vol. 191, no. 5 the american naturalist may 2018

Synthesis

Fifty Years of Mountain Passes: A Perspective on Dan Janzen's Classic Article

Kimberly S. Sheldon,[1,*] Raymond B. Huey,[2] Michael Kaspari,[3] and Nathan J. Sanders[4]

1. Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; 2. Department of Biology, University of Washington, Seattle, Washington 98195; 3. Geographical Ecology Group, Department of Biology, University of Oklahoma, Norman, Oklahoma 73019; 4. Environmental Program, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont 05405

Submitted July 31, 2017; Accepted November 7, 2017; Electronically published March 19, 2018

Online enhancements: supplemental material.

abstract: In 1967, Dan Janzen published "Why Mountain Passes Are Higher in the Tropics" in *The American Naturalist*. Janzen's seminal article has captured the attention of generations of biologists and continues to inspire theoretical and empirical work. The underlying assumptions and derived predictions are broadly synthetic and widely applicable. Consequently, Janzen's "seasonality hypothesis" has proven relevant to physiology, climate change, ecology, and evolution. To celebrate the fiftieth anniversary of this highly influential article, we highlight the past, present, and future of this work and include a unique historical perspective from Janzen himself.

Keywords: dispersal, geographic range size, seasonality, temperature variation, thermal sensitivity, tropics.

Prologue: Dan Janzen on How "Mountain Passes" Came to Be

As stated in the acknowledgments of the original article (Janzen 1967), the idea for "Why Mountain Passes Are Higher in the Tropics" emerged during the 1965 (summer) first Organization for Tropical Studies (OTS) course Fundamentals of Tropical Biology: An Ecological Approach, funded by the US National Science Foundation as part of the germination and early growth of the OTS in Costa Rica (Stone 1988). I was a new faculty member in the Entomology Department of the University of Kansas, coordinating the 2-month course. It was sequentially 2 weeks in (i) the cloud forest at high, cold elevations on Cerro de la Muerte (≥2,500 m); (ii) the lowland Guanacaste Province dry forest in the rainy season (60 m); (iii) the coastal marine ecosystem of Guanacaste Province; and (iv) the lowland northeastern rain forest (40 m; fig. 1).

The course had a Costa Rican teaching assistant (TA), born and raised in the San José area (1,000–1,300 m asl). He had been there essentially all his life. Unfortunately, I no longer have a record (paper in those days) of his name or whereabouts.

In the 2 weeks on Cerro de la Muerte—climate indicated by its name—the course fully occupied a generally unheated small hotel (pension). It was fieldwork in the day and lectures in the evening in a makeshift classroom. I stood in the back listening and casually studying the students, all from North America. The TA sat next to me to the right, back to the wall. After several days, I realized that he was always huddled under a pile of one to two blankets wrapped around his shoulders, long pants, long-sleeved shirt, and heavy undershirt and often wore a coat in the field in the daytime. Innocently thinking malarial chills, I asked him if he was sick; he replied no but said, "it sure is cold here." At the same time, my mental photo was of the 20 students seated calmly listening and taking notes, all in T-shirts, long-sleeved shirts rolled up, long hair, and relaxed; some in shorts during the day, and always just one shirt. The light bulb did not go off in my head, but the two photographs were there.

After 2 weeks on Cerro de la Muerte, we bussed directly down to 60 m in rainy season Guanacaste Province dry forest and occupied a large rented farm house and some sleeping cots outdoors. Lectures were held in the open air under the second floor in a work patio. Again, it was fieldwork in the day, lectures at night. Again, I was standing in the back watching and listening, the TA seated on my right. I looked down at him in a light T-shirt and his back and shirt were soaked in sweat, brow as well. First thought was, oops, sick. And then the light began to turn on. I looked carefully at the backs of 20 students wearing the same T-shirts and cotton long-sleeved shirts rolled up, the same clothing they wore

* Corresponding author; e-mail: ksheldon@utk.edu.

ORCIDs: Sheldon, https://orcid.org/0000-0002-3215-2223; Huey, https://orcid.org/0000-0002-4962-8670; Kaspari, https://orcid.org/0000-0002-9717-5768; Sanders, https://orcid.org/0000-0001-6220-6731.

Am. Nat. 2018. Vol. 191, pp. 553–565. © 2018 by The University of Chicago. 0003-0147/2018/19105-57853$15.00. All rights reserved.
DOI: 10.1086/697046

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

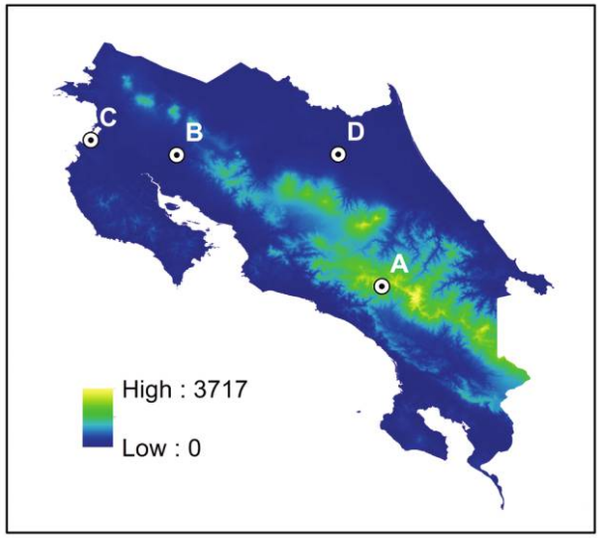


Figure 1: Map of Costa Rica showing the study locations of the 1965 course Fundamentals of Tropical Biology: An Ecological Approach. Participants in the course spent 2 weeks at each of the following sites: (*A*) in or near cloud forest at high elevations on Cerro de la Muerte in the province of Cartago (~3,100 m), (*B*) in lowland dry forest during the rainy season in the province of Guanacaste (~60 m), (*C*) on Playa Coco in the coastal marine ecosystem of Guanacaste (3 m), and (*D*) in the lowland northeastern rain forest near the town of Puerto Viejo de Sarapiqui in the province of Heredia (40 m).

on Cerro de la Muerte. Not a trace of sweat on anyone. That is when the light bulb turned fully on. If you grow up in a constant climate at midelevations (or anywhere), going into the upper-elevation cold or the lowland heat is a major shock, but not if you have lived your life annually fluctuating through summer, fall, winter, and spring, largely in non-air-conditioned buildings (it has never snowed in San José, and at 1,100 m it is more or less, to a North American, like being in a lightly air conditioned world nearly all the time). Therefore, mountain passes are higher in the tropics from the viewpoint of the physiological animal, and therefore montane barriers are greater in the tropics. Needless to say, the concept applies to any organism vis-à-vis the milieu in which it is situated.

—Daniel Janzen, January 17, 2017, Área de Conservación Guanacaste

Introduction

In the summer of 1965, Dan Janzen was a newly minted PhD teaching a tropical ecology course in Costa Rica (fig. 2). He was already a seasoned tropical biologist and a keen observer of the natural world, having cut his teeth on studies of the coevolution of ants and acacias in Central America (Janzen 1966). While teaching the tropical ecology course, he noted that a Costa Rican TA who was born and raised at a mid-elevation site near San José was freezing at cooler, high-elevation sites and overheating at warmer, low-elevation sites. In contrast, the students from North America who experienced both warm summers and cold winters were comfortable with the temperatures at a variety of elevations. As Janzen describes in the prologue to this article, these simple observations were the inspiration for his classic article "Why Mountain Passes Are Higher in the Tropics" (Janzen 1967), in which he linked fluctuation in temperature with its consequences for the physiology and dispersal of organisms.

Janzen (1967) proposed a simple hypothesis (Janzen's "seasonality hypothesis") consisting of two assumptions and two predictions. Assumption 1, the primary focus of his article, is that ecosystems vary not only in mean temperature but also in variation around the mean and that variation in temperature is relatively less in the tropics. Given that mean temperature decreases with elevation at all latitudes (Dillon et al. 2005), a corollary is that the climates at any two given points along a tropical elevational gradient will overlap less in their range of temperatures than will two equivalently separated temperate points (fig. 3). Assumption 2 is that populations (especially of ectotherms) are adapted to climates they experience; a corollary is that thermal specialists characterize less variable (i.e., tropical) climates, whereas thermal generalists are more prominent in variable (i.e., temperate) climates. From these two assumptions, Janzen derived the article's eponymous prediction 1,



Figure 2: Photo of Dan Janzen in Costa Rica teaching the course Fundamentals of Tropical Biology: An Ecological Approach in March 1967, just before "Why Mountain Passes Are Higher in the Tropics" was published. On the blackboard, Janzen drew "fairy insects"—imaginary insects he has drawn since childhood—to illustrate the differences between species richness and species evenness. Two years earlier, during the first iteration of the same course, Janzen formulated his ideas linking seasonality in temperature, thermal physiology, and range sizes. Photo credit: Carl Rettenmeyer.

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

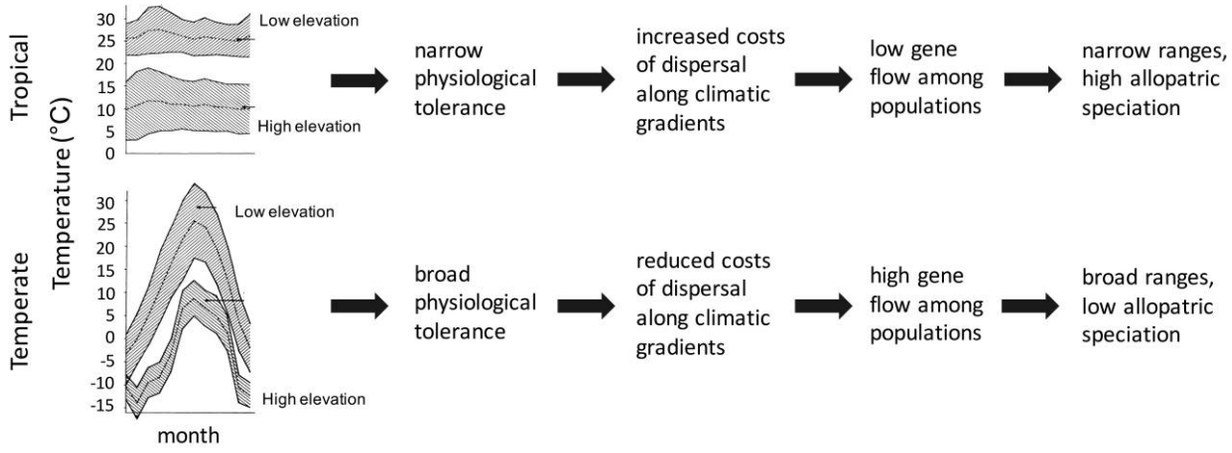


Figure 3: Schematic of Janzen's seasonality hypothesis (adapted from Ghalambor et al. 2006). The first panel shows one of the plates from the original article (Janzen 1967), all of which were hand drawn by Janzen.

which can be paraphrased as follows: take any two organisms, one tropical, one temperate, and let them climb a mountain; the tropical organism is more likely than the temperate organism to encounter climates for which it is maladapted. As a consequence, Janzen reasoned, tropical mountain ranges are more likely to act as physiological barriers to movement (up or down a mountain) because thermal specialists are less able to acclimate to and survive the range of temperatures encountered on the journey. This leads to prediction 2: thermal specialists in the tropics will have reduced dispersal along climatic gradients and thus smaller elevational ranges than thermal generalists. Although Janzen (1967) did not explicitly discuss species range sizes, he views prediction 2 of the seasonality hypothesis—the link between barriers to dispersal and smaller elevational ranges—as implicit and self-evident, so much so that "stating it is redundant on what was said before." Thus, we view prediction 2 as part and parcel of Janzen's seasonality hypothesis.

The combination of assumptions and predictions in "Mountain Passes" is simple but appealing. Janzen marshalled temperature data to support assumption 1 but did not cite any references showing that tropical species were more likely to be thermal specialists with relatively limited acclimation abilities. Here he had to rely on intuition, as comparative studies of thermal specialization and acclimation were not yet available. Since then, a pattern of increased variance in body temperature with latitude has been documented in lizards (van Berkum 1988), but variance in body temperature can nonetheless be substantial in high-elevation tropical ectotherms (Navas 1996; Navas et al. 2013). Moreover, a pattern of greater thermal specialization in the tropics has been well established (Sunday et al. 2011). However, Payne and Smith (2017) recently proposed an alternative explanation for global trends in thermal tolerance. Using a thermodynamics approach (i.e., transforming temperatures to presumed biological rates), they argue that tropical ectotherms have relatively narrow thermal tolerance and performance ranges because the tropics are relatively warm—thus, biological rates change relatively rapidly with temperature—and not because tropical temperatures are relatively constant. However, as Payne and Smith (2017) note, their hypothesis and the seasonality hypothesis need not be mutually exclusive. Finally, Janzen's assumption that tropical species have relatively limited acclimation ability is still debated (Gunderson and Stillman 2015; Seebacher et al. 2015; Vinagre et al. 2016).

When Janzen submitted his manuscript to *The American Naturalist* in November 1966, he corresponded with the journal's coeditor, Richard C. Lewontin (supplemental material, available online). We know from this correspondence that Lewontin sent the manuscript to two reviewers, Monte Lloyd and one anonymous reviewer whom Lewontin described as "an eminent person in the field." Both reviewers gave the article their "highest recommendation." The anonymous reviewer wrote, "The contribution is original and significant. It crystallizes what many of us who work in the tropics have understood vaguely—so vaguely that we have never articulated the idea in any way that counts. Janzen hammers it into shape in a sharp and authoritative manner, and his article will be quoted for a long time to come."

The anonymous reviewer's expectation has proven correct: due to the mechanistic nature of the seasonality hypothesis and its implications for latitudinal and elevational patterns of biodiversity, Janzen's unique synthesis has inspired 50 years of research in biogeography, physiological ecology, evolution, and global change biology. However, interest in the article was slow to develop. In a recent correspon-

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

dence, Janzen wrote the following of "Mountain Passes": "Once published, it created no interest. I did not flog it. . . . If I had made a career of talking about it and its relevance at meetings and in more papers, it would have gotten more attention. But that is not something I cared about or enjoyed."

Consistent with Janzen's statement, the article generated limited interest—at least as indexed by citations—in the early years. Of the 610 times the article has been cited (Web of Science through April 2017), more than 75% have come in the last 10 years (fig. 4). The recent uptick in citations may be due in part to Ghalambor and colleagues (2006), who, revisiting their yellowed copies of "Mountain Passes," outlined the assumptions and predictions of Janzen's original work and introduced a new generation of scientists to this important article. Additionally, Janzen's assumption 2 has become critically relevant to discussions about the vulnerability of tropical species to climate warming (e.g., Deutsch et al. 2008). With a renewed appreciation for "Mountain Passes," Janzen's article has become increasingly influential and is widely regarded as a classic. Here we discuss how the predictions of "Mountain Passes" have been examined and what questions remain unanswered.

Mapping the Geography of Physiological Performance

Janzen's seasonality hypothesis explicitly focuses on mountain ranges as barriers to dispersal, but the cornerstone underlying the hypothesis is the importance of considering environmental gradients as physiological rather than physical barriers. Here's the key statement in Janzen's article: "It is the temperature gradient across a mountain range which determines its effectiveness as a barrier, rather than the absolute height" (p. 233). In effect, Janzen's basic concept was to "map" or "transduce" elevational change onto its impact on physiological performance, as mediated by temperature change.

The perspective here is simple but profound, especially given that organismal performance is usually nonlinearly related to physical environmental factors. That is, a unit change in a physical factor should not imply a unit and parallel change in performance. In ectotherms, for example, performance generally increases gradually with body temperature up to some maximum level and then drops rapidly as temperatures approach a critical or lethal limit, so any given change in body temperature (with elevation, habitat, or climate) could enhance, reduce, or not affect performance, depending on the actual temperatures involved (Huey 1991). Furthermore, the same change in temperature can affect different species with different thermal optima in different ways. Consequently, any attempt to analyze the biological impacts of the physical environment—or of changes in that environment—requires "mapping" physical metrics onto physiological ones. While this concept was foreign to ecologists in 1967 (but see Fry 1947), it is now a standard consideration—although not without complications (e.g., Dowd et al. 2015; Kingsolver and Woods 2016; Sinclair et al. 2016)!

Why does mapping matter? In recent decades, air temperatures have increased most rapidly in the Arctic, followed by northern temperate regions and then the tropics. This observation led to the prediction that biological impacts are likely to be greatest in the Arctic and in northern temperate

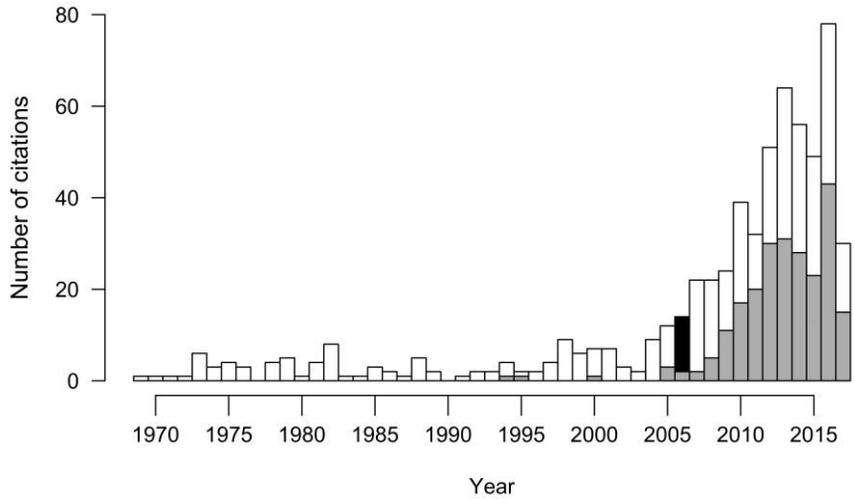


Figure 4: Citation history of "Why Mountain Passes Are Higher in the Tropics" showing how interest in the article increased over time. The white bars show all citations by year, the black bar shows the year Ghalambor et al. (2006) revisited Janzen's original article, and the gray shading shows the number of citations that mention "climate change," "global warming," or "climate warming" in the title, abstract, or keywords of the article. Results are from a Web of Science search in April 2017.

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

regions (Root et al. 2003). However, biological impacts depend not only on the magnitude of temperature change but on the physiological sensitivity of species (Deutsch et al. 2008). Many physiological functions of ectotherms, such as reproduction and growth, increase exponentially—not linearly—with temperature up to an optimum temperature and then decline rapidly to an upper maximum. Because tropical species are thermal specialists, the range of temperatures over which they can function is narrower than that of temperate species, and they are active at temperatures nearer to the threshold temperature where performance decreases. When projected changes in air temperature were mapped onto population growth curves, the biggest declines in organismal fitness were in the tropics, not the temperate region, suggesting that tropical species are more vulnerable to temperature changes (Deutsch et al. 2008).

In principle, any physical factor (e.g., pH, salinity, O_2) can be mapped onto a performance trait, such that Janzen's mapping concept is broadly applicable (Huey and Ward 2005). Moreover, multiple environmental factors often interactively affect physiological performance, complicating any mapping exercise. As an example that is relevant to mountain gradients, organismal heat tolerance can be affected interactively by temperature and O_2 (Pörtner 2002; Smith et al. 2015; Gunderson et al. 2016), both of which decline with elevation. Analytical approaches are being developed to map multiple physical factors onto physiological performance and tolerance (Porter et al. 1984; Deutsch et al. 2015).

Maps of Temperature Mean and Variation

Elevation

Janzen's seasonality hypothesis is based on two climatological patterns: (1) that daily and seasonal variation in air temperatures are lower in the tropics than at higher latitudes and (2) that air temperatures decline roughly linearly with elevation anywhere on the globe (Dillon et al. 2005). These facts were widely known, but Janzen's insight was to merge those two observations and then to realize that low- and high-elevation sites on a tropical mountain would be climatologically more different from each other than would equally separated low- and high-elevation sites on a temperate mountain. To demonstrate this point, he compiled temperature data from several pairs of sites on mountains and then computed an index of seasonal temperature overlap between low- and high-elevation sites. In a series of graphs, Janzen showed clearly that low- and high-elevation sites in the tropics had much less thermal overlap than did temperate sites. All else equal, this implies that a tropical organism dispersing up or down a mountain would be more likely (relative to a temperate-zone disperser) to encounter a thermal regime that differs from the one in its "home" environment and thus would be more likely to encounter a physiological barrier to further dispersal (Janzen 1967).

We will soon return to this issue, but we first must emphasize that the climate patterns in Janzen (1967) were based on shaded air temperatures from weather stations: thus, the derived elevational and latitudinal patterns of temperature overlap would apply strictly to the rare organisms that are always in shade (Ghalambor et al. 2006). Most organisms live in a mix of sun and shade or may shift from shadier habitats at low elevation to open habitats at high elevation (Hertz 1992). For such organisms, what matters for physiological performance are operative temperatures, which, for organisms exposed to the sun, can be dramatically higher than air temperatures (Bakken 1992), especially in the tropics (Sunday et al. 2014).

Buckley et al. (2013*a*) took a fresh look at climate overlap and contrasted patterns based on air versus operative temperatures. They noted that shaded temperatures decline with elevation but that radiation levels increase. As a consequence, surface soil temperatures in the sun—and operative temperatures of ectotherms—decline with elevation but do so much less rapidly than air temperatures. When they substituted operative temperatures to compute climate overlap, Buckley et al. (2013*a*) found that the "height of mountain passes" in tropical and temperate regions can sometimes be very similar. Computations of operative temperatures in Sunday et al. (2014) show similar patterns. But as Buckley et al. (2013*a*) note, other factors, like local cloud cover and behavioral thermoregulation, complicate specific elevational overlaps. Thus, the degree of temperature overlap among sites separated by elevation will depend on a host of variables, such as habitat, local climate, behavioral shifts, and the species of concern (Hertz 1992; Buckley et al. 2013*a*).

Vertical Layers of Ecosystems

Physiological ecologists have developed maps of temperature mean and variation and found that local differences in temperatures can arise from the fact that ecosystems often have vertical layers (Huey et al. 2009; Denny et al. 2011; Kaspari et al. 2015). Consider the diverse insects of a forest. An ant crawling on a branch in the sun-drenched canopy may experience super-heated air of the boundary layer (Oke 1978; Woods 2013), at least until it crawls to the shaded side of the branch. Below, in the shaded leaf litter of the forest floor, an ant will be cooler still and encounter fewer temperature hotspots—and, hence, less temperature variation. When night falls, the temperatures of the canopy and forest floor converge (Kaspari et al. 2015). Down into the soil, temperatures further stabilize and are invariant year-round (Coleman and Crossley 1996). A similar pattern occurs in Earth's oceans, from the warm, variable surface waters to the cold, constant abyssal depths (Pacanowski and Philan-

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

der 1981). Maps of temperature mean and variation across the vertical layers of ecosystems thus differ in a useful way from Janzen's maps across latitude: layers closer to the sun (i.e., forest canopies and surface waters) are likely to be warmer on average than those below, as well as more variable. This effectively reverses the latitudinal correlation of temperature mean and variation and provides a second way to test assumption 2 of Janzen's seasonality hypothesis—that variable environments select for temperature generalists—but *within* local communities.

And More . . .

Janzen recognized that temperature mean and variation of an environment covary geographically, with potential ramifications for species traits and movement. For example, Janzen (1967) noted that terrestrial habitats near oceans often experience less temperature variation due to the higher specific heat of water than air. Likewise, the parasites and microbiomes of endotherms likely experience a warmer and less thermally variable environment than do those of ectotherms. Finally, like terrestrial species, aquatic species in temperate streams experience greater change in temperature mean and variation over the year, but unlike terrestrial species, the aquatic species experience roughly the same minimum temperature—the freezing point of water—regardless of elevation (Shah et al. 2017).

Janzen's observations open up many opportunities to test how these climatic maps predict changes in population traits and physiological performance. Biophysical modeling (Kingsolver and Watt 1983; Buckley et al. 2013*a*) can be used to explore these patterns, but ultimately an empirical approach is necessary and will involve monitoring body temperatures of free-ranging ectotherms of a given clade over 24-h days for a full year and then replicating these measurements at several elevations and several latitudes. The resulting data would provide insights into "realized" thermal overlap. Such a project is ambitious but feasible thanks to miniature data loggers. To our knowledge, it remains to be attempted.

Transducing Climatic Maps into Distribution, Diversity, and Function

Range Sizes

Janzen's seasonality hypothesis is focused on the impact of temperature variation on organismal dispersal—about whether an organism can cross a thermal barrier—and the resulting consequences for population isolation. Reduced dispersal in the tropics should lead to tropical species that have smaller elevational ranges than their temperate counterparts. Two extensions of this logic are that (1) greater seasonality on mountaintops should result in broader elevational range sizes of species living at higher elevations (Stevens 1992) and (2) reduced seasonality at lower latitudes presents a barrier to dispersal and should result in smaller latitudinal ranges for low-latitude species (i.e., Rapoport's rule; Stevens 1989; see below).

Wake and Lynch (1976) were the first to cite "Mountain Passes" in relation to range sizes when they discussed small elevational range sizes of tropical salamanders. Since then, studies have largely confirmed predictions that tropical taxa have smaller elevational ranges than their temperate counterparts. However, this pattern does not hold for all taxa. Elevational ranges are narrower in tropical herpetofauna, insects, and birds, but mammal groups are mixed: bats, but not rodents, have narrower elevational ranges in the tropics (Huey 1978; McCain 2009; Cadena et al. 2011; Sheldon and Tewksbury 2014). The lack of a consistent pattern in mammals is ironic considering that "Mountain Passes" was built on Janzen's observations of mammalian subjects. The prediction that range sizes should be greater at higher elevations has also received mixed results (Gaston and Chown 1999*a*; McCain and Knight 2013; Sheldon et al. 2015).

Studies examining Janzen's seasonality hypothesis and elevational range sizes may suffer from the use of proxies for temperature variation. For example, sites at the same latitude can have vastly different seasonalities depending on elevation and whether the site has a continental or maritime climate (Chan et al. 2016). In addition, temperature readings from weather stations do not represent microclimates important for the physiology of small ectotherms (Bartholomew 1966; Potter et al. 2013; Kaspari et al. 2015; Pincebourde and Suppo 2016). Even the temporal scales of temperature variation (i.e., seasonal vs. daily climate variation) can have differing influences on elevational range sizes depending on the region of interest (Chan et al. 2016). Thus, a better approach to test predictions about seasonality and range size would be to use temperature variation itself rather than latitude as an explanatory variable in models and to use "realized" seasonality, or the temperature variation species experience when active or at appropriate times in their life cycles (Ragland and Kingsolver 2008; Sheldon and Tewksbury 2014). Using appropriate seasonality requires an understanding of the natural history and phenology of a species and microclimates at a site (Kingsolver et al. 2011; Levy et al. 2015; Pincebourde and Casas 2015); this is nontrivial, as activity cycles vary with seasonality.

In addition to elevational ranges, Janzen's seasonality hypothesis has been extended to latitudinal ranges: reduced seasonality in the tropics presents a barrier to dispersal and should result in smaller latitudinal ranges for species at low latitudes (i.e., Rapoport's rule; Stevens 1989). Support for this extension is mixed, with some studies showing a trend toward smaller latitudinal ranges with decreasing latitude and others studies showing no relationship (Price et al. 1997; Ruggiero and Lawton 1998; Cruz et al. 2005).

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

The idea that physiological barriers to dispersal result in smaller range sizes hinges on the presence of allopatric sites with limited thermal overlap. Unlike montane gradients, where mean temperature shows a linear decline with elevation, mean temperature is not linear with latitude. Instead, mean temperature is relatively constant in a band around the equator from 25°N to 25°S (Terborgh 1973; Gaston and Chown 1999*b*). Outside this region, mean temperature declines linearly with increasing latitude toward the poles, but the decline is steeper in north temperate regions than in south temperate ones (Gaston and Chown 1999*b*; Colwell 2011). Thus, studies of lowland species outside the tropics—but not within the tropics—may well show a trend toward increasing latitudinal range size (e.g., Price et al. 1997). However, if Janzen's seasonality hypothesis explains latitudinal range sizes, then tropical species—at least lowland ones—could also have broad ranges (Gaston and Chown 1999*b*; Colwell 2011). Thus, a careful examination of range sizes across latitude must focus on temperature, not latitude, as the key factor.

Janzen's seasonality hypothesis can also be applied to map vertical distributions. This leads to a testable prediction: species that inhabit the stable temperatures of the soil or abyssal depths are less likely to disperse than those of forest canopies or surface water (Brown 2014; Tomillo et al. 2017). In other words, the soil, forest, or aquatic layer in which a population makes its home may shape the fraction of Earth it occupies. We know of no data for this conjecture, pro or con.

Characterizing the relationship between thermal physiology and range size is an important step forward in understanding the factors affecting species distributions. Janzen predicted that variation in temperature seasonality would influence dispersal, the degree of population isolation, and distributions of both temperate and tropical species, which was counter to discussions at the time that suggested that abiotic and biotic factors were the primary drivers of ecological and evolutionary patterns at higher and lower latitudes, respectively (Dobzhansky 1950; MacArthur 1969). The relative role that biotic versus abiotic factors play in species distributions is largely untested (Schemske et al. 2009; Jankowski et al. 2013). Closing this knowledge gap will help to illuminate range shifts of species in response to climate change and may help us to understand why range shifts have not always followed predicted responses (Lenoir et al. 2010; Chen et al. 2011).

Speciation in the Tropics

The two predictions stemming from Janzen's seasonality hypothesis are that tropical mountain ranges are more likely to act as physiological barriers to movement than temperate ones and that tropical species should thus have reduced dispersal and narrower elevational ranges. An extension of this logic, what we call prediction 3, is that reduced dispersal in the tropics should limit gene flow, resulting in greater population isolation and local adaptation and, thus, in increased rates of speciation in the tropics (Ghalambor et al. 2006; Ricklefs 2006; Martin et al. 2009). Surprisingly, prediction 3 was not the main focus of Janzen (1967). In fact, in the introduction of "Mountain Passes," Janzen (1967) specifically wrote that his article was "not an attempt to explain tropical species diversity . . . but rather to discuss a factor that should be considered in any discussion of the relation between topographic and climatic diversity, and population isolation" (p. 233). However, the idea posed by Janzen (1967) that tropical mountain ranges are more effective barriers to dispersal leads inexorably to reduced gene flow and likely to greater speciation in the tropics, all else equal. So why the contradiction? When asked about this, Janzen wrote,

> Back in those days, "tropical species diversity" was all the rage. I did not want the paper to be seen as one more . . . attempt to blame tropical species richness on one factor. Today I would have the prose maturity to separate the two more unambiguously such that it would not appear that I was . . . negating the obviously true "idea that greater effectiveness of tropical barriers leads inexorably to reduced gene flow and likely to greater speciation, all else equal." Of course it does. But rather, I wanted the readers to not think about that per se but rather about the physiological ecology of the phenomenon itself, because it applies to vastly more things and cases than just the old saw about tropical species richness.

Thus, Janzen had recognized that his seasonality hypothesis could be a mechanism for greater speciation in the tropics. Subsequent research shows that tropical populations have greater genetic (Martin and McKay 2004) and phenotypic (Martin and Tewksbury 2008) divergence, suggesting reduced dispersal, limited gene flow, and greater population isolation in the tropics. A recent analysis of New World mayflies uncovered greater diversity of cryptic species along elevational gradients in the tropics, supporting the idea that limited dispersal in tropical mountains promotes speciation (Gill et al. 2016). Not surprisingly, speciation in African forest biota was found to be greatest in areas characterized by topographic complexity (e.g., montane areas; Fjeldså and Lovett 1997).

The Microgeography of Traits in Ecological Communities

Scaling downward, microclimate gradients within local ecological communities can be used to predict how the mean

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

and range of thermal traits are distributed (Ruibal 1961; Otero et al. 2015).

For example, in a lowland forest in Panama, ants in the canopy experience daytime temperatures 4°–10°C warmer than those in the litter below, a temperature disparity that vanishes at night or under heavily overcast skies. The thermal ecology of the canopy and litter ants match their environment in the way that Janzen's seasonality hypothesis predicts (Kaspari et al. 2015, 2016): the mean thermal maxima of a canopy species averages 3.5°C higher and is broader than that of a species from the cooler, more thermally stable litter.

Studies of the thermal ecology of whole communities remain uncommon but hold the promise to partition drivers of thermal diversity by local versus latitudinal gradients in temperature. The importance of local drivers is hinted at by studies of plant functional traits that reveal a considerable fraction of global trait diversity residing within a given community (Kraft et al. 2008; Hillebrand and Matthiessen 2009; Messier et al. 2010). The Panama ant community described above (Kaspari et al. 2015) accounted for 74% of the thermal diversity found by the global survey of Diamond et al. (2012). Thus, local physiological diversity can be substantial, even in the tropics. What maintains such local variation? One suggestion: competition drives some populations to become "thermal outliers," diverging from the taxon's mean physiological optimum to access less crowded microclimates (MacArthur 1972; Cerda et al. 1998).

A final opportunity for applying Janzen (1967) to ecological communities lies in exploring the effects of seasonal variation on populations that may experience that seasonality very differently. For example, Janzen's OTS students, unlike the TA, had experienced thousands of daily and 20 or so annual temperature cycles during their individual ontogenies. Those 20 years of living in a variable environment were sufficient to generate the phenotypic differences between students and TA that were the genesis of Janzen's observations. However, a quarter of a century before Janzen (1967), Hutchinson (1941) asked us to match an organism's life history to its experience of environmental variation (Potter et al. 2013)—that the passing from one season to the next is a few months in the life of a 10-year-old fish but spans many generations for a unicellular lake phytoplankton. Each generation of algae, Hutchinson (1941) argued, grows up, lives, and dies in a relatively stable physiochemical environment, while the fish in the same pond endures five summers and winters. Across the diversity of life on Earth, the 10^{17} range in body mass generates an hours-to-century range in life spans, and thus we must consider how environmental variation is distributed within versus between generations (Levins 1968; Gilchrist 1995; Weiser et al. 2018). What implications does this have for the distribution of thermal traits with body size?

The Next 50 Years

"Mountain Passes" may have seemed like esoteric natural history in 1967, but Janzen's concepts are now foundational to our understanding of the effects of climate change and have been an integral part of ecology's global change toolkit (Deutsch et al. 2008; Bonebrake 2013). Generating future climatic maps of temperature mean and variation, predicting how they transduce organismal performance, and extrapolating to the geography of populations and communities has never been more relevant given contemporary climate change. How will Janzen (1967) contribute in the next 50 years?

What Is the Future of Temperature Mean and Variation?

Global change modelers working at large spatial scales are increasingly predicting increases in both temperature mean and temperature variation over time (Diffenbaugh and Scherer 2011). Understanding how these changes relate to the operative temperatures of organisms (i.e., translating microclimates into the equilibrium temperature of individuals) and to biological impacts remains a central challenge (Kearney and Porter 2009; Potter et al. 2013). Given that forests generate a variety of microclimates (Otero et al. 2015; Pincebourde and Suppo 2016; Scheffers et al. 2016), including cooler, more stable temperatures in their shaded understories, forests operate as major climate modifiers. Thus, one clear impact of large-scale climate change on the mean and variation of operative temperatures in forested regions would be the loss of forest canopy. Models have suggested that the combination of heat and drought is expected to convert lowland evergreen rain forests into more open, seasonal forests (Malhi et al. 2009) or savannah (Salazar et al. 2007). The resultant shifts in operative temperatures will likely swamp any direct shifts in air temperature. Recent patterns of both tropical and temperate tree mortality have begun to validate these predictions (Laurance et al. 1997; van Mantgem et al. 2009; Silva et al. 2013).

How Does Change in Temperature Variation Shape Individual Performance?

To examine the effects of climate change on species, researchers have typically used shifts in mean temperature to make predictions. Increasingly, ecologists studying the effects of climate change are recognizing something Janzen did 50 years ago: temperature variation is just as important as temperature mean in driving the ecology and evolution of species and, thus, responses to climate change (Gilchrist 1995; Martin and Huey 2008; Williams et al. 2016, 2017). Because species responses to temperature are not linear, small changes in temperature variation can have large biological consequences and greatly alter predictions of climate change

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

(Dillon et al. 2010; Vasseur et al. 2014; Sheldon and Dillon 2016). A productive step in climate change research will be to focus on how changes in temperature variation, rather than mean temperature, shape the physiology, ecology, and evolution of species.

What Are the Consequences for Populations and Communities along Elevational and Latitudinal Gradients?

Janzen's seasonality hypothesis, applied to populations, helps predict which are most at risk of extinction in a warming world. If aseasonal environments favor populations of thermal specialists, with thermal optima closer to thermal maxima, then a given increase in temperature is more likely to drive those species into a thermally untenable situation, resulting in extirpation (Deutsch et al. 2008). A literature review suggests that range contractions have resulted in more local extinctions in tropical (55%) than in temperate (39%) regions (Wiens 2016). At the same time, warming environments provide opportunities for range expansion, especially for ectotherms. Unfortunately, this suggests that tropical diseases, such as malaria, will reach higher latitudes and elevations as mosquito vectors expand their ranges (Siraj et al. 2014), leading to epidemics in areas where people lack immunity and greatly impacting the economies of tropical and extratropical countries (Gallup and Sachs 2001). A key knowledge gap is our ability to predict which populations will be more adept at dispersing to exploit the shifting geography of climate (Colwell et al. 2008; Buckley et al. 2013*b*).

Beyond a simple summation of population responses, Janzen's seasonality hypothesis can be applied to predict how the properties of communities will change in a warming world. First, when whole habitats disappear (e.g., the tundra of a mountaintop), then the assemblage of species specialized to that habitat will likely go with it (Colwell et al. 2008). Second, if populations are becoming extinct locally and colonizing new habitats in a changing world, then communities (assemblages of species) should be experiencing enhanced turnover, and this should be particularly true in the tropics (Lawler et al. 2009; Sheldon et al. 2011). A survey of species turnover across 13 assemblages over 10–159 years (Gibson-Reinemer et al. 2015) suggested mean species turnover of 12% per decade with little net change in diversity. Long-term monitoring studies will be vital to understanding whether community flux is enhanced in the Anthropocene. Perhaps the most intriguing puzzle is how the often considerable intrinsic diversity of a community—within and between species (Kraft et al. 2008; Hillebrand and Matthiessen 2009; Messier et al. 2010, Kaspari et al. 2015)—feeds into its resilience: the ability to retain abundance, form, and function in a changing world. This leads to a basic question, one that has enlivened more than one OTS classroom discussion over the years: Are the hyperdiverse tropics susceptible to disturbance because their populations are hyperspecialized, or are they resilient because they are genetically and phenotypically diverse?

Epilogue: Dan Janzen on the Importance of Natural History Observations

"Mountain Passes" is a natural history observation. Noticing it requires being in the middle of the perturbation and noticing its effects as displayed by the reactions of the participants. It requires no theoretical framework and of course can be "tested" if one has the desire. But it is one of the simple natural history observations that is so clear that replicate samples are likely to be superfluous. Obviously, this observation will not apply to all species and all mountain ranges. Wherein lies the variation can be determined only by experiments and more observations; of course, this was a naturally occurring experiment that alerted me to an ongoing process in nature.

It should be noted that this salami did not require being sliced very thin in order to have it be useful to others. They do their own salami slicing for their own sandwiches, allowing me to enjoy the luxury of being in the forest among many other salamis.

It is fair to say that every one of the papers or processes for which I am "famous" has its origin in such an observation. I did not theorize that acacia ants protect their ant acacias and then test it. I saw it happen in front of me and then decided to repeat it "experimentally" to probe its variation and variance for a formal dissertation (Janzen 1966). The same applies to herbivores and tropical trees (Janzen 1970), toxic seeds (Bell and Janzen 1971), why fruits rot (Janzen 1977), and tropical conservation through biodevelopment (Janzen and Hallwachs 2016). It is fair to acknowledge that the experiments, formalizations, and "theoretical" conceptualizations always came after seeing something happen that was, in effect, a naturally occurring experiment. Nature is full of them. The question is only which of them does *Homo sapiens* care to pay attention to, for whatever agenda, and which does one happen to be carrying enough other contextual information to stimulate noticing.

—Daniel Janzen, January 17, 2017, Área de Conservación Guanacaste

Acknowledgments

We are grateful to Dan Janzen for contributing the prologue, the epilogue, and the historical context for this article. We thank him for inspiring our own work and for his many contributions to research and conservation in the tropics. We thank R. Colwell and D. Kerkhoff for helpful comments on an early version of the manuscript.

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Literature Cited

Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32:194–216.

Bartholomew, G. A. 1966. Interaction of physiology and behavior under natural conditions. Pages 39–45 *in* R. I. Bowman, ed. The Galápagos. University of California Press, Berkeley.

Bell, E. A., and D. H. Janzen. 1971. Medical and ecological considerations of L-Dopa and 5-HTP in seeds. Nature 229:136–137.

Bonebrake, T. C. 2013. Conservation implications of adaptation to tropical climates from a historical perspective. Journal of Biogeography 40:409–414. doi:10.1111/jbi.12011.

Brown, J. H. 2014. Why marine islands are farther apart in the tropics. American Naturalist 183:842–846.

Buckley, L. B., E. F. Miller, and J. G. Kingsolver. 2013*a*. Ectotherm thermal stress and specialization across altitude and latitude. Integrative and Comparative Biology 53:571–581.

Buckley, L. B., J. J. Tewksbury, and C. A. Deutsch. 2013*b*. Can organisms escape the heat of climate change by moving? Proceedings of the Royal Society B 280:1765.

Cadena, C. D., K. H. Kozak, J. P. Gómez, J. L. Parra, C. M. McCain, R. C. Bowie, A. C. Carnaval, et al. 2011. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proceedings of the Royal Society B 279:194–201. doi:10.1098/rspb.2011.0720.

Cerda, X., J. Retana, and A. Manzaneda. 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117:404–412.

Chan, W.-P., I.-C. Chen, R. K. Colwell, W.-C. Liu, C.-y. Huang, and S.-F. Shen. 2016. Seasonal and daily climate variation have opposite effects on species elevational range size. Science 351:1437–1439.

Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Coleman, D. C., and D. A. Crossley. 1996. Fundamentals of soil ecology. Academic Press, New York.

Colwell, R. K. 2011. Biogeographical gradient theory. Pages 309–330 *in* S. M. Scheiner and M. R. Willig, eds. The theory of ecology. University of Chicago Press, Chicago.

Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261.

Cruz, F. B., L. A. Fitzgerald, R. E. Espinoza, and J. A. Schulte II. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. Journal of Evolutionary Biology 18:1559–1574. doi:10.1111/j.1420-9101.2005.00936.x.

Denny, M. W., W. W. Dowd, L. Bilir, and K. J. Mach. 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. Journal of Experimental Marine Biology and Ecology 400:175–190.

Deutsch, C., A. Ferrel, B. Seibel, H.-O. Pörtner, and R. B. Huey. 2015. Climate change tightens a metabolic constraint on marine habitats. Science 348:1132–1135.

Deutsch, C., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the USA 105:6668–6672.

Diamond, S. E., L. M. Nichols, N. McCoy, C. Hirsch, S. L. Pelini, N. J. Sanders, A. M. Ellison, N. J. Gotelli, and R. R. Dunn. 2012. A physiological trait-based approach to predicting the responses of species to experimental climate warming. Ecology 93:2305–2312.

Diffenbaugh, N. S., and M. Scherer. 2011. Observational and model evidence of global emergence of permanent, unprecedented heat in the 20th and 21st centuries. Climatic Change 107:615–624.

Dillon, M. E., M. R. Frazier, and R. Dudley. 2005. Into thin air: physiology and evolution of alpine insects. Integrative and Comparative Biology 46:49–61.

Dillon, M. E., G. Wang, and R. B. Huey. 2010. Global metabolic impacts of recent climate warming. Nature 467:704–706.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist 38:209–221.

Dowd, W. W., F. A. King, and M. W. Denny. 2015. Thermal variation, thermal extremes, and the physiological performance of individuals. Journal of Experimental Biology 218:1956–1967.

Fjeldså, J., and J. C. Lovett. 1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. Biodiversity and Conservation 6:325–346.

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Services 55:1–62.

Gallup, J. L., and J. D. Sachs. 2001. The economic burden of malaria. American Journal of Tropical Medicine and Hygiene 64(suppl.):85–96.

Gaston, K. J., and S. L. Chown. 1999*a*. Elevation and climatic tolerance: a test using dung beetles. Oikos 86:584–590.

———. 1999*b*. Why Rapoport's rule does not generalise. Oikos 84:309–312.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46:5–17.

Gibson-Reinemer, D., K. S. Sheldon, and F. J. Rahel. 2015. Climate change creates rapid species turnover in montane communities. Ecology and Evolution 5:2340–2347. doi:10.1002/ece3.1518.

Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. American Naturalist 146:252–270.

Gill, B. A., B. C. Kondratieff, K. L. Casner, A. C. Encalada, A. S. Flecker, D. G. Gannon, C. K. Ghalambor, et al. 2016. Cryptic species diversity reveals biogeographic support for the "mountain passes are higher in the tropics" hypothesis. Proceedings of the Royal Society B 283:20160553. doi:10.1098/rspb.2016.0553.

Gunderson, A. R., E. J. Armstrong, and J. H. Stillman. 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic environment. Annual Review of Marine Science 8:357–378.

Gunderson, A. R., and J. H. Stillman. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proceedings of the Royal Society B 282:20150401.

Hertz, P. E. 1992. Evaluating thermal resource partitioning. Oecologia 90:127–136.

Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405–1419.

Huey, R. B. 1978. Latitudinal pattern of between-altitude faunal similarity—mountains might be "higher" in the tropics. American Naturalist 112:225–229.

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

———. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91–S115.
Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. Álvarez Pérez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B 276:1939–1948.
Huey, R. B., and P. D. Ward. 2005. Hypoxia, global warming, and terrestrial Late Permian extinctions. Science 308:398–401.
Hutchinson, G. E. 1941. Ecological aspects of succession in natural populations. American Naturalist 75:406–418.
Jankowski, J. E., G. A. Londoño, S. K. Robinson, and M. A. Chappell. 2013. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography 36:1–12.
Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution 20:249–275.
———. 1967. Why mountain passes are higher in the tropics. American Naturalist 101:233–249.
———. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.
———. 1977. Why fruits rot, seeds mold, and meat spoils. American Naturalist 111:691–713.
Janzen, D. H., and W. Hallwachs. 2016. DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservacion Guanacaste, northwestern Costa Rica. Genome 59:641–660.
Kaspari, M., N. A. Clay, J. Lucas, S. Revzen, A. Kay, and S. P. Yanoviak. 2016. Thermal adaptation and phosphorus shape thermal performance in an assemblage of rainforest ants. Ecology 97:1038–1047.
Kaspari, M., N. A. Clay, J. Lucas, S. P. Yanoviak, and A. Kay. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Global Change Biology 21:1092–1102.
Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350. doi:10.1111/j.1461-0248.2008.01277.x.
Kingsolver, J. G., and W. B. Watt. 1983. Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. American Naturalist 121:32–55.
Kingsolver, J. G., and H. A. Woods. 2016. Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. American Naturalist 187:283–294.
Kingsolver, J. G., H. A. Woods, L. B. Buckley, K. A. Potter, H. MacLean, and J. K. Higgins. 2011. Complex life cycles and the responses of insects to climate change. Integrative and Comparative Biology 51:719–732.
Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582.
Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Morona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. Science 278:1117–1118.
Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. Ecology 90:588–597. doi:10.1890/08-0823.1.
Lenoir, J., J.-C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J.-C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33:295–303.
Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.
Levy, O., L. B. Buckley, T. H. Keitt, C. D. Smith, K. O. Boateng, D. S. Kumar, and M. J. Angilletta. 2015. Resolving the life cycle alters expected impacts of climate change. Proceedings of the Royal Society B 282:20150837.
MacArthur, R. H. 1969. Patterns of communities in the tropics. Biological Journal of the Linnean Society 1:19–30. doi:10.1111/j.1095-8312.1969.tb01809.x.
———. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row, New York.
Malhi, Y., L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences of the USA 106:20610–20615. doi:10.1073/pnas.0804619106.
Martin, P. R., F. Bonier, I. T. Moore, and J. J. Tewksbury. 2009. Latitudinal variation in the asynchrony of seasons: implications for higher rates of population differentiation and speciation in the tropics. Ideas in Ecology and Evolution 2:9–17.
Martin, P. R., and J. K. McKay. 2004. Latitudinal variation in genetic divergence of populations and the potential for future speciation. Evolution 58:938–945.
Martin, P. R., and J. J. Tewksbury. 2008. Latitudinal variation in subspecific diversification of birds. Evolution 62:2775–2788.
Martin, T. L., and R. B. Huey. 2008. Why suboptimal is optimal: Jensen's inequality and ectotherm thermal preferences. American Naturalist 171:E102–E118.
McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be "higher" in the tropics. Ecology Letters 12:550–560.
McCain, C. M., and K. Bracy Knight. 2013. Elevational Rapoport's rule is not pervasive on mountains. Global Ecology and Biogeography 22:750–759.
Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? a case for trait-based ecology. Ecology Letters 13:838–848.
Navas, C. A. 1996. Metabolic physiology, locomotor performance, and thermal niche breadth in Neotropical anurans. Physiological Zoology 69:1481–1501.
Navas, C. A., J. M. Carvajalino-Fernández, L. Saboyá-Acosta, L. A. Rueda-Solano, and M. A. Carvajalino-Fernández. 2013. The body temperature of active amphibians along a tropical elevation gradient: patterns of mean and variance and inference from environmental data. Functional Ecology 27:1145–1154.
Oke, T. R. 1978. Boundary layer climates. Routledge, Abingdon.
Otero, L. M., R. B. Huey, and G. C. Gorman. 2015. A few meters matter: local habitats drive reproductive cycles in a tropical lizard. American Naturalist 186:E72–E80. doi:10.1086/682359.
Pacanowski, R. C., and S. G. H. Philander. 1981. Parameterization of vertical mixing in numerical models of tropical oceans. Journal of Physical Oceanography 11:1443–1451.
Payne, N. L., and J. A. Smith. 2017. An alternative explanation for global trends in thermal tolerance. Ecology Letters 20:70–77.
Pincebourde, S., and J. Casas. 2015. Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. Ecology 96:986–997. doi:10.1890/14-0744.1.
Pincebourde, S., and C. Suppo. 2016. The vulnerability of tropical ectotherms to warming is modulated by the microclimatic heterogeneity. Integrative and Comparative Biology 56:85–97. doi:10.1093/icb/icw014.
Porter, W. P., R. Hinsdill, A. Fairbrother, L. J. Olson, J. Jaeger, T. Yuill, S. Bisgaard, W. G. Hunter, and K. Nolan. 1984. Toxicant-disease-

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

environment interactions associated with suppression of immune system, growth, and reproduction. Science 224:1014–1017.
Pörtner, H. O. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comparative and Biochemical Physiology A 132:739–761.
Potter, K. A., H. A. Woods, and S. Pincebourde. 2013. Microclimatic challenges in global change biology. Global Change Biology 19:2932–2939.
Price, T. D., A. J. Helbig, and A. D. Richman. 1997. Evolution of breeding distributions in the Old World leaf warblers (genus *Phylloscopus*). Evolution 51:552–561.
Ragland, G. J., and J. G. Kingsolver. 2008. Evolution of thermotolerance in seasonal environments: the effects of annual temperature variation and life-history timing in *Wyeomyia smithii*. Evolution 62:1345–1357.
Ricklefs, R. E. 2006. Global variation in the diversification rate of passerine birds. Ecology 87:2468–2478.
Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.
Ruggiero, A., J. H. Lawton, and T. M. Blackburn. 1998. The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. Journal of Biogeography 25:1093–1103. doi:10.1046/j.1365-2699.1998.00253.x.
Ruibal, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15:98–111.
Salazar, L. F., C. A. Nobre, and M. D. Oyama. 2007. Climate change consequences on the biome distribution in tropical South America. Geophysical Research Letters 34:L09708. doi:10.1029/2007GL029695.
Scheffers, B. R., D. P., Edwards, S. L. Macdonald, R. A. Senior, L. R. Andriamahohatra, N. Roslan, A. M. Rogers, T. Haugaasen, P. Wright, and S. E. Williams. 2016. Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica 49:35–44. doi:10.1111/btp.12355.
Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.
Seebacher, F., C. R. White, and C. E. Franklin. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. Nature Climate Change 5:61–66.
Shah, A. A., B. A. Gill, A. C. Encalada, A. S. Flecker, W. C. Funk, J. M. Guayasamin, B. C. Kondratieff, et al. 2017. Climate variability predicts thermal limits of aquatic insects across elevation and latitude. Functional Ecology 31:2118–2127. doi:10.1111/1365-2435.12906.
Sheldon, K. S., and M. E. Dillon. 2016. Beyond the mean: biological impacts of cryptic temperature change. Integrative and Comparative Biology 56:110–119. doi:10.1093/icb/icw005.
Sheldon, K. S, A. D. Leaché, and F. B. Cruz. 2015. The influence of seasonality in temperature on elevational range size across latitude: a test using *Liolaemus* lizards. Global Ecology and Biogeography 24:632–641. doi:10.1111/geb.12284.
Sheldon, K. S., and J. J. Tewksbury. 2014. The impact of seasonality in temperature on thermal tolerance and elevational range size of tropical and temperate beetles. Ecology 95:2134–2143. doi:10.1890/13-1703.1.
Sheldon, K. S., S. Yang, and J. J. Tewksbury. 2011. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. Ecology Letters 14:1191–1200.
Silva, C. E., J. R. Kellner, D. B. Clark, and D. A. Clark. 2013. Response of an old-growth tropical rainforest to transient high temperature and drought. Global Change Biology 19:3423–3434.
Sinclair, B. J., K. E. Marshall, M. A. Sewell, D. L. Levesque, C. S. Willett, C. D. G. Harley, D. J. Marshall, B. S. Helmuth, and R. B. Huey. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecology Letters 19:1372–1375.
Siraj, A. S., M. Santos-Vega, M. J. Bouma, D. Yadeta, D. Ruiz Carrascal, and M. Pascual. 2014. Altitudinal changes in malaria incidence in highlands of Ethiopia and Colombia. Science 343:1154–1158. doi:10.1126/science.1244325.
Smith, C., R. S. Telemeco, M. J. Angilletta, and J. M. VandenBrooks. 2015. Oxygen supply limits the heat tolerance of lizard embryos. Biology Letters 11:20150113. doi:10.1098/rsbl.2015.0113.
Stevens, G. C. 1989. The latitudinal gradient in geographical range—how so many species coexist in the tropics. American Naturalist 133:240–256.
———. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. American Naturalist 140:893–911.
Stone, D. E. 1988. The Organization for Tropical Studies (OTS): a success story in graduate training and research. Pages 143–187 *in* Tropical rainforests: diversity and conservation. California Academy of Sciences, San Francisco.
Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B 278:1823–1830.
Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proceedings of the National Academy of Sciences of the USA 11:201316145.
Terborgh, J. 1973. On the notion of favorableness in plant ecology. American Naturalist 107:481–501.
Tomillo, P. S., L. Fonseca, F. V. Paladino, J. R. Spotila, and D. Oro. 2017. Are thermal barriers "higher" in deep sea turtle nests? PLoS ONE 12:e0177256.
van Berkum, F. H. 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. American Naturalist 132:327–343.
van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.
Vasseur, D. A., J. P. DeLong, B. Gilbert, H. S. Greig, C. D. G. Harley, K. S. McCann, V. Savage, T. D. Tunney, and M. I. O'Connor. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proceedings of the Royal Society B 281:20132612.
Vinagre, C., I. Leal, V. Mendonça, D. Madeira, L. Narciso, M. S. Diniz, and A. A. V. Flores. 2016. Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms. Ecological Indicators 62:317–327.
Wake, D. B., and J. F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Scientific Bulletin, Natural History Museum of Los Angeles County 25:1–65.
Weiser, M. D., S. T. Michaletz, V. Buzzard, Y. Deng, Z. He, L. Shen, B. J. Enquist, R. B. Waide, J. Zhou, and M. Kaspari. 2018. Toward

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

a theory for diversity gradients: the abundance-adaptation hypothesis. Ecography 41:255–264. doi:10.1111/ecog.02314.

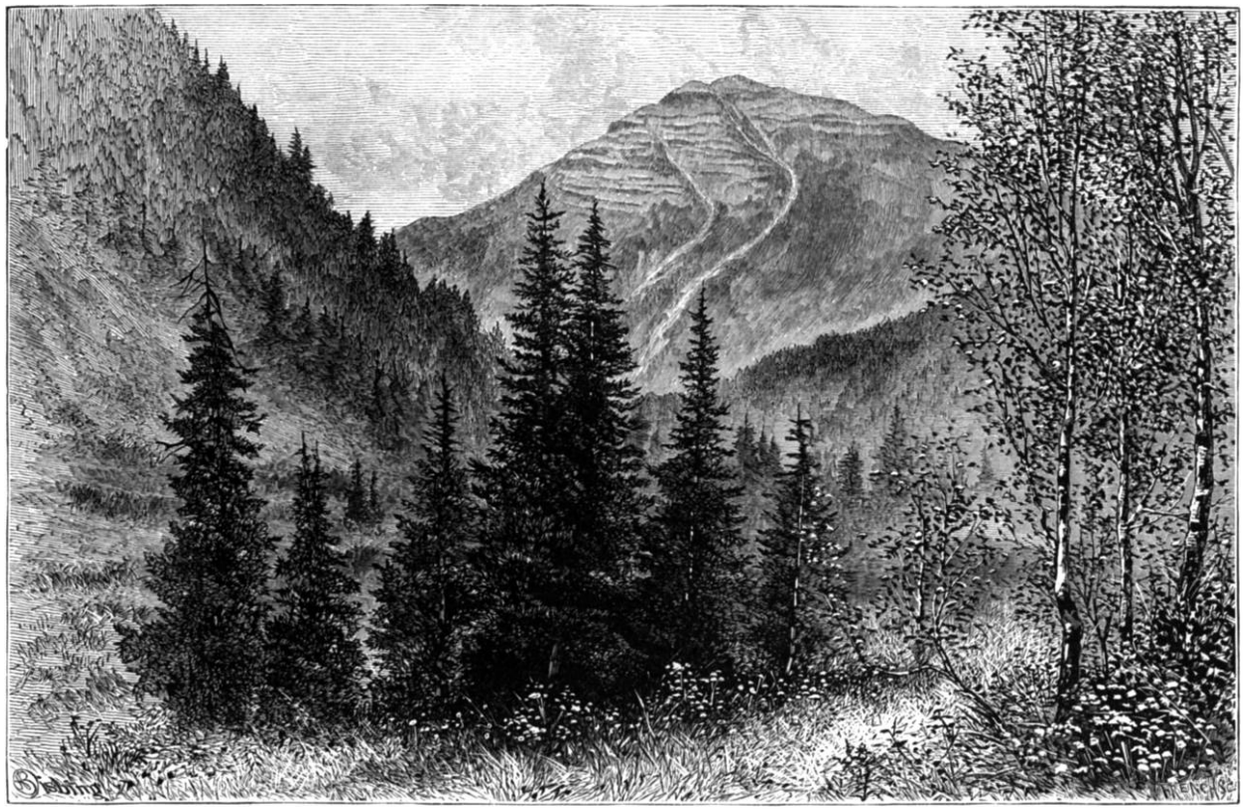
Wiens, J. J. 2016. Climate-related local extinctions are already widespread among plant and animal species. PLoS Biology 14:e2001104. doi:10.1371/journal.pbio.2001104.

Williams, C. M., L. B. Buckley, K. S. Sheldon, M. Vickers, H.-O. Pörtner, W. W. Dowd, A. R. Gunderson, K. E. Marshall, and J. H. Stillman. 2016. Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. Integrative and Comparative Biology 56:73–84.

Williams, C. M., G. J. Ragland, G. Betini, L. B. Buckley, Z. Cheviron, K. Donohue, J. Hereford, et al. 2017. Understanding evolutionary impacts of seasonality. Integrative and Comparative Biology 57:921–933. doi:10.1093/icb/icx122.

Woods, H. A. 2013. Ontogenetic changes in the body temperature of an insect herbivore. Functional Ecology 27:1322–1331.

Editor: Judith L. Bronstein



"*Teocalli mountain*.—On the west side of the Main or Wasatch range, in a nearly direct line from the Twin lakes, is a mountain peak of very singular but interesting appearance. . . . The name was given this peak by the Survey on account of its resemblance to the celebrated sacrificial mound of Mexico." From "Twin Lakes and Teocalli Mountain, Central Colorado, with Remarks on the Glacial Phenomena of that Region" by F. V. Hayden (*The American Naturalist*, 1880, 14:858–862).

This content downloaded from 198.137.018.118 on February 27, 2019 07:24:28 AM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).