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The Andes are a driver of physiological diversity in *Anolis* lizards

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ABSTRACT

The Andes, with its diverse topography and climate, is a renowned cradle for adaptive radiation, particularly for vertebrate ectotherms such as lizards. Yet, the role of temperature in promoting physiological specialization in the Andes remains unclear. Aseasonality in the tropics should favour physiological specialization across elevation in lizards, but empirical data are limited and equivocal. Determining how thermal tolerances are geographically and phylogenetically structured is therefore a priority, particularly as environments continue to change rapidly. However, there is a gap in our knowledge of thermal limits of species from the Andes, one of the planet's most biodiverse regions. Anoles, a diverse lizard group found across thousands of metres of elevation in the Andes, can offer insights into evolutionary adaptations to temperature. This study focused on 14 anole species from two clades (Dactyloa and Draconura) that independently diversified along elevational gradients in the Andes. We measured critical thermal limits (CT_{min} and CT_{max}) and found patterns of thermal tolerance specialization across elevation, both among and within species. Patterns of thermal specialization are similar among anole clades, indicating parallel responses to similar environmental pressures. Specifically, high-elevation anoles are more cold tolerant and less heat tolerant than their low-elevation counterparts, rendering thermal tolerance breadths stable across elevation (thermal specialization). Evolutionary rates of physiological traits were similar, reflecting parallel specialization in heat and cold tolerance across elevation. The adaptive radiation of anole lizards reflects physiological specialization across elevation, and the endemism such specialization favours, probably catalysed their remarkable diversity in the tropical Andes.

RESUMEN

Los Andes, con su diversa topografía y clima, son reconocidos por ser cuna de radiación adaptativa, especialmente para ectotermos como las lagartijas. Sin embargo, el papel de cómo la temperatura promueve la especialización fisiológica en los Andes sigue siendo incierto. La falta de estacionalidad en los trópicos podría favorecer la especialización fisiológica a lo largo de la elevación en lagartijas, pero los datos empíricos son limitados y ambiguos. Por esto, determinar cómo las tolerancias térmicas están estructuradas geográfica y filogenéticamente en lagartijas es de vital importancia, especialmente cuando el ambiente está en constante cambio. No obstante, existe una brecha en nuestro conocimiento sobre los límites térmicos de las especies de los Andes, una de las regiones más biodiversas del planeta. Los *Anolis*, un grupo diverso de lagartijas que se encuentra a lo largo del gradiente de elevación en los Andes, pueden ofrecer información sobre adaptaciones evolutivas a la temperatura. Este estudio se centró en 14 especies de *Anolis* que perteneces a dos clados (Dactyloa y Draconura) que se diversificaron independientemente a lo largo de gradientes altitudinales en los Andes. Para estas, medimos los límites térmicos críticos (CTmin y CTmax) y encontramos patrones de especialización en la tolerancia térmica a lo largo de la elevación, tanto entre como dentro de las especies. Los patrones de especialización térmica son similares entre los clados de *Anolis*, lo que indica respuestas paralelas a presiones ambientales similares. Específicamente, los *Anolis* de alta elevación toleran temperaturas más frías y son menos tolerantes al calor que sus contrapartes de baja elevación, lo que hace que los rangos de tolerancia térmica sean estables a lo largo de la elevación (especialización térmica). Las tasas evolutivas de los rasgos fisiológicos fueron similares, reflejando una especialización paralela en la tolerancia al calor y al frío a lo largo de la elevación. La radiación adaptativa de las lagartijas *Anolis* refleja una especialización fisiológica a lo largo de la elevación, y el endemismo que favorece dicha especialización, probablemente catalizó su notable diversidad en los Andes tropicales.

Keywords: *Anolis*; adaptive radiation; elevational gradient; thermal biology; thermal physiology

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INTRODUCTION

The Andes Mountains are a powerful engine for speciation and are considered one of the most biodiverse regions on the planet (Jiménez *et al.* 2009, Clapperton 2011, Hazzi *et al.* 2018, Rahbek *et al.* 2019, Alencar *et al.* 2024). The incredible biodiversity reflects, in part, the topographic complexity of the Andes, which range from sea level to more than 6000 m asl and host a correspondingly wide range of climatic niches (Rahbek *et al.* 2019). The pronounced climatic variation of the Andes provides a clear substrate for adaptive radiation involving physiological specialization to different thermal and rainfall regimes (Sheldon 2019). Although adaptive radiation involves multidimensional phenotypic evolution (Schluter 2000, Stroud and Losos 2016, Gillespie *et al.* 2020), it has most often been studied with respect to morphology (e.g. Warheit *et al.* 1999, Mahler *et al.* 2010, Moen *et al.* 2021, Patton *et al.* 2021, Ronco *et al.* 2021, Viertler *et al.* 2021, Burress and Muñoz 2022), with comparatively fewer physiological studies (e.g. Givnish *et al.* 2004, Givnish and Montgomery 2014, Muñoz *et al.* 2014, Salazar *et al.* 2019, Cicconardi *et al.* 2023, Alomar *et al.* 2024, Bodensteiner *et al.* 2024). As such, we know significantly less about the role of ecophysiological specialization in adaptive radiation, and even less about its role in diversification in the Andes.

This knowledge disparity is evident for anole lizards (genus *Anolis*), a classic example of adaptive radiation (e.g. Losos 2009, Muñoz *et al.* 2023). This group of lizards is characterized by the evolution of divergent structural habitat specialists, termed ecomorphs, bearing morphological and behavioural specializations to the specific type of vegetation strata they most often utilize (Williams 1972, Losos *et al.* 1998, Losos 2009, Huie *et al.* 2021). Yet, anoles are also diverse in their ecophysiology and have repeatedly specialized to different thermal microhabitats (e.g. shaded vs. open habitats), and to different macrohabitats across elevational gradients, from sea level up to 3700 m asl (Ruibal 1961, Rand 1964, Hertz *et al.* 2013, Muñoz *et al.* 2014, Gunderson *et al.* 2018, Salazar *et al.* 2019, Bodensteiner *et al.* 2024). While morphology is relatively well studied in anoles, including several Andean species, comparatively less is known about the patterns of physiological specialization in this lineage. This study focuses on expanding our understanding of ecophysiological evolution in anole lizards, focusing on their diverse radiation in the tropical Andes of Colombia.

Critical thermal limits define the acceptable thermal boundaries for organismal function, thus influencing species distribution ranges and vulnerability to temperature changes (Lancaster 2016, Bennet *et al.* 2019, Collin *et al.* 2021, Beauty *et al.* 2023, Bovo *et al.* 2023). Specifically, the critical thermal minimum (CT_{min}) and maximum (CT_{max}) represent the lower and upper temperatures, respectively, at which an individual loses its locomotor ability (Angilletta 2009). Here, we use 'cold tolerance' and 'heat tolerance' to describe the critical thermal minimum and maximum, respectively. Ectotherms like anoles rely on ambient temperature to regulate their body temperature and carry out basic metabolic functions (reviewed in Angilletta 2009). Given that the tropics are aseasonal environments, we can predict that anole species will exhibit thermal specialization across elevation: this expectation that tropical lineages are physiologically specialized across elevation due to low seasonality is known as Janzen's hypothesis (Janzen 1967, Ghalambor *et al.* 2006). Specifically, we predict that species found at low elevation should be more heat tolerant and less cold tolerant than their counterparts at high elevation. Under this scenario, heat tolerance and cold tolerance should evolve at equal rates across elevation, as both features simultaneously specialize to local thermal conditions, and thermal tolerance breadths (the range of temperatures separating critical limits) should remain unchanged with elevation.

Yet, there may be more complexity to this pattern because diurnal ectotherms like anoles may thermoregulate to maintain a certain body temperature, even in quite thermally different environments (Muñoz and Losos 2018). Across elevation, such thermoregulation should result in a similar physiological response among species, even when found in habitats that vary in average thermal conditions (Huey *et al.* 2003, Muñoz and Losos 2018). In this case, we would expect behavioural buffering to limit divergence in heat tolerance across elevation, a phenomenon termed the Bogert effect (Bogert 1949, Huey *et al.* 2003, Muñoz 2022). Anoles are inactive at night and nighttime temperatures become progressively lower with elevation, limiting behavioural refuges from the cold and favouring physiological specialization to low environmental temperatures (Muñoz *et al.* 2014, Muñoz and Bodensteiner 2019). As such, we can predict that cold tolerance will increase with elevation, regardless of whether lizards diurnally thermoregulate or not. In this case, we would expect the rate of cold tolerance evolution to outpace that of heat tolerance, suggesting that specialization in the Andes involves rapid specialization to minimum environmental temperatures more so than to maximum temperatures. Likewise, we would expect tolerance breadths to increase with elevation, reflecting a relatively inert heat tolerance and decreasing CT_{min} with elevation.

While critical temperature data on ectotherms available in the literature have expanded significantly across various taxa in recent decades, including reptiles (e.g. Huey *et al.* 2009, Muñoz *et al.* 2014, Gunderson and Stillman 2015, Piantoni *et al.* 2015, Andrango *et al.* 2016, Gunderson *et al.* 2018, Salazar and Miles 2024), amphibians (e.g. Gunderson and Stillman 2015, von May *et al.* 2017), insects (e.g. Gaston and Chown 1999, Hoffmann 2010, Stevens *et al.* 2010, Gunderson and Stillman 2015, Sinclair *et al.* 2016), and aquatic animals (e.g. Díaz *et al.* 2002, Dülger *et al.* 2012, Gunderson and Stillman 2015, Martinez *et al.* 2016, Sinclair *et al.* 2016, Yanar *et al.* 2019), there remains a notable gap in information on thermal limits for Andean-dwelling species (but see Méndez-Galeano and Calderón-Espinosa 2017, Méndez-Galeano *et al.* 2020, Montoya-Cruz *et al.* 2024, Pinzón-Barrera *et al.* 2024).

Andean anoles can be found from sea level to elevations of up to 3700 m, varying in the elevational range that they occupy, and different lineages have independently diversified across elevation (Moreno-Arias *et al.* 2021). This replicated diversification across elevation renders anoles an ideal system for comparative physiological inquiry. In the present study, we focused on 14 species from two anole clades, Dactyloa (comprising 138 species) and Draconura (comprising 69 species) (Poe *et al.* 2017), which independently diversified in the challenging environmental conditions of the Andean mountains. We investigated how thermal

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limits and thermal tolerance breadth vary with elevation within and among anole species. We compared the evolutionary rates of heat tolerance (the critical thermal maximum, CT_{max}) and cold tolerance (the critical thermal minimum, CT_{min}) within the two focal clades of anoles. Our study investigates how thermal variation across elevation predicts the evolution of two key physiological traits in tropical mainland ectotherms, and how thermal physiology has evolved in the Andean radiation of anole lizards.

METHODS

Study sites and species

We collected anole cold tolerance (CT_{min}) and heat tolerance (CT_{max}) measurements from December 2016 to November 2017 in five different localities from the Colombian Andes (Supporting Information Fig. S1): (i) Anchicayá Hydroelectric (3°26′27.12″N, 76°40′0.13″W; 192–639 m); (ii) Bitaco Forest Reserve (3°33′9.95″N, 76°35′1.52″W; 1973–2050 m); (iii) Parque Nacional Natural (PNN) Tatamá (5°13′47.96″N, 76°5′1.51″W; 1326–2330 m); (iv) PNN Farallones de Cali (3°24′41.65″N, 76°39′5.36″W; 1870–2369 m); and (v) Passiflora Reserve (4°55′59.59″N, 74°6′43.19″W; 2818m). We captured 367 individuals from 14 species (Fig. S2).

Nine species belong to the Dactyloa clade: *Anolis calimae* (2117–2240 m; $N = 4$), *A. chloris* (1341–1488 m; $N = 21$), *A. danieli* (1776–2330 m; $N = 8$), *A. eulaemus* (2042 m; $N = 1$), *A. heterodermus* (1345–2818 m; $N = 9$), *A. maculigula* (1389–1438 m; $N = 24$), *A. princeps* (527–1408 m; $N = 4$), *A. purpurescens* (formerly known as *A. chocorum*; 572–591 m; $N = 2$), and *A. ventrimaculatus* (1343–2369 m; $N = 142$). Five species belong to the Draconura clade: *Anolis antonii* (1326–2314 m; $N = 131$), *A. granuliceps* (586–639 m; $N = 2$), *A. lyra* (591 m; $N = 1$), *A. maculiventris* (256–624 m; $N = 16$) and *A. notopholis* (192–285 m; $N = 2$). Two species, *Anolis antonii* and *A. ventrimaculatus*, were sampled at multiple localities at different elevations. *Anolis antonii* was measured at PNN Farallones de Cali ($N = 30$) and PNN Tatamá ($N = 101$), and *A. ventrimaculatus* was measured at Bitaco Forest Reserve ($N = 53$), PNN Farallones de Cali ($N = 53$), and PNN Tatamá ($N = 36$). Most of the individuals in this study were found <2 m above the ground. Some of the species we measured (*A. chloris*, *A. calimae*, *A. eulaemus*, *A. heterodermus*, *A. princeps*, and *A. purpurescens*) are commonly found high up in trees; unfortunately, for these we were unable to precisely measure how high in the tree they were perched (Supporting Information Table S1).

Measurement of CT_{min} and CT_{max}

Lizard capture was mostly done during the night (between 6 p.m. and 2 a.m.), when anoles are easier to spot. Individuals were captured by hand, and for each we also recorded a GPS point. Temperature measurements during tolerance trials were taken following Muñoz *et al.* (2014) and Llewelyn *et al.* (2016) with the following modifications. We conducted all the physiological measurements at the field station near to the capture site of each individual. To record instant body temperature of larger species [snout–vent length (SVL) > 60 mm], a 2-mm thermocouple was inserted into the cloaca of adult individuals; for juveniles and adults of smaller species (SVL < 60 mm), a 0.22-mm thermocouple was used instead. The thermocouple was secured to the base of the tail using medical tape. To measure CT_{min} and CT_{max}, the anole was placed into a plastic container that was submerged in a cold-water ice bath or a warm-water bath, respectively. Each time the body temperature of the lizard changed one degree, the individual was turned, placing it on its back inside the container. If the lizard righted itself to its original position, we continued with the temperature reduction or increase procedure until it was not able to turn itself over, indicating a loss of locomotor function. At this point, the temperature was recorded as the CT_{min} or CT_{max}. At the end of the experiment, the individual was slowly returned (1°C every minute) to its initial temperature by means of a warm-water or cold-water bath. To minimize animal stress, only one measurement (either CT_{min} or CT_{max}) was collected per individual in the morning after they were captured; we performed both measurements only for species where we found one or two individuals (*A. eulaemus*, *A. granuliceps*, *A. lyra*, *A. purpurescens*, *A. notopholis*). The morning after thermal trials individuals were released at their capture site. Before releasing an individual, a mark was made on the belly using a permanent marker ink to avoid measuring the same individual twice. From CT_{min} and CT_{max} we calculated the thermal breadth (T_{br}; also referred as thermal tolerance range) for each species, such that $T_{br} = CT_{max} - CT_{min}$.

Environmental data

As a proxy for the general thermal conditions experienced by different lizard species, we extracted three ecologically relevant temperature variables from the WorldClim database (Fick and Hijmans 2017) for each of the sample sites of the study [Bio 1 (mean annual temperature), Bio 5 (maximum annual temperature), and Bio 6 (minimum annual temperature); Qu and Wiens (2020)]. These WorldClim layers are resolved to 1 km^2 and summarize thermal averages, extremes, and ranges. As these three climatic variables were highly correlated (Supporting Information Tables S2 and S3), we decided to use one variable (Bio 1) for our analyses. Using mean values from WorldClim data (Fick and Hijmans 2017) to represent the climatic niche may not reflect the microhabitat variation that lizards experience, and micro- and macroclimatic niches can vary in ectotherms (Velasco *et al.* 2016, 2020, Farallo *et al.* 2020, Muñoz *et al.* 2022). Nevertheless, these macroclimatic features do provide a coarse approximation for general thermal conditions experienced by lizards and can serve as a starting point to evaluate the relationship between thermal physiology and the macroenvironment. In addition, we also investigated the operative environmental temperatures experienced by lizards (described below).

Operative environmental temperature (T_e)

We used the R package 'NicheMapR' (Kearney and Porter 2017) to estimate the operative environmental temperatures (T_e) at each site. T_e is defined as the equilibrium body temperature of a non-thermoregulating organism in the open, accounting for the various sources of heat gain and heat loss. We estimated T_e where the anoles were found. By using 'NicheMapR' we can model microclimate by using locations, forest cover level, and other factors to calculate the microclimatic conditions that an ectotherm experiences (Kearney and Porter 2017, 2019). We acquired

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macroclimate data for the microclimatic analyses from the ERA5 fifth generation ECMWF global atmospheric reanalysis of global climate using the 'mcera5' package (Klinges *et al.* 2022). We acquired microclimatic data through the 'NicheMapR' function *micro_era5*, which is integrated with the 'microclima' package (MacLean *et al.* 2019). The output of *micro_era5* is used by the function *ectotherm* in 'NicheMapR' to generate a model of heat and water exchange. We obtained T_e estimates for each *Anolis* species at each site by using the default organismal parameters except for the mean body mass of each species. Because the species of *Anolis* in the data are arboreal, we set the parameter for climb equal to 1, which indicates that a species is arboreal. We estimated the mean monthly T_e values for the duration of the study period (December 2016 to November 2017). We only show the T_e mean results in the main text, and we provide the results for T_e minimum and T_e maximum in the Supporting Information.

Statistical and phylogenetic analyses

All statistical analyses were conducted using R v.4.3.2 (R Core Team 2023). Figures were made with the 'ggplot2' package (Wickham 2009). Before we conducted phylogenetic analyses, we evaluated whether CT_{min} and CT_{max} differed between sexes (adult males vs. adult females) and age classes (juveniles vs. adults). As we did not find variation among the categories, we combined data for all individuals (Supporting Information S1).

For the phylogenetic analysis, we used the Poe *et al.* (2017) phylogeny based on morphological and molecular data (MCC—maximum clade credibility tree) and species' averages for each trait. First, we quantified the amount of phylogenetic signal for CT_{min}, CT_{max}, and T_{br}, using the λ statistic (Pagel 1999) with the function *phylosig* in the R package 'phytools' (Revell 2012). We used this statistic to evaluate the phylogenetic dependence of the trait data. Pagel's λ ranges from 0 to 1, with values closer to 0 indicating weak phylogenetic signal, meaning that traits are evolving independent of relatedness, and values closer to 1 indicating greater phylogenetic structuring to the data, following expectations under a Brownian motion (BM) model of evolution (Pagel 1999). Less commonly, λ can exceed 1, indicating that traits are more similar than expected under BM (Pagel 1999). Intraspecific comparisons of thermal limits among populations of *Anolis antonii* and *A. ventrimaculatus* were performed with one-way ANOVA (separate for each species) with the mean for CT_{min}, CT_{max}, T_{br}, and elevation.

To evaluate the relationship between thermal limits (CT_{min}, CT_{max}), breadth (T_{br}), elevation (mean elevation for each species), and thermal environment (Bio 1, T_e mean) among the 14 species we used phylogenetic generalized least squares (PGLS) analysis using the *pgls.SEy* function in the package 'phytools' (Revell 2012); this function takes into account the standard error for each species. Before interpreting the PGLS results, we quantified the phylogenetic signal of the residuals using Pagel's λ to assess the influence of shared evolutionary history on the residual variation. Because we have only one T_{br} value per species, we were not able to run a *pgls.SEy*, and instead we ran a PGLS using the *pgls* function in the package 'caper' (Orme 2018). We compared the model fit using the Akaike Information Criterion for small samples sizes (AICc; Sugihara 1978, Burnham and Anderson 2002).

To compare the rate of physiological evolution for CT_{min} and CT_{max}, first we fitted five different models of evolution—BM, Ornstein–Uhlenbeck (OU), Early Burst (EB), Delta, and White Noise (WN)—to each physiological trait, using the *fitContinuous* function in the 'geiger' package (Harmon *et al.* 2008). We compared each model by examining the AICc.

We were also interested in whether the relationship between elevation and thermal physiology varied between clade of anoles or, instead, whether the effect of elevation was comparable among clades. To this end we conducted a phylogenetic analysis of covariance (pANCOVA; Revell and Harmon 2022) to evaluate whether the slopes and intercepts of the trait–environment relationships varied between anole clades (Dactyloa and Draconura).

We used Adams' (2013) method to compare the evolutionary rates (σ^2) of CT_{min} and CT_{max}. Specifically, we performed a likelihood-ratio test (LRT) to compare the likelihood of a model in which rates for CT_{min} and CT_{max} were constrained to be equal (i.e. $\sigma^2_{min} = \sigma^2_{max}$). To consider intraspecific measurement error, we did incorporate the standard error (corrected) into the analysis. We also show the results when we did not incorporate standard error (uncorrected). We used the 'ape' package in R to run the code provided by Adams (2013). Since CT_{min} and CT_{max} are correlated with elevation and might be correlated with each other, we set the *TraitCov* argument to *TRUE* to specify that both physiological traits may covary.

RESULTS

We measured CT_{min} and CT_{max} from 350 lizards (173 individuals for CT_{min} and 177 for CT_{max}; Table 1) from 14 species. These 350 individuals were 87 adult males (37 for CT_{min} and 50 for CT_{max}), 113 adult females (62 for CT_{min} and 51 for CT_{max}), and 123 juveniles (60 for CT_{min} and 63 for CT_{max}). Additionally, we found 27 individuals that we were not able to sex or age (14 for CT_{min} and 13 for CT_{max}). We found no difference in CT_{min} and CT_{max} between sexes and ages (Supporting Information S1, Fig. S3, Table S4), so we used the entire data set to conduct subsequent phylogenetic analyses.

Thermal habitat

There was a high correlation between CT_{min} and CT_{max} with both Bio 1 and elevation (Fig. 1), where CT_{min} and CT_{max} increase with mean annual temperature, and decrease with elevation. By contrast, T_{br} showed no relationship with Bio 1 or elevation and remained fairly constant across elevation (Fig. 1; Supporting Information Fig. S4 for Bio 5 and Bio 6, Tables S5 and S6). We found similar results for the correlations between CT_{min} and CT_{max} with T_e (Fig. 1 for T_e mean, Fig. S4 for T_e minimum and T_e minimum, Tables S5 and S6), where both CT_{min} and CT_{max} increase as T_e increases. We ran pgls (*pgls.SEy* and *pgls*) analyses for all species combined.

Interspecific variation in CT_{min}, CT_{max} and T_{br}

We found that Pagel's λ was low (0.00006), suggesting little to no phylogenetic structure to the trait data. We determined that the residual variation was largely independent of phylogeny, and used *pgls.SEy* for subsequent analysis (Fig. 2; Supporting Information

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Table 1. Average capture elevation, CT_{min}, CT_{max}, and T_{br} for each species.

Species	Elevation (m)	CT_{min} (°C)	CT_{max} (°C)	T_{br} (°C)
Dactyloa clade				
A. chloris[d]	1414 ± 178	12.97 ± 2.28 (18)	31.82 ± 1.07 (14)	18.85
A. danieli[d]	2109 ± 173	13.62 ± 1.47 (7)	30.10 ± 1.29 (5)	16.48
A. eulaemus[b]	2042	11.50 (1)	23.60 (1)	12.10
A. heterodermus[ce]	2182 ± 358	7.44 ± 2.33 (7)	30.36 ± 4.40 (8)	22.93
A. maculigula[d]	1409 ± 18	13.10 ± 1.62 (12)	29.58 ± 1.39 (8)	16.48
A. calimae[c]	2158 ± 53	13.59 ± 0.78 (2)	26.36 ± 3.24 (3)	12.77
A. princeps[a]	800 ± 425	13.109 ± 4.70 (4)	32.31 ± 6.60 (3)	19.22
A. purpurescens[a]	582 ± 13	18.97 ± 1.06 (2)	31.97 ± 0.76 (2)	13.00
A. ventrimaculatus[bcd]	1992 ± 217	11.93 ± 2.52 (45)	27.58 ± 2.99 (62)	15.66
Draconura clade				
A. antonii[cd]	1608 ± 333	13.36 ± 2.29 (60)	27.63 ± 1.99 (59)	14.26
A. granuliceps[a]	621 ± 37	15.50 ± 0.93 (2)	32.69 (1)	17.19
A. lyra[a]	591	17.86 (1)	36.50 (1)	18.64
A. maculiventris[a]	580 ± 88	17.98 ± 1.90 (10)	31.86 ± 0.79 (8)	13.88
A. notopholis[a]	239 ± 66	14.43 ± 0.64 (2)	32.41 ± 2.45 (2)	17.98

Mean and standard deviation are shown and the numbers in parentheses indicate sample size. The locality for each species is shown as follows: [a]Anchicayá Hydroelectric, [b]Bitaco Forest Reserve, [c]PNN Farallones de Cali, [d]PNN Tatamá, and [e]Passiflora Forest Reserve.

Table S7). The WN model best fit the CT_{min}, CT_{max} and T_{br} data (Table S8); this WN model indicates that the thermal traits evolved independently of the phylogeny, which corroborates Pagel's λ result (Table S9; Harmon *et al.* 2008, Muschick *et al.* 2014). Both thermal limits, CT_{min} and CT_{max}, decreased with elevation (Fig. 1; Table 2; Tables S5 and S6). We found that these relationships were similar, both in slope and in intercept, for species in the Dactyloa and Draconura clades (Table S10). We did not find differences in the evolutionary rate of the thermal traits (Table 3), meaning that CT_{min} ($\sigma^2 = 0.21$) and CT_{max} ($\sigma^2 = 0.19$) evolve at similar rates.

Intraspecific variation in CT_{min} and CT_{max}

We found that populations of *A. antonii* located at different elevations have different CT_{min} values (Fig. 3A), such that the higher elevation population is less cold tolerant (higher CT_{min}) ($t = 4.51$, $P < .001$, d.f. = 58). We did not detect differences in CT_{max} among populations ($t = -1.70$, $P = .09$, d.f. = 63). Similarly, for *A. ventrimaculatus*, we found that the populations that are found at high elevation are less cold tolerant (higher CT_{min}), and those found at low elevation are more heat tolerant (higher CT_{max}) (CT_{min}: $F_{2,54} = 9.03$, $P < .001$ and CT_{max}: $F_{3,72} = 5.2$, $P = .002$; Fig. 3).

DISCUSSION

The topographical complexity of the Andes forged a wide range of thermal habitats presenting the opportunity for physiological specialization across elevation. As predicted, we found that montane anoles tolerate lower temperatures better than their low-elevation counterparts, and that anoles closer to sea level were more heat tolerant than those found at high elevation. Similarly, numerous studies have found that tolerance to cold is enhanced in cooler environments across a wide range of ectotherm taxa (e.g. Araújo *et al.* 2013, Sunday *et al.* 2014, 2019, von May *et al.* 2017, Pintanel *et al.* 2019, Gonzalez *et al.* 2022). However, our finding that species in cooler environments are also less heat tolerant than their counterparts in warmer environments contrasts with other studies, including on anoles, in which heat tolerance remains relatively static across environmental clines (e.g. Muñoz *et al.* 2014, Shah *et al.* 2017, Qu and Wiens 2020). Such strong physiological structuring across altitudinal clines may help explain why phylogenetic signal is low as close relatives diverge in thermal tolerances across environmental boundaries, and appear physiologically specialized to their local conditions, as evidenced by the fact that thermal tolerance breadth (T_{br}) is unchanged across elevation (Fig. 1). The decrease in both cold and heat tolerance with elevation may also explain why rates of CT_{min} and CT_{max} evolution are indistinguishable. The adaptive radiation of Andean anoles therefore involves specialization in both heat and cold tolerance across elevation. Below, we unpack these findings in greater detail.

How thermal habitat influences the evolution of critical thermal limits

We observed a strong correlation between heat tolerance, cold tolerance, and the thermal environment (Fig. 1), suggesting that local climatic conditions favour thermal physiological specialization. Consistent with Janzen's hypothesis (Janzen 1967, Sheldon *et al.* 2018), tolerance breadths are stable across elevation, reflecting local adaptation in both cold and heat tolerance. Additionally, we found both clades, Dactyloa and Draconura, followed the same pattern of evolution, indicating parallel trends of thermal specialization among lineages that independently radiated in the Andes (Fig. 1; Supporting Information Fig. S4; Poe *et al.* 2017).

As both heat and cold tolerance decrease with elevation, we observed no differences in the evolutionary rate of these two traits. Previous studies on other ectotherm lineages have reported similar findings for CT_{min} and CT_{max} (Shah *et al.* 2017,

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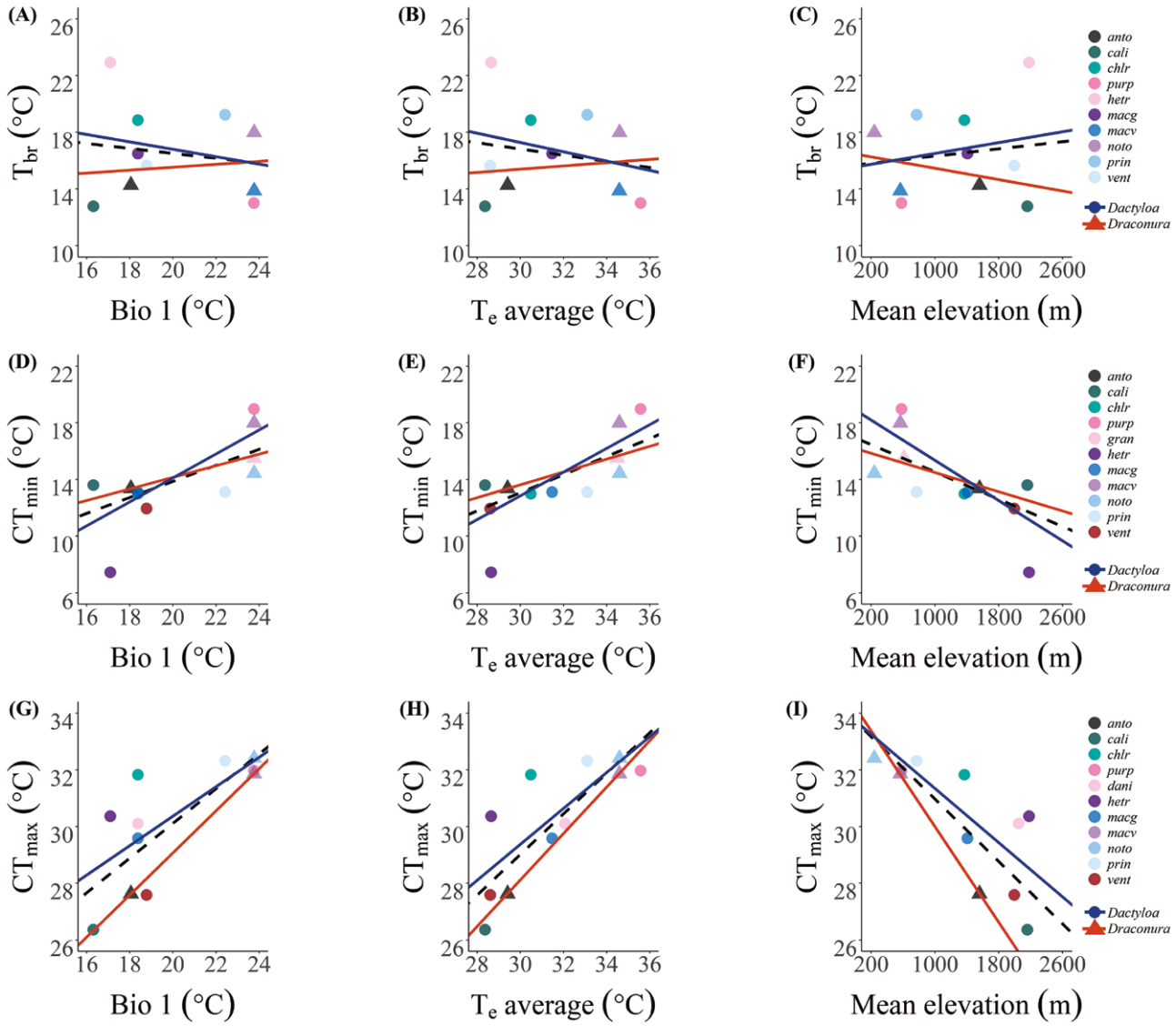

Figure 1. Relationship between species between T_{br} (top), CT_{min} (middle), and CT_{max} (bottom) with Bio 1 (mean annual temperature; A, D, G), T_e (operative environmental temperature; B, E, H), and mean elevation (C, F, I) *Anolis antonii—anto*, *A. calimae—cali*, *A. chloris—chlr*, *A. danieli—dani*, *A. granuliceps—gran*, *A. heterodermus—hetr*, *A. maculigula—macg*, *A. maculiventris—macv*, *A. notopholis—noto*, *A. princeps—prin*, *A. purpurescens—purp*, and *A. ventrimaculatus—vent*. Dashed lines represent the phylogenetic regression for all species. Coloured lines indicate the phylogenetic regression for Draconura species in green and Dactyloa species in brown. Each point corresponds to a different species of *Anolis* lizard. Circles indicate Dactyloa species; triangles indicate Draconura species.

von May *et al.* 2017, Pintanel *et al.* 2019, Gonzalez *et al.* 2022, Bovo *et al.* 2023, Bota-Sierra *et al.* 2022 [CT_{max} only]). Yet, prior work on Caribbean anoles found that heat tolerance does not vary across elevation, while cold tolerance does (Muñoz *et al.* 2014). Behavioural thermoregulation is a primary mechanism underlying this disparity between heat and cold tolerance adaptation: whereas behavioural thermoregulation 'shields' diurnal lizards like anoles from selection on upper thermal limits, behaviour is less effective at shielding them from selection on lower thermal limits (Muñoz and Bodensteiner 2019, Bodensteiner *et al.* 2021). This lopsided effect of thermal behaviour results in stability in heat tolerance across elevation (and a relatively slow rate of evolution) and lability in cold tolerance across elevation (and a relatively fast rate of evolution) (Muñoz 2022). While we did not consider thermal behaviour here, it is probable these Andean lizards are thermoconformers, as they tend to occupy dense, closed-canopy habitats, where the costs of thermoregulation are high owing to long transit distance between sun and shaded patches, meaning that the distance travelled may exceed the home range of an individual (Huey 1974). Moreover, these anoles tend to move relatively little (Losos 2009), reflecting greater predation risk on the South American mainland relative to the Caribbean, further limiting thermoregulatory behaviour.

Putting these pieces together, habitat structure and predation may favour thermoconformity in the Andes, which in turn favours physiological specialization across elevation and probably contributed to the anole adaptive radiation in the Andes. Under Janzen's (1967) hypothesis, this physiological specialization should limit dispersal across elevation, limit gene flow, and potentially help catalyse speciation, as has been observed in South

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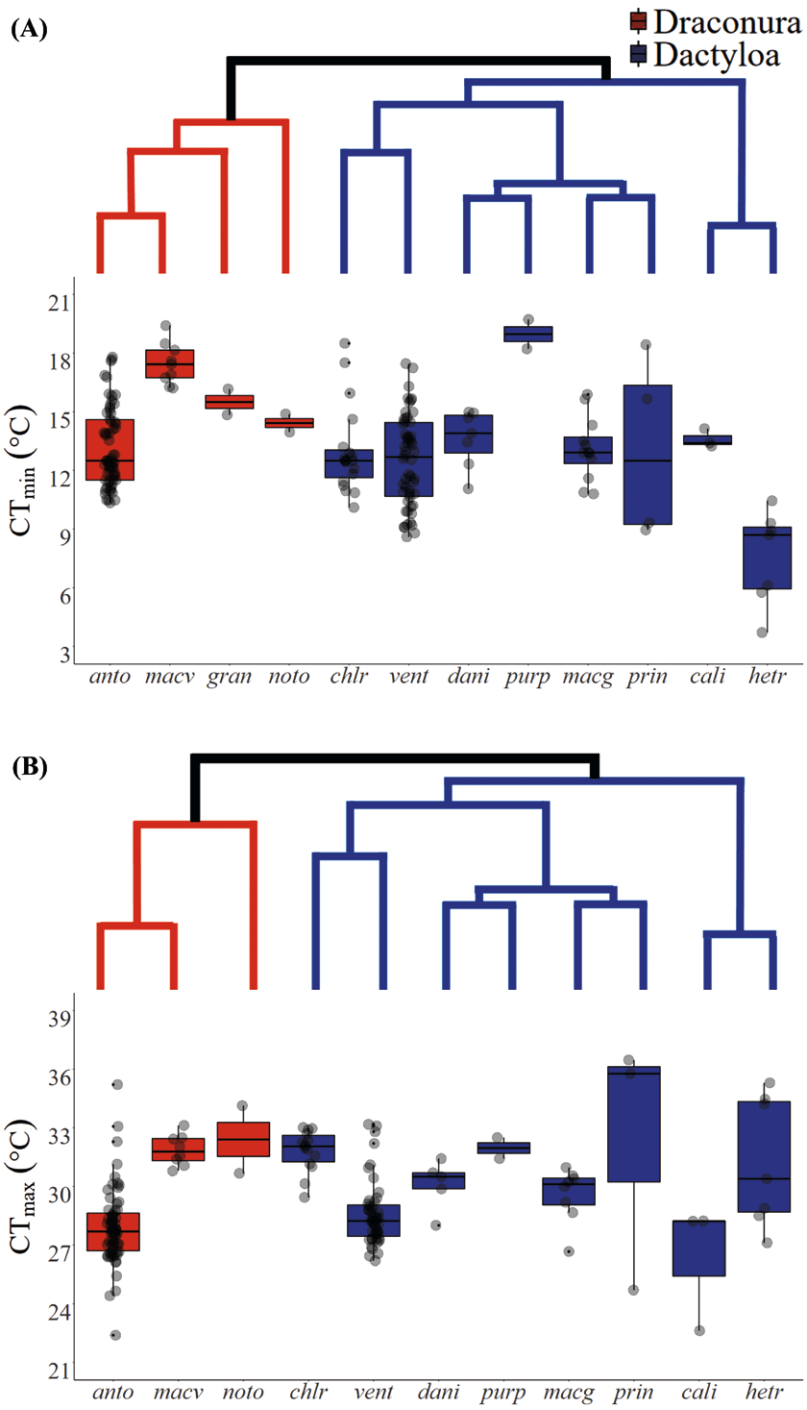

Figure 2. Interspecific divergence of (A) CT_{max} and (B) CT_{min} for Andean anoles. Species tree shows the relationship between 11 species for CT_{max} (top) and 12 species for CT_{min} (bottom). *A. antonii—anto*, *A. calimae—cali*, *A. chloris—chlr*, *A. danieli—dani*, *A. granuliceps—gran*, *A. heterodermus—hetr*, *A. maculigula—macg*, *A. maculiventris—macv*, *A. notopholis—noto*, *A. princeps—prin*, *A. purpurescens—purp*, *A. ventrimaculatus—vent*. Species are coloured according to their clade (Dactyloa—brown, Draconura—green).

American aquatic insects (Polato *et al.* 2018). We do note, however, that there may be some thermoregulation in some Andean anole species that may impact patterns of physiological specialization. For at least one Andean anole species, *A. heterodermus*, we know that activity changes throughout the day, decreasing as the day gets warmer (Méndez-Galeano and Calderón-Espinosa 2017, Méndez-Galeano *et al.* 2020). Therefore, the relationship between thermal behaviour and physiological specialization in Andean anoles awaits deeper exploration. Future studies on the thermal physiology of Andean anoles should also investigate how thermal plasticity might impact patterns of specialization in CT_{min} and CT_{max}. In some ectotherms, for example, limited plasticity has been observed (e.g. Domínguez-Guerrero *et al.* 2019, García-Robledo and Baer 2021). In one Central American anole (*Anolis apletophallus*), by contrast, high levels of plasticity have been found at different levels, phenotypic and

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Table 2. Results from phylogenetic generalized linear regression models for CT_{min}, CT_{max}, and T_{br} assuming Brownian motion as the evolutionary model.

Model	Coefficient	*P*-value	AIC	logLik
CT_{min} ~ elevation	*−0.0024*	*.015*	*50.00*	*−22.00*
CT_{min} ~ Bio 1	*0.57*	*.016*	*50.19*	*−22.09*
CT_{min} ~ T_e average	*0.64*	*.0073*	*48.41*	*−21.20*
CT_{max} ~ elevation	*0.57*	*.0077*	*48.25*	*−21.13*
CT_{max} ~ Bio 1	*0.61*	*.0047*	*47.12*	*−20.56*
CT_{max} ~ T_e average	*0.72*	*.0012*	*44.44*	*−19.22*
Model	**Coefficient**	***P*-value**	**R^2**	***F***
T_{br} ~ elevation	<0.0001	.70	.019	0.16
T_{br} ~ Bio 1	−0.18	.66	.026	0.21
T_{br} ~ T_e average	−0.22	.60	.035	0.29

Coefficient, *P*-value and AIC values are shown for the *pgls.SEy* results, and the coefficient, *P*-value, R^2 and *F*-value are shown for the *pgls* results. Significant results are shown in italics.

Table 3. Evolutionary rate comparison for CT_{min} and CT_{max}.

Pairwise comparison	Uncorrected $LRT_{d.f=1}$; *P*	Corrected $LRT_{d.f=1}$; *P*
CT_{min} vs CT_{max}	.03; .86	.03; .86
Confidence interval for evolutionary rate	Low	High
CT_{min}	.15	.28
CT_{max}	.13	.24

Pairwise comparison for evolutionary rates among traits. The results are given for two analyses, one in which we did not consider intraspecific measurement of error (uncorrected), and another in which we did incorporate the error (corrected). The confidence interval for the evolutionary rates for CT_{min} and CT_{max} are also shown.

genetic, at least for heat tolerance (Rosso *et al.* 2024). More generally, the degree of plasticity appears to vary among traits and lineages (Gunderson and Stillman 2015), underscoring the need for species-specific estimates. Nevertheless, to the extent that physiological evolution has contributed to the diversity of Andean anoles, thermoconformity may be a potent catalyst for their adaptive radiation.

Intraspecific variation in CT_{min} and CT_{max}

Contrasting differences in thermal limits were observed among populations of *A. antonii* and *A. ventrimaculatus* (Fig. 3) in CT_{min}. We found that, for both species, cold tolerance is lower at high-elevation sites and higher at the low-elevation site, while CT_{max} for *A. antonii* remains unchanged. In contrast, for *A. ventrimaculatus* (Fig. 3B) CT_{max} is higher at the low-elevation site and lower at high-elevation sites. Despite the counterintuitive nature of these patterns, our results suggest that factors beyond elevation may contribute to differences in thermal limits between populations and among species. However, there could be more factors playing a role in our findings including microhabitat segregation (Jenssen 1970, Hertz 1974, Du *et al.* 2000, Ramirez-Bautista and Benabib 2001, Herczeg *et al.* 2008, Tang *et al.* 2013, Muñoz *et al.* 2016), predator and competitor presence (Terborgh and Weske 1975, Huey and Kingsolver 1989, Helmuth *et al.* 2005, Jankowski *et al.* 2013, Salazar *et al.* 2019, Londoño *et al.* 2023), humidity (Hutchinson 1957, Wake and Lynch 1976), rainfall (Wake and Lynch 1976, Salazar and Miles 2024), morphology (Wegener *et al.* 2014), and plastic capacity (Llewelyn *et al.* 2016, Phillips *et al.* 2016, García-Robledo and Baer 2021, Rosso *et al.* 2024). This suggests that biotic and abiotic factors could play a role in local adaptation that is not captured in a broader, macro-evolutionary view across the lineage. Future studies should integrate these factors to understand their role in thermal physiology variation among species and populations, including behaviour during daytime.

Although climatic stability in tropical regions has historically been cited as a key factor in explaining species range limits, particularly along mountain ranges (Janzen 1967), the influence of climatic heterogeneity on species' physiological and evolutionary traits in these regions has often been overlooked (Boyle *et al.* 2020, Muñoz 2022). The geomorphological complexity of the Andes, spanning various valleys, slopes, and elevations, probably serves not only as a driver of faunistic diversity (Alencar *et al.* 2024), but also as a determinant of thermal physiology diversity (Velasco *et al.* 2016). Unfortunately, this geomorphological complexity of the Andes cannot be captured by WorldClim or NicheMapR data (Sears *et al.* 2019). To truly understand how environmental temperature affects thermal physiology evolution, we should use microclimatic data collected on-site. However, using Bio 1 and T_e mean we observed the same pattern for our three physiological variables (CT_{min}, T_{br}, CT_{max}) for all species in the two clades (Fig. 1). The diverse microclimates created by different topographical features impose unique thermal challenges among populations, leading to the observed differences in thermal physiology within species.

Although we discussed how temperature has contributed to the colonization and adaptation to the Andes climate, there are additional factors that could have affected our results. We have few individuals for some of the species we captured and measured, which may lead to biased estimates of CT_{min} and CT_{max}. Additionally, we used species from two different clades with few representatives from each. Furthermore, we have no knowledge of the genetic background of Andean anole species, which could alter our understanding of how these species have evolved to withstand low temperatures in the Andes. These are several factors that should be taken into consideration for further studies.

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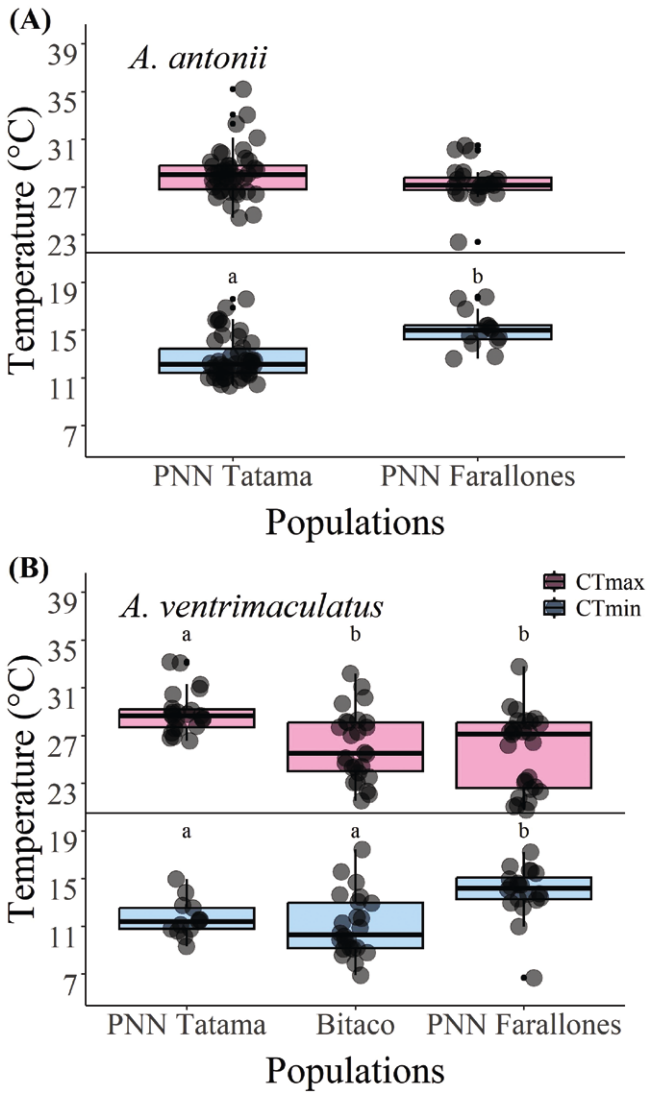

Figure 3. CT_{min} and CT_{max} comparison among populations of (A) *A. antonii* in PNN Tatamá (1392 m) and PNN Farallones (2115 m), and (B) *A. ventrimaculatus* in PNN Tatamá (1689 m), Bitaco Forest Reserve (2005 m), and PNN Farallones (2201 m). Lower-case letters a, b, and c indicate if CT values differ (different letter) or not (same letter) statistically. The boxes are coloured according to the thermal limits; blue for CT_{min} and red for CT_{max}.

Nevertheless, this work presents a significant advance forward: unlike in the Caribbean, mainland anoles are notoriously cryptic and exhibit lower densities (discussed in Losos 2009), which has surely contributed to the relative lack of physiological knowledge for continental species.

Just as important as the factors that shape the origin of biodiversity are those that threaten its loss. For ectotherms like anoles, the rapid rise of environmental temperatures presents an existential threat, and there is an urgent need to assess vulnerability across the animal tree of life (Deutsch *et al.* 2008, Huey *et al.* 2010, Muñoz and Moritz 2016, Stillman 2019). Even among ectotherms, tropical anoles like those studied here are expected to be particularly vulnerable, as they are already operating near their physiological limits (Huey *et al.* 2009, Sunday *et al.* 2014). Our data on Andean anoles are consistent with this perspective: whether near sea level or several kilometres above it, species are physiologically specialized to their local thermal conditions, and exhibit relatively narrow tolerance breadths, as predicted for tropical lizards (Huey *et al.* 2009).

The critical question remains whether species will be able to keep pace with the rapid rate at which climate change is affecting their natural environments. Studies should focus on understanding how future temperatures and rainfall patterns will affect the activity patterns, energetic balance, and population growth rates of Andean anoles to connect physiological variation to demographic patterns under rapid global change.

CONCLUSION

Our study on Andean anoles has yielded insights into their thermal physiology and adaptation to their environment. When compared to low-elevation anoles, those at high elevations demonstrated greater performance capacity at lower temperatures but were also less tolerant of higher temperatures. These results align with Janzen's (1967) hypothesis, as thermal breadth remains constant across elevation, reflecting local specialization in both heat and cold tolerance. We also observed that the evolution of cold and heat tolerance occurs at similar rates, and this occurred independently in the two anoles clades tested on this study, Dactyloa and Draconura. Phylogenetic analysis revealed that thermal limits vary among closely related species, indicating a departure from niche conservatism and reflecting lability in physiological tolerance as species diversified across elevation. Ecological and phenotypic divergence among close relatives is a canonical signature of adaptive radiation. The intricate geomorphological complexity of the Andes emerged as a key driver of thermal physiology diversity in the adaptive radiation of mainland anoles. Understanding the role of physiological diversity in diversification could offer valuable insights into how two clades from the genus with different evolutionary histories have similar evolutionary responses to adaption to mountainous environments. Future research should aim to elucidate the impact of the genetic background on the distribution and diversification of montane ectotherms, considering their evolutionary history and potential differential effects on lowland and highland species.

SUPPLEMENTARY DATA

Supplementary data are available at *Evolutionary Journal of the Linnean Society* online.

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CREDIT STATEMENT

Jhan C. Salazar (conceptualization, field work, experiments, analysis, manuscript draft), Gustavo A. Londoño (conceptualization, analyses, manuscript draft), Martha M. Muñoz (conceptualization, analyses, manuscript draft), Donald B. Miles (analysis, manuscript draft), and María del Rosario Castañeda (conceptualization, supervision of experiments, manuscript draft). All authors contributed to the discussion of the results and provided contributions to the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA AVAILABILITY

The complete dataset that supports the findings of this study is available online at: https://github.com/salazarjhan95/Anolis_Andes_2024/.

REFERENCES

Adams DC. Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Systematic Biology* 2013;**62**:181–92. https://doi.org/10.1093/sysbio/sys083

Alencar LRV, Schwery O, Gade MR *et al.* Opportunity begets opportunity to drive macroevolutionary dynamics of a diverse lizard radiation. *Evolution Letters* 2024;**8**:623–37. https://doi.org/10.1093/evlett/qrae022

Alomar N, Bodensteiner BL, Hernández-Rodríguez I *et al.* Comparison of hydric and thermal physiology in an environmentally diverse clade of Caribbean anoles. *Integrative and Comparative Biology* 2024;**64**:377–89. https://doi.org/10.1093/icb/icae030

Andrango MB, Sette C, Torres-Carvajal O. Short-term predicted extinction of Andean populations of the lizard *Stenocercus guentheri* (Iguanidae: Tropidurinae). *Journal of Thermal Biology* 2016;**62**:30–6. https://doi.org/10.1016/j.jtherbio.2016.09.012

Angilletta MJ. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. New York: Oxford University Press, 2009.

Araújo MB, Ferri-Yáñez F, Bozinovic F *et al.* Heat freezes niche evolution. *Ecology Letters* 2013;**16**:1206–19. https://doi.org/10.1111/ele.12155

Beauty F, Gehman ALM, Brownlee G *et al.* Not just range limits: warming rate and thermal sensitivity shape climate change vulnerability in a species range center. *Ecology* 2023;**104**:e4183. https://doi.org/10.1002/ecy.4183

Bennet S, Duarte CM, Marbà N *et al.* Integrating within-species variation in thermal physiology into climate change ecology. *Philosophical Transactions of the Royal Society B* 2019;**374**:20180550. https://doi.org/10.1098/rstb.2018.0550

Bodensteiner BL, Agudelo-Cantero GA, Arietta AZA *et al.* Thermal adaptation revisited: How conserved are thermal traits of reptiles and amphibians? *Journal of Experimental Zoology. Part A, Ecological and Integrative Physiology* 2021;**335**:173–94. https://doi.org/10.1002/jez.2414

Bodensteiner BL, Burress ED, Muñoz MM. Adaptive radiation without independent stages of trait evolution in a group of Caribbean anoles. *Systematic Biology* 2024;**73**:743–57. https://doi.org/10.1093/sysbio/syae041

Bogert CM. Thermoregulation in reptiles, a factor in evolution. *Evolution* 1949;**3**:195–211. https://doi.org/10.1111/j.1558-5646.1949.tb00021.x

Bota-Sierra CA, García-Robledo C, Escobar F *et al.* Environment, taxonomy and morphology constrain insect thermal physiology along tropical mountains. *Functional Ecology* 2022;**26**:1924–35. https://doi.org/10.1111/1365-2435.14083

Bovo RP, Simon MN, Provete DB *et al.* Beyond Janzen's hypothesis: how amphibians that climb tropical mountains respond to climate variation. *Integrative Organismal Biology (Oxford, England)* 2023;**5**:obad009. https://doi.org/10.1093/iob/obad009

Boyle WA, Shogren EH, Brawn JD. Hygric niches for tropical endotherms. *Trends in Ecology and Evolution* 2020;**35**:938–52. https://doi.org/10.1016/j.tree.2020.06.011

Burnham KP, Anderson DR. *Model Selection and Multimode Inference: A Practical Information Theoretic Approach*. New York: Springer, 2002.

Burress ED, Muñoz MM. Ecological opportunity from innovation, not islands, drove the anole lizard adaptive radiation. *Systematic Biology* 2022;**71**:93–104. https://doi.org/10.1093/sysbio/syab031

Cicconardi F, Milanetti E, Pinheiro de Castro EC *et al.* Evolutionary dynamics of genome size and content during the adaptive radiation of Heliconiini butterflies. *Nature Communications* 2023;**14**:5620. https://doi.org/10.1038/s41467-023-41412-5

Clapperton CM. *Glacial and Volcanic Geomorphology of the Chimborazo-Carihuairazo Massif, Ecuadorian Andes*. Cambridge: Cambridge University Pres, 2011.

Collin R, Rebolledo AP, Smith E *et al.* Thermal tolerance of early development predicts the realized thermal niche in marine ectotherms. *Functional Ecology* 2021;**35**:1679–92. https://doi.org/10.1111/1365-2435.13850

Deutsch CA, Tewksbury JJ, Huey RB *et al.* Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 2008;**105**:6668–72. https://doi.org/10.1073/pnas.0709472105

Díaz F, Sierra E, Re AD *et al.* Behavioural thermoregulation and critical thermal limits of *Macrobrachium acanthurus* (Wiegman). *Journal of Thermal Biology* 2002;**27**:423–8. https://doi.org/10.1016/S0306-4565(02)00011-6

Domínguez–Guerrero SF, Muñoz MM, Pasten–Téllez DJ *et al.* Interactions between thermoregulatory behavior and physiological acclimatization in a wild lizard population. *Journal of Thermal Biology* 2019;**79**:135–43. https://doi.org/10.1016/j.jtherbio.2018.12.001

Du WG, Yan SJ, Ji X. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. *Journal of Thermal Biology* 2000;**25**:197–202. https://doi.org/10.1016/s0306-4565(99)00022-4

Dülger N, Kumlu M, Türkmen S *et al.* Thermal tolerance of European Sea Bass (*Dicentrarchus labrax*) juveniles acclimated to three temperature levels. *Journal of Thermal Biology* 2012;**37**:79–82. https://doi.org/10.1016/j.jtherbio.2011.11.003

Farallo VR, Muñoz MM, Uyeda JC *et al.* Scaling between macro- to microscale climatic data reveals strong phylogenetic inertia in niche evolution in plethodontid salamanders. *Evolution* 2020;**74**:979–91. https://doi.org/10.1111/evo.13959

Fick CE, Hijmans RJ. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 2017;**37**:4302–15. https://doi.org/10.1002/joc.5086

García-Robledo C, Baer CS. Positive genetic covariance and limited thermal tolerance constrain tropical insect responses to global warming. *Journal of Evolutionary Biology* 2021;**34**:1432–46. https://doi.org/10.1111/jeb.13905

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Gaston KJ, Chown SL. Elevation and climatic tolerance: a test using dung beetles. *Oikos* 1999;**86**:584–90. https://doi.org/10.2307/3546663
Ghalambor CK, Huey RB, Martin PR *et al*. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* 2006;**46**:5–17. https://doi.org/10.1093/icb/icj003
Gillespie RG, Bennett GM, Meester LD *et al*. Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* 2020;**111**:1–20. https://doi.org/10.1093/jhered/esz064
Givnish TJ, Montgomery RA. Common-garden studies on adaptive radiation of photosynthetic physiology among Hawaiian lobeliads. *Proceedings Biological Sciences* 2014;**281**:20132944. https://doi.org/10.1098/rspb.2013.2944
Givnish TJ, Montgomery RA, Goldstein G. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany* 2004;**91**:228–46. https://doi.org/10.3732/ajb.91.2.228
Gonzalez VH, Oyen K, Vitale N *et al*. Neotropical stingless bees display a strong response in cold tolerance with changes in elevation. *Conservation Physiology* 2022;**10**:coac073. https://doi.org/10.1093/conphys/coac073
Gunderson AR, Stillman JH. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings Biological Sciences* 2015;**282**:20150401. https://doi.org/10.1098/rspb.2015.0401
Gunderson AR, Mahler DL, Leal M. Thermal niche evolution across replicated Anolis lizard adaptive radiations. *Proceedings Biological Sciences* 2018;**285**:20172241. https://doi.org/10.1098/rspb.2017.2241
Harmon LJ, Weir JT, Brock CD *et al*. GEIGER: investigating evolutionary radiations. *Bioinformatics* 2008;**24**:129–31. https://doi.org/10.1093/bioinformatics/btm538
Hazzi NA, Moreno JS, Ortiz-Movliav C *et al*. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* 2018;**115**:7985–90. https://doi.org/10.1073/pnas.1803908115
Helmuth B, Kingsolver JG, Carrington E. Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology* 2005;**67**:177–201. https://doi.org/10.1146/annurev.physiol.67.040403.105027
Herczeg G, Herrero A, Saarikivi J *et al*. Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. *Oecologia* 2008;**155**:1–10. https://doi.org/10.1007/s00442-007-0886-9
Hertz PE. Thermal passivity of a tropical forest lizard, *Anolis polylepis*. *Journal of Herpetology* 1974;**8**:323–7. https://doi.org/10.2307/1562901
Hertz PE, Arima Y, Harrison A *et al*. Asynchronous evolution of physiology and morphology in *Anolis* lizards. *Evolution* 2013;**67**:2101–13. https://doi.org/10.1111/evo.12072
Hoffmann AA. Physiological climatic limits in Drosophila: patterns and implications. *The Journal of Experimental Biology* 2010;**213**:870–80. https://doi.org/10.1242/jeb.037630
Huey RB. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 1974;**184**:1001–3. https://doi.org/10.1126/science.184.4140.1001
Huey RB, Kingsolver JG. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution* 1989;**4**:131–5. https://doi.org/10.1016/0169-5347(89)90211-5
Huey RB, Hertz PE, Sinervo B. Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist* 2003;**161**:357–66. https://doi.org/10.1086/346135
Huey RB, Deutsch CA, Tewskury JJ *et al*. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences* 2009;**276**:1939–48. https://doi.org/10.1098/rspb.2008.1957
Huey RB, Losos JB, Moritz C. Are lizards toast? *Science* 2010;**328**:832–3. https://doi.org/10.1126/science.1190374
Huie JM, Prates I, Bell RC *et al*. Convergent patterns of adaptive radiation between island and mainland *Anolis* lizards. *Biological Journal of the Linnean Society* 2021;**134**:85–110. https://doi.org/10.1093/biolinnean/blab072
Hutchinson GE. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 1957;**22**:415–27. https://doi.org/10.1101/sqb.1957.022.01.039
Jankowski JE, Londoño GA, Robinson SK *et al*. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. *Ecography* 2013;**36**:1–12. https://doi.org/10.1111/j.1600-0587.2012.07785.x
Janzen DH. Why mountain passes are higher in the tropics. *The American Naturalist* 1967;**101**:233–49. https://doi.org/10.1086/282487. https://www.jstor.org/stable/2458977
Jenssen TA. The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). *Journal of Herpetology* 1970;**4**:1–38. https://doi.org/10.2307/1562700
Jiménez I, Distler T, Jørgensen PM. Estimated plant richness pattern across northwest South America provides similar support for the species-energy and spatial heterogeneity hypotheses. *Ecography* 2009;**32**:433–48. https://doi.org/10.1111/j.1600-0587.2008.05165.x
Kearney MR, Porter WP. NicheMapR – an R package for biophysical modelling: the microclimate model. *Ecography* 2017;**40**:664–74. https://doi.org/10.1111/ecog.02360
Kearney MR, Porter WP. NicheMapR – an R package for biophysical modelling: the ectotherm and dynamic energy budget models. *Ecography* 2019;**43**:85–96. https://doi.org/10.1111/ecog.04680
Klinges DH, Duffy JP, Kearney MR *et al*. mcera5: Driving microclimate models with ERA5 global gridded climate data. *Methods in Ecology and Evolution* 2022;**13**:1402–11. https://doi.org/10.1111/2041-210x.13877
Lancaster LT. Widespread range expansions shape latitudinal variation in insect thermal limits. *Nature Climate Change* 2016;**6**:618–21. https://doi.org/10.1038/nclimate2945
Llewelyn J, Macdonald SL, Hatcher A *et al*. Intraspecific variation in climate-relevant traits in a tropical rainforest lizard. *Diversity and Distributions* 2016;**22**:1000–12. https://doi.org/10.1111/ddi.12466
Londoño GA, Gomez JP, Sánchez-Martínez MA *et al*. Changing patterns of nest predation and predator communities along a tropical elevation gradient. *Ecology Letters* 2023;**26**:609–20. https://doi.org/10.1111/ele.14189
Losos JB. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, CA: University of California Press, 2009.
Losos JB, Jackman TR, Larson A *et al*. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 1998;**279**:2115–8. https://doi.org/10.1126/science.279.5359.2115
Maclean IMD, Mosedale JR, Bennie JJ. Microclima: an r package for modelling meso- and microclimate. *Methods in Ecology and Evolution* 2019;**10**:280–90. https://doi.org/10.1111/2041-210x.13093
Mahler DL, Revell LJ, Glor RE *et al*. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution* 2010;**64**:2731–45. https://doi.org/10.1111/j.1558-5646.2010.01026.x
Martinez JD, Cadena CD, Torres M. Critical thermal limits of *Poecilia caucana* (Steindachner, 1880) (Cyprinodontiformes: Poeciliidae). *Neotropical Ichthyology* 2016;**14**:e150171. https://doi.org/10.1590/1982-0224-20150171
Méndez-Galeano MA, Calderón-Espinosa ML. Thermoregulation in the Andean lizard *Anolis heterodermus* (Squamata: Dactyloidae) at high elevation in the Eastern Cordillera of Colombia. *Iheringia, Série Zoologia* 2017;**107**:e2017018. https://doi.org/10.1590/1678-4766e2017018
Méndez-Galeano MA, Paternima-Cruz RF, Calderón-Espinosa ML. The highest kingdom of *Anolis*: thermal biology of the Andean lizard *Anolis heterodermus* (Squamata: Dactyloidae) over an elevational gradient in the Eastern Cordillera of Colombia. *Journal of Thermal Biology* 2020;**89**:102498. https://doi.org/10.1016/j.jtherbio.2019.102498
Moen DS, Ravelojaona RN, Hutter CR *et al*. Testing for adaptive radiation: a new approach applied to Madagascar frogs. *Evolution* 2021;**75**:3008–25. https://doi.org/10.1111/evo.14328

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Montoya-Cruz A, Díaz-Flórez RA, Carvajalino-Fernández JM. Thermal balance in Andean lizards: a perspective from the high mountains. *Austral Ecology* 2024;**49**:313578. https://doi.org/10.1111/aec.13578

Moreno-Arias RA, Velasco JA, Urbina Cardona JN *et al. Atlas de la Biodiversidad de Colombia Anolis*. Bogotá: Instituto Humboldt Colombia, 2021.

Muñoz MM. The Bogert effect, a factor in evolution. *Evolution* 2022;**76**:49–66. https://doi.org/10.1111/evo.14388

Muñoz MM, Bodensteiner BL. Janzen's hypothesis meets the Bogert effect: connecting climate variation, thermoregulatory behavior, and rates of physiological evolution. *Integrative Organismal Biology (Oxford, England)* 2019;**1**:oby002. https://doi.org/10.1093/iob/oby002

Muñoz MM, Losos JB. Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. *The American Naturalist* 2018;**191**:E15–26. https://doi.org/10.1086/694779

Muñoz MM, Moritz C. Adaptation to a changing world: Evolutionary resilience to climate change. In: Losos JB, Lenski RE (eds). *How Evolution Shapes Our Lives: Essays on Biology and Society*. Princeton, NJ: Princeton University Press, 2016, 265–81.

Muñoz MM, Stimola MA, Algar AC *et al.* Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proceedings Biological Sciences* 2014;**281**:20132433. https://doi.org/10.1098/rspb.2013.2433

Muñoz MM, Langham GM, Brandley MC *et al.* Basking behavior predicts the evolution of heat tolerance in Australian rainforest lizards. *Evolution* 2016;**70**:2537–49. https://doi.org/10.1111/evo.13064

Muñoz MM, Feeley KJ, Martin PH *et al.* The multidimensional (and contrasting) effects of environmental warming on a group of montane tropical lizards. *Functional Ecology* 2022;**36**:419–31. https://doi.org/10.1111/1365-2435.13950

Muñoz MM, Frishkoff LO, Pruett J *et al.* Evolution of a model system: new insights from the study of *Anolis* lizards. *Annual Review of Ecology, Evolution, and Systematics* 2023;**54**:475–503. https://doi.org/10.1146/annurev-ecolsys-110421-103306

Muschick M, Nosil P, Roesti M *et al.* Testing the stages model in the adaptive radiation of cichlid fishes in East African Lake Tanganyika. *Proceedings Biological Sciences* 2014;**281**:20140605. https://doi.org/10.1098/rspb.2014.0605

Orme D. The caper package: comparative analysis of phylogenetics and evolution in R. *R Package Version* 2018;**5**:1–36.

Pagel M. The maximum likelihood approach to reconstructing ancestral character States of discrete characters on phylogenies. *Systematic Biology* 1999;**48**:612–22. https://doi.org/10.1080/106351599260184

Patton AH, Harmon LJ, Castañeda MR *et al.* When adaptive radiations collide: different evolutionary trajectories between and within island and mainland lizard clades. *Proceedings of the National Academy of Sciences* 2021;**118**:e2024451118. https://doi.org/10.1073/pnas.2024451118

Phillips BL, Muñoz MM, Hatcher A *et al.* Heat hardening in a tropical lizard: Geographic variation explained by the predictability and variance in environmental temperatures. *Functional Ecology* 2016;**30**:1161–8. https://doi.org/10.1111/1365-2435.12609

Piantoni C, Navas CA, Ibargüengoytía NR. Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology. *Animal Conservation* 2015;**19**:391–400. https://doi.org/10.1111/acv.12255

Pintanel P, Tejedo M, Ron SR *et al.* Elevational and microclimatic drivers of thermal tolerance in Andean *Pristimantis* frogs. *Journal of Biogeography* 2019;**46**:1664–75. https://doi.org/10.1111/jbi.13596

Pinzón-Barrera C, Suárez-Ayala N, Carrillo-Chávez LM *et al.* Unveiling critical thermal limits of *Anolis tolimensis* (Squamata, Anolidae) across an elevational landscape. *Current Herpetology* 2024;**43**:155–34. https://doi.org/10.5358/hsj.43.115

Poe S, Nieto-Montes de Oca A, Torres-Carvajal O *et al.* A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). *Systematic Biology* 2017;**66**:663–97. https://doi.org/10.1093/sysbio/syx029

Polato NR, Gill BA, Shah AA *et al.* Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proceedings of the National Academy of Sciences of the United States of America* 2018;**115**:12471–6. https://doi.org/10.1073/pnas.1809326115

Qu YF, Wiens JJ. Higher temperatures lower rates of physiological and niche evolution. *Proceedings Biological Sciences* 2020;**287**:20200823. https://doi.org/10.1098/rspb.2020.0823

R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2023. https://www.R-project.org/

Rahbek C, Borregaard MK, Colwell RK *et al.* Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* 2019;**365**:1108–13. https://doi.org/10.1126/science.aax0149

Ramirez-Bautista A, Benabib M. Perch height of the arboreal lizard *Anolis nebulosus* (Sauria: Polychrotidae) from a tropical dry forest of México: effect of the reproductive season. *Copeia* 2001;**2001**:187–93. https://www.jstor.org/stable/1448110

Rand AS. Ecological distribution in Anoline lizards of Puerto Rico. *Ecology* 1964;**45**:745–52. https://doi.org/10.2307/1934922

Revell LJ. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 2012;**3**:217–23. https://doi.org/10.1111/j.2041-210x.2011.00169.x

Revell LJ, Harmon LJ. *Phylogenetic Comparative Methods in R*. Princeton, NJ: Princeton University Press, 2022.

Ronco F, Matschiner M, Böhne A *et al.* Drivers and dynamics of a massive adaptive radiation in cichlid fishes. *Nature* 2021;**589**:76–81. https://doi.org/10.1038/s41586-020-2930-4

Rosso AA, Casement B, Chung AK *et al.* Plasticity of gene expression and thermal tolerance: Implications for climate change vulnerability in a tropical forest lizard. *Ecological and Evolutionary Physiology* 2024;**97**:81–96. https://doi.org/10.1086/729927

Ruibal R. Thermal relations of five species of tropical lizards. *Evolution* 1961;**15**:98–111. https://doi.org/10.2307/2405846

Salazar JC, Miles DB. The shape of water: physiological adaptations to habitat aridity in the ornate tree lizard (*Urosaurus ornatus*). *Integrative and Comparative Biology* 2024;**64**:390–401. https://doi.org/10.1093/icb/icae061

Salazar JC, Castañeda MR, Londoño GA *et al.* Physiological evolution during adaptive radiation: a test of the island effect in *Anolis* lizards. *Evolution* 2019;**73**:1241–52. https://doi.org/10.1111/evo.13741

Schluter D. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press, 2000.

Sears MW, Riddell EA, Rusch TW *et al.* The world still is not flat: Lessons learned from organismal interactions with environmental heterogeneity in terrestrial environments. *Integrative and Comparative Biology* 2019;**59**:1049–58. https://doi.org/10.1093/icb/icz130

Shah AA, Gill BA, Encalada CA *et al.* Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Functional Ecology* 2017;**31**:2118–27. https://doi.org/10.1111/1365-2435.12906

Sheldon KS. Climate change in the tropics: ecological and evolutionary responses at low latitudes. *Annual Review of Ecology, Evolution, and Systematics* 2019;**50**:303–33. https://doi.org/10.1146/annurev-ecolsys-110218-025005

Sheldon KS, Huey RB, Kaspari M *et al.* Fifty years of mountain passes: a perspective on Dan Janzen's classic article. *The American Naturalist* 2018;**191**:553–65. https://doi.org/10.1086/697046

Sinclair BJ, Marshall KE, Sewell MA *et al.* Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters* 2016;**19**:1372–85. https://doi.org/10.1111/ele.12686

Stevens MM, Jackson S, Bester SA *et al.* Oxygen limitation and thermal tolerance in two terrestrial arthropod species. *The Journal of Experimental Biology* 2010;**213**:2209–18. https://doi.org/10.1242/jeb.040170

Stillman JH. Heat waves, the new normal: summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology (Bethesda, Md.)* 2019;**34**:86–100. https://doi.org/10.1152/physiol.00040.2018

Stroud JT, Losos JB. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* 2016;**47**:507–32. https://doi.org/10.1146/annurev-ecolsys-121415-032254

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Sugihara N. Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics Theory Methods* 1978;**7**:13–26. https://doi.org/10.1080/03610927808827599

Sunday JM, Bates AE, Kearney MR *et al*. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America* 2014;**111**:5610–5. https://doi.org/10.1073/pnas.1316145111

Sunday JM, Bennett JM, Calosi P *et al*. Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2019;**374**:20190036. https://doi.org/10.1098/rstb.2019.0036

Tang XI, Yue F, He JZ *et al*. Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, *Eremias multiocellata*. *Zoology* 2013;**116**:331–5. https://doi.org/10.1016/j.zool.2013.08.006

Terborgh J, Weske JS. The role of competition in the distribution of Andean birds. *Ecology* 1975;**56**:562–76. https://doi.org/10.2307/1935491

Velasco JA, Martínez-Meyer E, Flores-Villela O *et al*. Climatic niche attributes and diversification in *Anolis* lizards. *Journal of Biogeography* 2016;**43**:134–44. https://doi.org/10.1111/jbi.12627

Velasco JA, Villalobos F, Diniz-Filho JAF *et al*. Macroecology and macroevolution of body size in *Anolis* lizard. *Ecography* 2020;**43**:812–22. https://doi.org/10.1111/ecog.04583

Viertler A, Salzburger W, Ronco F. Comparative scale morphology in the adaptive radiation of cichlid fishes (Perciformes: Cichlidae) from Lake Tanganyika. *Biological Journal of the Linnean Society* 2021;**134**:541–56. https://doi.org/10.1093/biolinnean/blab099

von May R, Catenazzi A, Corl A *et al*. Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. *Ecology and Evolution* 2017;**7**:3257–67. https://doi.org/10.1002/ece3.2929

Wake DB, Lynch JF. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. *Bulletin of the Natural History Museum of Los Angeles County* 1976;**25**:1–75.

Warheit KI, Forman JD, Losos JB *et al*. Morphological diversification and adaptive radiation: a comparison of two diverse lizard clades. *Evolution* 1999;**53**:1226–34. https://doi.org/10.1111/j.1558-5646.1999.tb04535.x

Wegener JE, Gartner GEA, Losos JB. Lizard scales in an adaptive radiation: variation in scale number follows climatic and structural habitat diversity in *Anolis* lizards. *Biological Journal of the Linnean Society* 2014;**113**:570–9. https://doi.org/10.1111/bij.12380

Wickham H. *ggplot2. Elegant Graphics for Data Analysis*. London: Springer, 2009.

Williams EE. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. In: Dobzhansky TH, Hecht ML, Steere WMC (eds). *Evolutionary Biology*. Berlin: Springer, 1972, 47–89.

Yanar M, Erdoğan E, Kumlu M. Thermal tolerance of thirteen popular ornamental fish Species. *Aquaculture* 2019;**501**:382–6. https://doi.org/10.1016/j.aquaculture.2018.11.041

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