# Are mountain passes higher in the tropics? Janzen's hypothesis revisited

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**Synopsis** In 1967 Daniel Janzen published an influential paper titled "Why Mountain Passes Are Higher in the Tropics." Janzen derived a simple climatic-physiological model predicting that tropical mountain passes would be more effective barriers to organismal dispersal than would temperate-zone passes of equivalent altitude. This prediction derived from a recognition that the annual variation in ambient temperature at any site is relatively low in the tropics. Such low variation within sites not only reduces the seasonal overlap in thermal regimes between low- and high-altitude sites, but should also select for organisms with narrow physiological tolerances to temperature. As a result, Janzen predicted that tropical lowland organisms are more likely to encounter a mountain pass as a physiological barrier to dispersal (hence "higher"), which should in turn favor smaller distributions and an increase in species turnover along altitudinal gradients. This synthetic hypothesis has long been at the center of discussions of latitudinal patterns of physiological adaptation and of species diversity. Here we review some of the key assumptions and predictions of Janzen's hypothesis. We find general support for many assumptions and predictions, but call attention to several issues that somewhat ameliorate the generality of Janzen's classic hypothesis.

## Introduction

How climate shapes variation in the physiology, ecology, and evolution of organisms is a fundamental issue for organismal biologists (Dobzhansky, 1950; Andrewartha and Birch, 1954; Pianka, 1966; MacArthur, 1972; Brown *et al.*, 1996; Spicer and Gaston, 1999; Chown *et al.*, 2004*a*). Biologists have long appreciated that abiotic (*e.g.*, temperature, solar radiation, humidity) as well as biotic factors (*e.g.*, competition, predation, parasitism) influence the conditions in which organisms can survive, grow, reproduce, and disperse (*e.g.*, Wallace, 1878; Hutchinson, 1957; Dobzhansky, 1950; Pianka, 1966; Porter and Gates, 1969; MacArthur, 1972; Holt, 2003). Nevertheless, the relative importance of these abiotic and biotic processes, and of their interactions, remains unsettled (Dobzhansky, 1950; MacArthur, 1972; Schemske, 2002; Chase and Leibold, 2003).

Studies of tropical *versus* temperate-zone organisms have been central to these debates, largely because latitudinal gradients in climate are striking and co-vary with conspicuous gradients in species diversity of many taxa (Wallace, 1878; Dobzhansky, 1950; Pianka, 1966; Brown and Lomolino, 1998; Willig *et al.*, 2003). A seminal contribution here is Janzen's (1967) paper "Why mountain passes are higher in the tropics." This paper developed a conceptual framework for examining how latitudinal variation in climate should shape the evolution of physiological tolerances and, in turn, should determine topographic resistance to dispersal and, through this, influence geographic range size. For many biologists, Janzen's paper provides a logical—indeed a necessary—starting place for discussions of latitudinal gradients in species diversity, physiological adaptation, and related phenomena.

Janzen (1967) began by explicitly assuming that the effectiveness of a topographic barrier to dispersal depends mainly on the magnitude of the temperature gradient across that barrier and less on the actual change in altitude. Thus mountain passes are *physiological*, not topographic, barriers to dispersal. Consequently, a mountain pass will be a greater physiological barrier *if* there is relatively little overlap in climate between a low-altitude valley and an adjacent high-altitude pass.

Janzen next argued that the greater seasonal uniformity of temperature at tropical localities would 1) necessarily result in low overlap in climate between valleys and mountain passes and 2) select for organisms that had narrow tolerances to temperature. He then linked these assumptions and predicted that tropical organisms would have greater difficulty crossing

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mountain passes (than would temperate-zone organisms) because they would be more likely to encounter a climate to which they were not adapted. Or, to use Janzen's own evocative words, "mountain passes are 'higher' in the tropics." Reduced dispersal across tropical passes should in turn lead to greater genetic divergence between populations, enhance allopatric speciation, and potentially result in greater species packing along altitudinal gradients.

The individual steps in Janzen's model seem logical and obvious in retrospect, but that was not the case in the 1960s. Janzen was ahead of the crowd and raised ideas that would later be embraced as areas of productive research. He was thinking about barriers to dispersal and isolation of populations long before many biologists became sensitized to population fragmentation. He appreciated the ecological and evolutionary effects of climate on physiological tolerances and capacities long before the field of evolutionary physiology existed (Garland and Carter, 1994). And, he challenged the contemporary dogma of his day (*e.g.*, Dobzhansky, 1950), which held that abiotic (climate) effects dominated ecological and evolutionary patterns in the temperate zones, whereas biotic effects dominated in the tropics. Thus, Janzen provided a novel perspective for the crucial role abiotic effects and physiological tolerance could play in understanding patterns observed in the tropics.

In the decades since its publication, Janzen's (1967) hypothesis has remained at the center of debates of latitudinal gradients in diversity and ecology (*e.g.*, Schemske, 2002); and it has inspired numerous studies in physiology, biogeography, and evolutionary ecology. Nevertheless, many of the assumptions and predictions of this hypothesis have never been systematically tested or critically evaluated.

Here we revisit Janzen's (1967) hypothesis. Our goals are to highlight general patterns and to lay a foundation for future inquiry, not to present an exhaustive review. We begin by re-describing the hypothesis itself. Then we evaluate some of its key assumptions and predictions. We draw largely on studies of vertebrate ectotherms (amphibians and lizards) because these taxa are physiologically sensitive to variation in temperature, because they have been studied extensively from the perspective of Janzen's hypothesis, and because these studies have used relatively consistent methodologies, thus facilitating comparisons.

## Janzen's hypothesis: A précis

Janzen's hypothesis is a consequence of a series of logical steps. It emerges fundamentally from considerations of climatic variation, then from the evolutionary impact of that variation on physiology, and finally from the role of physiology in determining differences in dispersal and biogeographic patterns between temperate and tropical environments.

That thermal regimes are more constant in the tropics compared to the temperate zones has long been common knowledge. However, Janzen focused on the consequences of that tropical constancy on the *overlap* in thermal regimes of sites separated by altitude (Fig. 1). He noted that lowland forests in the tropics are always warm, whereas high-altitude tropical forests are always significantly cooler. Consequently, altitudinally separated sites in the tropics will have little overlap in their thermal regimes at any given time or even over the course of a year (Janzen, 1967, pp. 236–237). Temperate zones show a strikingly different pattern because both low- and high-altitude sites experience marked seasonal variation in temperature. So, even though high-altitude sites in the temperate zones are of course colder at any given season than are low-altitude ones, high-altitude sites can nonetheless be warm in summer, whereas low-altitude sites can be cool in winter (Fig. 1). As a result, both low- and high-altitude sites in the temperate zones have considerable overlap in thermal regimes, at least computed over a full year (Janzen, 1967, pp. 236–237).

Janzen next explored the physiological consequences of climate variation. He explicitly assumed that organisms should evolve physiological adaptations that reflect the range of climatic variation typically encountered. Thus, temperate zone organisms would need to evolve broad thermal tolerances as well as marked acclimation capacities to cope with the large seasonal changes in climate. In contrast, tropical organisms would evolve narrow thermal tolerance and reduced acclimation responses, appropriate to the less variable climate of the tropics.

Janzen melded these climatic and physiological considerations into a bold prediction: tropical mountain passes should be more effective barriers to dispersal than temperate-zone passes of equivalent altitude, simply because tropical organisms attempting to move up (or down) a mountain would likely encounter temperatures to which they are neither adapted nor acclimated. By contrast, temperate-zone organisms should be less constrained by temperature when moving up or down a mountain pass. Thus, mountain passes should be physiologically "higher in the tropics" and impose greater fitness costs to dispersal (Fig. 1).

Janzen (1967) emphasized that he did not intend his model to serve as an explanation for tropical species diversity. Even so, his model is relevant to this issue because his arguments lead directly to the prediction that altitudinally separated populations in the tropics will experience reduced gene flow leading to greater

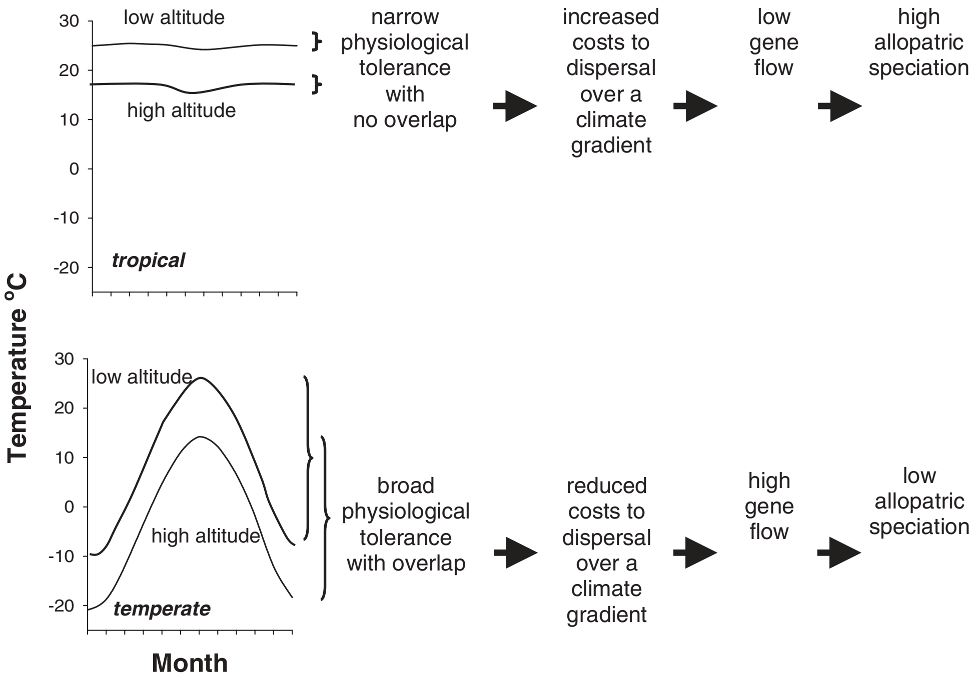


**Fig. 1** A schematic summary of the primary steps making up Janzen's (1967) hypothesis. Shown are seasonal changes in air temperature for low- and high-altitude sites in a tropical and temperate location. Seasonality in the temperate zone results in the broad overlap of temperatures experienced at high and low altitudes, but a lack of seasonality in the tropics results in no overlap. Janzen (1967) assumed that this climatic difference should favor broadly overlapping physiological tolerances between populations separated by altitude in the temperate zone, leading to a reduction in dispersal costs over an altitudinal gradient. In contrast, he predicted that a lack of seasonality in the tropics should favor narrow tolerances with little overlap between populations separated altitudinally and increased costs to dispersal. The obvious consequence is high rates of dispersal and gene flow between populations and a reduction in the potential for population differentiation and speciation in the temperate zone, whereas, in the tropics gene flow is reduced and the potential for population differentiation and speciation is increased.

genetic divergence, setting up the conditions that favor accelerated rates of allopatric speciation (Fig. 1).

## Key assumptions

At first glance, Janzen (1967) provides a simple and elegant hypothesis that links climate, physiology, and dispersal. However, many of the assumptions underlying the hypothesis have not been critically examined. Here we revisit four key assumptions and then examine the main predictions derived from this hypothesis.

### Assumption 1: The effectiveness of a topographic barrier depends on the magnitude of the temperature gradient across that barrier

Janzen (1967, p. 234) proposed that a mountain pass is a barrier to dispersal primarily because of the climatic challenges it imposes on the physiology of organisms. For example, a lowland organism, which should be adapted to warm temperatures, might not be able to withstand the low temperatures it would encounter at high elevations when attempting to cross a mountain pass. Janzen presented no data to bolster this assumption. Mountains do pose significant barriers to dispersal in diverse taxa (*e.g.*, Slechtova *et al.*, 2004; Forister *et al.*, 2004; Funk *et al.*, 2005; Huey and Ward, 2005). For example, the lowland Puerto Rican lizard (*Anolis cristatellus*) survives for only a few hours at the minimum temperatures occurring at 600 m (Heatwole *et al.*, 1969). However, it is still not known whether the cause is the magnitude of the temperature gradient or some other factor that covaries with altitude, or even whether the same factors are most important across taxa. Even so, Janzen's assumption seems reasonable for many ectotherms, though it would be less so for endotherms, which are relatively buffered against environmental temperatures (Porter and Gates, 1969). Identifying the relative importance of temperature in constraining dispersal patterns across altitudinal gradients is of growing interest given the prospects for climate change (*e.g.*, Porter *et al.*, 2002).

We see two general ways to test the role of temperature change in limiting dispersal across a topographic barrier. One approach involves developing theoretical models that integrate operative environments (see *Assumption 2*, below), bioenergetics and physiological structure, with population dynamics (Dunham *et al.*, 1989; Porter, 1989; Dunham, 1993; Porter *et al.*, 2002; Buckley and Roughgarden, 2005). Such models are increasingly powerful and predict how population energetics and dynamics change with local climate (Porter *et al.*, 2002). Thus, one test of Janzen's assumption is to compute the "potential" altitudinal ranges of tropical and temperate zone species; if Janzen is correct, tropical species should have narrower potential ranges than do temperate zone species.

Alternatively, one might do reciprocal transplants, such as to transplant low-altitude individuals to various higher altitudes, and then determine empirically the maximum altitude at which they can grow and reproduce. An elegant example of this approach is work by Angert and Schemske (2005) with monkey flowers (*Mimulus*) in the Sierra Nevada of California. If parallel studies were done on related species in both the tropics and in the temperate zones, one could not only determine whether tropical species sustain populations over smaller altitudinal ranges than do temperate zone species, but also elucidate the role climatic factors play in causing variation in fitness (see Angert and Schemske, 2005). To our knowledge, such matched reciprocal transplants have never been done at different latitudes.

Note that neither approach quantifies dispersal ability per se; rather, they estimate the range of altitudes over which populations are sustainable. Certainly, many animals can disperse though environments that are otherwise unsuitable on a long-term basis, yet few studies to date have considered how habitat suitability shapes dispersal and colonization patterns. One weakness of this assumption—as Janzen appreciated—is that many environmental variables (not just temperature) may influence dispersal patterns and altitudinal ranges (Porter, 1989; Porter *et al.*, 2002; Gaston, 2003; Navas, 2005). For example, biotic interactions such as interspecific competition can also modulate ranges (Davis *et al.*, 1998*a*, *b*; Porter *et al.*, 2002; Case *et al.*, 2005; Buckley and Roughgarden, 2005). Moreover, different taxa may be limited by different variables—many plants, for example, may be limited by patterns of water availability, rather than temperature (Hawkins *et al.*, 2003). Thus even if insects that rely on these plants are limited by temperature, they are further constrained by the precipitation requirements of their host (Huey, 1978). Further, slope, insolation (*i.e.*, amount of incoming solar radiation), and canopy structure could also have important interacting influences (Porter *et al.*, 2002). Thus, testing this assumption by identifying factors responsible for limiting dispersal and geographic ranges is likely to be a challenging endeavor.

### Assumption 2: Latitude, seasonality, and altitude influence between-altitude climate overlap

Janzen's second assumption is actually an insightful observation; the overlap in temperature regimes over a year between low- and high-altitudes is greater in the temperate zones than in the tropics. He illustrated this pattern with graphs of seasonal changes in air temperature at low- versus high-altitude sites from the tropics and the north temperate zone and showed quantitatively that the between-altitude overlap in temperature was much greater in the temperate zone than in the tropics (Janzen, 1967, *pp.* 235–237).

Janzen's global climatic template is inarguable, as it follows directly from the angle of the earth's axis of rotation relative to the sun (MacArthur, 1972), and from the independence of the adiabatic lapse rate with latitude (Dillon *et al.*, 2005). Even so, several other climatic issues complicate this pattern and have implications for the patterns of physiological adaptation we should expect in temperate and tropical organisms. We discuss some of these complications below.

Janzen's hypothesis is driven by the greater seasonal variation in temperature in temperate, but not tropical locations. However, marked seasonal variation occurs mainly at temperate latitudes in the northern hemisphere (Addo-Bediako *et al.*, 2000; Chown *et al.*, 2004*b*), not in the southern hemisphere (Fig. 2A), where the proximity of the oceans buffers winter temperatures (Addo-Bediako *et al.*, 2000; Chown *et al.*, 2004*b*). Thus, had Janzen (1967) compared temperatures from his sites in Costa Rica with sites in either the southern Andes or southern Africa, he might have been somewhat less impressed about the "low" height of temperate zone mountain passes. Moreover, increased seasonality at high latitudes in the northern hemisphere is primarily driven by cold winter temperatures (Fig. 2B), as warm summer temperatures vary less with latitude (Fig. 2C). Clarifying these climatic patterns is important, because they provide insight into the kinds of physiological adaptations to temperature we should expect at a global scale. For example, if large seasonal changes in temperature select for a broad physiological tolerance, then organisms at high latitudes in the northern hemisphere should show a much greater tolerance than organisms occupying equivalent latitudes in the southern hemisphere: this is indeed the case in insects (Addo-Bediako *et al.*, 2000). In addition, because seasonality is primarily driven by cold winter temperatures in the north, physiological adaptation

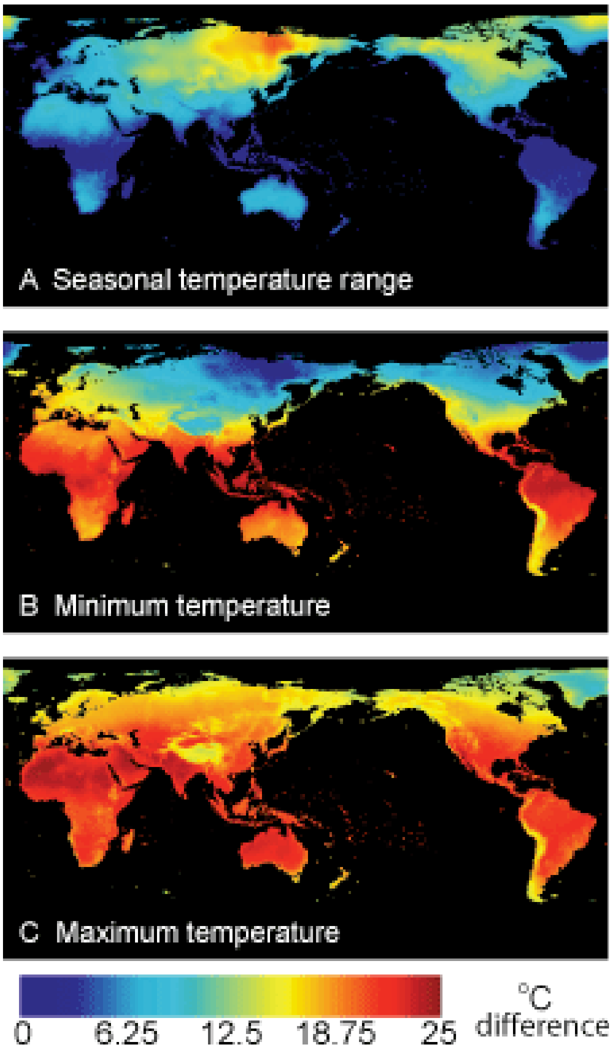


**Fig. 2** Global patterns of temperature, showing that the latitudinal gradient of seasonality is caused mainly by a strong gradient in minimum temperature and less by the gradient in maximum temperature. A) Seasonal range of monthly temperatures (mean daily maximum of the warmest month minus mean daily minimum of the coldest month). B) Mean daily minimum temperature of the coldest month. C) Mean daily maximum temperature of the warmest month. In A) colors are normalized to the site with the least seasonal variation (set to deep blue). In B) colors are normalized from the coldest site (set to deep blue). In C), colors are normalized to the warmest site (set at deep red); Temperature data are from New *et al.* (1999) and are based on 720 by 360 grid.

should be driven more by a greater tolerance to cold temperatures at high latitudes in the north, rather than greater tolerance to warm temperatures near the equator (see below).

Janzen (1967) emphasized the importance of *seasonal* changes in temperature. However, *diurnal* changes in temperature may also drive physiological adaptation, especially at high altitudes in the tropics (see below). Insolation and diurnal temperature fluctuations are generally greater in low-latitude mountains than in high-latitude ones and the magnitude of daily variation in temperature at high altitude in the tropics can match the magnitude of seasonal variation in the temperate north because of the combination of thin air and the vertical angle of the sun's rays near the equator (Mani, 1968; Sarmiento, 1986). In other words, at very high altitudes in the tropics, organisms may experience summer-like conditions during the day and winter-like conditions at night every day of the year (Mani, 1968). Therefore, with increasing altitude, tropical organisms might need to evolve relatively broad thermal tolerances to cope with the increasing diurnal changes in temperature, contrary to Janzen's expectation.

Although seasonal variation in atmospheric temperature is great at high latitudes, organisms living there might nonetheless be active over relatively narrower ranges of *body* temperatures or simply escape unfavorable climatic conditions. Indeed, ectotherms typically restrict activity periods in seasonal environments (Stevenson, 1985) and spend prolonged periods of hibernation in protected sites (Mani, 1968). Similarly, endothermic mammals and birds at northern latitudes exhibit hibernation and migration strategies that have no equivalent in the tropics. As a result, selection for broad thermal tolerances might be somewhat buffered by behaviors that shield organisms from the seasonal changes in temperature (Huey *et al.*, 2003).

Finally, Janzen (1967) focused on air temperature ($T_a$). However, the thermal environment of organisms is now known to be better characterized (Bakken, 1992) by operative environmental temperature ($T_e$, for ectotherms) and by standard operative temperature ($T_{es}$, for endotherms). Because $T_e$ estimates the equilibrium body temperature of a specified ectotherm in a specified spot, it is the preferred index of the thermal environment for ectotherm physiology and ecology (Huey, 1991; Dunham, 1993; Porter, 1989). An interesting exercise would be to repeat Janzen's computation of between-altitude overlap in climate but to substitute $T_e$ for $T_a$.

## Assumption 3: Tropical organisms have narrow ranges of thermal tolerance independent of altitude

Janzen (1967, p. 241) stated that organisms are less likely to "... evolve mechanisms to survive at a given temperature if that temperature falls outside of the temperature regime of the organism's habitat than if it falls within it." Thus, tropical organisms should have relatively narrow thermal tolerances (*e.g.*, difference between critical thermal minimum [$CT_{min}$] and maximum [$CT_{max}$] temperatures). This assumption can be tested with various lines of evidence. First, determine whether tropical organisms experience narrower ranges of body temperature ($T_b$) than do temperate zone organisms. Second, determine whether tropical organisms have narrow tolerance zones. Finally, determine whether overlap in thermal tolerance among altitudinally separated tropical populations is reduced compared to temperate populations. If Janzen is right, then high-altitude populations in the tropics should have a narrow tolerance for cooler temperatures whereas low-altitude populations should have a narrow tolerance for warmer temperatures.

Testing whether tropical organisms experience a more narrow range of $T_b$ can be complicated by a variety of factors. For example, even though temperate zones have relatively variable thermal regimes, organisms living there might not have relatively variable $T_b$: as noted above, many ectotherms have effective thermoregulatory behaviors that reduce variation in $T_b$ (Stevenson, 1985), and others simply migrate or hibernate during cold periods. Unfortunately, data on latitudinal patterns in $T_b$ variability (on daily or seasonal bases) have not been compiled systematically. However, despite these complications, the few available compilations of $T_b$ data are consistent with the expectation that $T_b$ variability is reduced in the tropics and increases with latitude in both salamanders (Feder and Lynch, 1982) and lizards (van Berkum, 1988).

Do high- and low-altitude tropical species have narrow ranges of $T_b$? Janzen assumed this was the case. However, the marked diurnal shifts in operative environmental temperature at high altitude in the tropics (driven by high radiant heat loads during the day and by cold nights) might well increase variance in $T_b$. For example, $T_b$ of the lizard *Liolaemus multiformis* (at altitude of 4,300 m in tropical Peru) covers a large range from $\sim 7°$ to 33°C during the day (Pearson and Bradford, 1976) which is comparable to temperate zone lizards. To date, the magnitude of such diel shifts remains to be quantified systematically with respect to latitude, but this pattern is supported by data on other lizards (van Berkum, 1988). Moreover, mean $T_b$ often decreases with increasing elevation in tropical *Anolis* lizards (Heatwole *et al.*, 1969; Ruibal and Philibosian, 1970; Huey and Webster, 1976; Hertz, 1981; van Berkum, 1986) and in tropical salamanders (Feder and Lynch, 1982). Interestingly, mean $T_b$ also drops significantly with increasing altitude in tropical *Sceloporus* (a group known to use behavioral thermoregulation) but not in temperate zone species (Andrews, 1998), suggesting that tropical species at high altitude are either more cold adapted or unable to maintain a preferred $T_b$ (Andrews, 1998).

Do temperate zone organisms have relatively broad thermal tolerances, and (if so), do broad thermal tolerances reflect mainly increased cold tolerance, as suggested by climate data (Fig. 2)? Using data from Brattstrom (1968) for amphibians, Snyder and Weathers (1975) showed that tolerance ranges do increase with latitude and consistent with the observation that temperate zone seasonality is driven by cold winter temperatures, this increase is driven by changes in $CT_{min}$ (Fig. 3). Van Berkum (1988) and Addo-Bediako *et al.* (2000) found similar latitudinal patterns for lizards and insects, respectively, and in both cases, changes in $CT_{min}$ are greater than changes in $CT_{max}$. Furthermore, high-latitude insects in the Southern Hemisphere have markedly narrow tolerance ranges compared to high-latitude species in the Northern Hemisphere, again consistent with the greater seasonality in the Northern Hemisphere (Addo-Bediako *et al.*, 2000; Fig. 2A).

Are narrow tolerance ranges characteristic of high-altitude as well as low-altitude species in the tropics, and are high-altitude tropical species specialized for lower temperatures than are low-altitude tropical species? Janzen's (1967) hypothesis assumes that both are true and are the underlying reason for greater species turnover along tropical altitudinal gradients. However, although lowland tropical species generally do have narrow tolerance ranges (see above), results to date show that high-altitude tropical species in fact can have broad tolerance ranges. For example, tolerance ranges (Brattstrom, 1968) of some high-altitude tropical amphibians converge on those of high-altitude temperate zone species (Fig. 4), mainly because $CT_{min}$ declines relatively quickly within increasing altitude in tropical species. More recent studies (*e.g.*, Navas, 1996, 2005; Luddecke and Sanchez, 2002) also suggest that high-altitude tropical amphibians perform well over broader ranges of temperatures than do their low-altitude counterparts. This pattern of increasing tolerance with increasing altitude in the tropics is also observed in the less seasonal south temperate zone. For example, lizards from the mountains of central Chile (Carothers *et al.*, 1997) and southeastern Australia (Spellerberg, 1972), which are temperate zone areas but with low seasonality (Fig. 2A), also show an increasing thermal tolerance range with increasing altitude, mainly because of a decline in $CT_{min}$, suggesting that physiological adaptations to altitude may be similar between the tropics and south temperate zone.

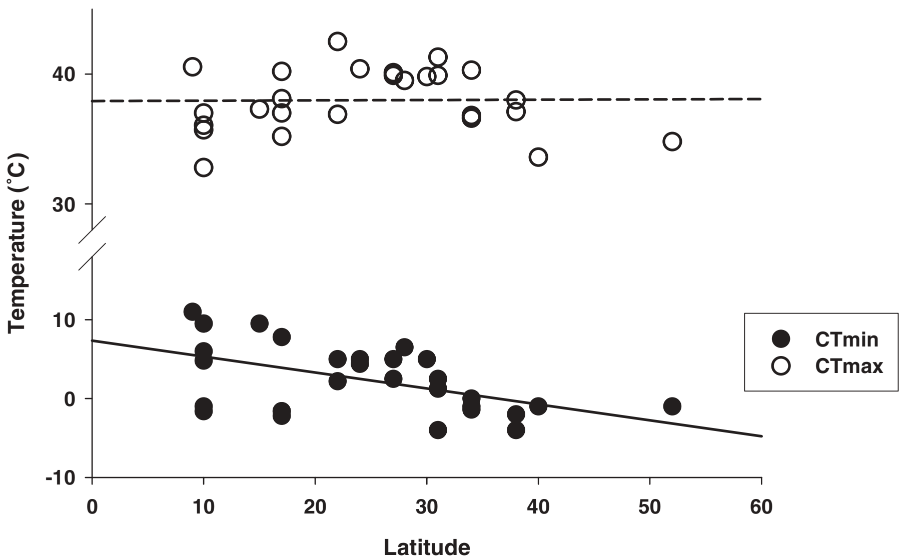


**Fig. 3** Changes in $CT_{min}$ and $CT_{max}$ as function of latitude in frogs (data from Brattstrom 1968). $CT_{min}$ (filled circles) is highly negatively correlated with latitude ($p < 0.05$). $CT_{max}$ (open circles) represent individuals acclimated between 26°C and 30°C (if more than one value existed for a species the mean was taken). $CT_{max}$ is not correlated with latitude ($p > 0.70$).

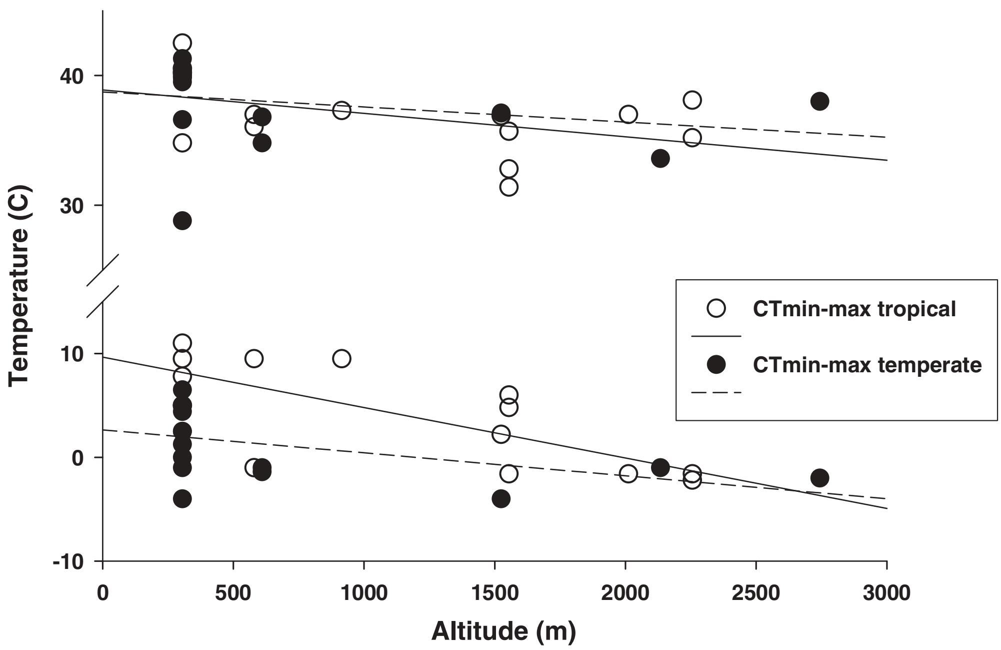


**Fig. 4** Change in $CT_{min}$ and $CT_{max}$ in temperate and tropical frogs as a function of altitude (data from Brattstrom 1968). $CT_{min}$ decreases with increasing altitude in tropical ($p < 0.01$), but not temperate ($p > 0.05$) frogs, although the interaction between the two is not significant ($p = 0.12$). $CT_{max}$ was not significantly correlated with altitude ($p > 0.05$) in both tropical and temperate species.

Compilations of temperature and tolerance data are obviously limited, but available patterns are generally consistent with Janzen's (1967) assumptions. Specifically, north temperate zone species have more variable $T_b$ than do tropical species; and temperate zone species have relatively broad thermal tolerances, primarily because they are much more cold tolerant. Nevertheless, tropical species living at high altitude can have variable $T_b$ and can also be relatively cold and warm tolerant, probably reflecting the consistent cooler temperatures and marked diurnal, rather than seasonal, shifts in temperature (see also Gaston and Chown 1999). Thus, not all tropical species have narrow tolerance ranges. What are needed now are systematic studies that explore how altitude affects $T_b$ variation, tolerance zones and "performance breadths," for example, VanDamme *et al.* (1989) of tropical and temperate-zone representatives of diverse taxa.

## Assumption 4: Tropical organisms evolve limited acclimation responses

Janzen (1967) predicted that tropical organisms would not only have relatively small tolerance zones, but also have limited acclimation responses. Janzen presumably assumed that acclimation is favored only in seasonal environments, where the benefits of physiological compensation would outweigh the costs (*e.g.*, Hoffmann, 1995) of maintaining the capacity to acclimate.

Only a year after Janzen (1967), Brattstrom (1968) reported that temperate and tropical amphibians had similar ranges of acclimation ability. (Note: Most of Brattstrom's tropical species died (85%) when acclimated to low temperature (5°C), whereas most of his temperate zone species survived (25%). Thus, acclimation responses were measured over a relatively broader range of temperatures for the temperate zone species, confounding this tropical versus temperate-zone comparison.). However, subsequent studies generally support Janzen's expectation (1967) that acclimation responses increase with latitude. Feder (1978, 1982) found that all temperate zone amphibians ($N = 22$) showed significant acclimation of metabolism to temperature, but that only one of seven tropical species did so. Similarly, Tsuji (1988) showed that two populations of a temperate zone lizard showed greater metabolic acclimation to temperature than did a related tropical species.

Whether acclimation ability varies with altitude for a broad range of organisms (and does so differently in the tropics and the temperate zones) is currently unclear, simply because too few studies are available. Interestingly, however, those tropical amphibians that do show acclimation responses are from high altitude (see Brattstrom, 1968). Moreover, Patterson (1984) found that high-altitude (but not low-altitude) populations of the lizard *Mabuya striata* from tropical Africa exhibit significant thermal acclimation in resting metabolic rate. In contrast, Rogowitz (1996) found no difference in acclimation between high- and low-altitude *Anolis* from Puerto Rico; but the maximum altitude on Puerto Rico is less than 1400 meters.

Although empirical data are limited, tropical organisms—at least low-altitude ones—seem to show relatively limited acclimation responses as Janzen (1967) expected. Even so, some tropical species at high altitude may experience selection for enhanced acclimation in response to diurnal rather than seasonal fluctuations in temperature.

## Main predictions: Tropical organisms have reduced dispersal across elevational gradients and have reduced between-altitude overlap of their distributions

Janzen's (1967) main prediction is that mountain passes in the tropics are more effective "physiological" barriers to dispersal than are passes in the temperate zones. If so, two patterns should be evident. First, tropical species should have relatively reduced rates of dispersal up and down mountains. Second, tropical species should have relatively restricted altitudinal ranges, such that between-altitudinal faunal and floral overlaps would be reduced.

Is dispersal reduced along tropical mountains? Unfortunately, such dispersal rates of tropical and temperate zone species have never been systematically compared, at least to our knowledge. However, molecular markers are increasingly being used to track patterns of gene flow; and this may represent a future opportunity to quantify the magnitude of dispersal patterns. The few studies along these lines so far hint that gene flow may be reduced in the tropics as a whole and also between tropical populations separated by altitude; Martin and McKay (2004) found that tropical species exhibit greater isolation by distance than do temperate species, consistent with an expectation of reduced dispersal in the tropics. In addition, tropical populations show reduced gene flow and greater isolation by distance in various insect (*e.g.*, Eber and Brandl, 1994; West and Black, 1998; Aulard *et al.*, 2002) and plant species (Arias and Rieseberg, 1994; Murillo and Rocha, 1999; Thomas *et al.*, 2002). Nevertheless, much more data are required before we know whether latitude influences altitudinal resistance to dispersal, much less the mechanisms behind those patterns.

Are altitudinal ranges relatively restricted in the tropics? Here available data are strongly supportive: this pattern seems general and is documented in comparisons of herpetofaunas (*e.g.*, Heyer, 1967; Wake and Lynch, 1976; Huey, 1978; Navas, 2002), birds (*e.g.*, Terborgh, 1977; Rahbek, 1997; Rahbek and Graves, 2001; Herzog *et al.*, 2005), and plants (*e.g.*, Smith, 1988; Lieberman *et al.*, 1996). Similarly, between-altitudinal faunal similarity of amphibians and reptiles is reduced in the tropics (Wake and Lynch, 1976; Huey, 1978; Fig. 5).

These biogeographic patterns are consistent with Janzen's (1967) predictions, but again the underlying mechanisms for these patterns remain largely untested. To be sure, the mechanisms limiting ranges are more complex than outlined in Janzen (1967), who focused more on current dispersal patterns and not necessarily

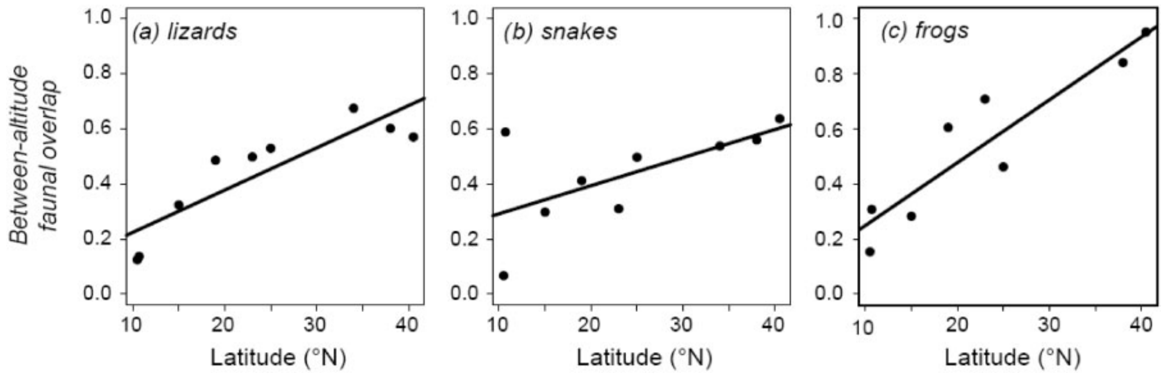


**Fig. 5** Patterns of between-altitude faunal overlap for lizards, snakes, and frogs versus latitude. Faunas separated by altitude are much more similar in the temperate zone than in the tropics (based on data in Huey, 1978).

on geographic ranges and distributions. Indeed, altitudinal ranges are often limited by biotic factors, not just by physiological ones (Davis *et al.*, 1998*a*,*b*; Gaston, 2003; Navas, 2005). For example, limits to ranges are thought to be constrained—or at least influenced—by biotic factors such as interspecific competition (Case and Taper, 2000; Case *et al.*, 2005), predation (Dekker, 1989), and parasitism (Briers, 2003). Thus many factors are likely to influence altitudinal range limits, and the primary factors setting these limits may vary even among close relatives (Carothers *et al.*, 1997, 2001).

## Discussion

Was Janzen (1967) right? Are mountain passes higher in the tropics? A definitive answer to this question remains elusive because of the difficulty in linking patterns to underlying processes. Nevertheless, considerable evidence supports many of the major assumptions and predictions.

Not surprisingly, Janzen's (1967) global climatic template is valid for temperature. Temperate zone sites do show much greater seasonal variation in ambient temperature than do tropical sites. Moreover, altitudinally separated sites in the temperate zones have greater overlap in ambient temperature than do similarly separated sites in the tropics. However, the seasonality of the temperate zones is now realized to be primarily a Northern Hemisphere phenomenon (Fig. 2), because the proximity of southern landmasses to oceans buffers climatic extremes there (see also Addo-Bediako *et al.*, 2000; Chown *et al.* 2004*b*). Thus tropical mountain passes may be higher than north temperate zone passes, but they are probably less so compared with south temperate zone ones. Moreover, high-altitude tropical sites can also experience greater daily fluctuations in temperature compared to similar altitudes in temperate locations. In any case, Janzen's global climatic template needs to be recomputed using operative environmental temperatures rather than ambient temperature (Bakken, 1992) and to allow for expression of behavioral and other adaptations that buffer variation in ambient temperatures (Stevenson, 1985; Cossins and Bowler, 1987; Huey *et al.*, 2003).

Janzen (1967) expected that the observed variation in climatic patterns would influence the evolution of physiological capacities. Specifically, he expected that body temperature variation, thermal tolerance ranges, and acclimation capacities would all increase with latitude. Available data generally support this expectation. However, some tropical species living at higher altitudes also appear to experience variable body temperatures, have broad tolerance ranges, and can acclimate to temperature; a result not anticipated by Janzen but still consistent with his general assumption that organisms adapt or acclimate to the temperatures they normally encounter.

What about Janzen's (1967) prediction that dispersal up and down a tropical mountain should be restricted relative to that in the temperate zones? To our knowledge, this prediction has never been directly tested. However, many tropical species have greater isolation by distance (Martin and McKay, 2004), do occupy relatively narrow altitudinal distributions (Wake and Lynch, 1976; Huey, 1978), and do show reduced overlap in altitudinal ranges (Huey, 1978: Lieberman *et al.*, 1996; Rahbek and Graves, 2001). This is consistent with the prediction that altitudinal dispersal is more restricted in the tropics than in the temperate zones (Wake and Lynch, 1976; Huey, 1978).

In addition to predicting that tropical mountains should be "higher," Janzen also predicted that tropical valleys should be "lower" for high-altitude species (Janzen, 1967, p. 243). However, the evidence to date suggests that high-altitude tropical species have broader thermal tolerances than do low-altitude species, primarily because they have relatively greater tolerance to cold (Figs. 3 and 4; Navas, 2005). Therefore, resistance to dispersal up versus down tropical mountains may be asymmetric. Lowland tropical species may be restricted to low altitude because of their limited tolerance to cold (*e.g.*, Heatwole *et al.*, 1969); but upland tropical species, which do have high heat tolerance as well as cold tolerance, should be able to move to relatively low altitudes.

How can we reconcile these patterns of thermal tolerance with the observed narrow altitudinal bands occupied by many upland tropical taxa? One possible explanation could involve evolutionary trade-offs between broad thermal tolerances and the competitive environment. For example, if broad thermal tolerances evolve at a cost to performance and to competitive ability (Huey and Slatkin, 1976; Gilchrist, 1995), then high-altitude species might be unable to disperse to lower elevations because they are competitively inferior to lowland species, not because they are physiologically incapable of surviving there. Indeed, range limits along elevational and other environmental gradients often reflect interactions between physiological tolerance and competitive interactions and are common in a wide range of taxa (Connell, 1961; Bovbjerg, 1970; Jaeger, 1971*a*, *b*; Morse, 1974; Chappell, 1978; Bertness, 1981*a*, *b*; Connell, 1983; Robinson and Terborgh, 1995; Griffis and Jaeger, 1998; Martin and Martin, 2001). Reciprocal removal studies might be an ideal way of determining whether biotic interactions prevent high-altitude species from moving down a tropical mountain and physiological constraints limit low-altitude species from moving up.

## Short-comings and caveats

The empirical data reviewed here represent an attempt to bring together a disparate literature on climate, thermal tolerance, acclimation ability, geographic ranges, and patterns of diversity. Unfortunately, no single study has examined all of the assumptions and predictions of Janzen's hypothesis; so our data are necessarily cobbled together from diverse studies, many of which were motivated by concerns other than Janzen's hypothesis (1967). This is hardly a strong foundation for comparative studies. Moreover, the comparative data we review here needs to be re-analyzed using phylogenetically based comparative methods (Felsenstein, 1985; Garland *et al.*, 1999); and future studies also need to control for parental and environmental effects that can confound the genetic basis of trait values (Garland and Adolph, 1991).

A more difficult challenge in testing many of the predictions of Janzen's hypothesis is that similar predictions emerge from other biogeographical, climatic, and historic hypotheses for latitudinal variation in population differentiation and speciation. For example, historic patterns of glaciation, lower energy at higher latitudes, and/or colder temperatures during the winter may cause higher rates of population extinctions, leading to higher recolonization rates at high latitudes (Martin and McKay, 2004). This process of extinction and recolonization can degrade both local adaptation to climate and population differentiation, resulting in similar patterns as those predicted by Janzen (Martin and McKay, 2004). Nevertheless, systematic tests of the assumptions and predictions of Janzen's hypothesis provide an opportunity to merge studies of climate, physiology, evolutionary ecology, and biogeography under a common conceptual framework.

## Final thoughts

We have focused our review primarily on studies of vertebrate ectotherms, a group that should be sensitive to the climatic (Porter and Gates, 1969) and physiological concerns raised by Janzen (1967). Whether other taxa show congruent patterns needs to be determined. Plants might show even more pronounced patterns: plants have limited ability to use behavior to avoid environmental influences and thus may experience stronger selection for physiological tolerance as well as greater population isolation (Bradshaw, 1965; Huey *et al.*, 2002). Endotherms, on the other hand, might show less pronounced patterns, because these organisms are relatively well buffered from climatic concerns (Porter and Gates, 1969). Birds, with their high mobility, might be even less impressed by the height of tropical mountain passes. These questions are important not only for testing the generality of whether mountain passes are higher in the tropics but also for generating testable hypotheses for linking climatic variation to the physiology, ecology, and evolution of species. In the face of a rapidly changing climate, the ability to make informed decisions about how certain groups (plants *vs.* animals) or certain communities (tropical low elevation *vs.* tropical high elevation) might respond is a pressing problem for organismal biologists. These are all appealing issues, and stand as a legacy of opportunities opened by Janzen (1967).

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