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Microgeography, Not Just Latitude, Drives Climate Overlap on Mountains from Tropical to Polar Ecosystems

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ABSTRACT: An extension of the climate variability hypothesis is that relatively stable climate, such as that of the tropics, induces distinct thermal bands across elevation that render dispersal over tropical mountains difficult compared with temperate mountains. Yet ecosystems are not thermally static in space-time, especially at small scales, which might render some mountains greater thermal isolators than others. Here we provide an extensive investigation of temperature drivers from fine to coarse scales, and we demonstrate that the degree of similarity in temperatures at high and low elevations on mountains is driven by more than just absolute mountain height and latitude. We compiled a database of 29 mountains spanning six continents to characterize thermal overlap by vertically stratified microhabitats and biomes and owing to seasonal changes in foliage, demonstrating via mixed effects modeling that micro- and mesogeography more strongly influence thermal overlap than macrogeography. Impressively, an increase of 1 m of vertical microhabitat height generates an increase in overlap equivalent to a 5.26° change in latitude. In addition, forested mountains have reduced thermal overlap—149% lower—relative to nonforested mountains. We provide evidence in support of a climate hypothesis that emphasizes microgeography as a determinant of dispersal, demographics, and behavior, thereby refining the classical theory of macroclimate variability as a prominent driver of biogeography.

Keywords: thermal ecology, climate variability hypothesis, biogeography, microclimate, macrogeography, forest canopy.

Introduction

Temperature is one of the most basic denominators on earth that governs the physiology, ecology, and evolution of organisms (Currie and Paquin 1987; Gaston 2000; Rahbek and Graves 2001; Ezard et al. 2011). Temperature changes spatially with latitude, elevation, and within and across habitats, but also temporally, from diel fluctuations to climatic shifts through geologic time (Adams and Woodward 1989; Campbell and Norman 2012; Elmendorf et al. 2012; Paaijmans et al. 2013). The spatial and temporal components of thermal change also interact; for example, habitats might undergo structural change in response to seasonal variation in climate, thereby amplifying or reducing the thermal flux to which organisms are exposed (Monteith and Unsworth 2013).

The concept that thermal gradients drive biogeography largely stems from observations of temperature overlap across mountain passes: when temperature bands at different elevations do not overlap, the movement of plants and animals may be hindered (Janzen 1967). Such thermal stratification has been observed in the tropics, in which habitats experience low thermal variability at a given elevation band (Janzen 1967; McCain 2009; Cadena et al. 2012). High elevations in the tropics present thermal regimes that low-elevation species are not adapted for and vice versa. As a consequence, owing to dispersal barriers, tropical communities remain segregated between sets of uniform thermal regimes, which reduces gene flow, creates conditions for allopatric speciation, and dictates colonization rates after extinction events (Janzen 1973; Duellman 1988; Fjeldså et al. 2012; Londoño et al. 2017; Noriega and Realpe 2018; Polato et al. 2018; Garcia-Porta et al. 2019).

The principles that guide macroecological studies of temperature likely break down at smaller scales when microgeographical complexity is taken into consideration (Potter et al. 2013; Woods et al. 2015; Pincebourde et al. 2016). Even when tropospheric temperature is uniform across a region, at finer spatial resolutions, factors such as topography and vegetation cover can reduce incoming radiation via shading, creating large variability in near-surface temperatures (Parker 1995; Geiger et al. 2009; Lenoir et al. 2017). In addition to showing high thermal variation across short distances horizontally, classic biophysical work has demonstrated the dramatic change in temperature vertically from belowground to several meters above it. Specifically, daytime temperatures are hotter (and due to patchy air mixing,

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more variable) near surfaces where solar radiation is intercepted: at the ground for unvegetated habitats and in the canopy for forests. Both below and above these surfaces, conditions are typically cooler and less variable—owing to lower heat transfer and more homogenous air mixing—which yields thermal buffering of soils relative to open air and of the forest floor relative to air within the forest canopy (Richardson 1922; Geiger 1942; Campbell and Norman 2012).

Vertically from ground to canopy in forests, many taxa exhibit strong associations with particular strata, including amphibians (Basham et al. 2018; Oliveira and Scheffers 2018), arthropods (Devries et al. 1997; Lindo and Winchester 2009; Ulyshen 2011; Basset et al. 2015; Ashton et al. 2016), fungi (Lodge and Cantrell 1995; Unterseher et al. 2007), lichens (Komposch and Hafellner 2000), and various microbiota (Lambais et al. 2006; Baldrian et al. 2012), and therefore distinct climatic niches may emerge for such stratified communities (Scheffers et al. 2017*b*). However, despite much work on how macroclimate influences biogeography at broad scales (Currie 1991; Gaston 2000; Parmesan and Yohe 2003; Evans et al. 2005), fewer attempts have been made to integrate knowledge of such vertically stratified microclimates into biogeographical theory pertinent to landscape and global scales (but see Diamond et al. 2012; Scheffers et al. 2017*b*; Oliveira and Scheffers 2018). Recent work suggests that, owing to high thermal variation in the canopy relative to the ground, thermal overlap between canopies of lowland and upland tropical rainforests overlap greatly, whereas little overlap exists across elevation for soil layers (Scheffers and Williams 2018). In this case, even though tropical landscapes undergo low thermal variability throughout the year, there are microhabitats that contain overlapping climates similar to those expected in temperate ecosystems. Conversely, foliage complexity in temperate ecosystems reduces exposure to solar radiation and buffers temperature extremes (Morecroft et al. 1998; Chen et al. 1999; De Frenne et al. 2019), which may create local thermal stability in temperate systems that is comparable to the tropics. Both microclimate variability and foliage thermal buffering therefore complicate the classical theory of macroclimate variability as a prominent driver of biogeography.

Here, we conducted a global synthesis of mountain temperatures from tropical to polar systems (fig. 1) and demonstrate that thermal overlap across mountains varies considerably by microhabitat, vegetation structure, and snow depth, as well as across latitudes—showcasing the complexity of the climate variability hypothesis. For the purpose of offering a simple framework to explore drivers of thermal overlap using empirical data, we explore three dimensions that enrich and complement classical theory on thermal overlap: (1) the height of a microhabitat below- or aboveground (microgeography), (2) spatial and temporal differences in foliage and snow cover between biomes and change in elevation (mesogeography), and (3) the magnitude of seasonality due to latitude (macrogeography).

In our study, we first quantify changes in thermal overlap between low and high elevations on mountains, as presented in Janzen's (1967) framework, using data from 29 mountains across the globe. We explore how thermal overlap across elevation differs for vertical microhabitats (belowground, at ground level, and in forest canopies) across spatial and temporal changes in foliage cover (dense broadleaf to nearly barren desert, and seasonal fluctuations in deciduous vegetation) and with snow depth. Through a series of mixed effects models, we quantify how parameters at macro-, meso-, and microgeographic scales explain variation in thermal overlap, and we demonstrate that change in elevation, variability in vegetation structure, depth of snow, and vertical stratification of microhabitats drive mountain climate separation more strongly than latitude.

With these insights into how thermal overlap across elevation varies through space (microhabitats, biomes, and latitude) and time (transition of tree phenology and fluctuations in snow cover) for diverse mountain systems, we reevaluate the conclusions drawn by Janzen (1967) and present a nested framework of climate gradients from micro- to macroscales. Importantly, we demonstrate that the multidimensionality that exists in temperature gradients across elevation and latitude is largely due to factors acting at a fine resolution both in space and time. Drawing insight from the climate variability hypothesis, which relates species' physiological tolerance to temperature and geographic range sizes (Levene 1953; Rapoport 1982; Stevens 1989; Gilchrist 1995; Spicer and Gaston 2000; Chan et al. 2016), we discuss how distinct microclimates might interact with ecological processes such as site fidelity, dispersal, demographics, and behavior to determine broader patterns of biogeography (Kearney et al. 2009; Potter et al. 2013; Sheldon and Tewksbury 2014).

Methods

Microclimate Monitoring

We compiled published and unpublished temperature data from a combination of author field collection, personal communications, and public data repositories (see the "References Used for the Data" section) for a total of 29 mountains on six continents, representing gradients of vegetation, environmental degradation, and climate (table S1; fig. S1; tables S1–S6 and figs. S1–S5 are available online). Temperatures at low- and high-elevation sites were recorded on each mountain, as was the difference in elevation between low and high sites (of note is that not every low site was at the bottom of the mountain, nor was the high site always at the mountain peak; in addition, slope and aspect both varied

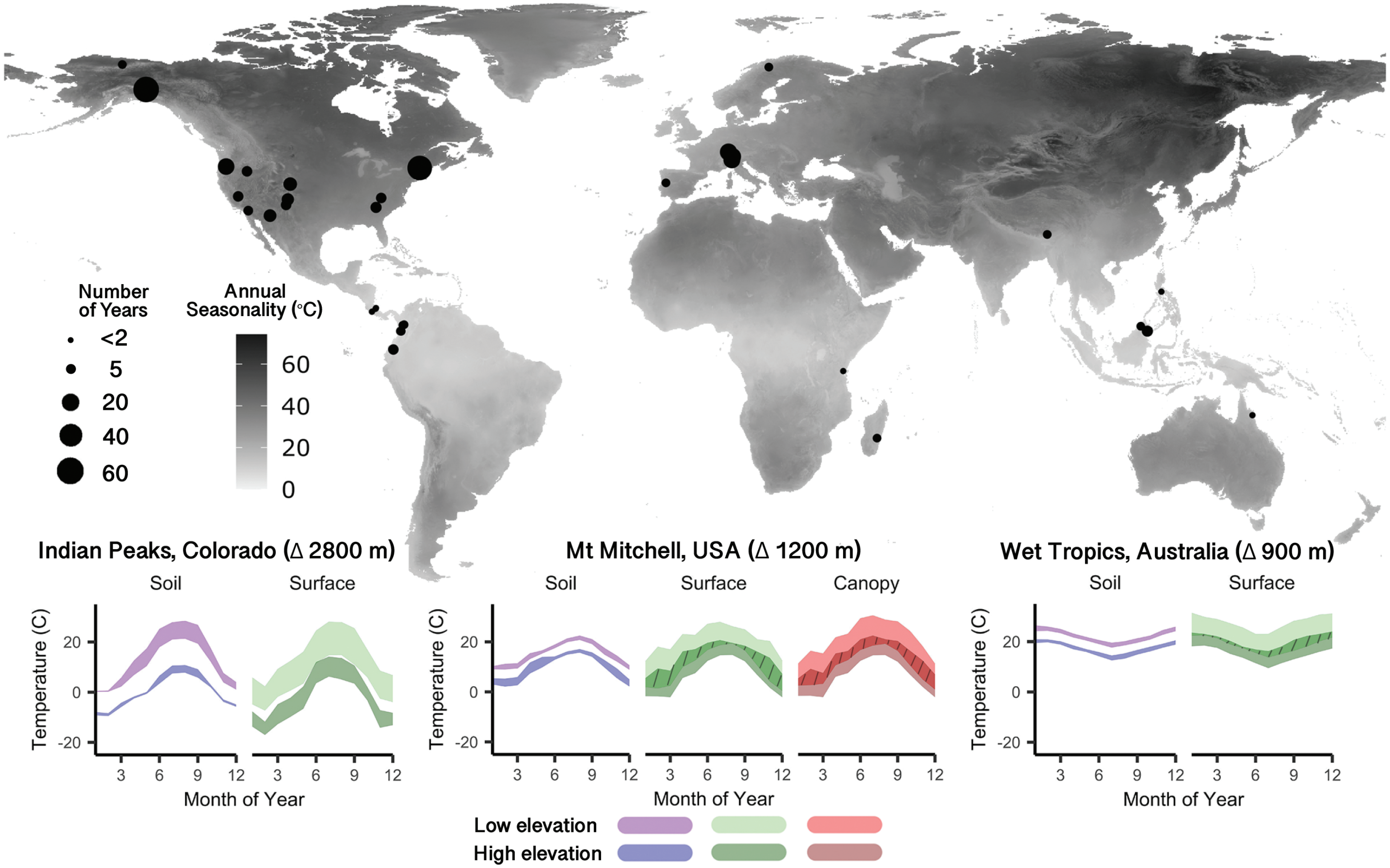

Figure 1: Locations of elevation gradients ($n = 29$) represented in the study spanning tropical to polar latitudes. Insets show temperatures of one sampled year (January–December) of low- and high-elevation sites on three of the sampled mountains (darker colors represent thermal regimes of high elevations). Greater amount of thermal overlap is indicated by the striped area shared between low- and high-elevation regimes. Aboveground microhabitats (surface and canopy labels) show more thermal overlap than belowground microhabitats (soil labels). Annual seasonality in the map background layer was measured as the difference between the average maximum and minimum annual temperatures between 1970 and 2000. Sites in close proximity to each other (<1° Euclidean distance) are jittered.

between sites). Difference in elevation between low and high sites (henceforth, "Δ elevation") was a parameter of interest (see "Mixed Effects Modeling"); therefore, a broad range of elevation gradients from 122 to 3,080 m was represented. Time series length varied from 74 days to 64 years; although sampling of 13 of the 29 mountains did not include every day of the year, seasonal coverage did not vary systematically (for how variation in time series length was accounted for, see "Mixed Effects Modeling"). At each elevation band (low and high), at least one of three vertically stratified microhabitats was monitored: soil, surface, and (in forests only) canopy. Of the 29 mountains, six sites had all three vertical strata represented, and 14 had at least two vertical strata represented. Soil temperature sensors varied in depth from 2 to 12 cm into topsoil (although 71% of sensors were between 7 and 10 cm in depth), surface-level sensors were 1–3 m above the ground, and canopy sensors were typically between 19 and 25 m high, placed within canopy foliage. When available, temperatures from multiple plots at the same approximate elevation on a mountain—that is, less than 5% of Δ elevation apart—were averaged. All thermal sensors included in our study were shielded from direct radiation (table S1), which is common in ecological research. While shielding reduces irregular sensor performance due to high solar radiation, it also dampens variation, depending on shielding methods (Terando et al. 2017). As a result, our estimates of microclimate variation may be conservative, but the majority of sites (17 of 29) followed best practices as recommended by global micrometeorological networks (Beeck et al. 2018; Rebmann et al. 2018). Both microhabitat category (soil, surface, canopy; henceforth, "vertical microhabitat") and depth belowground or height aboveground of sensor (henceforth, "microhabitat height") were used in analyses.

Vegetation Structure, Foliage Cover, and Snow Depth

All sensors were in locations representative of the dominant vegetation present on the mountain (e.g., under forest cover for a predominantly forested mountain). For each site (low and high) on all mountains, we spatially extracted 1 km^2 resolution canopy height (Simard et al. 2011) and 1 km^2 resolution tree density (Crowther et al. 2015) and used the product of canopy height and tree density as a score of vegetation structure. For mountains with seasonal change in foliage cover (fig. 2*A*), we then multiplied vegetation structure scores by the estimated daily proportion of foliage cover, using gap-filled phenological data or below-canopy light-intensity measurements (Moritz and Bartz-Beielstein 2017; for sources of phenological and light data, see the "References Used for the Data" section). In addition, because the presence of snow buffers thermal variation and furthermore decouples temperature from that above the surface (Körner 2003; Graae et al. 2012; fig. 2*B*), snow-depth measurements were extracted from gauges near each thermal data sensor site on each mountain (for sources of phenological and light data, see the "References Used for the Data" section).

Deriving Thermal Variation and Overlap

Three methods of calculating overlap in temperature between high and low elevations were employed: kernel density coefficient of overlapping (Ridout and Linkie 2009), D-score overlap (Janzen 1967), and thermal absolute overlap (Chan et al. 2016). Because models corresponding to all three methods yielded similar results, kernel density coefficient of overlapping is described and visualized in the main text; for results of other methods, see the supplemental PDF (available online).

For each vertical strata at low and high elevations on each mountain, we aggregated thermal data to daily mean, minimum, and maximum to standardize temporal sampling rates. From these daily values we derived monthly kernel density estimated (KDE) distributions of temperature. Monthly resolution was designated as appropriate as it (*a*) represents an intragenerational timestep for many organisms (Kingsolver et al. 2011; Li et al. 2016) and is therefore important for driving thermal specialization (Gilchrist 1995) and (*b*) enables us to derive overlap at the same temporal resolution as Janzen (1967). We then measured the overlap between KDE thermal distributions of high and low elevations using the overlap function of the overlapping R package (Pastore 2018), which calculates the area of integration between two distributions:

$$\Delta(f,g) = \int \min\{f(x),g(x)\}dx,$$

where $\Delta(f, g)$ is a measure of the overlapping proportion of the combined areas of two distributions $f(x)$ and $g(x)$ and is henceforth referred to as "thermal overlap." For our purposes, $f(x)$ and $g(x)$ correspond to the monthly thermal distributions of low and high elevations.

Univariate Rank Sum Tests and Regressions

To determine drivers of climate variability and separation, we regressed daily thermal variation and monthly thermal overlap across primary environmental parameters: latitude, microhabitat height, foliage cover, and snow depth. Here, for ease of interpretation, we used univariate regression to derive coefficients that characterize an effect of a single variable. We also conducted Kruskal-Wallis (KW) ranked sum tests to determine how thermal overlap varied with presence of leaf cover (for deciduous forests only, leaf on or leaf off) and between vertical microhabitats (soil,

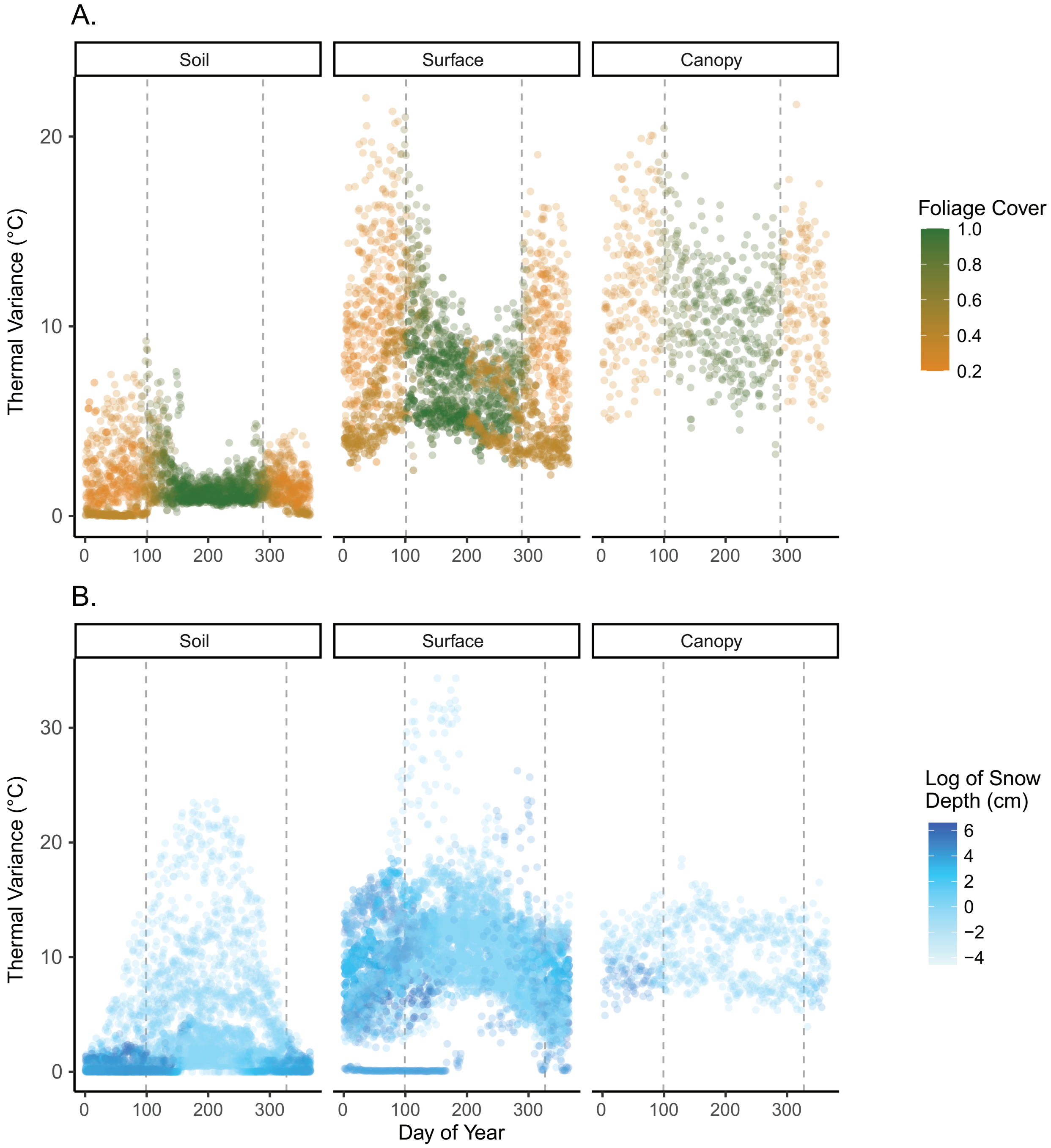

Figure 2: Average daily thermal variation (difference between daily minimum and daily maximum at a single elevation) on mountains varies temporally. *A*, For just sites with deciduous forest cover in the northern hemisphere ($n = 8$), thermal variation was low in the middle of the year (summer) when foliage cover is ubiquitous relative to the beginning or end of the year (winter) when only evergreen foliage is present. Foliage cover indicates estimated proportion of trees that are foliated at each site. Dashed lines indicate average first and last days of deciduous foliage. *B*, For sites ($n = 26$) with an average snow depth of at least 5 cm during the northern hemisphere winter (days of year 0–90 and 275–365), increasing snow depth buffers thermal regimes, especially for fossorial microhabitats, resulting in temporal trends in thermal variation that are opposite of those generated by foliage cover. Dashed lines indicate average first and last days of snow cover, and snow depth was log transformed for display purposes only (average daily snow depth values ranged from 0 cm to 415 cm).

surface, and canopy). All univariate regressions and KW ranked sum tests were performed using the residuals of a linear model of overlap across Δ elevation to control for the dominant effect of Δ elevation on thermal overlap.

Mixed Effects Modeling

We constructed a series of linear mixed effects models of thermal overlap by maximum likelihood estimation (Laplace approximation) using the lme4 package in R (Bates et al. 2015). To measure the relative predictive power of parameters, statistically important parameters were considered those with 95% confidence intervals (CIs) of coefficient estimates that did not include zero (Burnham and Anderson 2002; Baecher and Richter 2018). Prior to modeling, all continuous covariates were scaled between 0 and 1 to standardize contributions of each parameter in the analysis. Because we obtained empirical temperature measurements from each site rather than derived values such as coefficient estimates, there was no need to weigh overlap values by variance or sample size as is best practice for meta-analyses (Gurevitch et al. 2018). However, we took several measures to account for variable time series length (see "Testing effect of temporal coverage" in the supplemental PDF).

With the final set of parameters, we developed three sets of mixed effects models to explore drivers of thermal overlap, conducting model selection and averaging within each model set. First, we modeled thermal overlap separately for macrogeographic (latitude), mesogeographic (Δ elevation, vegetation structure, snow depth), and microgeographic (microhabitat height) parameters. Second, we conducted a global model that combined all of these parameters as predictors of thermal overlap. Third, we reran this global model (except with the covariate for microhabitat height removed) with only data from each vertical microhabitat category separately (soil, surface, canopy). All mixed effects models contained mountain identity as a random effect. We performed model selection based on Akaike's information criterion (AIC), selecting models with delta AIC scores less than 4 (Mazerolle 2006). Using this selection of models, we conducted multimodel inference (Burnham and Anderson 2002) with the MuMIn R package (Bartoń 2019) to determine the relative contribution of each predictor covariate using model-averaged estimated effect size ($\bar{\beta}$; for a complete list of models fitted for the global model [table S4], see the supplemental PDF).

All data processing and analysis was conducted in R 3.6.1 (R Core Team 2019). Along with other R software packages described above, tidyverse (Wickham et al. 2019*a*) and lubridate (Spinu et al. 2018) were used for data curation; raster (Hijmans et al. 2019) and rgdal (Bivand et al. 2019) were used for geospatial processing; scales (Wickham et al. 2019*b*), gridExtra (Auguie and Antonov 2017), and ggpmisc (Aphalo and Slowikowski 2020) were used for plotting and visualizations; and vegan (Oksanen et al. 2019) and fitdistrplus (Delignette-Muller et al. 2015) were used for model fitting and statistical analysis.

Results

Counter to predictions from past research, thermal overlap only weakly increased with latitude in a univariate linear model (linear regression; $\beta = 0.13$, $R^2 = 0.02$). Moreover, when we included latitude in the global multivariate mixed effects framework, latitude was absent from the most parsimonious model (table S4). To better demonstrate the (minimal) contribution of latitude compared with other parameters of interest, the next best model is reported, which includes coefficient estimates that are within 2% of those in the top model. Estimates of the effect of latitude on thermal overlap were relatively small, and the 95% CI of the coefficient estimate for latitude contained zero in the global model ($\beta = -0.021$, 95% CI: -0.197, 0.155; fig. 3). When thermal overlap was modeled separately for each vertical microhabitat, there was not a clear relationship between latitude and overlap for soil ($\beta = 0.025$, 95% CI: -0.206, 0.554), surface ($\beta = 0.020$, 95% CI: -0.051, 0.305), or canopy ($\beta = 0.052$, 95% CI: -0.094, 0.534) microhabitats (fig. S3; table S3).

Across sites, Δ elevation change ranged from 122 m to 3,080 m, and in our mixed effects models, change in elevation had the strongest effect on thermal overlap of all parameters in the global model ($\beta = -0.690$, 95% CI: -0.921, -0.458), showing the importance of mountain height in driving climate separation (fig. 3). Thermal overlap was higher in nonforested habitats than in forested habitats ($\chi^2 = 16.583$, $P < .001$; fig. 4); in deciduous forests, thermal overlap was lower when foliage was present than when foliage was absent (KW $\chi^2 = 7.811$, $P = .005$), and thermal variation moderately decreased with increasing foliage cover (linear regression; $\beta = -4.29$, $R^2 = 0.080$; fig. 2). When comparing leaf-on versus leaf-off conditions across all mountains, foliage decreased thermal overlap, on average, by 5.3°C (2.23°C for soils, 7.54°C for surface, and 15.41°C for canopy). Depth of snow ranged from monthly averages of 0 cm to 86 cm, and especially for soil microhabitats snow acted as a thermal insulator (figs. 2, S3). When snow was present, soil temperatures remained largely invariable around 0°C, resulting in little thermal overlap across elevation. Although snow depth was negatively correlated with thermal overlap, it explained a small amount of variation in overlap ($\beta = -0.17$, $R^2 = 0.02$). However, when only mountains at high latitudes (>23°; above the tropics) were included in a linear regression, snow depth improved slightly as a predictor of thermal overlap ($\beta = -0.27$,

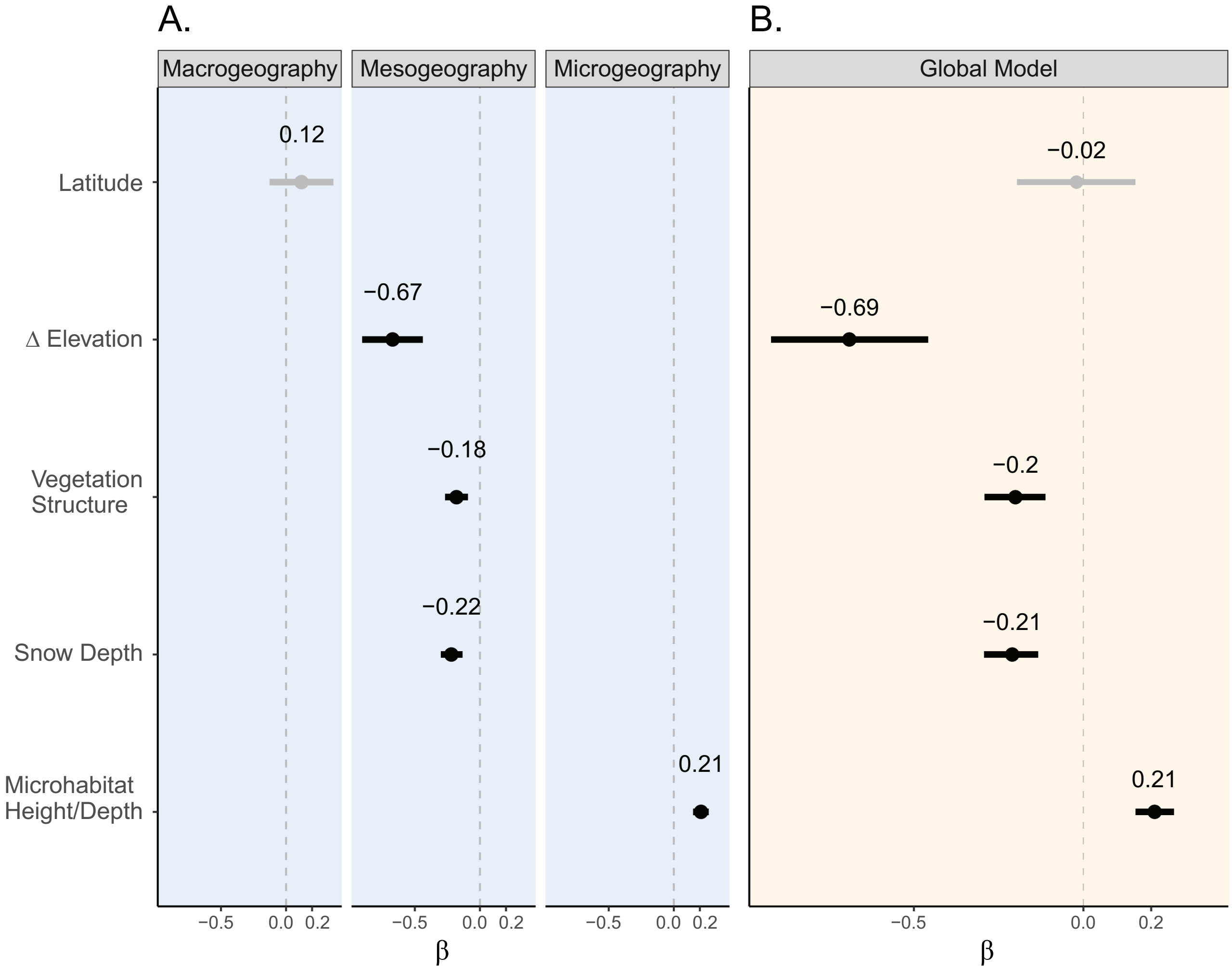

Figure 3: Estimates of β coefficients for parameters included in models of thermal overlap. Sign of β (+/−) indicates direction of influence on thermal overlap. Bars show 95% confidence intervals (CIs); black points/bars (all parameters except latitude) show 95% CIs that do not include zero and thus indicate statistically meaningful relationships. Overlap was modeled separately for macrogeographic, mesogeographic, and microgeographic parameters (*A*), as well as with all parameters included simultaneously in a global model (*B*). Here, the difference in elevation between high and low sites (Δ elevation) explained the most variation in thermal overlap, and vegetation structure and snow depth had strong negative effects on thermal overlap. Increasing height of microhabitat sampled (from belowground up to forest canopy) yielded an increase in thermal overlap. Latitude did not have a clear negative or positive effect on thermal overlap in either macrogeographic or global models, as in both models coefficient estimates were low and 95% CIs crossed zero.

$R^2 = 0.08$). In mixed effects modeling, thermal overlap decreased with depth of snow in the global model ($\beta = -0.212$, 95% CI: −0.293, −0.133; fig. 3), although when thermal overlap was modeled for each microhabitat separately, this trend only held for soils (soil: $\beta = -0.353$, 95% CI: −0.470, −0.236; surface: $\beta = -0.006$, 95% CI: −0.125, 0.006; canopy: $\beta = 0.084$, 95% CI: −0.048, 0.569; fig. S3).

Microhabitat height, spanning just belowground up to the canopy, positively predicted overlap in our mixed effects models and was a strong predictor of overlap in the global model (fig. 3; $\beta = 0.211$, 95% CI: 0.154, 0.267). When linear regression was performed to test the univariate relationships between microhabitat height and thermal overlap ($\beta = 0.16$, $R^2 = 0.04$) and latitude and thermal overlap ($\beta = 0.13$, $R^2 = 0.02$), models predicted that an increase in 1 m of microhabitat height yields an increase in thermal overlap (0.33°C increase) corresponding to a change in air temperature across 5.26° of latitude. Of note is that little variation in overlap is explained by these univariate models (denoted by R^2 values). In addition, relationships between several parameters (e.g., microhabitat height, latitude) and overlap may be nonlinear, and our choice of linear fits may not provide entirely suitable estimates of overlap for the tops of tall forest canopies or extreme polar latitudes. However,

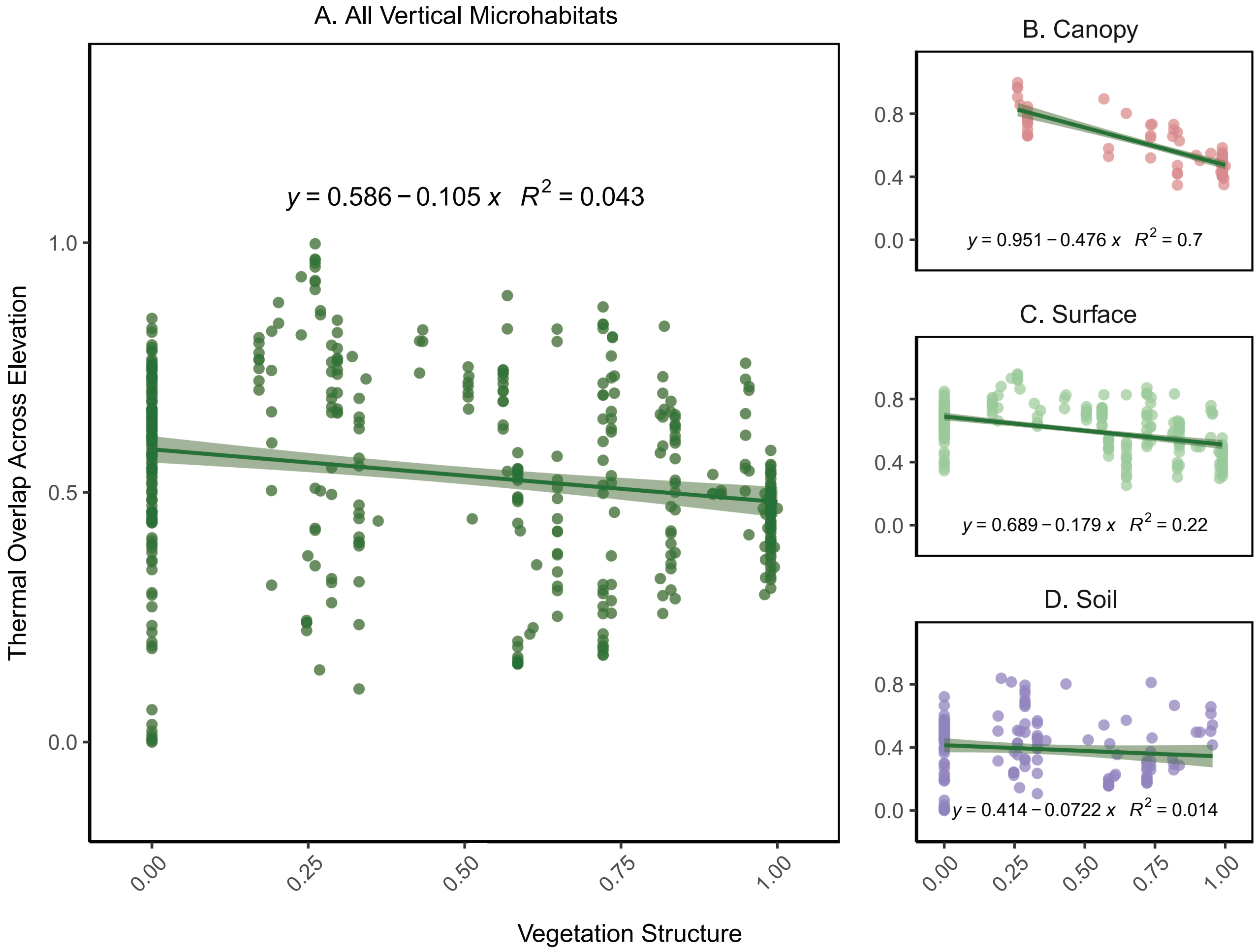

Figure 4: *A*, Thermal overlap, denoting similarity between thermal regimes at high and low elevations, decreases with increasing vegetation structure (the product of average canopy height and tree density, weighted according to seasonal changes in proportion of foliated trees). When temperature data from vertical microhabitats are separated, this trend is especially apparent for aboveground environments (*B*, *C*), but it is less so belowground (*D*). Each point corresponds to the thermal overlap value of 1 month at one site, and fits correspond to univariate linear regressions. Thermal overlap scores are corrected for differences in mountain heights in *A*–*D* by extracting the residuals of a linear model of overlap across the difference in elevation between high and low sites (Δ elevation).

preliminary model fitting suggested that a linear fit was more appropriate than several tested asymptotic models, and we see these as shortcomings that do not detract from the biological relevance of the findings toward near-surface systems.

Data used in analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.w3r2280nf; Klinges and Scheffers 2020).

Discussion

Drivers of Climate Separation on Mountains from Micro- to Macroscales

Our study provides, to the best of our knowledge, the most extensive investigation of near-surface thermal separation on mountains from fine to coarse scales using empirical data and demonstrates that the temperature gradient across a mountain (and therefore its effectiveness as a physiological barrier) is driven by more than just absolute mountain height and latitude. Leveraging a database of 29 mountains across six continents (cumulative 11,775,331 measurements spanning 524 sampling years; fig. 1), we show that micro- and mesogeography consistently predict thermal overlap across elevation better than macrogeography via mixed effects modeling (fig. 3) and that mountain climate separation operates within a nested space-time framework (figs. 5, 6).

Unsurprisingly, thermal regimes change more across taller mountains than shorter ones. In the global model, Δ elevation from lowlands to uplands explained the most

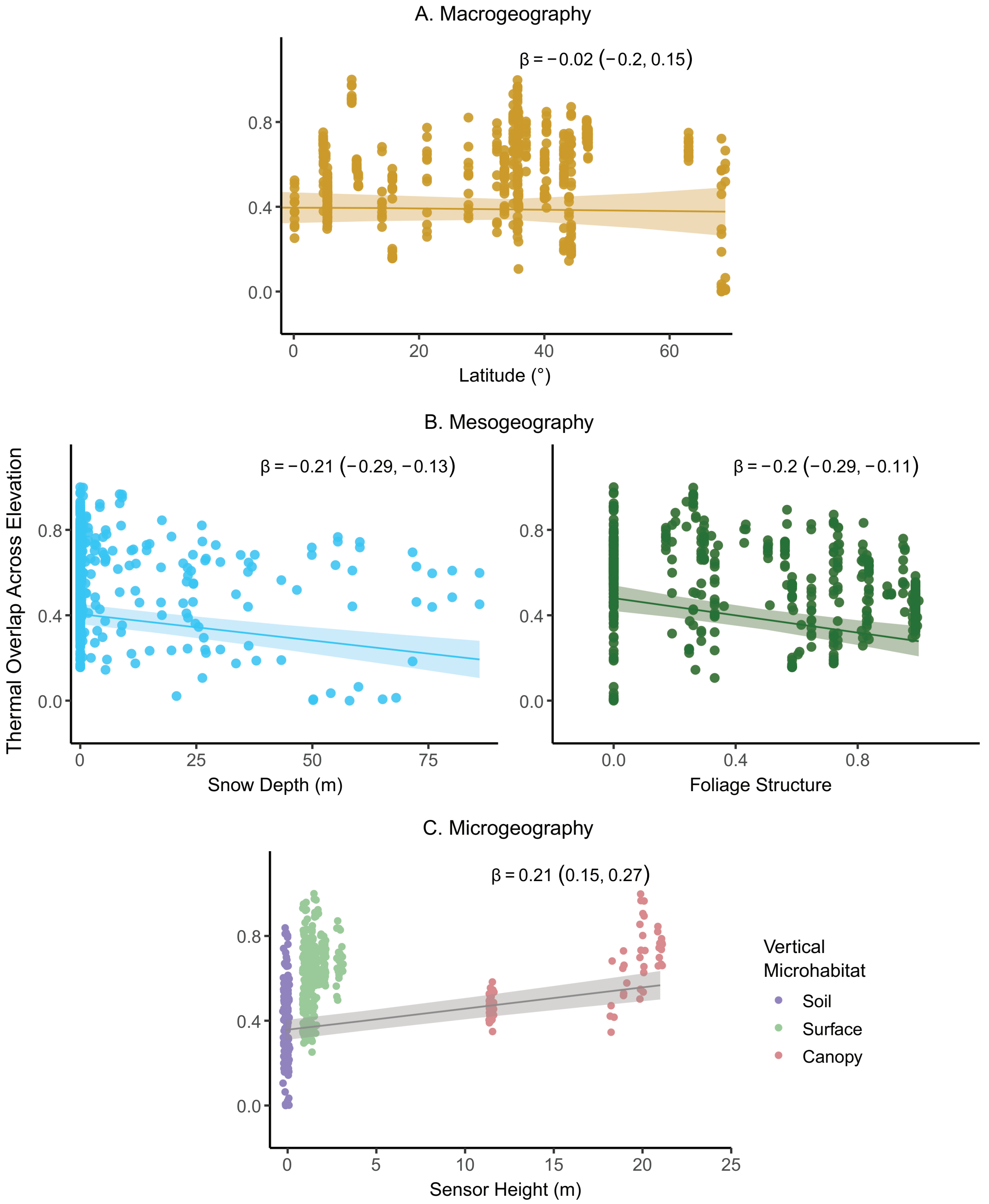

Figure 5: Thermal overlap as explained from macro- to microscales. *A–C* show raw observations along with coefficients (estimates and 95% confidence intervals) and predictions from the global mixed effects model. *A*, Thermal overlap demonstrates no clear trend with latitude from tropical to polar latitudes, as indicated by model predictions. *B*, Trends are more apparent at the mesoscale, however, where increases in snow depth and foliage structure are associated with decreases in thermal overlap. *C*, At the microhabitat scale, thermal profiles change considerably according to height of measurement (and therefore microhabitat sampled), leading to lowest overlap across mountains for belowground environments and highest in forest canopies. Latitudes are provided as absolute values, and thermal overlap scores are corrected for differences in mountain heights in *A–C* by extracting the residuals of a linear model of overlap across the difference in elevation between high and low sites (Δ elevation). Each point corresponds to the thermal overlap value of 1 month at one mountain.

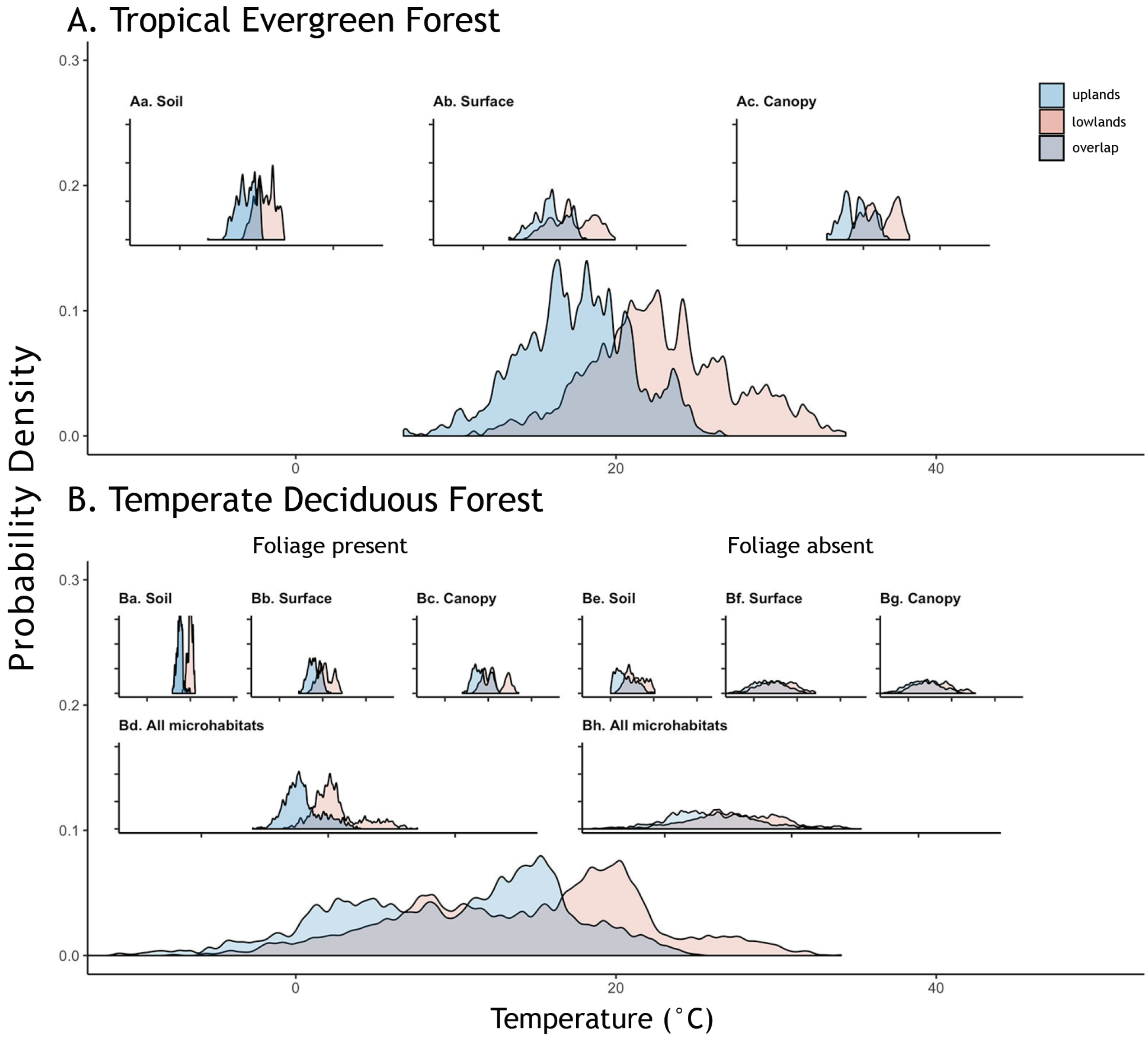

Figure 6: Distribution and degree of overlap of temperature (C°) among lowlands and uplands in the Australian Wet Tropics (*A*) and in North Carolina (*B*); gray area in each plot corresponds to the amount of thermal overlap. Overlap is nested in time and space, across microgeographic scales (soil, surface, canopy), and with seasonal structural changes (presence and absence of deciduous foliage). Thermal regimes of temperate forests during leaf-on conditions (Ba-Bd) closely resembled those of tropical forests (*A*). In temperate forests, overlap was lower during leaf-on conditions (Ba-Bd) than leaf-off conditions (Be-Bh), and across latitudes soil microhabitats experienced less overlap than surfaces or canopies (Aa, Ba, Be). Curves were generated from Gaussian kernel density estimates of thermal regimes and correspond to the relative likelihood of a temperature occurring in a system. All plots are scaled to the same axes.

variation in thermal overlap ($\beta = -0.590$, 95% CI: -0.921, -0.458, fig. 3), providing more evidence for the foundational role that mountains play in biogeography. Since the first descriptions of climate and organismal zonation by Alexander Humboldt (1817), and later studies of how mountains act as dispersal barriers and drivers of allopatric speciation (Mayr 1942; Simpson 1964; Körner 2007), focus has been placed on elevation change in formulations of biogeographical hypotheses. Yet we show that what influences overlap between thermal regimes is more nuanced than simply latitude and altitude but rather contingent on habitat composition, microgeography, and time of year—drivers of temperature that have been well understood for decades (Geiger 1942), but the biogeographical implications of which are not. This suggests that previously hypothesized relationships between latitude and thermal niches, which only used surface-level and open-air temperatures (Janzen 1967; McCain 2009) or focused on only one habitat type (e.g., streams, Polato et al. 2018), may not accurately capture the biogeography of many taxa such as forest-dwelling or fossorial organisms.

Reframing the Climate Variability Hypothesis (CVH) as a Nested Framework

A long-standing framework, serving as the bedrock of study into biogeographical patterns between tropical and temperate latitudes, is that of the importance of thermal variability within a system, and thermal similarity between adjacent systems, for determining physiological tolerance and therefore species distributions (Janzen 1967; Stevens 1989; Gilchrist 1995; Ghalambor et al. 2006). Through this direct test of the mountain passes hypothesis (Janzen 1967) unifying micro-, meso-, and macrogeography, our study suggests that the CVH may function within a highly nested multidimensional framework across space and time and reframes the comparison of climate across latitude: local conditions play just as important a role in establishing thermal regimes and forming climate separation (see fig. 3 and table S2 for coefficient estimates of parameters). The elevation-for-latitude hypothesis (or Humboldt's law) suggests that species' elevation ranges should change predictably along latitudinal gradients, for example, with a reduction of treeline elevation with increasing latitude (Humboldt 1817; Randin et al. 2013). Our study suggests that such a species range–environmental equilibrium may scale down even more, especially for small-bodied organisms with smaller areas of operation, to microhabitats created by forests and soils. In addition, the temporal window of activity determines thermal exposure: organisms active only during the summer in forests with seasonal foliage change operate within a narrower thermal environment than organisms active year-round, and therefore they might remain climatically isolated. Thus, climate separation for a species is not simply a result of latitude, but rather depends on where a species lives within a system and, especially for high-latitude species, when a species is active throughout the seasonal calendar (Angilletta Jr. 2009; Sunday et al. 2012; Sheldon and Tewksbury 2014; Chan et al. 2016; Pincebourde et al. 2016; Scheffers et al. 2017*b*).

Latitude is not to be discounted as a prominent driver of thermal biogeography, as studies of single species or clades found across latitudes demonstrate relationships between the thermal tolerance of species and their geographic location (Polato et al. 2018). Yet much variation exists when plotting species' physiological thermal limits across latitude (Sunday et al. 2011), and some single-species studies have found the opposite or no trend (Kimura et al. 1994; Gilman et al. 2006) or mixed evidence (Addo-Bediako et al. 2000) with latitude. This contributes to the mounting evidence in support of the role that microgeographic processes play in driving variation in ecophysiology (Freidenburg and Skelly 2004; Kearney et al. 2009; Pincebourde and Casas 2015; Woods et al. 2015; Isaak et al. 2017; Nowakowski et al. 2017). Decreased activity during hours of extreme temperatures (Sunday et al. 2014) or use of microhabitats (Scheffers et al. 2014) can mitigate the effect of extreme temperatures, so that the realized thermal exposure does not match ambient temperatures. Thus, consideration of such fine-scale phenomena may harmonize some of the discordant findings of thermal performance and tolerance across latitude (Ghalambor et al. 2006).

Spatial Considerations for the CVH

Thermal variability was lower on mountains with dense and tall vegetation, thereby effectively making forested mountains taller than equivalent mountains with little to no vegetation cover (figs. 2, 4). Full-year sampling of deciduous forest mountains also demonstrated the absolute effect of seasonal vegetation, which increases thermal separation between uplands and lowlands during the summer relative to winter (fig. 2). Forests increase climate separation on mountains, on average, by 3.32°C when compared with nonforested mountains, and for deciduous mountains, the presence of summer foliage increases climate separation by 7.13°C when compared with leaf-off winter conditions (fig. S2). The thermal regimes of elevation bands on a temperate forested mountain thus procure stability and separation when leaf cover is present (Janzen's tropical mountain) and overlap considerably when leaf cover is absent (Janzen's temperate mountain; fig. 6). This finding of a steep climate gradient created by forest vegetation expands on the recent body of work demonstrating the thermal insulation that forests provide (Laurance 2004; De Frenne et al. 2013, 2019; Scheffers et al. 2014; Frey et al. 2016; González del Pliego et al. 2016; Senior et al. 2017).

In addition, increasing snow depth reduced thermal overlap ($\beta = -0.212$, 95% CI: -0.293, -0.133 in the global model), although when vertical microhabitats were analyzed separately, this effect was only found in soil systems (fig. S3). The presence of snow offsets the thermal regimes of subterranean habitats from those above the surface in some places by 10°C or more (Grundstein et al. 2005; Graae et al. 2012), not only by reducing exposure to warm extremes but also by reducing exposure to freezing conditions (Venn and Green 2018). For plants, snow cover and depth are important regulators of growth (Happonen et al. 2019), sometimes extending or limiting the length of the growing season (Braun-blanquet 1932), and may rescue some species from distribution declines induced by macroclimate warming (Niittynen et al. 2018). For animals, snow may both reduce susceptibility to extreme cold as well as the metabolic costs of hibernation (Pauli et al. 2013; Kearney 2020), but such effects are highly species specific, depending on physiology, overwintering behaviors, and cold stress tolerance (Kearney 2020).

Thermal overlap also varied considerably between vertical microclimates. For instance, thermal overlap across elevation in the canopy of a deciduous forest in North Carolina was 12.6°C higher than overlap for the soils below, greater than the difference in overlap (11.7°C) between the surface temperatures of mountains in Costa Rica and California, which are 25° of latitude apart, as reported by Janzen (1967). Such changes in thermal variability with height may act as a principle driver of observed vertical community stratification. Across taxonomic groups, empirical evidence is mixed on the relationship between thermal tolerance and vertical life strategy (Tracy et al. 2010; Diamond et al. 2012; Baudier et al. 2015; Kaspari et al. 2015; Scheffers et al. 2017*b*), although the most taxonomically diverse of these works suggests that arboreality is associated with high dispersal potential and increased tolerance to environmental instability (Scheffers et al. 2017*b*). Microscale climate gradients extend beyond forests to other structurally or topographically complex systems, such as subterranean caves, in which increasing depth underground has been shown to decrease the thermal tolerance and elevation range of *Troglohyphantes* spiders (Mammola et al. 2019). Thus, to better understand thermal biogeography at ecologically relevant scales, ecologists should consider not only latitude and altitude but also how temperatures shift across the vertical climate axis with respect to the ground—perhaps appropriately termed "vertitude." More direct comparisons of physiology from the subsurface to canopy are encouraged to elicit how populations and communities respond to vertitudinal climate gradients.

Temporal Considerations for the CVH

Duration and time of year of activity also may determine the thermal environment experienced by an organism and thereby drive biogeography (Sheldon and Tewksbury 2014). Although seasonality of ambient climate tends to increase with latitude, organisms may partition activity or ontogeny across seasons to avoid or adapt to thermal variation (Angilletta Jr. 2009; Kingsolver et al. 2011). During a temperate winter, aboveground thermal variability is high (fig. 2), yet species can mediate their exposure to harsh cold temperatures by retreating within soil microhabitats, especially when covered in snow, and thus remain within a stable thermal regime (Storey and Storey 1992), or migrate to tropical latitudes and thus escape winter variability altogether (Newton 2007). Our study also suggests that during summer months, when activity in temperate systems is pronounced, forest organisms living within specific elevation ranges would be climatically isolated due to thermal buffering by vegetation. This seasonal dichotomy may serve as the evolutionary basis of organisms with seasonal fluctuations in dispersal strategy, phenology, or ontogeny, an important consideration for species redistribution science (Sheldon and Tewksbury 2014; Bonebrake et al. 2018). As Janzen (1967, p. 242) suggested, "by regulating its activity, [an organism] places itself in a more uniform environment during major activity periods," and, as such, metabolic activity only during times of thermal stability may result in community turnover across climate gradients such as elevation (Lomolino 2001; Sanders et al. 2009; Hu et al. 2018). Gamma diversity is therefore likely driven by life-strategy responses to climate as well as by microhabitat and biome occupancy within communities (Kearney et al. 2009; Scheffers et al. 2014; Stein et al. 2014; Sunday et al. 2014; Muñoz and Bodensteiner 2019). Moreover, seasonal mitigation of extreme exposure alongside microclimatic buffering might explain why species are capable of overfilling their fundamental thermal niche at high latitudes where temperatures fall below their minimum thermal tolerance (Sunday et al. 2012), but this hypothesis warrants further study.

Other Considerations for Thermal Biogeography across Mountains

When attempting to traverse novel landscapes such as mountain passes, dispersal ability and speed determine the thermal regimes an organism is exposed to and whether a physiological threshold is reached. For instance, some extremely mobile species like migratory birds may be able to traverse a mountain pass within a few hours or days, while a sessile organism with passive dispersal may take multiple generations to traverse the same distance. In this latter example, dispersal across mountains can be achieved despite climate separation as long as successive generations progressively adapt to moderately novel conditions. Thus, thermal overlap across elevation at a monthly resolution, as we have used, may not equally apply across taxa. Furthermore, the study of thermal biogeography cannot be simplified to exploring temperature similarity across elevation bands, as climate space can be defined in many ways. For instance, also noteworthy is the range of possible temperature values across a spatial scale: although vertical height was a good predictor of thermal overlap in our models, the magnitude of temperature change is considerably higher between tropical and polar latitudes than it is between the floor and canopy of forests. Frequency and intensity of climate extremes such as frost and drought will act as filters to dispersal (Easterling et al. 2000), and these factors are not fully captured by our measurements of thermal overlap (although likely correlated with overlap). Certainly many environmental factors besides climate delineate species ranges (Janzen 1970; Connell 1971; Villard and Metzger 2014), and such environmental, ecological, and evolutionary filters will shift in relative importance from individual to ecosystem levels.

Conclusion

Our study provides a nested space-time conceptual basis for the climate variability hypothesis extending from the growing field of microgeography (Freidenburg and Skelly 2004; Potter et al. 2013; Stein et al. 2014; Lenoir et al. 2017; Nowakowski et al. 2018; Sheldon et al. 2018; Suggitt et al. 2018). Our study advances, but does not finalize, integration of microgeographic dynamics across landscapes and into biogeographical theory. Capturing climatic data at fine resolution, as opposed to relying on generalizations from measurements by weather stations, is critical to understanding ecological patterns arising from climate (De Frenne and Verheyen 2016; Senior et al. 2018; Lembrechts et al. 2020), and accounting for such fine-resolution thermal variability over broad scales, as we have done here, provides a more accurate representation of the multidimensional environments biota are exposed to (Hertz 1992; Oke and Thompson 2015; Scheffers et al. 2017*a*; Suggitt et al. 2018). We show that thermal overlap varies considerably between microhabitats (figs. 1, 6) and with vegetation structure (figs. 4, 5), especially relative to latitude, and discuss how these phenomena might influence the evolution and ecology of species. Climate separation across elevation is not unique to the tropics, but exists at higher latitudes, which may restrict the mobility of species—especially those occupying forested or fossorial habitats, and during summer months when activity is pronounced in the temperate zone. We recommend that ecological communities be examined in the context of spatial and temporal complexity within and across habitats of mountain ecosystems to reach a more complete understanding of how micro-, meso-, and macroclimates dictate biogeography.

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Statement of Authorship

D.H.K. and B.R.S. designed the research; B.R.S. collected field data; D.H.K. compiled and curated the data and performed the analysis; and D.H.K and B.R.S. wrote the manuscript.

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