

# The Future of Tropical Species on a Warmer Planet

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**Abstract:** *Modern global temperature and land cover and projected future temperatures suggest that tropical forest species will be particularly sensitive to global warming. Given a moderate greenhouse gas emissions scenario, fully 75% of the tropical forests present in 2000 will experience mean annual temperatures in 2100 that are greater than the highest mean annual temperature that supports closed-canopy forest today. Temperature-sensitive species might extend their ranges to cool refuges, defined here as areas where temperatures projected for 2100 match 1960s temperatures in the modern range. Distances to such cool refuges are greatest for equatorial species and are particularly large for key tropical forest areas including the Amazon and Congo River Basins, West Africa, and the upper elevations of many tropical mountains. In sum, tropical species are likely to be particularly sensitive to global warming because they are adapted to limited geographic and seasonal variation in temperature, already lived at or near the highest temperatures on Earth before global warming began, and are often isolated from cool refuges. To illustrate these three points, we examined the distributions and habitat associations of all extant mammal species. The distance to the nearest cool refuge exceeded 1000 km for more than 20% of the tropical and less than 4% of the extratropical species with small ranges. The biological impact of global warming is likely to be as severe in the tropics as at temperate and boreal latitudes.*

**Keywords:** climate change, cool refuges, extinction threat, global warming, land cover, mammals, range shift, range extension, tropical forest

El Futuro de Especies Tropicales en un Planeta más Caliente

**Resumen.** *La temperatura global y la cobertura de suelos actuales y las temperaturas futuras proyectadas sugieren que las especies de bosques tropicales serán particularmente sensibles al calentamiento global. En un escenario de emisiones de gases de invernadero moderadas, 75% de los bosques tropicales presentes en 2000 experimentarán temperaturas medias anuales en 2100 mayores a la temperatura media anual más alta de los actuales bosques de dosel cerrado. Las especies sensibles a la temperatura quizás extiendan sus rangos a refugios frescos, definidos como áreas donde las temperaturas proyectadas para 2010 sean iguales a temperaturas de la década de 1960. Las distancias a esos refugios frescos son mayores para las especies ecuatoriales y son particularmente grandes para áreas tropicales clave incluyendo las cuencas de los ríos Amazonas y Congo, el oeste de África y las altitudes mayores de muchas montañas tropicales. En suma, es probable que las especies tropicales sean particularmente sensibles porque están adaptadas a una limitada variación geográfica y estacional en la temperatura, ya vivían en o cerca de las temperaturas más altas de la Tierra antes de que comenzara el calentamiento global y a menudo están aisladas de los refugios frescos. Para ilustrar estos tres puntos, examinamos las distribuciones y las asociaciones de hábitat de todas las especies actuales de mamíferos. La distancia al refugio fresco más cercano fue mayor a 1000 km para más de 20% de las especies tropicales y menos de 4% de las especies no extratropicales con rangos de distribución pequeños. El impacto biológico del calentamiento global probablemente es tan severo en los trópicos como en las latitudes templadas y boreales.*

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**Palabras Clave:** amenaza de extinción, bosque tropical, calentamiento global, cambio climático, cambio de rango, cobertura de suelo, extensión de rango, mamíferos, refugios frescos

## Introduction

Wild species will respond to global warming through acclimation, evolutionary adaptation, and range shifts to cool refuges—insofar as biology and geography allow. The ability of species to respond to global warming is likely to vary with latitude because of latitudinal differences in (1) expected temperature increases, (2) species' inherent sensitivity to temperature change, (3) proximity to cooler refuges, and (4) the potential for interaction with species adapted to warmer climates. The first factor is widely recognized—temperature increases have been and will continue to be larger at higher latitudes in the Northern Hemisphere than in the tropics (Trenberth et al. 2007), presenting an absolutely greater challenge to high-latitude species. Many North Temperate and Arctic species are already responding to longer growing seasons through earlier migration, earlier reproduction, and range extensions to higher latitudes and elevations (Parmesan 2006). Nevertheless, the other factors are just as important in understanding the relative challenges that species will face and are perhaps less widely appreciated.

The second reason global warming impacts will vary with latitude is that low-latitude species are likely to be more sensitive to a given temperature change. Lowland mean annual temperatures (MAT) range from just 24 to  $-27^{\circ}\text{C}$  over 31 million  $\text{km}^2$  and  $47^{\circ}$  of latitude between the Tropics of Cancer and Capricorn (Terborgh 1973). Seasonal temperature variation is also limited—the classic Köppen definition of tropical climates holds that monthly temperature averages  $>18^{\circ}\text{C}$  year-round. The physiologies of many tropical species have evolved to function optimally within these narrow temperature ranges (Janzen 1967; Ghalambor et al. 2006). With their physiology finely tuned to temperature, tropical species are likely to have a limited ability to acclimate to global warming (Deutsch et al. 2008; Tewksbury et al. 2008). Even small temperature increases might exceed fundamental temperature tolerances and cause ranges to retract to cooler refuges (Colwell et al. 2008). Furthermore, even if individual animal species could tolerate changed climates, the plant species on which they depend for food and habitat might not. Tropical forests are home to the majority of terrestrial species; thus, any contraction in their area from changed climates would have major implications for biodiversity.

The third reason global warming impacts are likely to vary with latitude concerns the potential for temperature-sensitive species to shift their ranges to cool refuges. A strong latitudinal temperature gradient averages  $1^{\circ}\text{C}$  for each 145-km change in latitude between the Tropics and

Polar Regions but approaches zero between the Tropics of Cancer and Capricorn (Terborgh 1973). The latitudinal temperature gradient will facilitate range extensions to cool refuges for extratropical species. In contrast, the potential for range shifts to cool refuges will be limited for tropical species except near mountains (Colwell et al. 2008). Elevational temperature gradients are similar at all latitudes; however, mountains are far from uniformly distributed over the planet.

The final reason global warming impacts are likely to vary with latitude concerns the potential for interactions with species adapted to warmer climates. As global temperatures increase, immigrants from warmer areas are likely to be better adapted to new, warmer climates than are the original residents of formerly cooler areas (Bush 2002). The combination of warmer temperatures and new arrivals adapted to those temperatures will challenge the original residents, causing ranges to retract not only where temperatures exceed fundamental tolerances, but also potentially where competitors, predators, and parasites from warmer areas have immigrated. Such interaction-induced contractions are likely to be common at higher latitudes, where continuous latitudinal temperature gradients provide a ubiquitous source of species adapted to warmer climates. In the tropics the potential threat is likely to be greatest for montane species because the surrounding lowlands provide a nearby source of species adapted to warmer climates. In contrast, the lowland tropics support the highest MATs and species adapted to warmer climates are missing; thus, lowland tropical species might lack the added challenge posed by the arrival of species adapted to warmer climates.

These four considerations suggest how the modern distribution of climate and species will mediate the biodiversity threat posed by global warming. We analyzed the global distribution of modern climates, land cover, mammal distributions, and projected future temperatures to quantify latitudinal variation in these factors, with a focus on a comparison of tropical and extratropical latitudes. To quantify potential differences in the temperature variation to which modern species are accustomed, we examined how MAT and the seasonal temperature range (STR) vary latitudinally. To evaluate potential differences in forest-cover sensitivity, we examined the range of MAT that supports broadleaf, closed-canopy forest in the Tropics and North Temperate Zone. We also examined whether tropical lowland forests occupy the warmest modern climates and the types of land cover present in the warmest modern climates. To quantify variation in the dispersal challenges required to track climates, we determined how proximity to cool refuges differs between

the Tropics and North Temperate Zone as well as regionally within the Tropics. Finally, we analyzed the ranges and habitat requirements of extant mammal species to quantify the challenges posed by global warming. We determined the number of tropical forest species that also occur outside the tropics or in warmer nonforest habitats and the number restricted to montane forests. The former are likely to have access to cool refuges, whereas the latter are particularly likely to interact with warm-adapted immigrants from the surrounding lowlands as ranges change in response to global warming. We also examined how distances to cool refuges differ between tropical and temperate mammal species with small range sizes.

## Methods

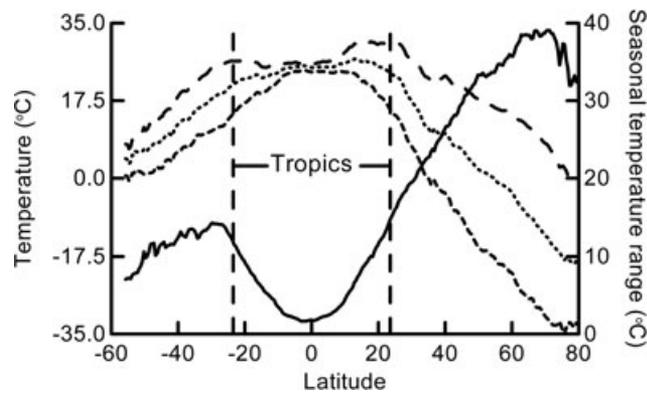
We superimposed 1960s temperatures, 2000 land cover, projected 2100 temperatures, and mammal distributions. We used ARCGIS software (ESRI, Redlands, California) to calculate area for key land-cover types with respect to latitude, MAT, and mean annual precipitation (MAP). We dichotomized latitude to contrast the Tropics (23.5°N–23.5°S) and the North Temperate Zone (23.5–60°N). We used 0.5° latitude–longitude resolution climate data for the 1960s (IPCC 2007) and calculated annual MAT and MAP from monthly values. The seasonal temperature range (STR) equaled the difference between maximum and minimum mean monthly temperatures. We downloaded 1-km spatial resolution land-cover data from the Global Land Cover 2000 Project (2007). These data are from daily satellite imagery acquired over the entire globe for 14 months (November 1999 through December 2000) by the VEGETATION instrument on the SPOT 4 satellite. We calculated distributions of (1) tropical land area with respect to MAT and MAP, (2) tropical land-cover types with respect to MAT, and (3) closed-canopy broadleaf forest with respect to MAT and latitude. For 3, we included broadleaf evergreen, broadleaf deciduous, and mixed coniferous-broadleaf cover (land-cover types 1, 2, and 6 of the Global Land Cover 2000 Project). For 2, we distinguished tree cover (land-cover types 1–9), shrub cover (11–12), herbaceous cover (13–15), agriculture (16–18), and bare ground (19). Agriculture included “cultivated and managed areas” and mosaics of cropland and natural vegetation. We excluded four minor land-cover types: burned tree cover, water bodies, snow and ice, and artificial surfaces.

Some species will extend their ranges into previously cooler regions as global temperatures increase. To evaluate the potential for such range extensions in 2100, we calculated the minimum distance between every 0.5° latitude–longitude block and a second destination block such that 2100 temperatures projected for the destina-

tion block equaled or were cooler than 1960s temperatures in the origin block. Distances were calculated as great-circle distances, which incorporate the curvature of the Earth’s surface. We estimated 2100 temperatures for each 0.5° of latitude from a strong relationship between latitude and 23 regional temperature projections (Supporting Information,  $R^2 = 0.78$ ,  $p < 10^{-6}$ ). Regional temperature projections were median terrestrial values calculated for 21 global climate models under the moderate (A1B) greenhouse-gas emissions scenario of the IPCC (Supporting Information). We compared distributions of these minimum distances for 20° latitudinal bands and the four tropical bioregions: Neotropic, Afrotropic, Indo-Malay, and Australasian (Olson et al. 2001).

Mammal range and habitat data are from Schipper et al. (2008). The ranges of 5286 terrestrial mammal species are available as GIS polygons. We excluded extinct species and calculated the area and latitudinal limits of the breeding ranges of the 5257 remaining species. We obtained habitat associations from the International Union for Conservation of Nature (IUCN) Red List (IUCN 2008). We distinguished extratropical forest (IUCN habitats 1.1–1.4), tropical/subtropical lowland forest (1.5–1.8), tropical/subtropical montane forest (1.9), all other natural terrestrial habitats (2–8), and artificial terrestrial habitats (14). These habitats included 5029 species. There were 4972 species with both habitat and breeding range data.

We evaluated minimum distances to cool refuges for small-range species. We restricted our analysis to species with ranges of  $<3136 \text{ km}^2$  to minimize complications introduced by climate variation within a species’ range. Our range-size cutoff is approximately equal to the area of one 0.5° latitude–longitude cell at the equator ( $56 \times 56 \text{ km}$ )—the resolution of the IPCC climate data used in our analysis. Climate variation at smaller scales cannot be resolved with these climate data and thus is appropriately ignored here. We calculated distances between midpoints of a range and a destination block such that 2100 temperatures at the destination block equaled or were cooler than 1960s temperatures in the modern range. We used midpoints rather than the nearest edge of the range or destination block because distances were pooled into broad categories for analysis, which makes the small distances between midpoints and edges inconsequential. We performed two-way contingency analyses with ordered distance categories to evaluate the null hypothesis that distances were equal for tropical versus extratropical species. We defined tropical species as those endemic to tropical latitudes and extratropical species as those whose breeding range extended to or lay entirely outside the tropics. Distance ( $d$ ) categories were  $d \leq 125$ ,  $125 < d \leq 250$ ,  $250 < d \leq 500$ ,  $500 < d \leq 1000$ ,  $1000 < d \leq 2000$ , and  $d > 2000 \text{ km}$ . We repeated the contingency analysis for all species and for the subset of species that inhabit forest (IUCN habitats 1.1–1.9).



**Figure 1.** Latitudinal variation in mean annual temperature (dotted line), maximum (long-dash line) and minimum (short-dash line) mean monthly temperatures, and seasonal temperature range (STR, solid line). The STR equals the difference between maximum and minimum mean monthly temperatures. Values are medians for  $0.5^\circ$ -longitude bands calculated from 1960s monthly mean temperatures provided by the IPCC (2007).

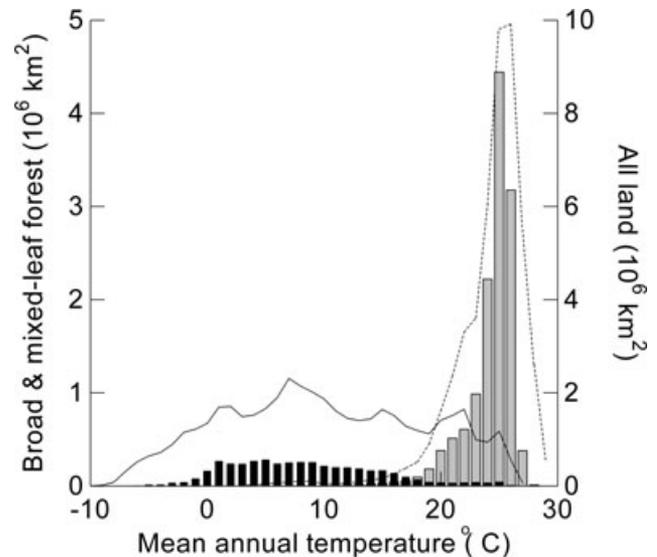
## Results

### Seasonal Temperature Variation

Latitudinal temperature variation occurred well inside the Tropics (Fig. 1). Minimum mean monthly temperatures were relatively constant with respect to latitude within just  $10^\circ$  of the equator, declined steadily with larger latitudes, and declined much more rapidly in the Northern than Southern Hemispheres. In contrast, MAT and maximum mean monthly temperatures varied little inside the Tropics and declined steadily with latitude outside the Tropics. Consequently, STR averaged  $<4^\circ\text{C}$  between  $10^\circ\text{S}$  and  $10^\circ\text{N}$ , but reached  $15.4^\circ\text{C}$  and  $11.5^\circ\text{C}$  at the Tropics of Cancer and Capricorn, respectively. This was 39% and 74% of the Northern and Southern Hemisphere maxima of  $39.3^\circ\text{C}$  and  $15.4^\circ\text{C}$ , respectively. Thus, 1960s STR was consistently small in the low-latitude tropics, reached relatively large values at higher latitudes within the tropics, and differed strongly between the Northern and Southern Temperate Zones (Fig. 1).

### Forest Cover and Climate

Broadleaf and mixed coniferous-broadleaf forests occurred over a wide 1960s MAT range in the North Temperate Zone and a relatively narrow 1960s MAT range in the Tropics (Fig. 2). Total tropical land area dropped precipitously from 9.9 to 5.5, to 2.6, and to 0.53 million  $\text{km}^2$  for mean annual temperatures of 26, 27, 28, and  $29^\circ\text{C}$ , respectively (Fig. 2). The forested area dropped even more precipitously at these highest MATs from 3.2 to 0.38, to 0.012, and to 0 million  $\text{km}^2$ , respectively. The natural veg-



**Figure 2.** Area of closed-canopy forest in 2000 (y-axis) with respect to 1960s mean annual temperature (MAT) for the Tropics (gray) and the North Temperate Zone (black). Solid and dashed lines represent all land in the North Temperate Zone and between the Tropics of Capricorn and Cancer, respectively. Forest includes broadleaf evergreen, broadleaf deciduous, and mixed coniferous-broadleaf leaf types. The MAT is the average of monthly means from the IPCC (2007). Land cover is from the Global Land Cover 2000 project (2007).

etation where MAT was 28 or  $29^\circ\text{C}$  included a limited area of shrub cover, herbaceous cover or grasslands, and bare ground or desert (Fig. 3).

The distribution of MAP contributed to and perhaps controlled the precipitous decline in forest cover with MAT in the tropics (Fig. 4). MAP of 1 m approximates the lower limit for closed-canopy tropical forest (Holdridge 1967). The percentage of tropical land area with larger MAP fell from 68% to 38%, to 5.6%, and to 0% for MAT of 26, 27, 28, and  $29^\circ\text{C}$ , respectively (Fig. 4).

### Distances to Potential Cool Refuges

Distances to potential cool refuges varied greatly across the globe depending on topography, latitude, and projected temperature increases (Fig. 5). Minimum distances to  $0.5^\circ$  latitude-longitude blocks whose projected 2100 temperatures were equal to or cooler than observed 1960s temperatures in the origin block were shortest in and near adiabatically cooled mountains—except of course at the highest local elevations (Fig. 5). Latitudinal variation in distances to cool refuges incorporates latitudinal temperature gradients and projected temperature increases. Projected temperature increases for 2100 under the A1B scenario averaged  $3.3^\circ\text{C}$  across the tropics, increased with latitude north of about  $30^\circ\text{N}$ , and decreased with latitude south of about  $20^\circ\text{S}$  (Supporting

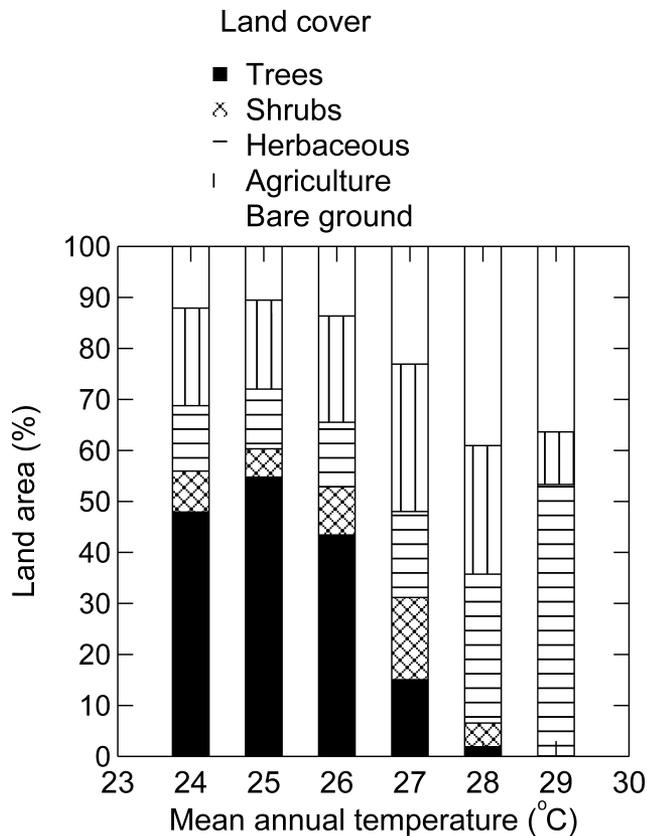


Figure 3. Tropical land-cover types with respect to mean annual temperature. Data sources are described in the caption of Fig. 2.

Information). Consequently, the distances to potential cool refuges tended to be shortest at intermediate latitudes, where latitudinal temperature gradients tended to offset projected temperature increases over short distances, and larger near the equator, where latitudinal temperature gradients are largely absent, and above 50 °N, where the projected temperature increases were largest (Fig. 6). Distances to cool refuges varied little among the four tropical bioregions (data not shown).

### Mammal Ranges and Climate Challenges

There are 4351 terrestrial mammal species (83% of the 5257 species with known ranges) whose geographic ranges include tropical latitudes. Among these, 2814 species (54%) had ranges restricted to tropical latitudes (Fig. 7). These 2814 species lacked direct contact with latitudinal gradients in MAT and maximum mean monthly temperature (Fig. 1) that might facilitate dispersal to cool refuges as global warming proceeds (Fig. 5). Of these, 1224 species (23%) were restricted to the low-latitude tropics (10 °S–10 °N) (Fig. 7). These 1224 species also experienced minimal seasonal variation in temperature (Fig. 1) and would likely be particularly sensitive to global warming.

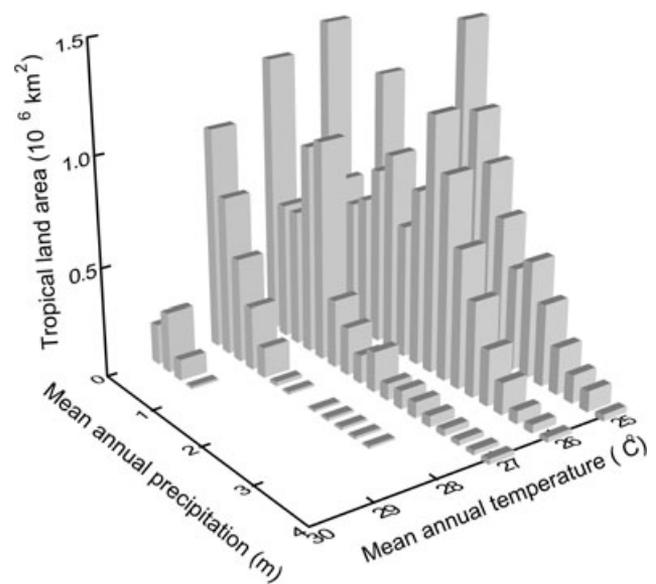


Figure 4. Tropical land area with respect to mean annual temperature (MAT) and mean annual precipitation (MAP) for the 1960s and MAT  $\geq 25$  °C and MAP  $\leq 4$  m. The MAT scale is reversed. Data sources are described in the caption of Fig. 2.

The habitat associations of 2672 terrestrial mammal species (53% of 5029 species with known habitat associations) included lowland tropical forest. The geographic ranges of 1795 of these species were restricted to tropical latitudes. Just 30% of these 1795 species inhabited other potentially warmer nonforest habitats. The remaining 1262 forest species lacked contact with latitudinal temperature gradients and populations adapted to warmer, nonforest habitats. Cool refuges were available to these species only on mountains within the tropics and through very long-distance dispersal to latitudinal temperature gradients outside the tropics.

The habitat associations of 1549 terrestrial mammal species (31% of 5029 species with known habitat associations) included montane tropical forests. The geographic ranges of 1130 of these species were restricted to tropical latitudes. Sixty-nine percent of these 1130 species inhabited potentially warmer habitats, largely lowland forests. The remaining 350 montane species lacked contact with latitudinal temperature gradients that might facilitate range extensions to cool refuges, lacked populations adapted to warmer climates, and would be likely to interact with immigrants adapted to the warmer climates of the surrounding lowlands as elevational ranges change with global warming.

A total of 657 terrestrial mammal species had geographic ranges of  $<3136$  km<sup>2</sup>. For these species, the minimum distance to a potential cool refuge was significantly greater for tropical endemics than for species whose ranges included extratropical latitudes (ordered

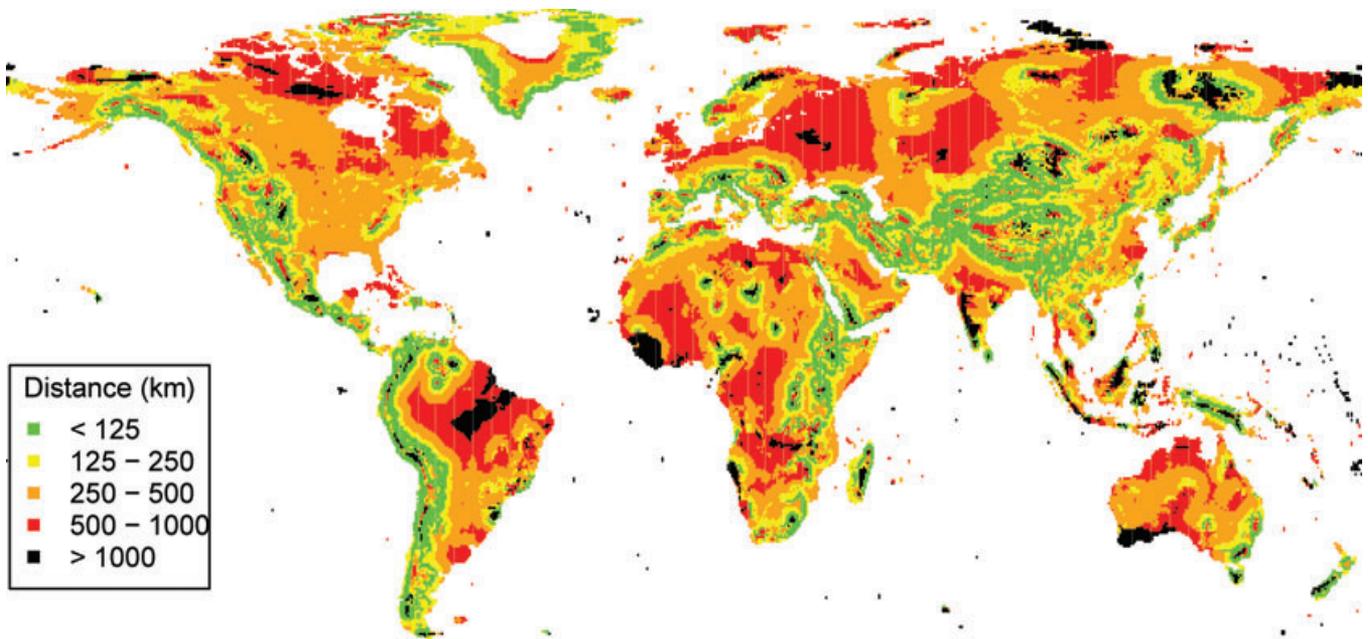


Figure 5. Global map of distances to potential cool refuges for each  $0.5 \times 0.5^\circ$  latitude-longitude block on land and north of  $60^\circ$  S latitude. Distance to potential refuges is defined as the shortest distance to a destination block whose projected 2100 temperatures equal or are cooler than the observed 1960s temperatures in the origin block.

Goodman-Kruskal  $\gamma$  [ $\pm 1$  asymptotic SE] =  $0.33 \pm 0.060$ ; unordered  $\chi^2 = 35.2$ ,  $df = 5$ ,  $p < 10^{-5}$ ). Distance to a cool refuge was also significantly greater for tropical endemics for the subset of 441 small-range species that inhabit forest (Goodman-Kruskal  $\gamma$  [ $\pm 1$  asymptotic SE] =  $0.35 \pm 0.10$ ;  $\chi^2 = 15.7$ ,  $df = 5$ ,  $p < 0.01$ ).

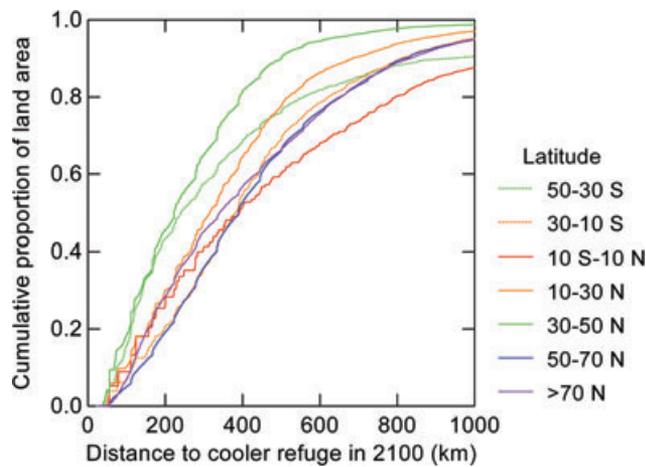


Figure 6. The proximity of cool refugia in 2100. The x-axis presents the minimum distance separating temperatures observed in the 1960s from equal or cooler temperatures projected for 2100 under the A1B greenhouse gas emissions scenario. The y-axis presents the cumulative proportion of land area for  $20^\circ$  latitudinal bands (see inset key).

## Discussion

Global climate is changing rapidly as emission rates of anthropogenic greenhouse gases accelerate (Raupach et al. 2007). In the tropics, temperature increases have averaged  $0.26^\circ\text{C}$  per decade since the 1970s (Malhi & Wright 2004). Globally, temperature, rainfall, and sea level are all increasing at rates similar to or larger than the fastest rates predicted by global climate models (Gu et al. 2007; Rahmstorf et al. 2007; Wentz et al. 2007). By many measures, the tropical belt has already expanded by  $2\text{--}4^\circ$  of latitude (Seidel et al. 2008). The acceleration of these changes lends urgency to our first attempts to understand their implications for tropical species.

### Temperature Dependence of Tropical Forests and Species

At first glance, the precipitous decline in tropical forest area with respect to mean annual temperature (Fig. 2) suggests that global warming could have severe consequences for tropical forest species. The warmest modern closed-canopy forests occur where MAT is  $28^\circ\text{C}$  (Fig. 2). If tropical temperatures increase by  $3.3^\circ\text{C}$ , as projected for 2100 under the IPCC's intermediate (A1B) greenhouse-gas emissions scenario (Christensen et al. 2007), then temperatures will exceed  $28^\circ\text{C}$  for 75% of the tropical forest present in 2000 (Fig. 2). Today, areas with similar MAT generally support relatively species-poor grasslands and deserts (Figs. 3 & 4), but these areas are also dry. The future climates of areas supporting tropical forests today will be wetter than modern tropical grasslands and deserts and warmer than modern tropical

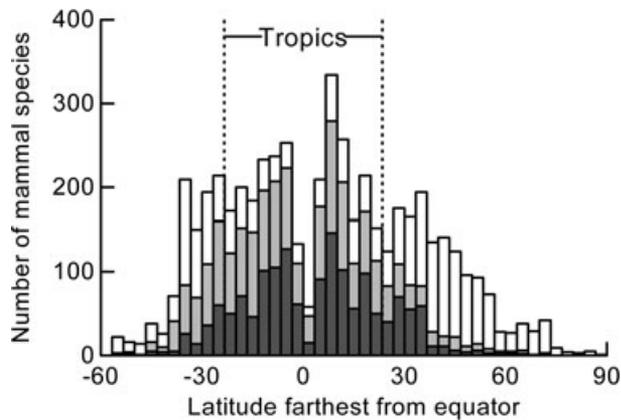


Figure 7. Number of mammal species with respect to the latitude farthest from the equator within their geographic ranges (open bars, all 5257 terrestrial species with known ranges; gray bars, subset of species that inhabit tropical lowland or montane forest; dark bars, subset of species that inhabit tropical montane forests). Species ranges are from Schipper et al. (2008).

forests. The biodiversity threat posed by global warming depends on how tropical forest species respond to these warmer wet climates—climates unlike any encountered on Earth today (Williams et al. 2007).

The generation times of many tropical trees are long relative to rates of temperature change—individual trees can be 300–1400 years old (Chambers et al. 1998). Thus, the acclimation capacity of individual trees is critically important. Mounting evidence suggests this capacity is limited in wet forests. Bole respiration increases by 8% for each 1 °C temperature rise at La Selva, Costa Rica (Ryan et al. 1994). Plant respiration is highly sensitive to mean monthly temperature in Hawaii, where total ecosystem respiration increases by 16% for each 1 °C temperature rise even though soil respiration is unrelated to temperature (G.P. Asner, personal communication). Tree growth rates in old-growth forests are inversely related to MAT at La Selva (Clark et al. 2003) and declined over 15–25 years as temperatures increased at Barro Colorado Island, Panama, and the Pasoh Forest Reserve, Malaysia (Feeley et al. 2007). Physiological considerations, however, suggest that observed temperature changes are insufficient to have caused the observed increases in respiration and declines in growth (Lloyd & Farquhar 2008). Because observation and theory diverge, the acclimation capacity of tropical trees to climate change remains a pressing research priority.

The sensitivity of tropical ectotherms to temperature reinforces concern for the future of tropical species on a warmer planet (Deutsch et al. 2008; Tewksbury et al. 2008). This sensitivity is likely to be greatest in the low-latitude tropics, where the seasonal temperature range is smallest and physiologies are most likely to be finely tuned to temperature (Fig. 1). Deutsch et al. (2008) docu-

mented the relationship between fitness and temperature for 38 insect species and estimated changes in fitness associated with temperatures projected for 2100. Temperate insects live well below their temperature optima today, and their fitness actually increases at projected 2100 temperatures. In contrast, equatorial insects live near their temperature optima today, and their fitness declines at projected 2100 temperatures. In most species, fitness declines precipitously with small increases above optimum temperatures. Short-lived insects may adapt evolutionarily to rapid climate change; however, these precipitous declines in fitness with small temperature increases heighten concern for the future of many tropical ectotherms.

### Potential Range Shifts Toward Cool Refuges

Temperature-sensitive species may disperse to cool refuges to escape global warming (Bush 2002; Colwell et al. 2008). The potential for such dispersal and successful range shifts depends in part on the distances to cool refuges. These distances tend to be largest near the equator, where there is no latitudinal temperature gradient to facilitate dispersal, shortest for mid-temperate latitudes (30–50° in both hemispheres), and large again at high North Temperate and Arctic latitudes (>50° N), where large projected temperature increases offset the latitudinal temperature gradient (Figs. 5 & 6).

Mammals with small geographic ranges illustrate the strong difference in distances to potential cool refuges between tropical and extratropical species. Species with small geographic ranges tend to be associated with mountains (Ohlemüller et al. 2008) and therefore with adiabatic temperature gradients. Nonetheless, it is more than 1000 km to the nearest location where projected temperatures in 2100 match temperatures in the modern range for 20.4% of tropical mammal species with small ranges. The comparable figure is just 3.8% for extratropical species. This tropical–extratropical discrepancy is likely to be even larger for species with larger ranges because mammal range size increases with latitude in the Northern Hemisphere (Schipper et al. 2008) and larger ranges are likely to include larger temperature ranges and require shorter distances to reach cool refuges.

Distances to cool refuges are particularly large for key tropical forest regions. This includes the Amazon and Congo River basins, most of equatorial West Africa, and isolated highlands and mountains (Fig. 5). Distances to cool refuges exceed 2000 km for several tropical mountain ranges. Examples include the Eastern Rift Mountains of Africa; the Western Ghats of India; and the highlands and mountains of Borneo, Madagascar, New Guinea, and Sumatra (Fig. 5). The vertebrates of one such mountain range in tropical Queensland, Australia, are known to be highly sensitive to temperature (Williams et al. 2003).

Levels of endemism are high on many tropical mountains, and elevational ranges are already moving upward (Pounds et al. 1999; Peh 2007; Raxworthy et al. 2008; Chen et al. 2009). Temperature-sensitive species on isolated tropical mountains can only survive global warming in place because cool refuges other than local peaks are thousands of kilometers distant.

### Climate Change, Species Composition, and Extinction

Novel biotic interactions will further challenge species as climate changes. There will be two sources of novelty in biotic interactions. First, climate-dependent performance will alter interactions among long-term sympatric species (Tylianakis et al. 2008). Second, range extensions and contractions will vary from species to species, and species will mix in novel combinations in the future (Bush et al. 2008). In these novel interactions, some species will do relatively poorly, whereas others will do relatively well.

The implications for local extirpations and global extinctions are uncertain. Negative density dependence stabilizes modern communities by favoring rare species and penalizing abundant species (Chesson 2000) and was pervasive in a meta-analysis of 1198 time series of animal abundances (Brook & Bradshaw 2006). As species' abundances change in response to climate change, the influences of negative density-dependent factors on their vital rates will shift accordingly, stabilizing the new communities. The balance of these forces and of direct climatic influences on vital rates will ultimately determine whether individual species go extinct locally and even globally. Climate change will surely cause large changes in species composition. The threat of extinction is uncertain, however, except where fundamental temperature or moisture tolerances are exceeded throughout the geographic range of a species and nearby areas that can be reached through dispersal.

### Conservation Implications

Climate change presents special challenges in the tropics. A paucity of long-term tropical studies hinders the detection of biological responses to climate change (Clark 2007). Key biological processes are poorly understood for tropical organisms including dispersal capacity, environmental control of phenology, community composition during warmer paleoclimates, and mechanisms that maintain diversity in modern communities. To anticipate tropical responses to climate change and take measures to avoid the worst outcomes, research is urgently needed (Clark 2007).

Climate change also presents opportunities for conservation funding. The other major threats to tropical biodiversity—habitat loss and direct persecution of game species and other charismatic species—are ultimately the responsibility of local governments and people. In con-

trast, a small number of wealthy countries caused a disproportionate share of the greenhouse gas emissions responsible for climate change (Millennium Ecosystem Assessment 2005). These wealthy countries must shoulder a similarly large share of the costs of conserving biodiversity in the face of climate change.

The most straightforward way to mitigate the effects of climate change on tropical diversity is to reduce the magnitude of change by controlling atmospheric greenhouse gases. Tropical land-use transitions offer a cost-effective means to reduce current greenhouse gas emissions and to remove carbon dioxide from the atmosphere. Tropical deforestation contributes approximately 20% of current greenhouse gas emissions (Millennium Ecosystem Assessment 2005). The inclusion of reduced emissions from deforestation and degradation (REDD) as a mechanism for mitigating climate change within United Nations climate-change agreements will enable payments to conserve tropical forests and thereby reduce greenhouse gas emissions. Secondary succession removes carbon from the atmosphere more quickly in tropical forests than in any other biome (Brown & Lugo 1990). Additional payments could help expand tropical forest cover on marginal agricultural land, which is often abandoned anyway (Asner et al. 2009 [this issue], Chazdon et al. 2009 [this issue]), and link existing nature reserves to provide dispersal corridors that are likely to become essential as climate change proceeds. The wealthy countries that are disproportionately responsible for climate change should contribute to realize these opportunities.

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### Supporting Information

An analysis of the relationship between latitude and projected temperature increases for 2100 under an intermediate greenhouse gas emissions scenario is available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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