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Biotic attrition from tropical forests correcting for truncated temperature niches

KENNETH J. FEELEY and MILES R. SILMAN

Department of Biology, Wake Forest University, Winston Salem, NC 27109, USA

Abstract

Species migration in response to warming temperatures is expected to lead to 'biotic attrition,' or loss of local diversity, in areas where the number of species emigrating or going locally extinct exceeds the number immigrating. Biotic attrition is predicted be especially severe in the low-lying hot tropics since elevated temperatures may surpass the observed tolerances of most extant species. It is possible, however, that the estimated temperature niches of many species are inaccurate and truncated with respect to their true tolerances due to the absence of hotter areas under current global climate. If so, these species will be capable of persisting in some areas where future temperatures exceed current temperatures, reducing rates of biotic attrition. Here, we use natural history collections data to estimate the realized thermal niches of >2000 plant species from the tropical forests of South America. In accord with the truncation hypothesis, we find that the thermal niches of species from hot lowland areas are several degrees narrower than the thermal niches of species from cooler areas. We estimate rates of biotic attrition for South American tropical forests due to temperature increases ranging from 1 to 5 °C, and under two niche assumptions. The first is that the observed thermal niches truly reflect the plant's tolerances and that the reduction in niche breadth is due to increased specialization. The second is that lowland species have the same mean thermal niche breadth as nonlowland and nonequatorial species. The differences between these two models are dramatic. For example, using observed thermal niches we predict an almost complete loss of plant diversity in most South American tropical forests due to a 5 °C temperature increase, but correcting for possible niche truncation we estimate that most forests will retain >50–70% of their current species richness. The different predictions highlight the importance of using fundamental vs. realized niches in predicting the responses of species to global climate change.

Keywords: Amazon, bioclimatic niche modelling, climate change, extinction, fundamental niche, GBIF

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Introduction

As global temperatures increase, species will likely shift their distributions, or 'migrate' in order to remain within the bounds of their thermal niches (e.g. Walther *et al*., 2002, 2005; Thomas *et al*., 2004; Beckage *et al*., 2008; Kelly & Goulden, 2008; Lenoir *et al*., 2008; Chen *et al*., 2009). These migrations are predicted to adversely affect many species by reducing the areas of climatically suitable habitat that is available (Thomas *et al*., 2004). Another less appreciated consequence of species migrations is that some regions may decrease in local diversity due to 'biotic attrition' in which the number of species emigrating or going locally extinct exceeds the number of species immigrating into the region (Colwell *et al*., 2008). The most extreme cases of biotic attrition are likely to occur in the lowland tropics since species from these areas may have narrow climatic tolerances due to high niche specialization (Janzen, 1967; McCain, 2009) and since there is often no pool of species from hotter areas available to replace those that leave due to elevated temperatures. Indeed, under the most basic climate change models in which temperature is increased independent of other climatic factors, much of tropical South America and the Amazon Basin would be left virtually devoid of species as the elevated temperatures surpass species' known tolerances.

There is, however, reason to believe that biotic attrition and species loss will not be as drastic as this conjecture would predict. One of the primary means through which species' climatic niches are modeled is on the basis of observed occurrences, natural history collections, and/or plot data (e.g. Graham *et al*., 2004; Araujo *et al*., 2005; Colwell *et al*., 2008; Thuiller *et al*.,

Correspondence: Kenneth J. Feeley, Florida International University and The Fairchild Tropical Botanic Garden, Miami, FL 33199, USA, e-mails: kjfeeley@gmail.com, silmanmr@wfu.edu

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2008). In the hot tropics, the resultant estimated climatic niches may underestimate the fundamental thermal niches of many species (Grytnes & Vetaas, 2002; Hannah *et al*., 2007; Svenning & Condit, 2008). This is because species' ranges may be truncated due to the absence of any areas with higher temperatures under Earth's current climate. In other words, the fundamental niches of some species may be broader than observed and include hotter temperatures, but there are simply no areas in the Neotropics that currently offer these conditions (e.g. Jackson & Overpeck, 2000). If the ranges of species are truncated with respect to their true climatic tolerances, some species may in fact be able to persist in hot lowland areas despite an increase in temperatures beyond their current realized thermal limits.

Here we use natural history collections data for >2000 plant species from South America's tropical moist forests to estimate rates of biotic attrition due to temperature increases ranging from +1 to +5 °C, and under two niche assumptions. First, we calculate rates of biotic attrition assuming that the observed thermal niches accurately reflect the full range of temperatures under which a species may persist. Second, we calculate rates of biotic attrition correcting for the possibility that the observed niches of lowland species are truncated by replacing them with randomly sampled niche breadths measured for species from higher elevations on the assumption that within wet tropical forests there is no relationship between fundamental thermal niche breadth and upper thermal niche limit.

Materials and methods

We downloaded all available herbarium records for plants identified to species and including geographic coordinates collected from South America through the Global Biodiversity Information Facility data portal (GBIF, http://www.gbif.org; specific databases accessed are provided in the supporting Table S3). We excluded duplicate records and all records with obvious geographic or elevational errors (e.g. those occurring over bodies of water or at elevations >5000 m). We further screened the data by limiting herbarium records to just specimen collected from the 'Tropical and Subtropical Moist Broadleaf Forests' biome of South America (Olson *et al*., 2001).

We estimated the mean annual temperature (or range of temperatures as described below and in the supplemental online materials) at which each individual specimen was collected by using the listed geographic coordinates to extract data from the WorldClim interpolated climate surface (http://www.worldclim.org; Hijmans *et al*., 2005). However, as we show elsewhere, geo-referencing errors of herbarium records may be severe and cause large inaccuracies in estimates of climatic niches (Feeley & Silman, 2009b). Geo-referencing errors are most problematic for collections from the Andes, where because of the high topographic relief even small horizontal displacements can result in large vertical shifts. Because of the relationship between elevation and temperature, this translates into large temperature shifts. Furthermore, extreme topographic variation can cause temperatures to vary by more than 5 °C within a climate database's single grid cell (i.e. $0.0083^\circ \times 0.0083^\circ$ latitude × longitude, or approximately 0.9 km × 0.9 km, in the case of the WorldClim database used here). For any specimen recorded as having been collected from above 1000 m elevation, we therefore applied a correction to the inferred temperature using the difference between the inferred collection elevation (i.e. the elevation extracted from a 90 m SRTM Digital Elevation Model containing the recorded collection coordinates) and the elevation recorded with the specimen itself assuming an adiabatic lapse rate of $-5.5\,^\circ\mathrm{C}\,1000\,\mathrm{m}^{-1}$ gain in elevation as previously measured for the region (Terborgh, 1977; Bush *et al*., 2004).

For each of the 2151 well-collected species (defined as having ≥30 specimens with temperature estimates; Wisz *et al*., 2008) we estimated the upper and lower limits of the thermal niche as the 2.5% and 97.5% quantiles, respectively, of the collection temperatures. Quantiles were used rather than absolute maximum and minimums in order to reduce the impacts of outliers potentially caused by errors in species identification, geo-referencing, or digitizing (Feeley & Silman, 2009b).

We divided the moist forests of South America into 1° temperature zones of 23.3–24.3, 24.3–25.3, 25.3–26.3, 26.3–27.3, and 27.3–28.3 °C (Table 1, Fig. 1). For each temperature zone, we calculated the rate of biotic attrition, or percent species loss, per degree of warming. The rate of biotic attrition (A) was calculated as $A = (1 - S_f/S_c) \times 100$ where S_c is the number of species that occur in the zone at present and S_f is the number of species predicted to be capable of occurring in the zone in the future with global warming (i.e. species whose thermal niche limits include the elevated temperature of +1 through +5 °C).

Next, we estimated the rate of species loss from each zone correcting for truncated thermal niches. To generate the corrected thermal niche limits, we assumed that there is no relationship between the breadth of a species' fundamental thermal niche and the upper thermal niche limit. Following this assumption, we replaced each of the potentially truncated niches (i.e. of species with upper thermal limits ≥25.5 °C; see 'Results') with one of the nontruncated niches (i.e. of species with upper thermal limits >20 °C and <25.5 °C) sampled at random with replacement. We then calculated the rate of biotic attrition as above but using the adjusted thermal niche limits. We iterated this process 10 000 times to generate 95%

Table 1 Species richness and approximate area (km^2) of climatic zones within the 'Tropical and Subtropical Moist Broadleaf Forests' biome of South America

Zone	Mean annual temperature range (°C)	# of species (% total)	Area (% biome*)
a	27.3–28.3	370 (17.20%)	740 000 (4.05%)
b	26.3–27.3	1430 (66.48%)	2 250 000 (12.35%)
c	25.3–26.3	1677 (77.96%)	2 610 000 (14.31%)
d	24.3–25.3	1761 (81.87%)	620 000 (3.38%)
e	23.3–24.3	1761 (81.87%)	30 000 (0.18%)

Zones are defined by mean annual temperatures. Zones are mapped in Fig. 1.
*Land areas do not add to 100% since some of the 'Tropical and Subtropical Moist Broadleaf Forests' falls outside of the selected temperature zones.

confidence intervals of calculated rates of biotic attrition per degree warming with error estimates incorporating the natural intraspecific variation that occurs even among nontruncated niches.

We also conducted all analyses estimating the thermal niches of species as the difference in the maximum (97.5% quantile) mean daily maximum temperature of the hottest month and minimum (2.5% quantile) mean minimum daily temperature of the coldest month from which samples have been collected in order to account for seasonality and diurnal temperature variation. Results did not differ qualitatively and are presented in the 'Supporting information'.

Results

In accord with the expectations of the truncated niche hypothesis, average thermal niche breadth changed in

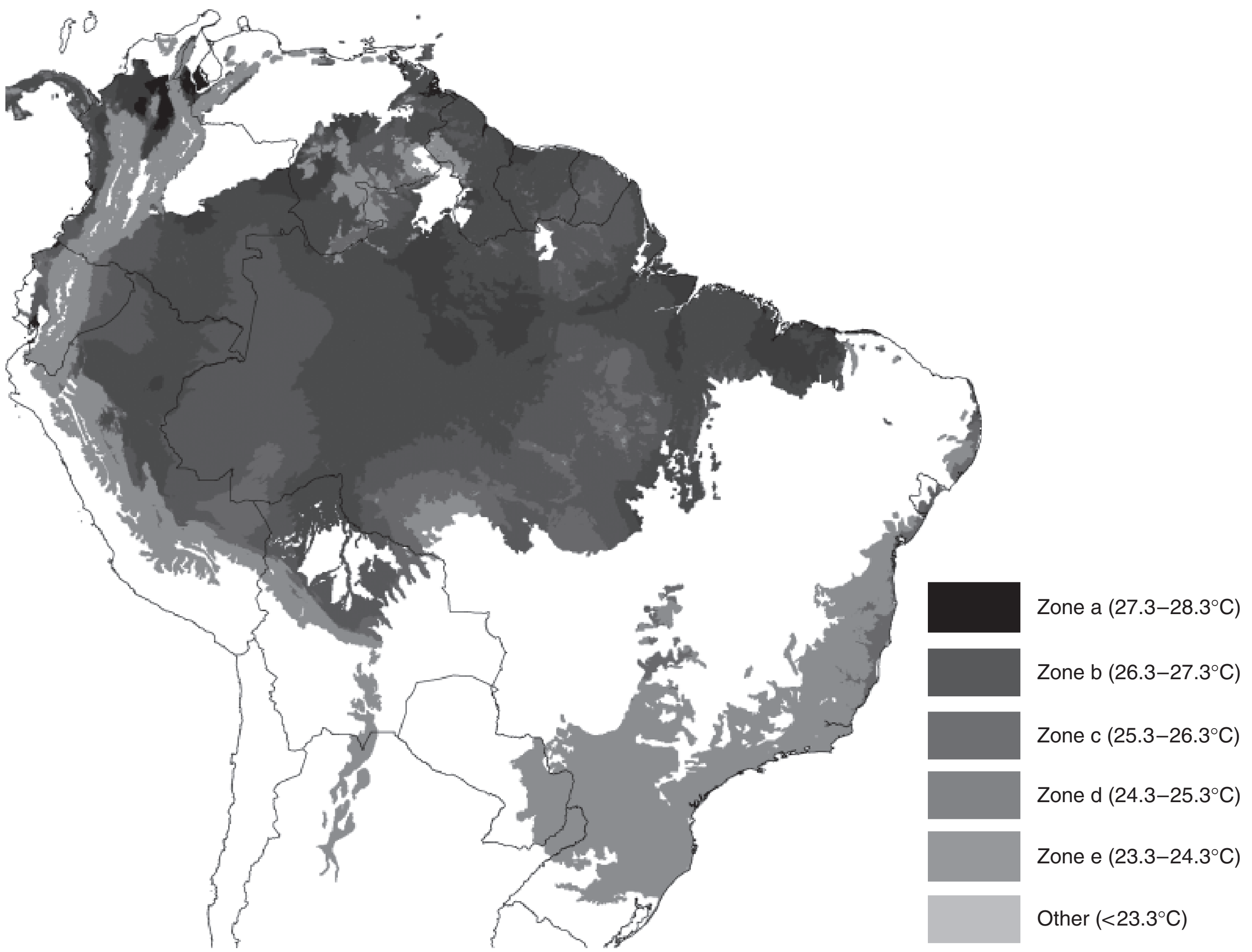

Fig. 1 Map of tropical South America indicating the location of climatic zones, as defined by mean annual temperature, within the 'Tropical and Subtropical Moist Broadleaf Forests' biome of South America (areas outside study biome not colored). The approximate land area and the number of plant species with thermal niches overlapping each zone are listed in Table 1.

relation to the species' upper thermal niche limit. Specifically, realized thermal niche breadth decreased sharply for species with upper thermal limits greater than approximately 25.5 °C mean annual temperature (Fig. 2). This is despite the fact that the range of possible niche breadths increases with hotter upper thermal limits (e.g. a species with a maximum thermal limit of 28 °C can potentially occur over a greater range of temperatures than can a species with a maximum thermal limit of only 22 °C; supporting Fig. S3). We also found a reduction of thermal niche breadths in species with maximum thermal limits less than approximately 20 °C (Fig. 2). This may be due to the truncation of lower thermal niche limit due to the lack of colder habitat especially within the bounds of Tropical Moist Forests with a minimum mean annual temperature of 2.9 °C ('Supporting information'). For species with upper thermal limits >20 °C and <25.5 °C (326 species), the mean thermal niche breadth is 10.42 ± 0.28 °C (95% CI based on bootstrapping with 10 000 samples). For species whose upper thermal limit exceeds 25.5 °C (1648 species), the mean thermal niche breadth is only 6.59 ± 0.14 °C (Fig. 2).

Using observed thermal niches, increasing temperatures will cause high rates of biotic attrition (A) over vast areas of South America's tropical forests, with all zones predicted to lose 100% of diversity under a + 5 °C warming scenario. If we adjust for the possibility that plants species' observed thermal niches are truncated by current climatic conditions and poorly reflect their true tolerances, estimated rates of biotic attrition from these forests decrease significantly (Table 2, Fig. 3). For example, using observed thermal niches we predict an almost complete loss of plant diversity in most South American tropical forests due to a 5 °C temperature increase, but correcting for possible niche truncation we estimate that most forests will retain >50–70% of their current species richness (Table 2).

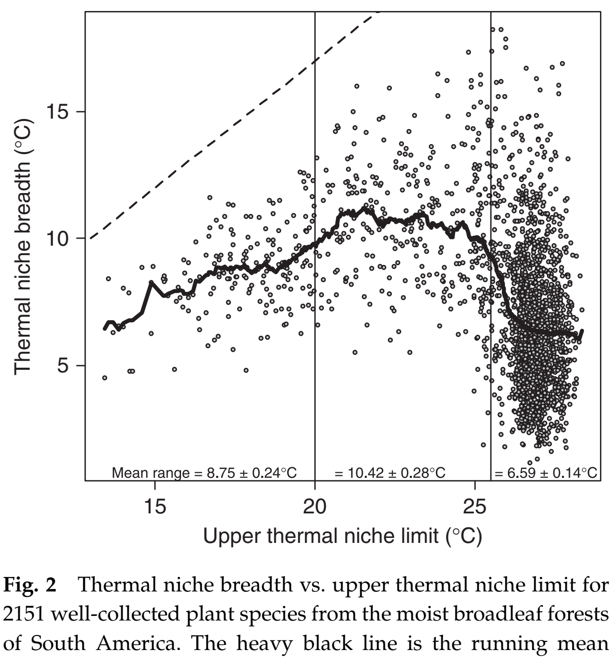

Fig. 2 Thermal niche breadth vs. upper thermal niche limit for 2151 well-collected plant species from the moist broadleaf forests of South America. The heavy black line is the running mean (averaged over 1 °C). The breadth of thermal niches decreases for species with upper thermal limits <20 °C or >25.5 °C (vertical lines). The dashed line indicates the maximum possible thermal niche breadth (minimum mean annual temperature within study biome = 2.9 °C). Mean thermal niche breadths ± 95% CI for species within each bin are indicated.

Discussion

A general prediction of global warming, as now supported by several long-term studies showing changes in plant species distributions (e.g. Dobbertin *et al.*, 2005; Walther *et al.*, 2005; Beckage *et al.*, 2008; Kelly & Goulden, 2008; Lenoir *et al.*, 2008), is that species will migrate upward and/or poleward tracking their preferred temperatures (Rosenzweig *et al.*, 2007; Thuiller, 2007). An inherent and alarming consequence of these distributional shifts toward colder climates is that vast areas of the low-lying hot tropics may suffer substantial biotic attrition and loss of species diversity (Colwell *et al.*, 2008). Temperatures have already risen measurably throughout much of the tropics over the past several decades (Vuille & Bradley, 2000; Malhi & Wright, 2004; Magrin *et al.*, 2007) but there have been no reports of the expected mass losses of species from low-lying hot areas. How are species able to persist in the hot tropics despite temperatures now exceeding their known tolerances? Species loss may be mitigated by factors other than temperature changes such as rising CO_2 and/or changes in precipitation (Tyree & Alexander, 1993; Rickebusch *et al.*, 2008). It is also possible that the changes in temperature have been so rapid that there has been insufficient time for biotic attrition to occur and that these forests are now full of the 'living dead'; or in other words, that the remaining species have already become committed to local extinction. Another possibility, which we explore here, is that estimates of thermal niches derived from observations or collection records are inaccurate and truncated due to the absence of hotter areas under current climate (Broennimann & Guisan, 2008). Consequently, even as temperatures increase to the point that they exceed the observed upper thermal limits of most species, they may still be within the fundamental tolerances of many, allowing them to persist.

The thermal niches as estimated from collections for plant species from the hottest forests of South America do in fact tend to be several degrees narrower than those of plant species from cooler climates (Fig. 2; supporting Fig. S3). One possible explanation for the observed pattern of narrower niches at hotter tempera-

Table 2 Rates of biotic attrition (*A*, equivalent to percent species loss), for climatic zones within the study biome (as defined by mean annual temperatures) predicted per degree of warming using observed thermal niches and correcting for truncated thermal limits (95% Confidence Intervals)

	Biotic attrition (*A*)				
	Zone				
Temperature increase (°C)	a	b	c	d	e
Using observed thermal niches					
1	100.00	74.13	14.73	4.77	0.00
2	100.00	100.00	77.94	18.80	4.77
3	100.00	100.00	100.00	78.99	18.80
4	100.00	100.00	100.00	100.00	78.99
5	100.00	100.00	100.00	100.00	100.00
Using corrected thermal niches					
1	7.16–10.09	5.01–7.42	5.36–7.34	9.63–11.28	1.31–2.6
2	16.98–20.96	12.62–15.96	10.74–13.5	13.64–15.94	8.87–10.72
3	28.7–33.16	21.96–26.01	17.96–21.38	18.95–21.87	14.31–16.71
4	41.23–45.99	32.96–37.44	26.86–30.76	26.03–29.33	19.39–22.14
5	53.96–58.83	44.83–49.44	37.18–41.34	34.47–38.12	25.97–29.14

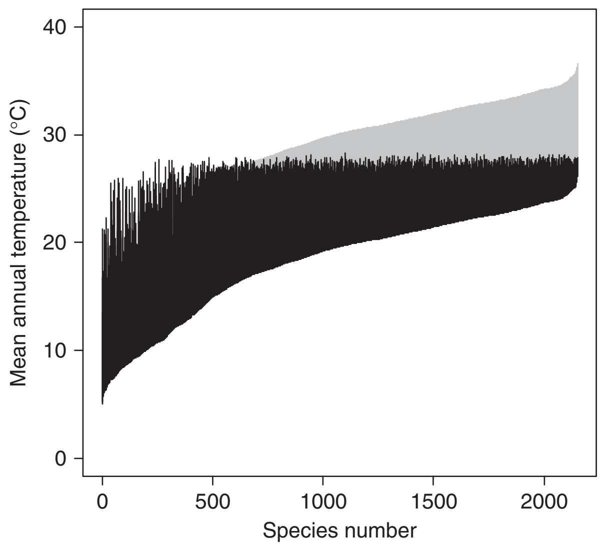

Fig. 3 Observed and corrected thermal niches for each of the 2151 study species (ordered by lower thermal niche limits to improve visual clarity). Black vertical lines indicate the observed thermal niches and gray lines indicate the mean corrected thermal niches applied to species with observed upper thermal limits $\geq$ 25.5 °C.

tures is that the thermal niches of species from the hot tropics are truly reduced relative to species from cooler regions of the tropics. This could be the result of greater climatic specialization in the hot lowlands where climate is more temporally stable (Janzen, 1967; Ghalambor *et al*., 2006; Deutsch *et al*., 2008; McCain, 2009). An alternative explanation is that the observed niche breadths of species from hot tropical forests are similar to those from other areas but are truncated under the current climatic regime. Experimental or manipulative studies are called for to distinguish between these two competing hypotheses (e.g. Duncan *et al*., 2009).

Assuming that the thermal niches of many species are truncated at the hottest temperatures, we estimate that rates of biotic attrition due to future warming will be markedly less than predicted using observed niches. Under a scenario of 5 °C temperature increase (the approximate temperature increase expected for these areas over the next 100 years; Carter *et al*., 2007; Magrin *et al*., 2007; Urrutia & Vuille, 2009), using the observed thermal niches predicts a 100% loss of diversity over more than 7 billion km^2 of South America's tropical forests, encompassing virtually the entire forested Amazon basin. In contrast, under the same warming scenario but using thermal niches which have been corrected for possible truncation, we estimate that in even the very hottest areas the maximum rate of attrition will not exceed 60% and that most South American forests will retain $>$50–70% of their current species richness (Table 2).

While estimates of biotic attrition show large differences under our competing assumptions regarding fundamental niche breadths, the true rates of species loss will almost certainly be intermediate and will likely depend heavily on a variety of other factors not taken into account when estimating thermal niches based on species occurrences. For example, regarding climatic variables, our models did not account for changes in moisture balance either due to changes in precipitation or changes in water use efficiency due to increasing atmospheric CO_2 (Tyree & Alexander, 1993; Rickebusch *et al*., 2008). Current species distributions are strongly

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associated with gradients in water balance (Gentry, 1988; Kreft & Jetz, 2007) and thus changes in precipitation and water use efficiency will almost certainly have strong impacts on future species distributions. Perhaps even more importantly, in our model we did not account for deforestation, land-use change, or other anthropogenic disturbances which may greatly influence the distribution of species (Feeley & Silman, 2009a). In order to accurately predict the impacts of climate change on species diversity, factors such as these will need to be included (Duncan *et al*., 2009).

Despite these concerns, our results clearly show that future studies must also account for, and correct, possible discrepancies between species' realized and fundamental climatic niches. To conclude, we point out that even our best case scenario, in which the thermal niches of all lowland species are assumed truncated, still predicts that some areas of the Amazon Basin may lose as much as 50% of plant species diversity due to the changes in temperature that are predicted over just the next century. Efforts are clearly called for to slow global warming and mitigate the effects on tropical forests (Killeen & Solorzano, 2008).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Thermal niche breadth vs. upper thermal niche limit for 2151 well-collected plant species from the moist broadleaf forests of South America with niches defined on the basis of maximum and minimum mean daily temperatures of the hottest and coldest months. The heavy black line is the running mean (averaged over 1 °C). The breadth of thermal niches decreases for species with upper thermal limits >30.5 °C or <26 °C (vertical lines). The dashed line indicates the maximum possible thermal niche breadth (minimum temperature $=-4.5$ °C). Mean thermal niche breadths $\pm$ 95% CI for species within each bin are indicated.
Figure S2. Observed and corrected thermal niches as defined on the basis of maximum and minimum mean daily temperatures of the hottest and coldest months for each of the 2151 study species (ordered by lower thermal niche limits to improve visual clarity). Black vertical lines indicate the observed thermal niches and gray lines indicate the mean corrected thermal niches for species with observed upper thermal limits ≥ 30.5 °C (see text).
Figure S3. Thermal niche breadth vs. upper thermal niche limit for 2151 well-collected plant species from the moist broadleaf forests of South America. The heavy black line is the running mean (averaged over 1 °C; see main text). The shaded area shows the 95% Confidence Interval for expected mean values based on simulations where species are distributed at random with regards to temperature and niche breadth, but truncation is not permitted (i.e., any species with a simulated niche breadth extending beyond the observed temperature limits were discarded). According to this null model, species occurring in hotter areas will tend to have broader niches than species with colder upper thermal niche limits.
Table S1. Species richness and approximate area (km^2) of climatic zones within the 'Tropical and Subtropical Moist Broadleaf Forests' biome of South America. Zones are defined by mean maximum daily temperature of the hottest month.
Table S2. Rates of biotic attrition (*A*, equivalent to percent species loss), for climatic zones within the study biome (as defined by mean maximum daily temperature of the hottest month) predicted per degree of warming using observed thermal niches (as defined by the difference in the maximum mean daily maximum temperature of the hottest month and minimum mean minimum daily temperature of the coldest month from which samples have been collected in order to account for seasonality and diurnal temperature variation) and correcting for truncated thermal limits (95% Confidence Intervals).
Table S3. Herbaria contributing tropical plant collections. All collections accessed through the Global Biodiversity and Information Facility (www.gbif.org) between 1/2008–2/2008.

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