting some measure of behavioural control (assuming access to relevant microclimates) over the survivorship and development of offspring (Pruett et al., 2020). Concerns about reproductive phenology are especially relevant given that plasticity in heat tolerance is often quite limited (Gunderson et al., 2020; Gunderson & Stillman, 2015), and adaptation is generally sluggish for this trait (Qu & Wiens, 2020, but see Campbell-Staton et al., 2020; Domínguez-Guerrero et al., 2021).

While our study provides a perspective on some key aspects of vulnerability, further studies are necessary to explore whether those same patterns are shared among other dimensions of vulnerability. To be clear, our goal was to assess whether signatures of vulnerability differ among ecological axes. While this outcome is well supported by our results, our broader point is that the ultimate fate of these (and other) species under warming is an inherently multidimensional (perhaps *n*-dimensional) problem: we posit that embracing such nuance among axes better reflects the patchwork nature of climate warming impacts on organismal vulnerability (e.g. Huey et al., 2012). More precisely, a more dimensional perspective can help identify the axes of greatest concern, which may assist with conservation efforts. In the case of these anoles, for example, our perspective suggests that macrohabitat loss is a proximate concern for the viability of these montane species under warming.

4 | CONCLUSIONS

A species' vulnerability to climate warming reflects the combined effects of its intrinsic sensitivity to temperature, and how often their environments supply dangerously hot temperatures (Deutsch et al., 2008; Huey et al., 2012). Warming, therefore, can induce varied patterns of vulnerability, even among close relatives (Diamond et al., 2012; Huey et al., 2009; Riddell & Sears, 2015). With respect to activity patterns, *Anolis armouri* and *A. shrevei* appear behaviourally resilient. We suspect that their relatively warm-adapted ecophysiology reflects their preference for edge/open habitat, as they behaviourally capitalize on steep sun-shade structure provided by forest edges, which facilitates thermoregulation. By contrast, tropical species specialized to closed-canopied habitats, like rainforest interiors, tend to be relatively cool-adapted and, correspondingly, more vulnerable to warming (Huey et al., 2009; Muñoz et al., 2016). Even warm-adapted species at low elevation are often at risk (albeit lower risk) because their environments are already quite warm (Huey et al., 2009). Capturing such nuance in microgeography and ecophysiology underscores the value of an explicitly mechanistic approach (Sears & Angilletta, 2011). To illustrate this point, we built correlative models (based only on museum records of capture sites) for these same montane anole species. These models, which were scrubbed of any trait-based information, clearly predicted warming-driven extirpation driven by the loss of thermally suitable habitat (Supplementary Methods, Figure S7; Table S7).

More broadly, these tropical montane anoles are not ecophysiological anomalies for being relatively warm adapted: ectotherms (even closely related taxa) vary in their basking preferences and thermal physiology (Bodensteiner et al., 2021; Muñoz et al., 2016; von May et al., 2019) and in their ability to adaptively modify their physiological phenotypes (Gunderson & Stillman, 2015). The patterns we observe here might, therefore, characterize many other montane organisms. As such, the remarkable diversity that tropical mountains host may be more behaviourally resilient to environmental warming than generally appreciated. Yet, patterns of intrinsic vulnerability will vary within and among lineages: for example, many montane anoles (particularly those from the Latin American mainland) thermoregulate less and are more physiologically specialized (Salazar et al., 2019; Velasco et al., 2016). In those cases, behavioural resilience might correspondingly be more limited. Given just how variable behavioural and physiological patterns can be, even among related species, generalizations about vulnerability are likely tenuous, necessitating detailed organismal data (Bodensteiner et al., 2021). Behavioural resilience can nonetheless be undermined by vulnerability along ecological axes, underscoring the multivariate impacts of warming on species' distributions. Correspondingly, the common reshuffling of animal assemblages across elevation (e.g. Gibson-Reinemer et al., 2015; Bender et al., 2019) may often reflect the indirect effects of warming on key macrohabitat distributions or important ecological resources, rather than the direct effects of warming on their physiology. Signatures of vulnerability can (and clearly do) vary among ecological axes: much work still remains in discovering how patchwork patterns interact to determine the fate of organisms in a changing world.

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CONFLICT OF INTEREST

The authors state no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.M.M. designed the study, acquired the data, contributed to analysis and interpretation, and wrote the first draft of the article; K.J.F. contributed to analyses and interpretation, and contributed to manuscript writing; P.H.M. acquired the data, contributed to analysis interpretation and contributed to manuscript writing; V.R.F. contributed to analyses and interpretation and to manuscript writing. All authors gave approval for the final manuscript.

DATA AVAILABILITY STATEMENT

Data upon which this study is based are available through the Dryad Digital Repository https://doi.org/10.5061/dryad.t1g1jwt36 (Muñoz et al., 2021).

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