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Widespread but heterogeneous responses of Andean forests to climate change

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Global warming is forcing many species to shift their distributions upward, causing consequent changes in the compositions of species that occur at specific locations. This prediction remains largely untested for tropical trees. Here we show, using a database of nearly 200 Andean forest plot inventories spread across more than 33.5° latitude (from 26.8° S to 7.1° N) and 3,000-m elevation (from 360 to 3,360 m above sea level), that tropical and subtropical tree communities are experiencing directional shifts in composition towards having greater relative abundances of species from lower, warmer elevations. Although this phenomenon of 'thermophilization' is widespread throughout the Andes, the rates of compositional change are not uniform across elevations. The observed heterogeneity in thermophilization rates is probably because of different warming rates and/or the presence of specialized tree communities at ecotones (that is, at the transitions between distinct habitats, such as at the timberline or at the base of the cloud forest). Understanding the factors that determine the directions and rates of compositional changes will enable us to better predict, and potentially mitigate, the effects of climate change on tropical forests.

As global temperatures rise, species are predicted to shift their geographical distributions towards cooler latitudes and elevations[1]. These 'species migrations' (here referring to all modes of range changes, including expansions, contractions and shifts[2,3]) have been observed in many different species and systems[2,4,5]. However, the vast majority of studies that have investigated species migrations are from temperate or boreal systems, and little information is available about the responses of tropical and subtropical species—and in particular tropical plant species—to climate change[2,6]. This is despite the fact that tropical plants may be especially susceptible to climate change because of their narrow thermal niches[7], and the fact that species migrations out of tropical lowlands can cause biotic attrition[8] and losses of local biodiversity.

Species migrations of tropical plants

For tropical and subtropical plants, only a small set of studies have researched species migrations. The most direct approach to detect species migrations is to quantify changes in the ranges of species over time, usually by tracking shifts in the mean or upper elevational range limits of species. For example, in the alpine Himalayas (>4,000 m above sea level, (m a.s.l.)), the upper range limits of nearly 90% of investigated plant species have risen since 1850[9]. In another study, 58% of plant species studied in Taiwan shifted their ranges upwards over a 100-year period[10]. In Hawaii, 67% of the studied grass species increased their maximum elevation levels over a 42-year period[11], and in Ecuador, 88% of the studied alpine plant species expanded their upper range limits to higher elevations over a 200-year period[12]. Although these species-specific studies provide compelling evidence that many tropical and subtropical plant species are shifting their ranges upslope, the approach is of limited applicability because it requires accurate maps of the ranges of individual species, or range limits, at multiple times. Long-term species-specific data are not available for the majority of tropical species. Indeed, even the current ranges of most tropical plant species remain unknown, making it impossible to test for temporal range shifts. For example, the Himalayan study included only 124 species and the Taiwanese study 24 species—small fractions of the total plant diversity in either of these areas. Thousands of other species from throughout the tropics and subtropics are similarly excluded from these types of studies because of the lack of accurate distribution data[6,13].

Another approach that enables the integration of data that are more-readily available from more areas and for more species is to analyse changes in the taxonomic or functional composition of communities over time[5]. More specifically, a community temperature index (CTI) can be used to characterize communities based on the relative abundances of species with different thermal affiliations, or optima, and to test the prediction that species migrations should cause directional changes in composition over time[14]. For example, upward species migrations will result in greater relative abundances of more-thermophilic species from relatively warmer climates at any given elevation. In other words, upward species migrations should cause increases in the CTI of communities—a phenomenon referred to as 'thermophilization'. Changes in the CTI and thermophilization have been used as evidence of latitudinal migrations of bird and butterfly species[15], as well as temperate lowland[16] and alpine plant species[17]. Changes in CTI, or other analogous indices, have also been calculated from fossil pollen records to estimate rates of plant species migrations in response to past climate change[18].

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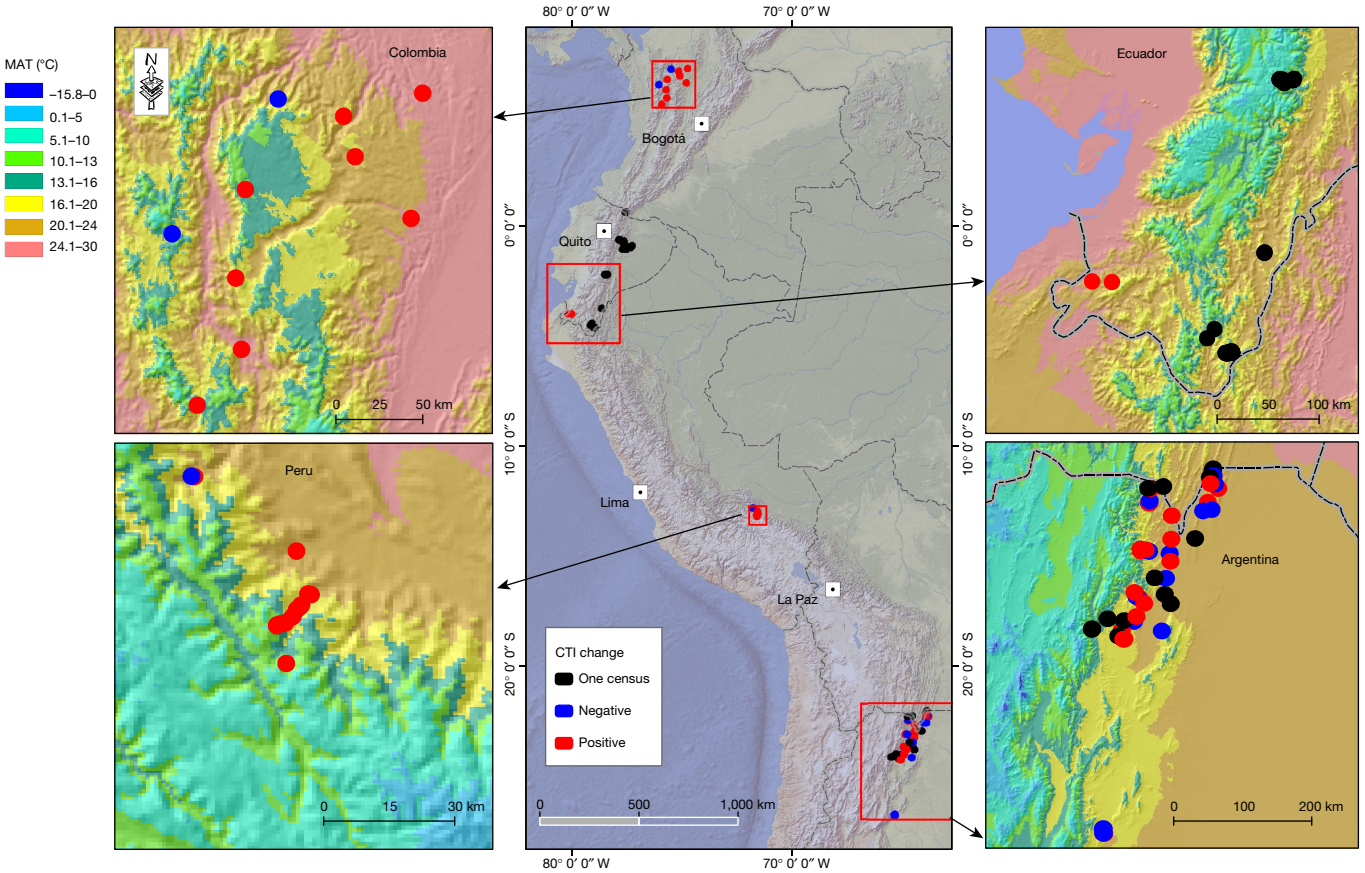

Fig. 1 | Map of Andean forest plot locations. The map shows the locations of the 186 Andean forest plots that are included in the analyses. Red points indicate plots with positive TR_{plot} (which is the annualized change in the CTI of a plot); blue points are plots with negative TR_{plot}; black points are plots with only one census and for which it was therefore not possible to calculate the TR_{plot}.

Tracking changes in the CTI is an especially useful tool for analysing the effects of climate change in hyperdiverse systems, such as tropical forests, because it does not require precise information about the range limits of individual species and enables the integration of census data from multiple locations and years. Several recent studies have used the CTI to characterize changes in the composition of tree species in tropical montane forests owing to contemporary species migrations. These studies from Peru, Costa Rica and Colombia found that focal tree communities mostly show increases in their CTI over time[19–21]. The thermophilization of these forests was hypothesized to be due primarily to increased mortality of the more heat-sensitive (that is, less-thermophilic) tree species as temperatures increased[21].

The above studies indicate that climate change is causing rapid shifts in the distributions of many tropical trees, which in turn is leading to directional changes in forest composition. However, important questions remain about the generalizability of these results. Specifically, it remains unclear how widespread and uniform the process of thermophilization is in tropical forests and what factors cause variation in thermophilization rates between different communities. In this study, we address these questions in the Tropical Andes Biodiversity Hotspot, from Colombia to Argentina in South America. We assess variability in rates of thermophilization between sites to gain insights into the factors that may be slowing, or preventing, species migrations in some areas.

Thermophilization of Andean forests

To examine temporal changes in the composition of tropical tree species at a large spatial scale, we collated a database of forest censuses from 186 inventory plots spread throughout the tropical and subtropical Andes Mountains of Colombia, Ecuador, Peru and northern Argentina[22] (Fig. 1). The plots span an elevation gradient of more than 3,000 m, corresponding to a gradient of approximately 14 °C in mean annual temperature (MAT). A total of 120 plant families, 528 genera and 2,024 tree species (including palms, tree ferns and lianas) occur in the study plots and were included in our analysis (further information about the plots is provided in Table 1 and in Supplementary Table 1). Using this dataset of tree-species composition in Andean forests, we analysed the relationships between the CTI and the environmental temperature and elevation of the plots. We then tested for thermophilization—that is, increases in CTI over time—in the plots that had been censused repeatedly ($n = 64$). We also applied a new analytical approach to the combined dataset of all plots ($n = 186$) to determine how rates of thermophilization relate to elevation and temperature across the Andes.

To look at patterns of species composition and compositional change, we first calculated the CTI (°C) for each plot during each census. CTI is the mean of the thermal optima of all species that were found in a plot weighted by their relative abundances. The thermal optimum of each species was calculated as the mean of the MATs[23] at the locations where each species are known to occur based on collection records obtained through the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/).

We next analysed the relationship between the CTI and the MAT of the plots to assess the role of regional temperatures in structuring community assembly. The average CTI of the plots ranged from 12.2 to 23.8 °C and was strongly positively correlated with MAT (slope = 0.71, $R = 0.92$, $P < 0.001$; Extended Data Fig. 1a). This indicates that the functional composition (that is, the relative abundances of species with different thermal optima) of the plots is strongly determined by temperature. In other words, plots at similar regional temperatures have similar CTI because of similar relative abundances of more- or less-thermophilic species, even if the plots are separated by as much as 4,000 km (for example, plots in Argentina versus Colombia) and have little to no taxonomic overlap in species. Given the strength of

Table 1 | Description of the Andean forest plot database

Countries	Argentina	Colombia	Ecuador	Peru	Total
Number of plots	52 (48)	10 (10)	110 (6)	14 (14)	186 (78)
Total plot area in ha	55.84	10	16.72	14	96.56
Number of plots with multiple censuses	38 (34)	10 (10)	2 (2)	14 (14)	64 (60)

The number of 1-ha plots is shown in brackets.

MAT in determining the functional composition of Andean forests, global warming should manifest as temporal increases in the CTI of the study plots.

To test for thermophilization, we first looked at changes in CTI over time in all plots that had been censused more than once. We calculated the annualized rate of change in the CTI of each plot in all possible census intervals ($n = 176$ census intervals, Fig. 2) and used the rate of change in CTI between the initial and final censuses as the best estimate of the thermophilization rate of each plot (TR_{plot}). Of the 64 plots with repeated census data, 46 (72%) increased in CTI (that is, had positive thermophilization rates), indicative of increasing relative abundances of species from relatively warmer climates. The number of plots with positive TR_{plot} is more than expected under the null expectation of equal proportions of plots with positive and negative TR_{plot} values that would occur due to random fluctuations in composition over time (binomial probability <0.001). Of the 23 plots that were censused repeatedly, 43% consistently increased in CTI and had positive TR_{plot} over all intervals. By contrast, only one of the plots (4%) had negative TR_{plot} in all intervals. The mean thermophilization rate measured across all census intervals was 0.0066 °C per year (95% confidence interval = 0.004– 0.009 °C per year) (see Methods and Extended Data Fig. 2 for an alternative method of calculating TR_{plot}).

To assess how thermophilization rates relate to plot temperatures and elevations, we integrated the compositional information from all 186 inventory plots, including those that had been censused only once, and calculated a running mean of CTI per MAT in overlapping five-year census intervals between 2000 and 2015 (Fig. 3a). We then calculated the thermophilization rate (TR_{MAT}) as the slope of the linear least-square regression between its mean CTI and the midpoint of the respective time period (Fig. 3b). TR_{MAT} was significantly positive at most MATs and elevations, consistent with the widespread thermophilization observed in the per-plot analysis described above. Using a linear mixed-effect model of CTI versus year with plot identity included as a random effect ($n = 283$), we estimated that the mean TR_{MAT} was 0.003 °C per year (95% confidence interval = 0.002–0.004 °C per year). The difference between the mean TR_{MAT} and TR_{plot} is due to the inclusion of plots with single censuses and the fact that TR_{MAT} incorporates temporal changes in the CTI both within and between plots.

Ecotonal barriers to species migrations

Our results support the hypothesis that increasing temperatures are causing thermophilization of montane forests across much of the tropical and subtropical Andes. Although thermophilization is widespread, we also find that the rates of thermophilization are heterogeneous throughout the MAT and elevation gradients. Specifically, thermophilization rates were positive on average, but TR_{MAT} was negative or not significantly different from zero at the coldest and middle MATs (that is, at the highest and mid-elevations, respectively). This result mirrors patterns that have been observed within individual elevation gradients in Peru, Colombia and Costa Rica[19–21]; in all three of these gradients, the lowest thermophilization rates occurred at mid- and high elevations.

Although the tropical Andes have been identified as a 'warming hotspot'[24], some studies indicate that the warming rates vary between elevations[25]. As such, one possible explanation for the absence of significant thermophilization at high and mid-elevations is that warming rates may be slower at these elevations. Indeed, when we compare TR_{plot} to the estimated mean warming rates at each plot location (overall mean warming = +0.06 °C per year since 1990), we find that there is an overall positive correlation ($R = 0.30$, $P < 0.01$) and that TR_{plot} is negative at six out of the seven sites at which temperatures decreased (Fig. 4). We also find a generally positive relationship between warming rates and TR_{MAT} (Extended Data Fig. 3). Although these analyses suggest that differences in regional warming rates may be contributing to variation in thermophilization rates, the relationships are fairly weak and it is probable that other factors—as discussed below—are also important in determining rates of compositional change in Andean forests.

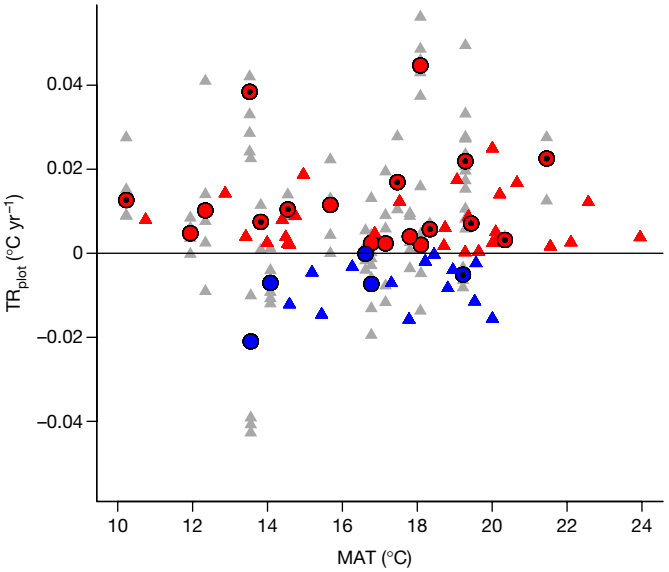

Fig. 2 | Thermophilization rates of repeatedly censused plots. TR_{plot} and MAT values were calculated for the Andean forest plots with multiple censuses. $n = 64$. Triangular grey points represent the annual change in the CTI for each of the possible census intervals ($TR_{interval}$); coloured triangular points represent plots with only two censuses and therefore only one interval. Circular points represent the average annual change in the CTI over the complete study period for plots with more than two censuses (that is, the annualized difference between final and initial CTI). Positive and negative thermophilization rates are coloured red and blue, respectively. Circles with black centres indicate plots for which the CTI changed consistently in one direction (that is, positive or negative) across all intervals.

An alternative or additional factor that may be driving differences in thermophilization rates across elevations is the presence of several distinct ecotones along the slopes of the Andes; for example, the transition from montane rainforest to cloud forest (that is, the cloud base) at mid-elevations and the transition from closed-canopy forest to open alpine grasslands (that is, the timberline) at high elevations. Conditions at ecotones can be biotically and abiotically distinct from surrounding forests, potentially reducing establishment success of colonizers and favouring stability of incumbent communities. For example, the cloud-base ecotone represents an inflexion point in many environmental variables such as precipitation, diurnal temperature range[26], soil water content[27] and light availability[28]. If the tree communities in and around ecotones are comprised predominantly of specialist species able to cope with the unique conditions that occur at these sites, then it may be harder for the composition to change, because any change will require the encroachment of non-specialized species. As one conceptual example, many high-elevation forests are dominated by just a single to few species of trees that are specifically adapted to the unique environmental conditions that occur near the timberline. Even if rising temperatures cause decreased reproduction, performance and/or increased mortality of these species (or even the complete loss of some species), changes in the CTI will be small because all of the remaining species will have similar thermal optima. In cases such as these, thermophilization can only occur if a species from lower elevations (that is, with higher thermal optima) expands its range and recruits into the ecotonal forest. In

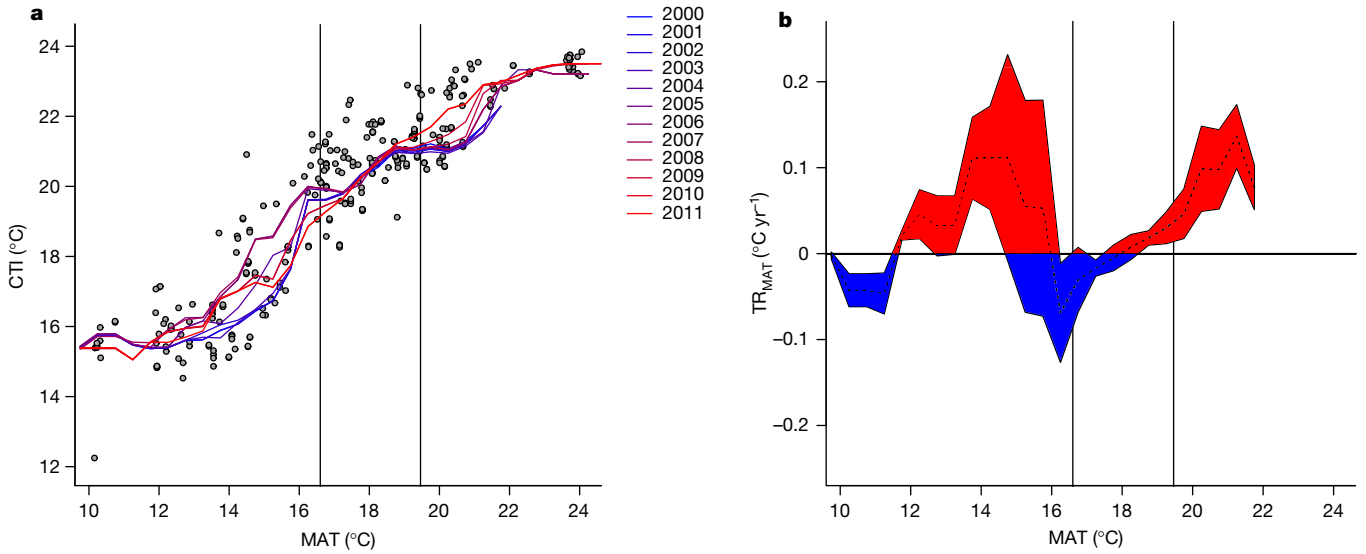

Fig. 3 | Thermophilization rates of Andean forest plots. a, The CTI and MAT values for all plot censuses are shown as points. $n = 283$. The lines indicate the mean CTI compared to MAT, calculated for overlapping five-year time periods from 2000 to 2015. **b**, The thermophilization rates for thermal bands (TR_{MAT}; the annualized change in the mean CTI of all plots within a thermal band) was compared to MAT values. $n = 283$ plot censuses, assigned to 28 thermal bands. The dashed line indicates the mean TR_{MAT} and the coloured area indicates the 95% confidence interval of TR_{MAT} with positive and negative values coloured red and blue, respectively. The black rectangle encompasses the approximate MATs encompassing cloud base in each country (Argentina, 1,000 m a.s.l.; Ecuador, 1,400 m a.s.l.; Colombia, 1,500 m a.s.l.; Peru, 1,600 m a.s.l.). Timberline occurs at approximately 5–7 °C MAT.

support of this hypothesis, we find that (1) plots with negative thermophilization rates have lower species richness than expected based on their MAT (Extended Data Fig. 4), (2) more-specialized communities have slower rates of thermophilization as indicated by a positive correlation between measures of intraspecific variation in the thermal optima of co-occurring species and the corresponding TR_{plot} (Extended Data Fig. 5) and (3) the absolute abundance (basal area) of more-thermophilic species (that is, with thermal optima higher than the CTI of the plot) remained stable or decreased in low- and mid-temperature plots, but generally increased in high-temperature plots (by contrast, the absolute abundance of less-thermophilic species with thermal optima below the CTI of the plot increased at mid-temperatures) (Extended Data Fig. 6). In other words, slow or negative thermophilization rates are associated with areas in which warming rates are slower, and/or with lower-diversity and more-specialized forests near ecotones in which there is little ingrowth or recruitment of more-thermophilic species.

In addition, variation in thermophilization rates can increase if the ranges of some species are limited by biotic interactions[29], non-climatic factors (for example, topography or soil-nutrient composition) or climatic factors that do not change concomitantly with temperature (for example, cloud cover or water availability)[30]. For example, if water availability decreases with elevation, then changes in precipitation and rising temperatures could cause drought-sensitive species to migrate downslope[31], resulting in negative TR_{plot} estimates. Similarly, changes in other environmental constraints such as light exposure or the frequency of frost events can change in unexpected and nonlinear ways (for example, owing to changes in cloud cover or 'cloud lifting'), potentially leading to downward migrations of some species in some areas. For example, there is evidence that the upper range limits of some Andean tree species are set by cold night-time temperatures and frost events. Despite rising MATs, the frequency and magnitude of frost events is increasing in some areas; this could prevent upward migrations and potentially cause the downward migrations of some species[32].

Finally, we cannot rule out the influence of idiosyncratic processes or events on community composition and thus thermophilization rates[33]—especially given the relatively short duration of this study in relation to the lifespans of most trees. In particular, the two plots with the most-negative TR_{plot} values may have been influenced by site-specific factors including increased understory recruitment due to reduced herbivory[34] and high growth rates of less-thermophilic understory species during certain years[35]. For this study, we focused exclusively on the effects of rising temperatures on tree species composition, but multiple forces (both climatic and non-climatic) can undeniably affect the suitability of habitats for different species[36] and, therefore, the CTI[33]; uncovering and integrating these other factors must be a priority of future studies.

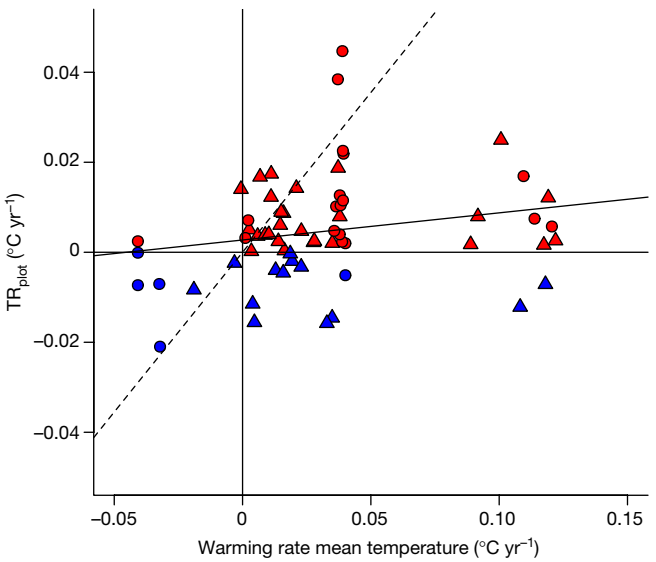

Fig. 4 | Mean warming rate at plots. The TR_{plot} was compared to the estimated warming rate (average annual change in mean temperature between 1990 and 2013) at each of the plot locations. $n = 64$ plots, Spearman correlation two-sided $R = 0.30$, 95% confidence interval = 0.06–0.50, $P < 0.01$; solid diagonal line. The triangular points are plots with only two censuses and the circular points represent plots with more than two censuses. Plots with positive and negative TR_{plot} are coloured red and blue, respectively. The dashed line shows the expected relationship between TR_{plot} and warming rate based on the observed relationship between CTI and MAT ($TR_{plot} = 0.71 \times \Delta MAT$).

Discussion

Our analyses indicate widespread thermophilization but with rates of compositional change that vary across elevation—potentially owing to differences in warming rates, the occurrence of ecotonal 'roadblocks' and/or the influence of factors other than temperature in setting the range limits of some species. Although we are confident that these findings are robust, we acknowledge two limitations of this study. First, the data used in our analyses come from a single, albeit extremely important, region of the tropics—the Tropical Andes Biodiversity Hotspot[37]—and it remains uncertain how other tropical forests and ecosystems are responding to climate change. Although comparable studies are clearly needed for other tropical and subtropical regions, there is good reason to suspect that other forests are undergoing similar changes in composition. As discussed above, studies from other parts of the tropics have all shown evidence of species migrations and thermophilization of plant communities[9–12,19–21]. Similarly, studies from various regions of the tropics have shown evidence of upward migration of animal species (for example, birds, insects and herpetofauna) and communities[38–40]. Second, although the observed shifts in the composition of tropical and subtropical Andean forests towards having greater relative abundances of thermophilic species is consistent with upward species migrations, these data alone cannot be used to determine which species are migrating or the specific manner in which the ranges of individual species are changing over time (for example, by range expansion, contraction or shifts)[2]. To help to resolve these questions, species-specific analyses looking at population demographics and range dynamics are required. In addition, experimental studies will be crucial for determining the specific way(s) in which changes in different climatic factors are affecting individual species and the consequences for ecosystem processes and services[41].

Despite these limitations, this study provides comprehensive evidence that many tropical and subtropical forests are changing directionally in composition over time, most probably as a response to global warming. It is troubling to note that in all but a few plots, rates of compositional change are markedly slower than regional warming (Fig. 4). Indeed, given that global temperatures have been rising for over a century, the 'slow' rates of compositional change that are observed here (on average 10 times slower than changes in regional MAT) suggest that many tropical tree species may already be occurring in sub-optimal conditions. The disequilibrium between rates of compositional and climate change[42], together with potential ecotonal barriers to species migrations[30], raises concerns regarding the future of tropical montane forests and the many important ecosystem services that they provide. Andean forests must be added to the growing list of ecosystems and species that lack the ability to quickly and cohesively respond to climate change[15,16,43] and thus face high risk of extinction, biodiversity loss and functional collapse[44]. Modelling and conservation efforts must account for compositional lags and prepare for the likelihood that as global warming continues to accelerate, tropical forests will fall even further behind.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41586-018-0715-9

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METHODS

Data reporting. No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Data. We collated census data from 186 Andean forest inventory plots (http://redbosques.condesan.org/). Plots were originally established as parts of seven independent projects with differing motivations and methods but with common core data on the identity and size of all trees (including palms, tree ferns and lianas) that were found within each plot (first census in 1991). A subset of 64 plots had been censused repeatedly (median number of censuses = 2, maximum number of censuses = 6) providing additional data on temporal changes in species composition. In collaboration with plot managers, the collated database was cleaned and corroborated to maximize accuracy of plot metadata, species identifications and stem diameter measurements. Plots with observations that indicated secondary forest composition were excluded from the database; however, two of the included plots from Argentina showed some signs of successional processes[35] or recovery from past disturbances (cattle)[34] that may affect their understory composition (excluding these plots had no observable effects on the results). Plot elevations were estimated based on their coordinates and the SRTM 1 ArcSec Global V3 (https://lta.cr.usgs.gov) 30-m-resolution digital elevation model (DEM). Plot elevations ranged from 360 to 3,360 m a.s.l., corresponding to a MAT gradient from 24.1 to 10.2 °C. The MAT of each plot was estimated by extracting the CHELSA BIO1 values[23] (30-arcsec resolution; approximately 1 km at the equator) at the plot locations. We subsequently down-scaled these estimates to a resolution of 30 m by applying a geographically weighted regression (GWR) model[45]. For the GWR model, we used the environmental and climate data from a total of 745,878 pixels. These included the pixels that contained each of the study plots, all pixels within a 100-m radius around each of the plots, and 20,000 pixels sampled randomly from across the entire Andean study area (bounding box coordinates: 83.0° W, 63.0° W, 9.9° N, 30.0° S). In the GWR, CHELSA BIO1 (that is, MAT) was disaggregated to a 30-m resolution and included as the dependent variable. Elevation, slope and aspect[46], derived from the 30-m DEM (topographic variables calculated using the Raster package in R[47]), were set as the independent variables. Bandwidth of the GWR was set automatically based on preliminary analyses with 100,000 sample points. The relationship between plot elevation and MAT is shown in Extended Data Fig. 1c.

The combined list of tree species from all plots was submitted to the Taxonomic Name Resolution Service (TNRS; http://tnrs.iplantcollaborative.org/) version 3.0 for homogenization and validation of species names. The processing mode was 'name resolution' and the selected sources were The Plant List[48], the Global Compositae Checklist[49], the International Legume Database and Information Service[50], Tropicos[51] and USDA's Plants Database[52]. The family classification was based on Tropicos. The match accuracy threshold was set to 0.05 with partial matches allowed. All species with invalid original names (for example, sp1, indet, and so on) were assigned as 'undetermined'. Any species with an unassigned TNRS-accepted name and taxonomic status of 'no opinion', 'illegitimate' or 'invalid' were manually reviewed. The proper name was added if the species name could be confirmed on The Plant List or Tropicos; if the proper species name could not be confirmed, but the genus was valid, it was assigned the genus name and a unique species identifier. All TNRS species names with taxonomic status 'accepted' but with matching scores lower than 0.9 were also manually checked and modified following the same criteria. Families and genera were changed in accordance with the new species name. If a full species name was not provided or could not be found, the genus and/or family name were kept from the original file.

CTI. Using previously established protocols[19,21], we estimated the thermal distributions of all tree species that occurred in the inventory plots based on the locations of herbarium specimens reported for these species from the tropical and subtropical Andes. More specifically, for all species found in the study plots, all available georeferenced herbarium data records from the Andean countries of Colombia, Ecuador, Peru, Bolivia and northern Argentina (latitude <30° S) were downloaded through the GBIF data portal (https://www.gbif.org/; data downloaded on 9 October 2015, https://doi.org/10.15468/dl.bmz3hf). Any records that were tagged by the GBIF as having possible coordinate issues or that had obvious georeferencing errors (for example, falling in large bodies of water or outside the Andean study region) were discarded. The MAT at the collection locations of all specimens were estimated by extracting the MAT values from the CHLESA BIO1[23]-extrapolated climate map at a spatial resolution of 30 arcsec. We did not down-scale the climate map when extracting MAT values at collection locations owing to the low resolution and potential inaccuracies of the georeferencing data. Only a single occurrence per species was retained from each climate cell. Finally, the most climatically extreme records (that is, those outside the species' central 95% quantile of MAT) for each species were discarded to help to minimize the influence of outliers or remaining georeferencing errors.

For each species represented by ≥10 observation records (n = 1,220), we estimated the thermal optimum as the mean MAT (°C) of the collection locations (we also calculated thermal optima based on median MAT values but this did not significantly change the results). This method of estimating the thermal optimum is appropriate for mountain species as their full thermal ranges can be expressed. By contrast, lowland species may have truncated thermal ranges and therefore their geographical distributions may not provide accurate estimates of their thermal optima[53]. For species with <10 available records (n = 500) or identified at the genus level (n = 264), we estimated the thermal optimum as the average collection temperature calculated from all available records for congeneric individuals in the Andean region (changing minimum sample size criteria did not have qualitative effects on the results). Any species not identified to genus or that had insufficient records available at either the genus or species levels (n = 40) was excluded from subsequent analyses.

We calculated the CTI of each plot as the average thermal optima of the species weighted by their relative total basal area (summed cross-sectional stem area of all conspecifics measured at breast height (1.3 m above ground)) in that plot. Changes in the CTI therefore integrate the effects of tree growth, recruitment and mortality on community composition. The CTI of a plot is calculated as:

$$\mathrm{CTI} = \sum_{i=1}^{n} (\mathrm{SpOptT}_i(\mathrm{BA}_i / \mathrm{BA}_{\mathrm{plot}})) / \mathrm{BA}_{\mathrm{plot}}$$

in which n is the number of species in the focal plot, SpOptT_i is the thermal optimum for species i, and BA_i and $\mathrm{BA}_{\mathrm{plot}}$ are the basal area of species i and of the plot, respectively. All individuals available in the plot inventory datasets, regardless of minimum criteria for the diameter at breast height, were included in the analyses presented in the main text. We reran all analyses using standard criteria of including only stems with a diameter at breast height of ≥10 cm; results of these analyses are shown in Extended Data Table 1. The relationships between the plot CTI and MAT and between the plot CTI and elevation are shown in Extended Data Fig. 1a, b.

$\mathrm{TR}_{\mathrm{plot}}$. To test for changes in the species composition of the study plots over time, we calculated the annualized difference in CTI between all possible censuses for each plot that was censused more than once ($\mathrm{TR}_{\mathrm{interval}}$). The rate of change in CTI between the initial and final census was used as the best estimate of the $\mathrm{TR}_{\mathrm{plot}}$ of each plot. We then calculated the mean $\mathrm{TR}_{\mathrm{plot}}$ using the generalized linear model of $\mathrm{TR}_{\mathrm{interval}}$ (CTI change per interval, n = 176) with plot identity included as a random effect. We used a binomial probability test to determine whether the number of plots with positive $\mathrm{TR}_{\mathrm{plot}}$ values differed significantly from the null expectations of equal positive and negative changes. We also performed a Student's t-test between $\mathrm{TR}_{\mathrm{plot}}$ and a null hypothesis of no change. We repeated the above analyses using only the 61 plots with an area ≥1 ha and with ≥2 censuses and obtained nearly identical results (Extended Data Table 1). As an alternative means of calculating the overall change in the CTI of a plot over time, we also calculated $\mathrm{TR}_{\mathrm{plot}}$ as the slope of the linear least-square regression between CTI and census year. Results did not differ qualitatively from the $\mathrm{TR}_{\mathrm{plot}}$ estimates explained above (Extended Data Fig. 2).

$\mathrm{TR}_{\mathrm{MAT}}$. To integrate data from plots with single censuses and investigate how thermophilization rates vary across the MAT and elevation gradients, we analysed temporal changes in the running average of CTI versus MAT. More specifically, we divided the census data into overlapping five-year periods from 2000 to 2015 (that is, period 1 = 2000–2005, period 2 = 2001–2006, period 3 = 2002–2007…period 11 = 2010–2015). For each time period, we calculated the mean CTI of all plots that occurred within overlapping 1.5-°C thermal bands (equivalent to approximately 250 m elevation based on the regional adiabatic lapse rate) between 10 and 25 °C MAT such that band 1 = 10–11.5 °C, band 2 = 10.5–12 °C, band 3 = 11–12.5 °C… band 28 = 23.5–25.0 °C (plots were assigned to thermal bands based on their downscaled CHELSA BIO1 values (see above) such that the MAT and thermal band assignments of a plot did not change over time). To calculate the average CTI per thermal band per time period, plots were weighted by their area. For any plot censused more than once in a given time period, we used the average CTI of that plot within that period. For each thermal band with ≥10 plots, we then calculated the $\mathrm{TR}_{\mathrm{MAT}}$ as the slope of the linear least-square regression between average CTI and year (mid-point of the five-year time period). We used the same regression analyses to estimate the 95% confidence interval around the $\mathrm{TR}_{\mathrm{MAT}}$ estimates, which then allowed us to assess the significance of $\mathrm{TR}_{\mathrm{MAT}}$ at specific MATs. We calculated the mean $\mathrm{TR}_{\mathrm{MAT}}$ using the generalized linear model of CTI (n = 283) versus census year with plot identity included as a random effect.

Historic temperature change for the study area. We downloaded monthly mean temperature data at 30-arcsec resolution from 1990 to 2013 from the CHELSA Timeseries dataset (http://chelsa-climate.org/timeseries/). We extracted the information for the plot locations and calculated the annualized change in mean temperature as the slope of the linear least-square regression of temperature versus date. For plots with multiple censuses, we performed a Spearman correlation between the warming rate and $\mathrm{TR}_{\mathrm{plot}}$. We also replicated the $\mathrm{TR}_{\mathrm{MAT}}$ calculation substituting MAT with warming rate ($\mathrm{TR}_{\mathrm{warm}}$) (average thermophilization rates calculated at intervals of 0.01 °C between −0.05 and 0.15 °C).

Species richness. For 1-ha plots with multiple censuses, we calculated species richness as the count of species that were found in the focal plot. We combined all morpho-species according to their genus assignments and added the genus to the species counts. We performed a linear model between MAT and species richness.
Range of thermal optima within plots. For plots with multiple censuses, we calculated the range of thermal optima (SpOptT) for all species that occurred within each plot as the difference between maximum and minimum SpOptT of the co-occurring species. We performed a linear model between the range of thermal optima and TR_{plot} values of the plots.
Change in basal area of more- versus less-thermophilic species per plot. For plots with multiple censuses, we calculated the change in basal area per plot generated by recruitment and growth (increase in basal area) versus mortality (decrease in basal area) for more-thermophilic species (that is, species with thermal optima above the CTI of a plot) and less-thermophilic species (that is, species with thermal optima below the CTI of a plot). For this analysis, we only included species for which the species thermal optima (SpOptT) were calculated using species-level GBIF records; we did not include species for which the thermal optima were estimated based on the distribution of congeners. We standardized the change in basal area by plot size and express the change as a percentage of the initial basal area. We performed a loess regression analysis between the basal area of more- versus less-thermophilic species and the MAT of the plots.
Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The plot data that support the findings of this study are available from the Red de Bosques (https://redbosques.condesan.org/) upon reasonable request. The list of species included in the analysis with their number of GBIF records after filtering and their estimated thermal optima is available in Supplementary Table 2.

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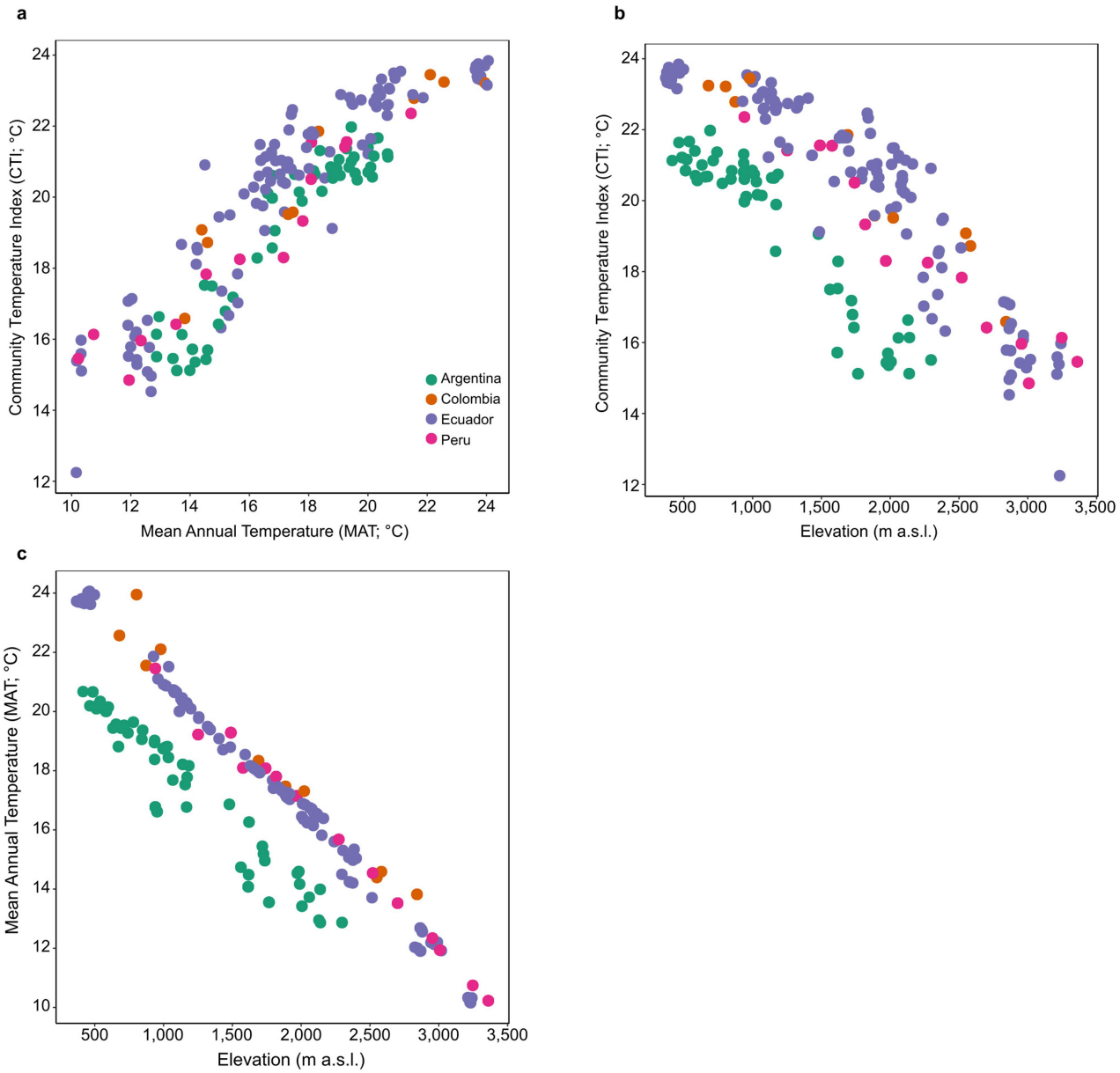
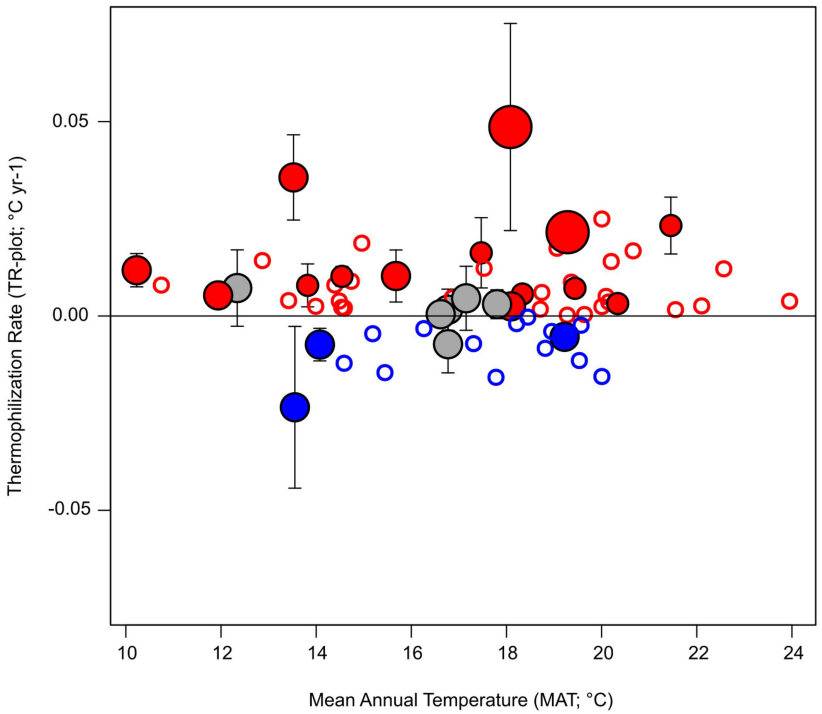
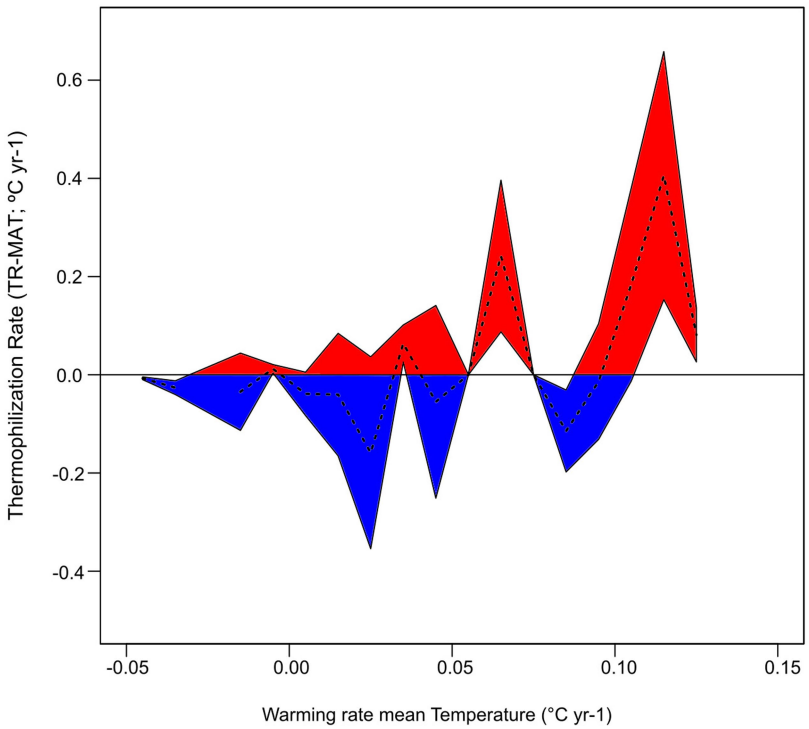


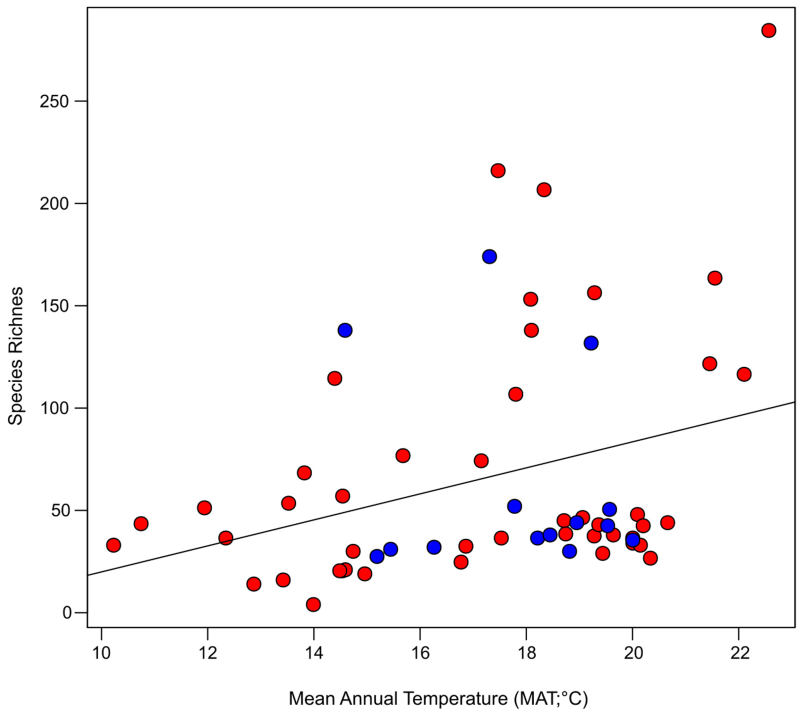
Extended Data Fig. 1 | CTI, MAT and elevation of study plots. a, The relationship between the mean CTI for each of the Andean forest plots (averaged across all censuses) and the MAT at the plot locations. $n = 186$, slope = 0.71, $R = 0.92$, 95% confidence interval = 0.88–0.93, $P < 0.001$. **b**, The relationship between the mean plot CTI and plot elevation. $n = 186$, $R = -0.77$, 95% confidence interval = −0.82 to −0.7, $P < 0.001$. **c**, The relationship between plot MAT and plot elevation. $n = 186$, $R = -0.92$, 95% confidence interval = −0.93 to −0.88, $P < 0.001$. All analyses are two-sided Spearman correlations.



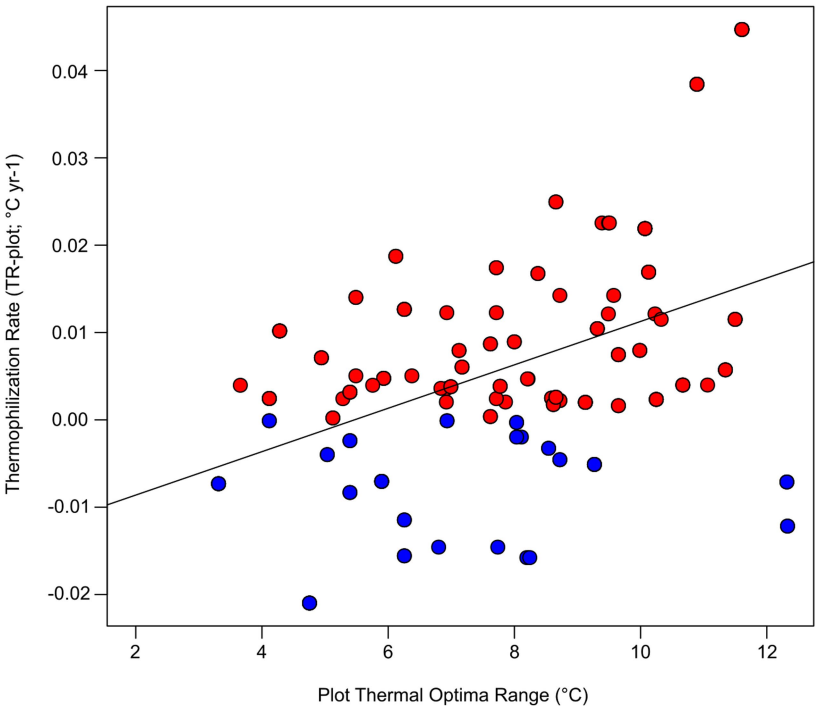
Extended Data Fig. 2 | Regression-based thermophilization rates of repeatedly censused plots. TR_{plot} was compared to the MAT for the Andean forest plots with multiple censuses ($n = 64$). Each point represents one plot and the size of the point is proportional to the number of censuses. Error bars are 95% confidence intervals based on the linear least-square regressions of the CTI versus census year of each plot. Grey points represent plots with non-significant TR_{plot} values and filled, coloured points represent plots with significant TR_{plot} values; hollow points are plots with only two censuses and for which the significance of the TR_{plot} could therefore not be determined. Positive and negative TR_{plot} are coloured red and blue, respectively.



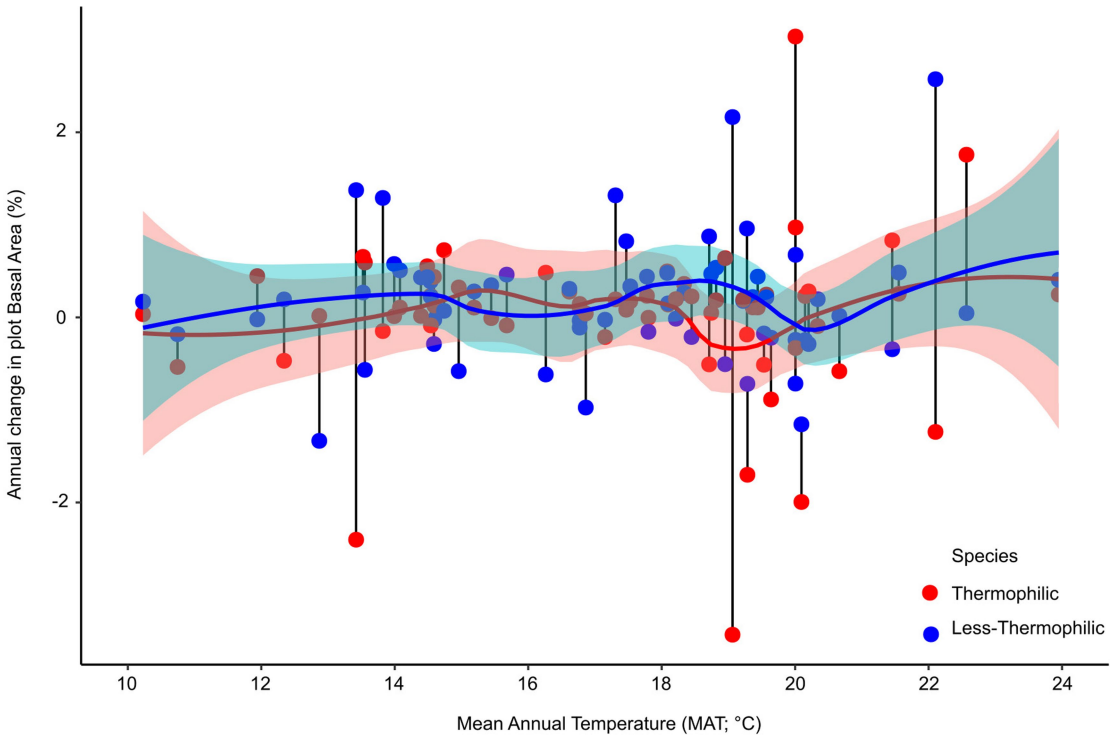
Extended Data Fig. 3 | Thermophilization rates for areas with different warming rates. The thermophilization rates in areas with different warming rates (TR_{warm}; the annualized change in the mean CTI of all plots within a band of equitable warming rate) were compared to the warming rate. $n = 283$ plot censuses, assigned to 20 warming bands. The dashed line indicates the mean TR_{warm} and the coloured shaded area indicates the 95% confidence interval of TR_{warm}. Positive and negative TR_{warm} is coloured red and blue, respectively.



Extended Data Fig. 4 | Species richness of repeatedly censused 1-ha plots. Species richness versus MAT in the 1-ha Andean forest plots with multiple censuses. $n = 61$. Each point represents one plot and the red and blue colours indicate positive and negative TR_{plot} values, respectively. The line shows the linear regression between MAT and species richness. $R^2 = 0.10$, $P < 0.05$.



Extended Data Fig. 5 | Range of the thermal optima in study plots. The range of thermal optima of co-occurring species versus TR_{plot} in the plots with multiple censuses. $n = 64$. Each point represents one plot and the red and blue colours represent positive and negative TR_{plot} values, respectively. The line shows the linear regression between the range of the thermal optima of the plots and TR_{plot}. $R^2 = 0.19$, $P < 0.001$.



Extended Data Fig. 6 | Basal area change in species composition. Percentage change in absolute basal area per plot for more-thermophilic (species thermal optimum > plot CTI) and less-thermophilic (species thermal optimum < plot CTI) species versus MAT in plots with multiple censuses ($n = 64$). The more- and less-thermophilic species are coloured red and blue, respectively. Lines show loess regression fits between the percentage change in basal area and MAT, and the shaded areas represent the 95% confidence intervals around the loess regressions.

Extended Data Table 1 | Results for alternative calculations of TR_{MAT} and TR_{plot}

		All data	Stems ≥ 10cm dbh	Plots size ≥ 1ha
	N. plots	186	186	79
	N. plots with ≥ 2 census	64	64	61
TR_{MAT}	CTI ~ Year +(1|plot id)	0.0029	0.0029	0.0061
	St. Error	0.001	0.001	0.001
TR_{plot}	pbinom	<0.001	<0.001	<0.001
	Upward m yr−1	1.7	1.7	2.1
	% Plots positive	72	72	75
	% Plots negative	28	28	25
	$TR_{interval}$ ~ +(1|plot id)	0.0066	0.0066	0.0084
	St. Error	0.002	0.002	0.002
	t.test	<0.001	<0.001	<0.001

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☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
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☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	Data downloaded from https://lta.cr.usgs.gov - SRTM 1 ArcSec Global V3 http://chelsa-climate.org - CHELSA BIO1 and Timeseries https://www.gbif.org/ Taxonomic Name Resolution Service (TNRS; http://tnrs.iplantcollaborative.org/) version 3.0)
Data analysis	R Core Team. 2018 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. version 3.5

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The plot data that support the findings of this study are available from the Red de Bosques (https://redbosques.condesan.org/) upon reasonable request. The list of species included in the analysis with their number of GBIF records used after filtering and their estimated Thermal Optima is available in Supplementary Table 2

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Study description	We collated census data from 186 Andean forest inventory plots (redbosques.condesan.org) and tested for Thermophilization on Andean plant communities by calculating the Thermophilization rate per plot and the Thermophilization rate per thermal band. For the TRplot we grouped or data based on plot identity and for the TRband we grouped the plots in thermal bands based on the Mean Annual Temperature of the plot location. The total number of census available is 293. A subset of 64 plots has been censused repeatedly (median number of censuses = 2, maximum number of censuses = 6).
Research sample	We used plot data available from 'Red de Bosques'. The extensive latitudinal and elevational range of the plots guarantees that multiple environmental conditions and corresponding plant communities are represented. This dataset represents the largest compilation of Andean forests plots so we hoped our sample would be as representative as possible for the Andean forests. The only manipulation performed to the original datasets was the standardization of species names. The plot data used in the analysis comes from 7 independent projects, led by the co-authors, with core data on the identity and size of all trees occurring within each plot. In this project, we also use GBIF data to calculate the species Thermal Optimum. GBIF data comes from multiple sources and it is publically available.
Sampling strategy	No sample-size calculation was performed. We used all plot data available from 'Red de Bosques'; this dataset represents the largest compilation of Andean forests plots. The extensive latitudinal and elevational range of the plots guarantees that multiple environmental conditions and corresponding plant communities are represented.
Data collection	We collated data from pre-existing plots. The information on the plot PI's is shown in Supplementary Information Table 1.
Timing and spatial scale	There is no rationale behind the start or timing of data collection other than availability of plot data. All plots are located within the tropical and subtropical Andes
Data exclusions	Plots on the Red de Bosques database with comments indicating secondary forest status were not included on any analysis in order to avoid the inclusion of confounding factors affecting changes in species composition. We also excluded plots on elevations with Mean Annual Temperature (MAT) higher than 25ºC for being outside the study area (Andes) and plots with MAT lower than 10ºC for lacking enough sample size. The exclusion of these plots was pre-established; the excluded plots were not used for any calculation or summary included in the manuscript.
Reproducibility	All results can be reliably reproduced by using the written R code based on publically available R packages.
Randomization	Each plot had associated coordinates and census years that were used to calculate Mean Annual Temperature (MAT) and Community Thermal Index (CTI). Plots were not clumped into groups but subsets were used to calculate the Thermophilization Rate per plot (TRplot) (only plots with multiple census) or to calculate the Thermophilization Rate per thermal band (TRmat) (plots on an specific MAT moving range).
Blinding	Plots included in the analysis were part of seven independent projects, leaded by different researchers, and established for different purposes. These plots were not initially established in order to test for thermophilization but to understand forest dynamics, biomass and diversity. Other than that, blinding to group allocation is not relevant nor possible in this study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging