Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics

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Many studies suggest that global warming is driving species ranges poleward and toward higher elevations at temperate latitudes, but evidence for range shifts is scarce for the tropics, where the shallow latitudinal temperature gradient makes upslope shifts more likely than poleward shifts. Based on new data for plants and insects on an elevational transect in Costa Rica, we assess the potential for lowland biotic attrition, range-shift gaps, and mountaintop extinctions under projected warming. We conclude that tropical lowland biotas may face a level of net lowland biotic attrition without parallel at higher latitudes (where range shifts may be compensated for by species from lower latitudes) and that a high proportion of tropical species soon faces gaps between current and projected elevational ranges.

Recent global climate change has already begun to affect species' geographic ranges. Poleward shifts in range limits correlated with warming climate and changes in precipitation have been documented for a wide spectrum of temperate and subtropical species, and phenological changes portend poleward shifts in even greater numbers (1). Corresponding

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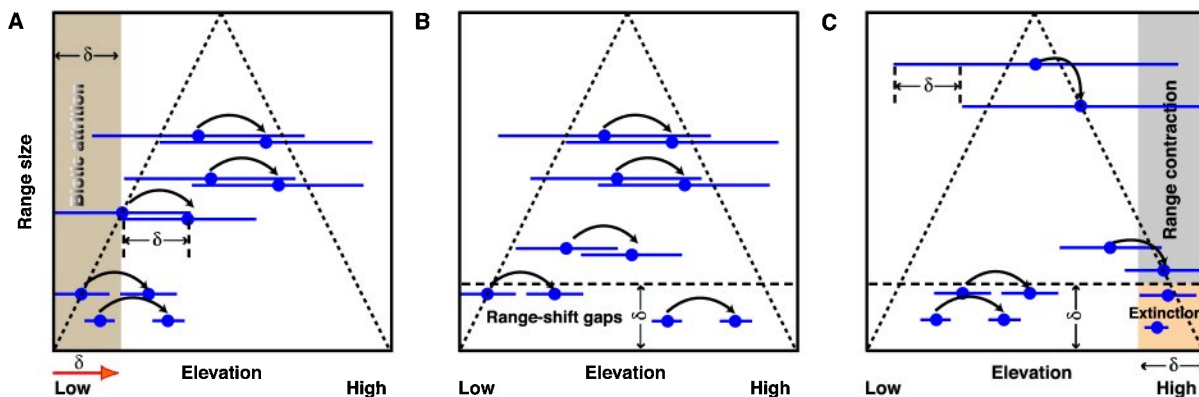†These authors are listed alphabetically.

upslope shifts in range boundaries along temperate elevational gradients have also been detected for both plants and animals (1–3).

In contrast, no study has documented climate-driven, contemporary latitudinal range shifts in the tropics. Biogeographical baseline data and resurveys at the high resolution required to document incipient range shifts are still scarce for tropical regions. More fundamentally, however, the steady latitudinal temperature gradients that characterize temperate latitudes level off to a broad plateau within the tropics (fig. S1). For midtropical species of restricted geographical range and limited capability for rapid range shift, the shallow latitudinal temperature gradient within the tropics presents a daunting obstacle to poleward range shifts (4).

In the tropics as elsewhere, however, elevational temperature gradients are steep—from 5.2°C

to 6.5°C decrease per 1000 m elevation (5)—nearly 1000 times as much as the latitudinal rate of decrease in temperature, per km, in the temperate zone (6.9° per 1000 km at 45° N or S) (fig. S1) and vastly greater than the modest latitudinal temperature gradient within the tropics. Consequently, for tropical species affected by warming climates, upslope range shifts appear far more likely than latitudinal shifts (4, 6). In fact, elevational shifts provide the only published evidence, to date, for contemporary range shifts within the tropics—a handful of examples, all for vertebrates, from Monteverde, Costa Rica (7).

To illustrate the potential for elevational range shifts in the tropics, we analyze elevational range data for four large survey data sets of plants and insects [epiphytes (8), understory Rubiaceae (5), geometrid moths (9), and ants (5)]. The data for all 1902 species were collected by the authors since 2001 from the Barva Transect, a continuously forested corridor ascending 2900 m up an elevational gradient from La Selva Biological Station, near sea level, to the top of Volcán Barva, in Costa Rica (8) (fig. S2). Before turning to an analysis of these data, however, we first examine the challenges that tropical species may face on such a gradient.

At temperate latitudes, resources released by poleward or upslope range shifts may be appropriated by species from lower latitudes or lower elevations—species already adapted to warmer temperatures—if suitable habitat corridors and dispersal mechanisms permit (1). Likewise, on tropical mountainsides, upslope range shifts may be compensated by the influx of species currently found at lower elevations or by expansion from small nuclei left over from previous warming episodes (4, 6). In the tropical lowlands, however, the parallels end. No community of species, now living in even hotter places, is available to replace tropical lowland species

Fig. 1. A simple graphical model of the potential effects of climate warming on the distribution of species ranges on a bounded elevational gradient. The elevational range size for each species (vertical axis) is plotted as a function of its elevational midpoint (horizontal axis), with corresponding range limits indicated by the solid horizontal lines. Because ranges cannot extend beyond the limits of the gradient, all range-size/range-midpoint coordinate pairs lie within the geometric constraint triangle (dotted lines). (The constraint triangle is not to be confused with a mountain.) An upslope shift in isotherms with warming climate is measured (in meters elevation) by δ, the sole parameter of the model. (**A**) Lowland biotic attrition. If lowland ranges shift δ m upslope, their new lower range limits must lie at or above δ m elevation, predicting a decrease in lowland richness. (**B**) Range-shift gaps. If elevational ranges follow isotherms upslope, no projected range smaller than δ m (plotted below the dashed horizontal line) will overlap its prewarming elevational range, posing challenges for dispersal and establishment. (**C**) Range contraction and mountaintop extinction. All ranges with upper limits less than δ m from the upper domain limit are predicted to contract, and the smallest of these (those less than δ m in extent) face local extinction.

that shift upslope with climate change or those that become extinct if no suitable habitat corridor to cooler climates is accessible.

How likely is "lowland biotic attrition," the net loss of species richness in the tropical lowlands from upslope range shifts and lowland extinctions driven by climate warming? Surprisingly, this question has scarcely been considered in a broad biogeographical framework. To explore it, we must ask whether tropical lowland species are already living near the thermal optimum of their climatic fundamental niche, above which fitness would decline in the absence of acclimation or adaptation. For plants, especially, because temperature and precipitation interact strongly through transpirational water loss, the answer depends on future changes in precipitation as well as in temperature. Wallace wrote that "[i]n the equable equatorial zone there is no ... struggle against climate. Every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little even throughout geological periods" (10). We now know that lowland tropical climates have changed substantially and relentlessly ever since species-rich forests resembling modern ones first

occupied the lowland wet tropics in the mid-Tertiary (6). Although the notion of long-term constancy of tropical climates is now universally dismissed, Wallace's view of tropical climates as benign lingers on (11), underlying the apparently widespread conviction that "[m]any tropical species may well be able to withstand higher temperature[s] than those in which they currently exist" (12).

Global climate has been cooling since the Middle Miocene [14.5 million years before the present (yr B.P.)], a trend punctuated, but not reversed, by the repeated, dramatic temperature fluctuations of the Quaternary glacial cycles (1.8 million yr B.P. to present). Pollen core data and plant microfossils from tropical sites, worldwide, show plant species moving downslope during the Last Glacial Maximum (20,000 yr B.P.), and back up again with the Holocene warming (10,000 yr B.P.) (13, 14). For the Andes, similar records span multiple Pleistocene glaciations (4).

Although the climatic changes driving them were complex (4, 15), these range shifts attest to the sensitivity of montane tropical species to temperature regimes (indeed, it is routine to estimate paleotemperatures from paleovegetation). Are tropical lowland species somehow exceptional,

having retained the tolerance for high-temperature environments of their Tertiary ancestors? If so, that tolerance has survived the adaptive demands of multimillennial glacial episodes when the lowland tropics averaged some 5°C cooler than now (a mean temperature currently characteristic of 30° N or S latitude), with much colder extreme events in some regions (6, 13, 16). Although habitat heterogeneity certainly mitigated extinction (4), lowland species or genotypes especially well adapted to warm climates, which "had nowhere to go" (6) during glacial episodes, would seem the least likely to have survived these cold periods unchanged, because of adaptive tradeoffs (17).

The warm interglacial periods of the Pleistocene, instead of Tertiary climates, might provide more appropriate adaptive benchmarks for warm climate tolerance. Current evidence, however, suggests that contemporary warming, 0.25°C decade^{-1} since 1975 in the tropical lowlands (15), has already driven global mean temperature to within ~1°C of Earth's maximum temperature in the past million years, exceeding the Holocene maximum (9000 to 5000 yr B.P.) of the current interglacial (18). In short, tropical climates are now warmer than at any time during at least the past two million years (4).

These considerations suggest, on evolutionary grounds, that many lowland tropical species may be in for trouble if they do not shift to higher elevations or to cooler, wetter microhabitats in coming decades—and trouble may already be at hand for some. Experimental studies indicate that tropical ectotherms are living at temperatures already near their thermal optimum, with early fitness declines expected under current projections for climate warming (19). The growth rate of individual lowland tropical trees is slowing, correlated on a year-to-year basis with increasing mean annual temperature in Costa Rica (20) (at La Selva) (fig. S2), and plot-level measurements in Panamanian and Malaysian forests show similar trends (21). In the Amazon, elevated atmospheric CO_2 itself may be interacting with increasing temperatures to drive changes in tropical forest composition (22), and distribution models for individual species project widespread range contractions and declines in tree viability and species richness (23), based on current bioclimatic envelopes. Some global climate models suggest that Amazonian forest may be approaching a "critical resiliency threshold," beyond which the system may lose its capacity to counter the effects of warming on tropical plants (24)

Species will respond individualistically to tropical climate change, just as they have in the past (4, 14), and vegetation types may expand or contract (6, 15). Nevertheless, the tropical lowlands are likely to experience decreased species richness, with novel plant communities (25) composed of heat-tolerant species [including fire-adapted, drought-tolerant species in areas subject to decreased precipitation (14, 15, 26)]. Early successional species, adapted to germination at higher soil temperatures, may thrive at the
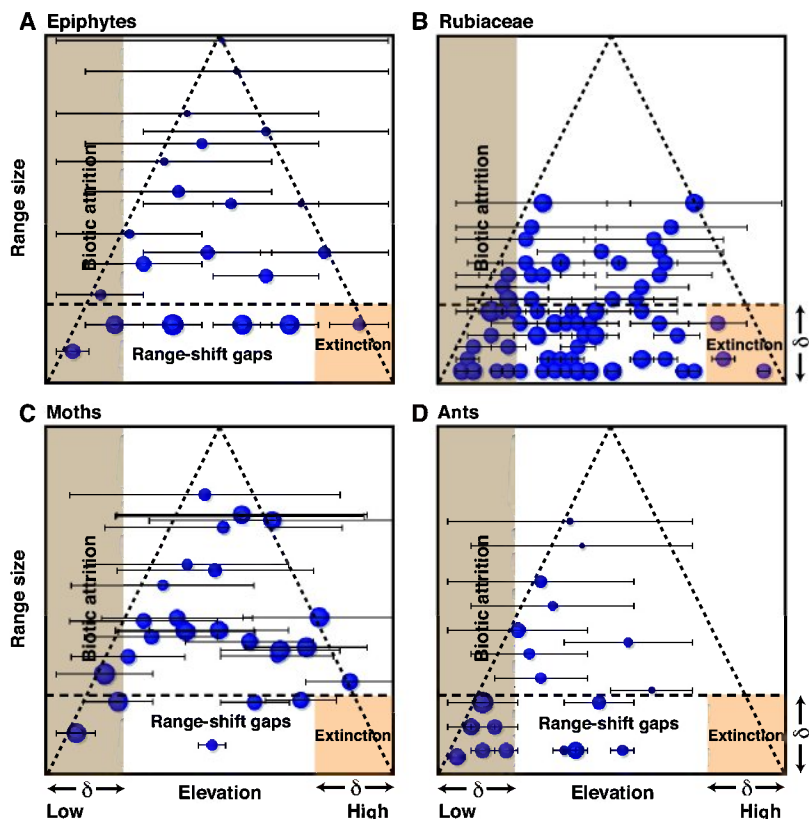

Fig. 2. The model in Fig. 1 applied to four groups of species on the Barva Transect (30 to 2900 m elevation) in Costa Rica (fig. S2). An upslope range shift of 600 m elevation is assumed, based on 3.12°C climate warming [the Intergovernmental Panel on Climate Change median regional rate for the next century (32) is 3.2°C] and locally measured lapse rate (5). Each blue disc represents the midpoint-range coordinate pair for n species (symbol size proportional to $\sqrt{n}$) (see Fig. 1 legend for details). (**A**) Data for 555 species of epiphytes (8) sampled at six elevations. (**B**) Data for 82 species of understory Rubiaceae (5) sampled at 28 elevations. (**C**) Data for 739 species of geometrid moths (9) sampled at six elevations. (**D**) Data for 495 species of ants (5) sampled at six elevations.

expense of late-successional species that require cooler microhabitats. Anthropogenic habitat alteration, shifts in land use patterns, and exotics and invasives (*27, 28*) can be expected to exacerbate many of these effects (*4, 26*).

Lowland biotic attrition is not the only biogeographic consequence of warming climate that is likely to be a greater problem in the tropics than in the temperate zone. Gaps between current and projected ranges ("range-shift gaps"), a concern at all latitudes, are especially worrisome on tropical elevational gradients because of the great number of tropical species with narrow elevational ranges. If tropical elevational ranges are narrower than their temperate counterparts [as widely believed, albeit on sparse evidence (*29*)], then tropical species are more likely than temperate species to experience range-shift gaps for a given upslope shift in climatic isotherms. Species already living near the top of elevational gradients face "mountaintop extinction" unless they have disjunct populations elsewhere on higher mountains or at cooler latitudes (*3, 25, 27, 30, 31*).

To illustrate the potential for lowland biotic attrition, range-shift gaps, and mountaintop extinctions in the wet tropics, we analyzed data for 1902 species of epiphytes, understory rubiaceous plants, geometrid moths, and ants on the Barva Transect, spanning 2900 m elevation (*8*) (fig. S2). Species distribution modeling (e.g., *12, 23, 30, 31*), commonly used to project range shifts under climate change, requires data for the full geographical ranges of species and corresponding environmental variables. Unfortunately, such data do not exist for the vast majority of tropical species (including those in this study), with the principal exception of the best-known vertebrate groups (e.g., *31*). Instead, we designed a simple graphical model (Fig. 1) that relies on temperature to assess potential elevational range shifts for transect data. In Figs. 2 and 3, we apply the model to illustrate the potential consequences of

warming-driven, elevational range shifts for the four groups of organisms surveyed on the Barva Transect.

Because the four groups of species differ substantially in statistical distribution of elevational range extents and in patterns of range location along the elevational gradient (Fig. 2), they project different patterns of potential range-shift effects (Fig. 3) (*5*). Overall, for a 600-m upslope shift in isotherms, driven by a 3.2°C temperature increase over the next century (*32*), about half (53%) of the 1902 species in this study (those that currently reach the lowest elevations) are candidates for lowland biotic attrition, and about half (51%) may be faced with range-shift gaps. The potential for mountaintop extinctions for these groups on the Barva Transect is minimal for a 600-m shift in isotherms (Fig. 3A) but begins to appear at about a 1000-m range shift (Fig. 3B). Although mountaintop extinction has been the focus of attention in most discussions of elevational range shifts (e.g., *2, 27, 31*), in the near term a far greater proportion of the tropical species in this study, and elsewhere, are threatened with lowland attrition or are challenged by early spatial discontinuities between current and projected elevational range (range-shift gaps). Many face both challenges.

In many respects, the predictions illustrated in Fig. 3 must be considered worst-case scenarios, even if warming occurs as assumed. Estimating elevational range limits from local inventory data is likely to underestimate regional elevational range, even accounting for local undersampling (*5*). Our projections share with species distribution models (*12, 23, 30, 31*) the assumptions that the fundamental climatic niche of each species is fully expressed by current distributions; that the effects of climate outweigh any idiosyncratic effects of species interactions, dispersal limitation, demographic patterns, or historical contingency; that change will be too rapid for adaptation to warmer temper-

atures at lower range limits (*1, 4, 30*); and that habitats at the landscape scale are homogenous with regard to microclimate. In fact, species that currently occupy warmer microhabitats at their lower range limit, including lowland species, may shift to currently cooler (and wetter) refuges at the same elevation, in response to warming (*1, 4, 14, 16*).

On the other hand, our simple projections based on temperature fail to take account of factors that may exacerbate the challenges facing tropical species. In the lowlands, decreased precipitation and increased fire frequency may amplify the direct effects of increased temperature (*15, 26*). Anthropogenic habitat fragmentation and widespread interruption of elevational forest corridors, which may increase as cloud levels rise with climate warming (*4, 7, 26*), cannot fail to impede successful range shifts, particularly for forest-dependent species with limited dispersal potential (*4, 14, 26, 28*). As current local assemblages are shuffled by individualistic range shifts, key species interactions may be disrupted (*1, 4, 7, 28*). Narrow-ranged species faced with range-shift gaps will have to compete successfully with wide-ranged species that continue to occupy upslope portions of their current ranges (*14*). Range-shift projections focus on immediate consequences, ignoring long-term effects of decreased suitable habitat and smaller populations, where land area declines with increasing elevation (*27*) as it does on the Barva Transect (*33*). Finally, the current spectrum of climate types may contract or novel types appear, as thermal bands move upslope (*25*).

Wallace's impression of tropical heat as "genial" may have survived the dismissal of his view of tropical climates as unchanging, but we suggest that it is time to question the conventional wisdom that tropical climates are biologically benign by taking a closer look at the challenges that climate change poses for tropical species. In the tropics, successful latitudinal range shifts ap-
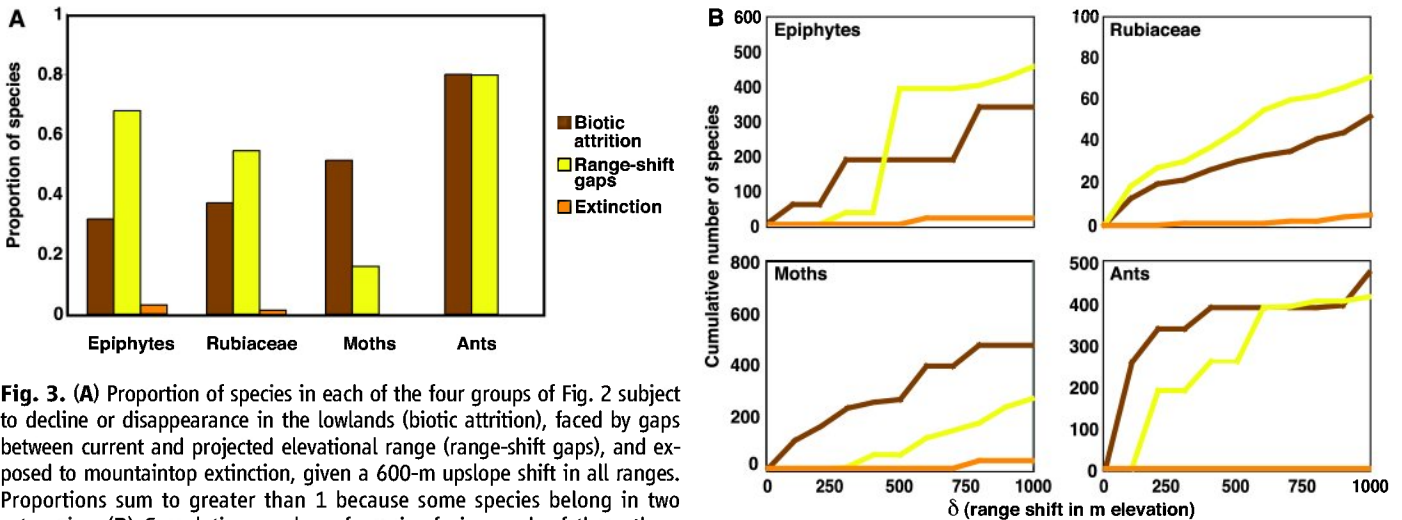
Fig. 3. (**A**) Proportion of species in each of the four groups of Fig. 2 subject to decline or disappearance in the lowlands (biotic attrition), faced by gaps between current and projected elevational range (range-shift gaps), and exposed to mountaintop extinction, given a 600-m upslope shift in all ranges. Proportions sum to greater than 1 because some species belong in two categories. (**B**) Cumulative number of species facing each of these three challenges as a function of warming-driven range shifts. The x axis represents model parameter δ, measured in meters of elevation range shift, on a continuous scale of warming-driven isotherm shifts of up to 5°C (nearly

1000 m), the upper range of projections for Central America for this century (*32*). The stairstep patterns are a consequence of sampling at discrete sites on the gradient (*5*).

pear unlikely, putting the focus on elevational gradients, where range-shift gaps will develop early for the great numbers of narrow-ranged species. The lowland tropics lack a source pool of species adapted to higher temperatures to replace those driven upslope by warming, raising the possibility of substantial attrition in species richness in the tropical lowlands.

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Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA

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We provide a century-scale view of small-mammal responses to global warming, without confounding effects of land-use change, by repeating Grinnell's early–20th century survey across a 3000-meter-elevation gradient that spans Yosemite National Park, California, USA. Using occupancy modeling to control for variation in detectability, we show substantial (~500 meters on average) upward changes in elevational limits for half of 28 species monitored, consistent with the observed ~3°C increase in minimum temperatures. Formerly low-elevation species expanded their ranges and high-elevation species contracted theirs, leading to changed community composition at mid- and high elevations. Elevational replacement among congeners changed because species' responses were idiosyncratic. Though some high-elevation species are threatened, protection of elevation gradients allows other species to respond via migration.

Although human-driven global warming (1) has changed phenology of species and contributed to range expansions (2–6), contractions of species' ranges are less well documented (7–10). Models of future climate-change scenarios predict large range shifts, high global extinction rates, and reorganized communities (11, 12), but model outcomes are also highly uncertain (13, 14). Most studies of species' responses span only a few decades—typically from the 1960 or 1970s, which was a relatively cool period, to the present. Such results can be confounded by decadal-scale climate oscillations (15) and landscape modification (8, 16). Furthermore, range shifts are uncertain when confounded by false absences due to limited historic sampling and inability to control for changes in detectability between sampling periods (17, 18).

We quantified the impact of nearly a century of climate change on the small-mammal community of Yosemite National Park (YNP) in California, USA, by resampling a broad elevational transect (60 to 3300 m above sea level) that Joseph Grinnell and colleagues surveyed from 1914 to 1920 (19) (Fig. 1). Their work documented the diversity and distribution of terrestrial vertebrates in California to establish a benchmark for future comparison (20), and led to the concept of the ecological niche, the importance of temperature as determinant of range boundaries, and the notion that species respond uniquely to environmental changes (21). In contrast to most early–20th century records, the "Yosemite Transect" was densely sampled across elevations (Fig. 1) and is amply documented by specimens (n = 4354), field notes (>3000 pages), and photographs (~700) (22), enabling precise identification of both species and sampling sites. From daily trapping records, we estimated detectability of species in historical as well as current surveys, permitting the unbiased estimation of species' "absences" from elevational bands in both periods (23). The transect spans YNP, a protected landscape since 1890, and allowed us to examine long-term responses to climate change without confounding effects of land-use change, although at low to mid-elevations there has been localized vegetation change relating to seral dynamics, climate change, or both (24). Finally, analyses of regional weather records pointed to substantial increase of the average minimum monthly temperature of 3.7°C over the past 100 years, with notable increases from 1910 to 1945 and from 1970 to the present (15, 22) (fig. S1).

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