Over the top: do thermal barriers along elevation gradients limit biotic similarity?

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Organismal dispersal through mountain passes should be more constrained by temperature-related differences between lowland and highland sites in montane environments. This may lead to higher rates of diversification through isolation of existing lineages toward the tropics. This mechanism, proposed by Janzen, could influence broad-scale patterns of bio-diversity across mountainous regions and more broadly across latitudinal gradients. We constructed two complementary analyses to test this hypothesis. First, we measured topographically-derived thermal gradients using recently-developed climatic data across the Americas, reviewing the main expectations from Janzen's climatic model. Then, we evaluated whether thermal barriers predict assemblage similarity for amphibians and mammals along elevational gradients across most of their latitudinal extent in the Americas. Thermal barriers between low and high elevation areas, initially proposed to be unique to tropical environments, are comparably strong in some temperate regions, particularly along the western slopes of North American dividing ranges. Biotic similarity for both mammals and amphibians decreases between sites that are separated by elevation-related thermal barriers. That is, the stronger the thermal barrier separating pairs of sites across the latitudinal gradient, the lower the similarity of their species assemblages. Thermal barriers explain 10–35% of the variation in latitudinal gradients of biotic similarity, effects that were stronger in comparisons of sites at high elevations. Mammals' stronger dispersal capacities and homeothermy may explain weaker effects of thermal barriers on gradients of assemblage similarity than among amphibians. Understanding how temperature gradients have shaped gradients of montane biological diversity in the past will improve understanding of how changing environments may affect them in the future.

Barriers to dispersal arising from pronounced changes in climatic conditions along elevation gradients may facilitate allopatric speciation by limiting species dispersal, which influences broad-scale patterns of species richness and composition (Janzen 1967, Ghalambor et al. 2006, Mittelbach et al. 2007, Buckley et al. 2013a). Reduced temperature seasonality in tropical environments is also likely to cause species to specialize on narrower climatic conditions and reduce their capacity to acclimate to the wide range of temperatures that challenge organisms in temperate or cold environments (Stevens 1989, Bonebrake 2013). In other words, allopatric speciation rates in mountainous areas depend strongly on climate and particularly on temperature (Janzen 1967). Because temperature seasonality is lower in tropical than temperate environments, a tropical species inhabiting a lowland area is unlikely to encounter tolerable temperatures at high elevations. In comparison, thermal regimes between lowland and highland areas overlap substantially in regions with more pronounced temperature seasonality. Organisms in such areas are, as a result, less likely to experience strong dispersal limitations arising from intolerance to temperature differences along elevation gradients (Ghalambor et al. 2006).

Species inhabiting tropical montane environments occupy smaller elevational ranges (Wake and Lynch 1976, Huey 1978, Navas 2002, Ghalambor et al. 2006, Orme et al. 2006, McCain 2009) and show narrower thermal tolerances than species in temperate montane environments (Addo-Bediako et al. 2000, Kozak and Wiens 2007, Deutsch et al. 2008, Cadena et al. 2012). Colder temperatures at high elevations represent thermal barriers that limit dispersal rates among species with such narrow thermal tolerances, reducing gene flow between subpopulations and increasing allopatric speciation rates. While this process could contribute to the origin and maintenance of global gradients of species diversity, there is mixed evidence that tropical speciation rates exceed those of temperate regions (Graham et al. 2004, Kozak and Wiens 2006, Rissler and Apodaca 2007, Peterson and Nyari 2008, Hua and Wiens 2010, Cadena et al. 2012). Niche conservatism could reduce the capacity of taxa originating under warm conditions to establish populations in higher elevation, cooler areas (Moritz et al. 2000, Wiens 2004, Wiens et al. 2010, Kozak and Wiens 2012) and climate change-related extinction risk for some taxa (Deutsch et al. 2008, Sinervo et al. 2010, Kerr et al. 2015). Understanding how climate interacts with species'

physiological characteristics (Buckley et al. 2013a, Coristine et al. 2014) and requirements for behavioral thermoregulation (Kearney et al. 2009, Meiri et al. 2013, Sunday et al. 2014) will help assessments of emerging conservation challenges for which responses to climatic conditions play a role (e.g. biotic homogenization; White and Kerr 2007).

Here, we test whether broad-scale gradients in assemblage similarity among mammals and amphibians relate to thermal barriers associated with dividing mountain ranges in western North and South America. We predict that increasing thermal barriers associated with gradients of temperature seasonality in mountainous areas across latitudes should lead to lower assemblage similarity among sites separated by those barriers. Population isolation is more likely in mountainous localities where temperature-related dispersal barriers are more persistent seasonally (Wiens and Graham 2005, Ghalambor et al. 2006, Kozak and Wiens 2007, Mittelbach et al. 2007, Buckley and Jetz 2008, McCain 2009, Cadena et al. 2012), leading to higher allopatric speciation rates. The spatial relationship between assemblage similarity and thermal barriers should be more pronounced among taxa that are more strongly affected by environmental temperatures (i.e. ectotherms) and those with lower dispersal capacities (Angilletta 2009).

Material and methods

Topography and thermal barriers

We constructed detailed measurements of thermal overlap between thermal regimes among sites across the Americas. We define a thermal regime as the temperature range between maximum and minimum monthly temperature observed throughout the year for a particular site. Thermal overlap is the similarity between thermal regimes. In areas where thermal regimes differ substantially (i.e. there is little or no thermal overlap), thermal barriers to dispersal are likely to be present. We measured thermal regimes at the resolution of the climate data (~ 1 km²) across mainland areas of the Americas using monthly temperature data from WorldClim for the 1951–2000 period. Cross-validated accuracy assessments of temperature measurements in the WorldClim dataset indicate that temperature normals for this period are usually within 0.3°C of observed values, with uncertainties in temperature measures rising in the most sparsely sampled and mountainous areas, respectively (Hijmans et al. 2005). The density of meteorological stations and availability of long term monitoring varies across the Americas and likely increases the uncertainty around estimates of thermal barriers that we hypothesize should limit species dispersal rates across mountainous regions. Geographic data were projected into Lambert Azimuthal Equal-Area projection and processed using ArcInfo Grid 10.3 (ESRI 2014).

We selected 404 focal sites (Fig. 1a) over which quadrats for biological measurements could be centred and temperature-related data extracted for subsequent analyses. This set of 404 focal sites includes 202 at low elevations (300 m a.s.l.) and 202 at high elevations (2000 m a.s.l.). Low and high elevation focal sites were each divided into 101 east-west pairs, separated by dividing mountain ranges (e.g. Andes).

Focal sites were situated from 69°N to 39°S with ~ 150 km latitudinal gaps between them (Fig. 1a). The two sets of 202 focal sites were divided evenly between eastern and western areas, so 101 focal sites on the eastern slopes were paired with 101 focal sites on western slopes at both low and high elevations (Fig. 1b). We computed the degree of thermal overlap between each focal site and all other pixels throughout the Americas, creating 404 thermal overlap surfaces relative to every focal site (e.g. thermal overlap map for an example focal site in Fig. 1).

For all pixels in the Americas, we extracted the maximum temperature of the warmest month and minimum temperature of the coldest month (Fig. 1c) (Hijmans et al. 2005). We measured temperature in kelvins to avoid negative values in later calculations. Then, we used resulting thermal regimes values to parameterize Eq. 1 (Fig. 1d), which measures pairwise thermal overlap between each focal site and all other areas in the Americas:

$$Overlap\ value = \sum_{i=1}^{12} \frac{d_i}{\sqrt{R_{1i} R_{2i}}}, \qquad (1)$$

where d_i is the temperature overlap between the focal site and each other site in the Americas for the ith month. R_{1i} is the difference in kelvins between the monthly mean maximum and minimum for the ith month of the focal site and R_{2i} is the corresponding value for each other site in the Americas. The maximum thermal overlap value is 12 if thermal regimes between two sites share identical monthly minimum and maximum temperatures throughout the year (Fig. 1e). Thermal overlap decreases as thermal regimes between sites grows more dissimilar. Zero values are possible if there is no overlap between thermal regimes between a focal site and another site and negative values will be observed if there is an annually persistent temperature difference (e.g. the maximum temperature of one site is always lower than the minimum temperature of another, Fig. 1e). Finally, we measured how thermal overlap changes along altitudinal gradients across the Americas by regressing observed thermal overlap values against elevation using ordinary least squares regression. We use the slope of these regressions to evaluate how thermal regimes vary with respect to elevation across the Americas. All data are available freely from <www.macroecology.ca/> and Supplementary materials Appendix 1, Fig. A1.

Assemblage similarity

We used distribution data for 1771 terrestrial mammal species (Patterson et al. 2007) from IUCN (<www.iucnredlist.org>) and 3131 amphibian species from Natureserve (<www.natureserve.org/>) in the western hemisphere. Distribution maps generally have fewer false absences than presence-only datasets but contain many false presences; compositional similarity between pairs of quadrats may appear misleadingly high using range map data. In addition, species distributions are less certain in tropical regions, a trend that is likely to be more pronounced at high elevations, where local distribution differences due to topographical complexity may be undetected. To our knowledge, this uncertainty has not yet been directly tested and is beyond the scope of this paper. Our results should be considered conservative (i.e. errors of commission
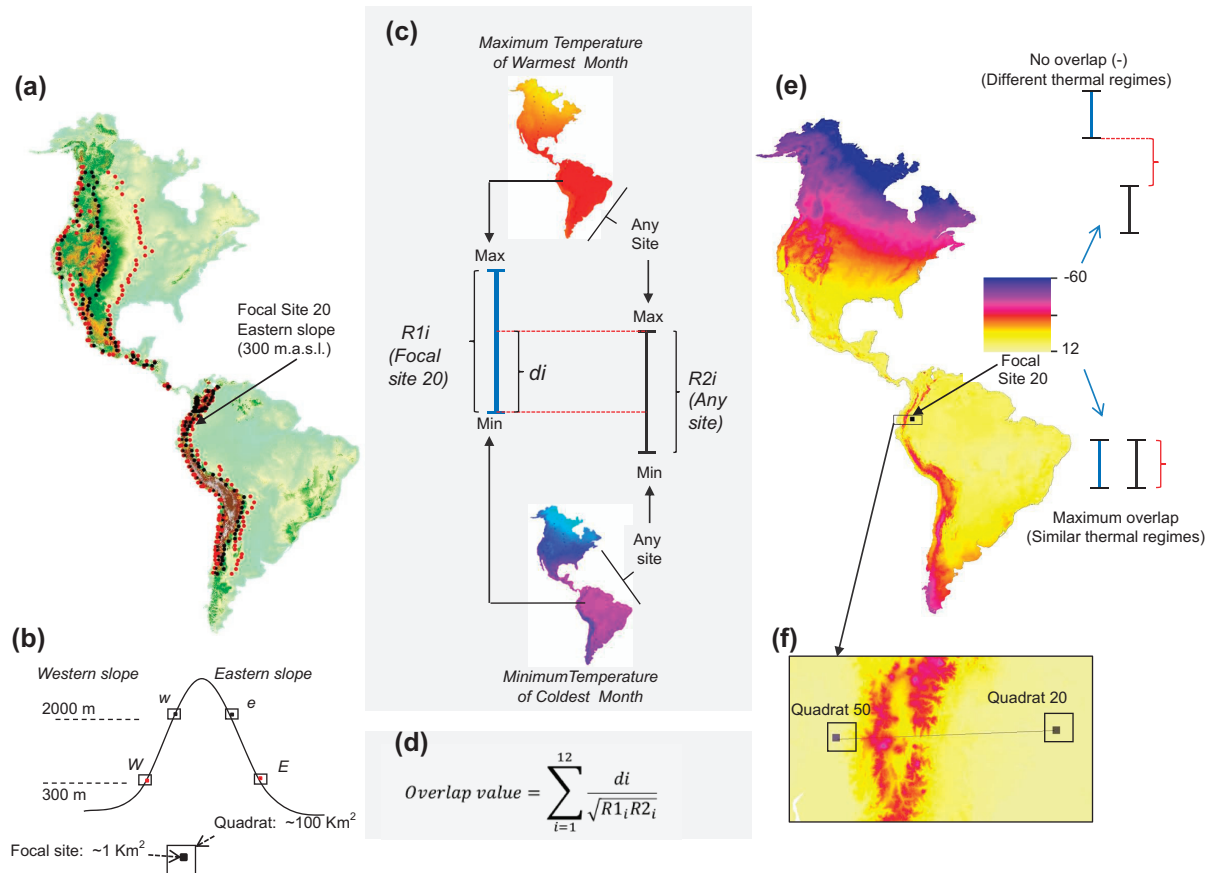
Figure 1. Conceptual diagram showing Janzen's approach (Janzen 1967), as adapted to measure the overlap between thermal regimes of 404 focal sites (a ~ 1 km² pixel) relative to all other sites in the Americas (a). These were divided into two sets of 101 focal site pairs at identical latitudes and elevations: the first set of 101 focal site pairs is at high elevation (2000 m a.s.l.), and the second set is at low elevation (300 m a.s.l.). The sites in each pair are separated by the dividing mountain ranges of the western Americas (b). We placed ~ 100 km² quadrats over each of focal sites to assess that area's assemblage of mammals and amphibians. Minimum and maximum monthly temperatures were extracted, pixel by pixel, throughout the Americas (c). We used these values to quantify thermal overlap between each focal site and all others using Janzen's equation (d). R_{1i} is the seasonal thermal regime of a focal site, R_{2i} is the thermal regime for a compared site, and d_i is the overlap between them. This resulted in 404 thermal overlap maps of the Americas, relative to each focal site (e). Thermal overlap ranges from pale yellow, which represents complete overlap between two thermal regimes for every month (a value of 12) to purple, which represents maximum observed separation between thermal regimes (i.e. areas with negative values indicates a substantial thermal regime difference with respect to this example focal site). A thermal barrier between two sites is the maximum difference in thermal overlap encountered between them (f).

in species range data are more common and increase apparent assemblage similarity among paired quadrats).

We measured species presences within quadrats of ~ 100 km² centered on each of the 404 focal sites, described above. A species was considered present if any portion of its range intersected a quadrat. We centered quadrats at 300 and 2000 m a.s.l. (and focal sites for thermal overlap calculations) to overcome two constraints. First, elevation contours at 2000 m a.s.l. are generally present across the study region of North and South America, while elevations greater than this are not. Second, some areas in Central America are narrow and have very small land areas near sea level, with steep slopes rising quickly above. In these areas, placing quadrats at 300 and 2000 m a.s.l., respectively, eliminated spatial overlap between adjacent quadrats, which would have misled measurements of similarity.

Pairwise similarity between species assemblages in site pairs was measured using the Sørensen coefficient in EstimateS ver. 9 (Colwell 2013). We constructed a presence/absence matrix for mammals and amphibians within each quadrat. We created two sets of pairwise comparisons: first between pairs of lowland quadrats (300 m a.s.l.) and a second between pairs of highland quadrats (2000 m a.s.l.) at the same latitude to the east and west of the dividing mountain range (Fig. 1f). We compared east-west pairs of quadrats (i.e. separated by dividing ranges, Fig. 1b) at the same elevation, which are more likely to represent biologically independent measurements, reducing potential area effects on biodiversity patterns that can mislead analyses in mountainous regions (Romdal and Grytnes 2007).

The Sørensen index uses presence–absence data and gives double weight to presences in two quadrats (Legendre and Legendre 1998). This measure is calculated as:

$$S_{ij} = \frac{2A}{2A+B+C} \tag{2}$$

where A is the number of species common to both quadrats i and j; B is the number of species present only at quadrat

i; and *C* is the number of species present only at quadrat *j* (Chao et al. 2005). Values range between 0 and 1, where 1 indicates that the two quadrats have the same species composition, and 0 means the two quadrats share no species.

Thermal barriers separating assemblages

We used the maximum difference in thermal regimes separating paired sites as an index of thermal barriers that organisms would encounter while moving from one quadrat to another across the dividing range. The biological impact of a thermal barrier should be greater if a dispersing organism encounters temperatures that are rarely or never present in the area from which it moved. Thermal barriers, as measured here (and described in Janzen 1967), measure the difference in thermal regimes between points of origin for dispersal (at low or high elevations) and the mountain passes that separate this point of origin from a quadrat at the same elevation across the dividing mountain range.

Statistical analysis

We constructed ordinary least squares regression models to test whether thermal overlap may limit assemblage similarity among pairs of quadrats across the Americas. Spatial autocorrelation normally influences broad-scale analyses across gridded sampling networks profoundly, which diminishes reliability of their probability tests by violating the assumption of independence of regression errors and biases predictor coefficients (Bini et al. 2009). Analyses here rely on assemblage similarity, a characteristic shared between paired sites separated by known distances. This pairwise distance measurement accounts for the extent to which purely spatial effects predict similarity, which decreases with geographic distance (Soininen et al. 2007). We included pairwise site separation as a covariate in all analyses. Distance and similarity were square root-transformed to improve normality and homoscedasticity of residuals (Nekola and White 1999).

We analyzed two sets of quadrats, which were centred on pairs of focal sites. First, we compared lowland quadrats (300 m a.s.l.; east-west, *EW* and west-east, *WE,* Fig. 1e) and, separately, highland quadrats on opposing sides of dividing ranges (2000 m a.s.l.; *ew* and *we*, Fig. 1e). The first letter indicates which focal site was used as the basis for thermal overlap calculations. For instance, *EW* pairwise comparisons of similarity as a function of thermal overlap use the thermal overlap value calculated from a site to the east (*E*, at 300 m a.s.l.). Finally, we tested for differences between regression slopes for similarity in paired quadrats in lowland and highland areas. Statistical analyses were performed in R ver. 3.2.1. (R Core Team).

Results

Thermal overlap along altitudinal and latitudinal gradients shows considerable variability. While the rate of change of thermal overlap with elevation is usually linear (Fig. 2; Supplementary material Appendix 1, Table A1 and Fig. A2a),

there is a region between 33°N and 48°N along the eastern side of the continental divide where that relationship is clearly nonlinear (Fig 2; see also Supplementary material Appendix 1, Table A1 and Fig. A2b). With respect to latitude, the greatest rates of change of temperature with respect to elevation are in the tropics, decreasing toward sub-tropical areas, and stabilizing between 20–40°S and 30–50°N (Fig. 2 and 3). Thermal regimes change similarly with elevation across the tropics and when measured from coastal areas of North America around 60°N (e.g. model estimates for a tropical region: $y = -6.6 \times 10^{-3}$ elevation $+ 12.005$; and model estimates for western North America at 60°N: $y = -6.7 \times 10^{-3}$ elevation $+ 12.312$; Fig. 2 and Supplementary material Appendix 1, Fig. A3). Thermal barriers along elevation gradients vary considerably more than simple latitudinal expectations suggest, so latitude cannot be used as a surrogate for the magnitude of thermal barriers (or as an indicator of the absence of thermal overlap between low and high elevation areas). Explicit measurements of thermal barriers are needed to test for their potential effects on gradients of similarity across the Americas (Supplementary material Appendix 1, Fig. A4).

Broadly, mammal and amphibian assemblages become less similar when separated by more substantial thermal barriers imposed by the steep elevation gradients of mountain ranges in the Americas. That is, the stronger the thermal barrier separating them, the lower the similarity of species composition between paired quadrats becomes (amphibians: $R^2 = 0.11–0.33$; mammals: $R^2 = 0.17–0.34$; Table 1). For pairwise comparisons of high elevation quadrats (i.e. at 2000 m a.s.l.), this result remains robust after accounting for separation distances between quadrats (amphibians: $R^2 = 0.33$; $F = 26.4$; DF $= 2,99$; p < 0.05; and mammals: $R^2 = 0.34$; $F = 26.9$; DF $= 2,99$; p < 0.05; Table 1a; Fig. 4a). However, the effect of thermal barriers on similarity is more variable when measured from west to east (amphibians: $R^2 = 0.20$; $F = 14.0$; DF $= 2,99$; p < 0.05; and mammals: $R^2 = 0.25$; $F = 18.3$; DF $= 2,99$; p < 0.05; Table 1b). For pairwise comparisons of low elevation quadrat pairs, the effect of thermal barriers on similarity decreases (amphibians: $R^2 = 0.22$; $F = 15.4$; DF $= 2,99$; p < 0.05; and mammals: $R^2 = 0.26$; $F = 19.2$; DF $= 2,99$; p < 0.05; Table 1c; Fig. 4b). The relationship between thermal barriers and biotic similarity at low elevations is not significant for mammals if measured from west-to-east ($F = 12.1$; DF $= 2,99$; p $= 0.17$; Table 1d) but is weakly significant for amphibians ($R^2 = 0.11$; $F = 7.5$; DF $= 2,99$; p < 0.05).

Discussion

Mechanisms governing the origin and maintenance of gradients of biological diversity remain the focus of intense interest in ecology and evolution (Currie et al. 2004, Hawkins et al. 2004, Hillebrand 2004, Kozak and Wiens 2010, Wiens et al. 2010). If mountain passes are 'higher' in the tropics (Janzen 1967), then population isolation and subsequent increase in speciation rate could contribute to gradients of species richness and turnover on a continental scale (Mittelbach et al. 2007, Buckley and Jetz 2008). Here, we measured and investigated spatial variation in thermal
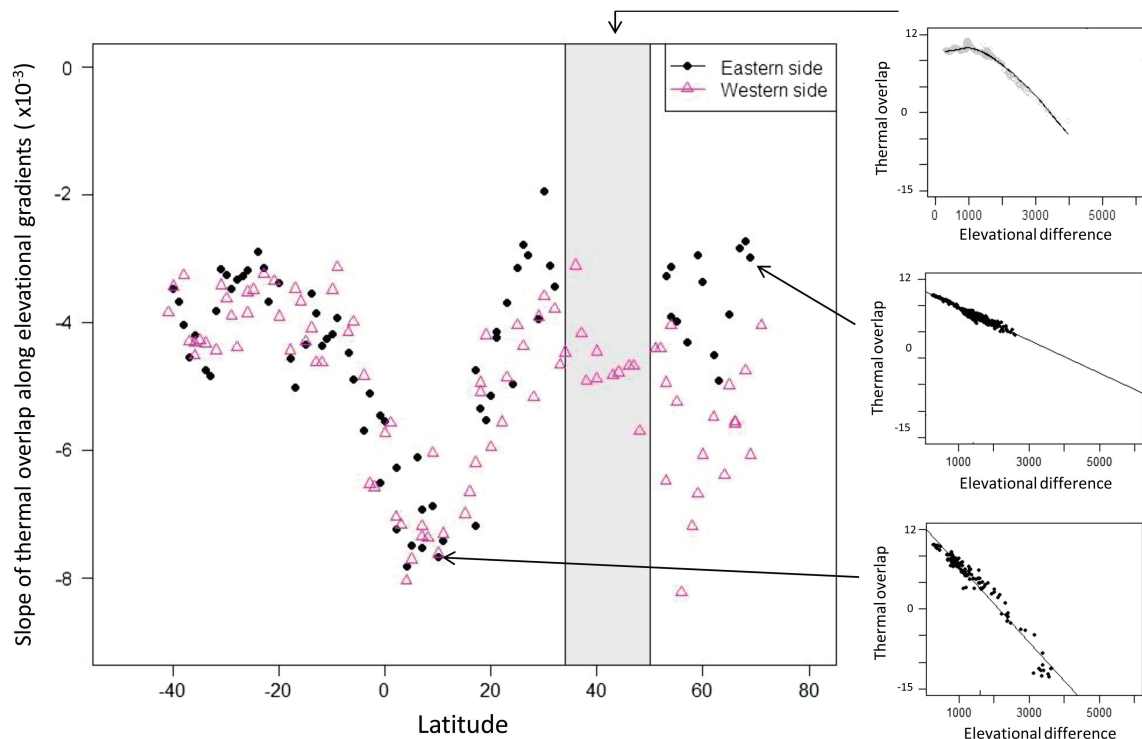
Figure 2. Changing thermal overlap relative to latitude along elevational gradients in the mountain ranges of the Americas. Black dots (left panel) represent slopes of thermal overlap relative to elevation measured from east of the dividing mountain ranges to the peak elevation within them, while magenta triangles represent same trend measured from the west. The gray region indicates an area where thermal overlap is not linearly related to elevation and linear regression slope values are consequently not shown. Two panels on the right give detailed examples showing how thermal overlap changes apparently linearly from low with elevation in many areas. The middle panel on the right shows a shallow thermal overlap slope ($s = -2.97 \times 10^{-3}$) for temperate zones and the third panel shows the steepest thermal overlap slope ($s = -7.23 \times 10^{-3}$) for tropical regions.

barriers along elevation gradients in mountain ranges and tested whether these barriers predict gradients of assemblage similarity across the latitudinal extent of those mountain ranges.

Mountain passes are 'higher' in biological terms when they are associated with strong thermal barriers, but these effects are not limited to the tropics. That is, the similarity of species assemblages decreases in comparisons of sites separated by more substantial thermal barriers associated with higher elevations. These effects are stronger for amphibians, which likely have lower effective dispersal rates than many mammal species and greater susceptibility to temperature fluctuations associated with ectothermy. However, we found robust evidence that thermal barriers, initially thought to be uniquely strong in tropical environments, can be comparably steep in temperate regions, particularly in western North America (Fig. 2 and 3). We find no evidence that thermal barriers are uniquely strong in tropical environments, although they are more widespread there.

Our results suggest that thermal barriers associated with mountain ranges limit species dispersal and increase potential for allopatric speciation. Comparisons between species assemblages in paired, highland sites showed a detectable and consistent effect of thermal barriers on assemblage similarity for both mammals and amphibians (Fig. 4 and Table 1). Temperature-related limitations on dispersal across high elevation areas could contribute to explanations of why patterns of assemblage similarity across broad areas

converge among different taxa (Buckley and Jetz 2008). Field measurements of thermal barriers can reflect sophisticated, location-specific information that reflect the operative temperature in an environment for a particular organism. Emerging techniques for measuring operative temperature account for factors such as incident solar radiation, wind speed, humidity, and ground temperature. Such approaches improve understanding of how short term environmental conditions influence species' behavioral thermoregulation requirements (Sunday et al. 2014) or species' dispersal and acclimation capacities in particular environments (Buckley et al. 2013a, b). Integrating such sophisticated metrics with spatially explicit dispersal rates estimates would enable tests of their potential effects on diversification rates and provide insight into processes that shape gradients of diversity.

Patterns of thermal overlap interact with species' dispersal capacities differently than suggested in simple tropical-temperate comparisons. For example, temperature-related dispersal barriers can be large if a species attempts to move inland from coastal North America, where areas with temperate rainforest have little or no thermal overlap with high elevation areas further inland. Nevertheless, mammal and amphibian species may filter around or through mountain ranges and the thermal barriers they impose. Many lowland species in tropical regions have broad geographical ranges spanning the Andes and these ranges were likely established as organisms dispersed through inter-Andean valleys at low altitude (Haffer 1967, Brumfield and Capparella 1996, Ron
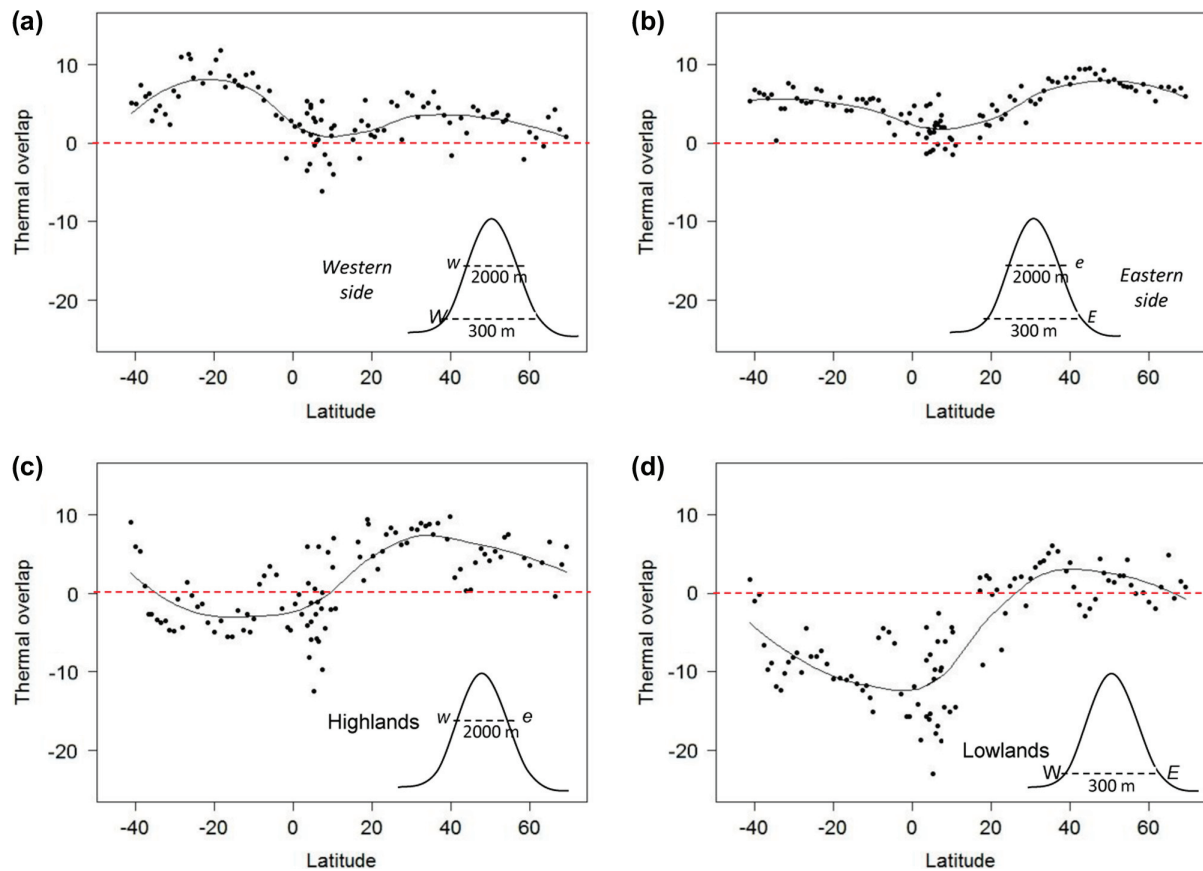
Figure 3. Maximum difference in thermal overlap between two sites across dividing mountain ranges in the Americas. Focal sites being compared along an elevational gradient are (a) low to high elevation focal sites on the western slopes of mountain ranges shown in Fig. 1a, (b) low to high elevation focal sites along the eastern slopes of those mountain ranges, (c) focal sites between high elevations and (d) focal sites between low elevations. For instance, (a) shows the maximum difference in thermal overlap encountered between a low elevation focal site at 300 m (*W*) and a nearby high elevation focal site at 2000 m (*w*). This difference in thermal overlap represents the thermal barrier that an organism must overcome when dispersing between focal sites. Scatterplots with Loess curves are shown. Dashed lines show the point at which thermal overlap declines to zero.

Table 1. Compositional similarity (COMP) as a function of the maximum thermal overlap (TOV) and accounting for geographical distance (DIST) for pairwise comparison of quadrats in the highlands (a, b) and lowlands (c, d) in the Americas.

	Amphibians							Mammals						
Predictor	Estimate	SE	t value	Pr(> t)	R²Adj	F	p	Estimate	SE	t value	Pr(> t)	R²Adj	F	p
a) Quadrats at Highlands (2000–2000 m), using TOV from east slope (ew†)														
Intercept	0.4466	0.0542	8.233	***	0.33	26.4	***	0.8953	0.0359	24.93	***	0.34	26.9	***
TOV	0.0339	0.0049	6.844	***				0.0167	0.0032	5.11	***			
DIST	−0.0094	0.0030	−3.121	**				−0.0115	0.0020	−5.74	***			
b) Quadrats at Highlands (2000–2000 m), using TOV from west slope (we)														
Intercept	0.4384	0.5941	7.379	***	0.20	14.0	***	0.8917	0.0381	23.34	***	0.25	18.3	***
TOV	0.0303	0.0063	4.815	***				0.0141	0.0040	3.48	***			
DIST	−0.010	0.0033	−2.99	**				−0.0117	0.0021	−5.45	***			
c) Quadrats at Lowlands (300–300 m), using TOV from east slope (EW)														
Intercept	0.6873	0.0782	8.782	***	0.22	15.4	***	1.0020	0.0642	15.59	***	0.26	19.2	***
TOV	0.0180	0.0039	4.521	***				0.0109	0.0032	3.36	**			
DIST	−0.0126	0.0023	−5.270	***				−0.0121	0.0019	−6.18	***			
d) Quadrats at Lowlands (300–300 m), using TOV from west slope (WE)														
Intercept	0.5541	0.0766	7.230	***	0.11	7.58	***	0.8478	0.0622	13.61	***	0.17	12.1	***
TOV	0.0109	0.0044	2.436	*				0.0002	0.0036	0.07	0.94			
DIST	−0.008	0.0022	−3.790	***				−0.0083	0.0018	−4.49	***			

Signif. codes (Pr(> t)): 0 '***', 0.001 '**', 0.01 '*' (DF = (2, 99) degrees of freedom).
†the first letter indicates which focal site was used to construct thermal overlap measurements for the linear model analysis. For instance, *ew* uses the thermal overlap value calculated from a focal quadrat *e* located in the eastern slope at 2000 m a.s.l.
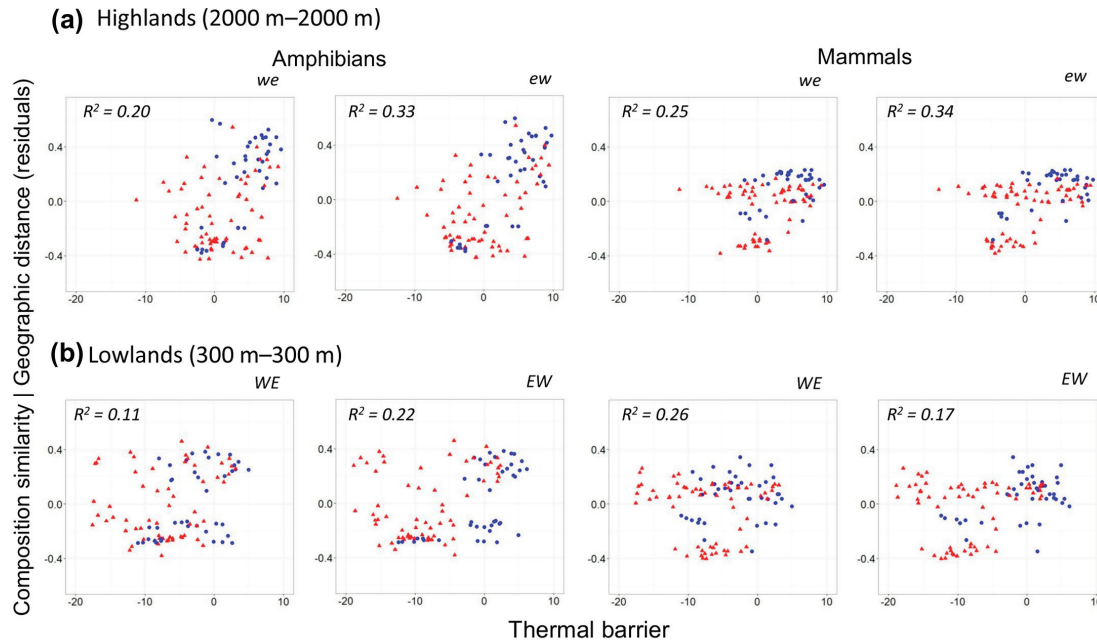
Figure 4. Relationships between assemblage similarity for amphibians and mammals as a function of the maximum thermal overlap (controlling for pairwise geographic distances) between quadrats located at (a) high elevations (2000 m) and (b) low elevations (300 m). Red triangles represent tropical pairwise comparisons and blue dots represent temperate ones. Letters in the top right of each graph indicate the focal site from which the thermal overlap was measured (note that quadrats are centered on each focal site). For instance, in the first graph, *we* indicates focal sites located at 2000 m, one set in the west (*w*) and the other set in the east (*e*). The first letter indicates which focal site was used to initiate thermal overlap measurements. For instance, *we* uses the thermal overlap value calculated from a focal site located to the west (*w*, at 2000 m), whereas in the second graph (*ew*), the thermal overlap value used is from a focal site located to the east of the dividing range (*e*, at 2000 m). Stronger thermal barriers between sites are suggested by negative thermal overlap values.

2000, Miller et al. 2008). Lineages inhabiting neotropical lowlands may have experienced initial isolation as a result of Andean uplift (Weir and Price 2011). However, trans-Andean dispersal events after Andean uplift reestablished contact among many such populations (Miller et al. 2008). Lowlands with similar thermal regimes near the northern limits of the Andes in Venezuela may have connected cis-Andean (east of the Andes) and trans-Andean (west of the Andes) biotas (Haffer 1967, Ron 2000). The Andalucia pass in Colombia and the Marańón and Porculla valleys in Peru, where thermal regimes differ by only small margins from neighboring lowlands, provide effective dispersal corridors connecting Amazonian, Pacific and Central American biotas (Haffer 1967, Vuilleumier 1971, Miller et al. 2008) (Supplementary materials Appendix 1, Fig. A5).

Thermal barriers are weaker or absent at low elevations (Wright et al. 2009, Salisbury et al. 2012) and our results cannot readily explain variation in species assemblages within such areas. Alternative explanations must be sought. It is possible that species within regions with relatively stable seasonal climates have lower dispersal capacities, making speciation more likely in the presence of any kind of barrier, thermal or otherwise (Jocque et al. 2010). If so, the intrinsic dispersal ability of species (Kodandaramaiah 2009, Smith and Klicka 2010) could generate structured gradients of species

richness across regions independently of in situ speciation rates (Cadotte 2006, Wiens 2011). Dispersal capacity also determines how rapidly organisms can track shifting environmental conditions (Ronce 2007, Leroux et al. 2013).

To the extent that thermal barriers limit species dispersal and contribute to the origins and maintenance of diversity gradients, rising temperatures in mountains that force upslope shifts in species' ranges (Dimitrov et al. 2012, Kerr et al. 2015) could erode species' geographical isolation and potentially confront distinctive, high elevation populations with influxes of individuals from historically disjunct areas. Such effects seem more likely for species in areas where thermal barriers associated with elevation are largest, which are most common in, but not restricted to, the tropics (Tewksbury et al. 2008, Dillon et al. 2010, Sinervo et al. 2010). If so, recently diverged populations may recombine. Mountainous areas have provided microrefugia for organisms during historical climatic changes (Jansson 2003, Willis and Bhagwat 2009, Scherrer and Korner 2011) and could improve species persistence following anthropogenic climate change (Ashcroft 2010, Moritz and Agudo 2013, Robillard et al. 2015). The role of such areas in maintenance, or erosion, of population isolation and allopatry relative to changing thermal barriers could be significant. Climate change offers pseudo-experimental opportunities (Kerr et al. 2007) to test

how thermal barriers associated with elevation gradients shape broad-scale gradients of assemblage similarity.

Processes intrinsic to the classic 'mountain passes' hypothesis (Janzen 1967) appear to contribute to the origins and maintenance of broad-scale gradients of biological diversity. This mechanism helps explain how environmental conditions shaped regionally-distinctive species assemblages in the past, integrating ecological perspectives on dispersal with evolutionary consequences for speciation. Yet, thermal barriers in some temperate regions are comparably strong to those observed in tropical areas. Differences in species assemblages across mountainous regions likely reflect some effect of those barriers, but other factors, whether historical or contemporary, must contribute to gradients of biological diversity. Understanding of such mechanisms will inform predictions of how assemblages may change in the future.

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