Title:

Amazonian and Andean tree communities are not tracking current climate warming

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Abstract

Climate change is shifting species distributions, leading to changes in community composition and novel species assemblages worldwide. However, the responses of tropical forests to climate change across large-scale environmental gradients remain largely unexplored. Using long-term data over 66,000 trees of more than 2,500 species occurring over 3,500 m elevation along the hyperdiverse Amazon-to-Andes elevational gradients in Peru and Bolivia, we assessed community-level shifts in species composition over a 40+ year time span. We tested the thermophilization hypothesis, which predicts an increase in the relative abundances of species from warmer climates through time. Additionally, we examined the relative contributions of tree mortality, recruitment, and growth to the observed compositional changes. Mean thermophilization rates across the Amazon-to-Andes gradient were slow relative to regional temperature change. Thermophilization rates were positive and more variable among Andean forest plots compared to Amazonian plots but were highest at mid-elevations around the cloud base. Across all elevations, thermophilization rates were driven primarily by tree mortality and decreased growth of highland (cool adapted) species rather than an influx of lowland species with higher thermal optima. Given the high variability of community-level responses to warming along the elevational gradients, the high tree mortality, and the slower-than-warming rates of compositional change, we conclude that most tropical tree species, and especially lowland Amazonian tree species, will not be able to escape current or future climate change through upward range shifts, causing fundamental changes to composition and function in Earth's highest diversity forests.

Keywords: Global warming, range shifts, species migration, thermal niches, tropical biodiversity

Significance statement

Our study investigates how climate change affects tree species composition in tropical forests across the Amazon-to-Andes elevational gradient. Using long-term data collected over more than four decades, we found that while species from warmer climates showed some increase in relative abundance (thermophilization), the process was slower than regional temperature increases. Thermophilization was highest at mid-elevations near the cloud base and was primarily driven by tree mortality and slowed growth of highland species rather than an influx of lowland species. Given the slow rate of compositional change and high variability in community responses, our study concludes that most tropical tree species, especially those in the Amazon, are unlikely to shift upward in range fast enough to adapt to ongoing climate change.

Introduction

Tropical regions have warmed at an average of >0.25 °C per decade since the mid-1970s (1), and in the Neotropics, contemporary rates of climate warming exceed those from any time in the last 50,000 years (2). Moreover, temperatures in some montane tropical ecosystems (e.g., the Andes) have increased approximately 0.11 °C per decade since 1939 (3) and are predicted to increase by an additional 2 – 4 °C this century (4, 5). Changes in precipitation, drought, fire, and nitrogen deposition are also associated with changes in temperature (6–8). The rapid pace of ongoing environmental changes presents unprecedented challenges to plant and animal species across tropical ecosystems, and species responses to these challenges are just beginning to be documented and understood.

Climate change is causing the displacement of species distributions along environmental gradients, resulting in compositional shifts and the emergence of novel species assemblages (9–11). Although these shifts have been well documented in the palaeoecological record, how they occur over shorter modern timescales and how they vary between different biogeographic regions remain key questions (12, 13). Within communities, the relative abundance of species adapted to cooler temperatures is predicted to decrease with warming, while the relative abundance of species adapted to hotter temperatures is predicted to increase, a pattern known as community thermophilization (14). The thermophilization hypothesis has been previously tested across montane tropical forests in the Andes using surveys of tree populations (15) and across ecoregions in the New World using plant collections (16). These studies show an overall increase in the abundance of warm-adapted species but also high heterogeneity in thermophilization rates across plant communities and regions. This heterogeneity remains unexplained. Furthermore, the thermophilization hypothesis is largely untested in lowland tropical ecosystems such as Amazonian forests (e.g., *floodplain* and *terra firme* forests), and the contributions of underlying demographic processes (growth, recruitment, mortality) to thermophilization are poorly characterized.

Differences in the thermophilization rates of forest communities along elevational gradients may result from several ecological processes. First, thermophilization rates may be faster at lower elevations due to faster rates of recruitment and mortality (i.e., faster turnover rates) (17, 18). Second, thermophilization may be influenced by differences in species' thermal tolerances. For example, species from lowland Amazonia are not only adapted to higher temperatures but also tend to have narrower thermal tolerances (i.e., smaller thermal safety margins) compared to species in the highlands (19–21). If lowland species are adapted to a smaller range of environmental conditions, they may be more sensitive to climate change (22), leading to faster thermophilization in lowland communities compared to montane forests. Third, thermophilization rates may be slower in lowland Amazonian forests than in Andean montane forests due to stronger effects of drought and biotic constraints at lower elevations. Increased drought severity and frequency in the Amazon (23) are shifting tree community composition toward more drought-tolerant species (24, 25). If drought-tolerance traits are uncorrelated with thermal-tolerance traits, then we might observe slower thermophilization rates in lowland forests due to the overriding effect of drought. In addition, theory and some empirical evidence suggest that lower elevational range limits of species are shaped more by biotic interactions than abiotic factors (26–28). If this is true, populations at higher elevations will respond more quickly to climate change, causing rapid shifts in species' upper range limits and increasing thermophilization of Andean communities relative to Amazonian communities. Finally, rates of thermophilization may be slower in the lowlands due to niche truncation and/or an absence of potential immigrants from hotter areas, which could allow incumbent species to persist even under suboptimal conditions (16).

Despite widespread interest in the demographic processes underlying community-level responses to climate change (29, 30), little is known about their relative importance in determining compositional change and thermophilization patterns in the Amazon and Andes. Thermophilization reflects the culmination of three non-mutually exclusive demographic processes that can influence species' relative abundances within communities: 1) faster tree growth of warm-adapted than cold-adapted species; 2) faster tree mortality of cold-adapted than warm-adapted species; and/or 3) faster recruitment of warm-adapted than cold-adapted species. Previous studies of montane tropical forests in the Colombian Andes (31) and tropical forests along an elevational gradient in Costa Rica (32) both concluded that tree mortality was the main driver of thermophilization. However, comparative studies of the demographic drivers of thermophilization across the Amazon-to-Andes elevational gradient are still lacking.

In this study, we tested the thermophilization hypothesis and the contributions of individual demographic processes to thermophilization across the hyper-diverse Amazon-to-Andes elevational gradient. We used two of the world's largest elevational transects located on the eastern slope of the Bolivian and Peruvian Andes, spanning lowland western Amazonian forests to the eastern Andean treeline. These elevational transects are represented through comprehensive networks of forest plots censused repeatedly over the last 44 years. Using long-term data from a combined total of 66 permanent forest plots (totaling 72.5 ha), we addressed three questions about the pace and underlying demographic basis of observed changes in tree community composition. Specifically, we asked: (1) Does the rate of thermophilization vary with elevation? 2) Do thermophilization rates differ between Amazonian and Andean forests? and 3) What are the individual contributions of tree mortality, recruitment, and growth to observed thermophilization rates? Our study provides novel insights into the patterns and causes of tropical forest responses to climate change.

Methods

Study area

The study was conducted on the eastern slopes of the Bolivian and Peruvian Andes (Central Andes) along two elevational gradients extending from the Andean treeline at ~3700 m to the lowland Amazon basin at 190 m. In Bolivia, the elevational gradient encompasses mature forests ranging from 200 m to 3400 m in the Madidi region, including the protected areas of Madidi National Park (13.80° S, 67.63° W), Apolobamba (14.99° S, 68.82° W), and the Pilon-Lajas Biosphere Reserve (15.00° S, 67.33° W). In Peru, the elevational gradient spans a stretch of unbroken mature forest ranging from 300 m to 3700 m in the Manu Biosphere Reserve (11.86° S, 71.72° W) and extends to 190 m in the nearby Tambopata National Reserve (12.92° S, 69.28° W) (Fig. 1a). In the study area, mean annual temperature (MAT) decreases linearly with increasing elevation along the gradient at an adiabatic lapse rate of -5.5 ºC km^{-1} with mean annual temperatures ranging from 26.6 ºC at the lowest elevations to 6.4 ºC at the treeline (2, 33, 34). Mean annual precipitation varies non-linearly across the gradient from 2448 to 10425 mm

yr^{-1}, with significant interannual variability throughout (34, 35). The study area has high cloud frequency in all seasons, and the cloud base zone is estimated to be between 1200 to 2000 m (34, 36). Temperatures in the study area have been increasing by approximately 0.03 °C y^{-1} in both the Amazon and the Andes since 1980 (http://berkeleyearth.org, Fig. 1b).

Forest monitoring data

Our dataset includes 66 permanent tree inventory plots (totaling 72.5 ha) from two large-scale forest plot networks in the Central Andes of Bolivia (28 plots) and Peru (38 plots) (Fig. 1a). The Bolivian elevational gradient encompasses 50 1-ha permanent plots, established and maintained by the Madidi Project at the Missouri Botanical Garden since 2002 (http://www.missouribotanicalgarden.org/plant-science/plant-science/south-america/the-madidi-project.aspx) but for this study, we used only a subset of 28 plots with repeated tree censuses ranging from 600 to 3300 m in elevation and established between 2005 to 2010. The Peruvian elevational gradient consists of 21 1-ha permanent plots established and maintained by the Andes Biodiversity and Ecosystem Research Group (ABERG; http://www.andesconservation.org/) located at elevations ranging from 400 to 3625 m and established between 2003 to 2017, and an additional 17 permanent plots located at 190 to 405 m elevation and established between 1979 to 2014 by various investigators, including J. Terborgh, P. Nuñez, O. Phillips, and A. Gentry. These lowland plots are currently maintained and monitored by the Amazon Forest Inventory Network (RAINFOR) through ForestPlots.net (http://www.forestplots.net/). By including western Amazonian forests below 500 m, we were able to include the lower limit populations of Andean tree species (down to 190 m) along their full realized elevational ranges (Supporting Information, Fig. S1). The Amazonian plots included a mix of *floodplain* and *terra firme* forests.

Floodplain forests are saturated or underwater for a significant portion of each year, while the adjacent *terra firme* forests occur on older and more highly weathered soils and rarely or never flood (37).

The forest plots included in this study were established and remeasured multiple times following highly standardized protocols (38, 39). The inventory plots were censused at least two times between 1979 and 2023 (total number of tree measurements = 252,075, total number of censuses = 334, average number of censuses per plot = 5, median number of censuses per plot = 5). The oldest plot was established in 1979 in the Tambopata *terra firme* rain forest of Peru and has the most censuses (n = 13; SI Appendix, Table S1). In total, the 66 permanent plots contained 66,715 stems ≥10 cm in diameter at breast height (d.b.h.).

Plant identifications

All botanical collections from the permanent plots were identified *in situ* and in different herbaria and were compared and standardized across sites in each country. The vouchers were deposited in Bolivian, Peruvian, and USA herbaria (CUZ, HOXA, HUT, LPB, MOL, USM, and DAV, MO, F, WFU). Additionally, local flora and plant checklists were used as references (40–46) and taxonomic experts also confirmed plant identifications. We combined and standardized the species names from all the permanent plots and the combined species list was submitted to the Taxonomic Name Resolution Service (TRNS version 4.0, http://tnrs.iplantcollaborative.org/) to standardize and validate the species names (47). All taxa identified to morphospecies [e.g., sp1(5984WFR)] or with invalid names (e.g., “indet”) were assigned as “undetermined.” We followed the APG IV plant classification for the valid species names (48). All TNRS “accepted” species names with an overall TNRS-score below 0.9 were manually reviewed, and the names were confirmed on The Plant List (http://www.theplantlist.org/) and Tropicos (http://www.tropicos.org) databases. We used the valid genus names as a unique species identifier if the specific epithet was not confirmed. Species with an unassigned accepted TNRS name (e.g., "invalid," "illegitimate" or "no opinion") were also manually reviewed, and the species names were corrected using The Plant List and Tropicos databases. Unidentified taxa at the genus level were excluded from subsequent analysis. In total, the plots included 2,523 arborescent species and morphospecies, including trees, tree ferns, and palms (hereafter, "trees").

Species thermal distributions and thermal optima

We used established protocols to estimate the geographic thermal distributions for all tree species occurring in the study plots (49). For each species, we downloaded all available georeferenced herbarium records from Andean-Amazonian countries (i.e., Bolivia, Colombia, Ecuador, Peru, and Venezuela) through the Botanical Information and Ecology Network (BIEN: http://bien.nceas.ucsb.edu/bien/). Plant records that were missing coordinates, records that were tagged by the BIEN as having coordinate errors or that had evident georeferenced errors (e.g., falling in large bodies of water), and duplicate records were all discarded. The mean annual temperatures (MAT) of all specimens were calculated at the collection locations by extracting the temperature values from the CHELSA (v.1.2 raster) BIOCLIM1 values at 30-arcsec resolution (50). We estimated the thermal optimum for each species represented by ≥ 10 herbarium collection records as the mean MAT (^{o} C) at the collection locations. For species with < 10 available records or identified at the genus level (2.5%), the thermal optimum was estimated as the average collection temperature calculated from all available records of congeneric individuals collected from the tropical Andean-Amazonian region (49). For a small number of species (~1.5%), there were insufficient records available at either the species or genus level; these species were excluded from relevant analyses.

Community temperature index (CTI) and thermophilization rates (TR)

The Community Temperature Index (CTI) was calculated for each forest plot in each census as the average thermal optimum of all the species recorded in the plot weighted by their relative abundances (49). We calculated CTI using two different metrics of relative abundances. First, we weighted CTI using just the numbers of individuals of each species, such that changes in CTI are only influenced by individuals dying or recruiting in a local population. Second, we weighted CTI using the total basal area of each species (i.e., the summed cross-sectional area of stems at 1.3 m above ground) such that changes through time are affected by tree growth in addition to individual mortality and recruitment. This second metric considers tree size as being ecologically important; for instance, the death of a large tree will affect ecosystem function more than the death of a small tree.

Because the central aim of our study was to understand changes in species composition due to climatic drivers, we excluded trees that likely died from major disturbances caused by landslides or fires, as these episodic non-climatic mortality events can potentially obfuscate thermophilization. Accordingly, we excluded from our analyses of CTI any trees that died in landslides that occurred over the census period in the SPD-01, TRU-02, and TRU-06 plots and that died in fires in the CUZ-01 plot (the affected trees were removed from all censuses pre- and post-disturbance). For each forest plot, we then calculated the thermophilization rate as the annual changes in CTI over all possible consecutive census intervals. The overall thermophilization rate of each plot (TR; °C yr^{-1}) was also calculated as the slope of the linear least-square regression between CTI and the census year (CTI calculated via the individual- and basal area-weighted approaches). A positive thermophilization rate indicates an increase through time in the relative abundance or basal area of species from warmer climates.

Contribution of demographic processes to community thermophilization

To assess the contributions of demographic processes to observed thermophilization patterns, we partitioned the observed thermophilization rates into three components attributable solely to tree basal area growth (TR_{growth}), tree basal area recruitment ($TR_{recruitment}$), and tree basal area mortality ($TR_{mortality}$) for each plot over each census interval. The TR_{growth} of a plot is the difference between the plot's CTI calculated using the initial and final basal areas of just the stems surviving through the census period. The $TR_{recruitment}$ of a plot is the difference between the CTI calculated using basal areas of all stems recorded at the end of the census interval and the CTI calculated using just the basal areas of stems that survived through the census interval. Finally, $TR_{mortality}$ is the difference between the CTI calculated using the initial basal areas of all stems recorded in the first census and the CTI calculated using the initial basal areas of just the stems that survived through the census interval (32). Positive TR_{growth} indicates that individuals of species from warmer climates have grown faster (i.e., increased faster in basal area) than species from colder climates during the census interval. A positive $TR_{recruitment}$ indicates faster basal area recruitment rates of species from warmer climates. A positive $TR_{mortality}$ indicates higher basal area mortality rates of species from colder climates.

Statistical tests

We calculated the overall mean TR with 95% confidence intervals across all forest plots. We used a binomial probability test to determine whether the proportion of plots with positive TR differed significantly from the null expectations of 50%. We used linear least squares regression of TR vs. plot elevation to test how TR varies with elevation. We also used the smoothing function of a generalized additive model (GAM) to fit response curves and to test the relationship between TR and elevation. To test whether TR differs between Amazonian and Andean forests, we first classified Amazonian forests as those below 500 m of elevation and Andean forests as those above 500 m (51). Then, we compared mean TR between the Amazonian and the Andean forests using a Mann-Whitney and two-tailed t-test. We also compared the levels of variability in TR between the Andes and the Amazon using Levene's test. To determine the contributions of tree mortality, recruitment, and growth to overall TR, we used the tree demographic components ($TR_{mortality}$, $TR_{growth,}$ and $TR_{recruitment}$) in a multiple linear regression model to explain variation in TR.

Results

Community temperature index (CTI)

The average CTI of the plots ranged from 13 to 25 °C and was strongly negatively correlated with plot elevation (Individual-weighted CTI: r = -0.97, $p < 0.0001$; basal area-weighted CTI: r = -0.96, $p < 0.0001$; Supporting Information Fig. S2). Although the use of herbarium records may introduce biases in estimating the thermal niches of tree species, the strength of the CTI vs. elevation relationship demonstrates the efficacy of the method and the importance of the thermal niche in controlling the geographic distributions of species and community composition across elevational gradients.

Thermophilization rates across the elevational gradient

CTI varied over time within the plots and along the gradient; however, some plots showed consistently positive (e.g., CUZ-04) or negative (e.g., TAM-02) changes in CTI since 1979 (Fig. 2a, b; Supporting Information, Fig. S3a, S3b). Annualized rates of thermophilization varied widely along the Amazonian-Andean elevational gradient, ranging from -0.019 to +0.023 °C yr^{-1} when using CTI based on the number of individuals and from -0.019 to +0.025 °C yr^{-1} when using CTI based on basal areas (Fig. 3a, b; Supporting Information, Table S2). The overall annual community TR across all forest plots was 0.0025 °C yr^{-1} (95% CI = 0.0004 - 0.0045 °C yr^{-1}) for the individual-weighted metric and 0.0022 °C yr^{-1} (95% CI = -0.0001 - +0.0043 °C yr^{-1}) for the basal area-weighted metric. Thermophilization rates were not significantly correlated with either the number of censuses or the number of years between censuses (Individuals-weighted: r = -0.05, *p* = 0.78; basal area-weighted: r = -0.02, *p* = 0.89; Supporting Information, Fig. S4).

Given the measured regional adiabatic lapse rate of 5.5 °C km^{-1} (2), the thermophilization rates reported here correspond to a plot-level mean upward elevational migration rate of 0.45 m yr^{-1} (95% CI = 0.04 – 0.85 m yr^{-1}) using the individual-weighted metric; and 0.40 m yr^{-1} (95% CI = -0.04 - +0.75 m yr^{-1}) using the basal area-weighted metric (Supporting Information, Table S2). Of the 66 plots, 62% and 59% had positive thermophilization rates using the individual-weighted (n = 41) and basal area-weighted (n = 39) metrics, respectively. However, the overall number of plots with positive thermophilization rates along the gradient was not more than expected under the null expectation (binomial probability; *p* = 0.06 and *p* = 0.18 for individual and basal-area metrics, respectively).

Differences in thermophilization rates between Amazonian and Andean forests

Along the elevational gradient, thermophilization rates were fastest and consistently positive at mid-elevations around the cloud base between 1200 m - 2000 m asl (Fig. 3, Supporting Information, Fig. S5). In contrast, the plots with negative TR were mainly located in the lowland Amazonian (< 500 m) and at higher elevations in upper montane forests (> 2500 m) (Fig. 3a, b Supporting Information, Table S2, Fig. S5). Because of the fast thermophilization at middle elevations, there was a non-linear relationship between thermophilization rates and elevation (Individuals-weighted: r = -0.01, *p* = 0.75; basal area-weighted: r = -0.006, *p* = 0.44; Fig. 3a, b).

The Amazonian tree communities are not changing directionally with regards to species' thermal niches [Amazon TR = 0.0007 °C yr^{-1} (95% CI = -0.0008 - +0.0023 °C yr^{-1}) for individuals, and -0.0007 °C yr^{-1} (95% CI = -0.0027 - +0.0013 °C yr^{-1}) for basal area-weighted], while Andean tree communities had very slow and heterogeneous rates of thermophilization [Andean TR = 0.0031 °C yr^{-1} (95% CI = -0.0001 - +0.0060 °C yr^{-1}) for the individual-weighted metric and 0.0032 °C yr^{-1} (95% CI = 0.0001 - 0.00005 °C yr^{-1}) for the basal area-weighted metric]. Mean thermophilization rates in lowland Amazonian plots (elevation < 500 m; n = 17 plots) were significantly slower than their Andean counterparts (elevation > 500 m; n = 49 plots) for the basal area-weighted metric (Two-tailed t-test, *p* = 0.04; Fig. 4), but were not significantly different for the individual-weighted metric (Mann-Whitney-Wilcoxon test; *p* = 0.26; Fig. 4).

Finally, TR was much more variable in the Andes than in the Amazon (Levene test; $p < 0.001$ for both individual and basal area metrics; Fig. 4).

Mortality, growth, and recruitment effects on community thermophilization

Across all plots along the Amazon-to-Andes elevational gradient, changes in plot-level TR were driven primarily by differential tree mortality ($TR_{mortality}$) as opposed to differential growth (TR_{growth}) or tree recruitment ($TR_{recruitment}$) (Fig. 5). In 61% of the forest plots, $TR_{mortality}$ accounted for the largest proportion of observed thermophilization. In contrast to TR_{growth} and $TR_{recruitment}$ were dominant drivers in just 26% and 13% of the plots, respectively. $TR_{mortality}$ showed strong positive correlations in plot-level thermophilization. TR_{growth} was also positively correlated with overall TR, whereas the $TR_{recruitment}$ showed no relationship with TR (Supporting Information, Table S3, Fig. S6). When analyzing Amazonian and Andean plots separately, we did not observe significant correlations between TR and $TR_{mortality}$, TR_{growth} or $TR_{recruitment}$ in the lowland Amazonian plots. In the Andean plots, in contrast, $TR_{mortality}$ had a strong positive correlation with TR. TR_{growth} had a significant positive correlation with TR, and $TR_{recruitment}$ had a significant negative correlation with TR (Supporting Information, Table S4, S5; Fig. S7, S8).

Discussion

Thermophilization rates are slower than warming rates

Using comprehensive long-term (40+ years) monitoring datasets from 66 forest plots spanning 3 degrees of latitude, 3500 m in elevation, and ~19 °C of temperature, we found little or no evidence of thermophilization of tree communities in both the lowland Amazonian or the high

Andes, but a strong signal of thermophilization in mid-elevation forests (~1200 – 2000 m). We find that mean observed thermophilization rates were more than an order of magnitude slower than regional warming rates, indicating that changes in community composition are not keeping pace with temperature increases, at least in the life-stages examined in this study. The overall rates of thermophilization averaged 0.0025 °C yr^{-1} (individual-weighted) to 0.0022 °C yr^{-1} (basal area-weighted). When viewed in the context of predicted climate change, our results suggest that by ~2100 the community temperature index (CTI) of Amazonian and Andean tree communities will only change by less than a quarter degree Celsius (0.19 - 0.17 °C, based on our current migration rates), while the ambient temperatures in this region are predicted to increase by 2 - 4 °C (4, 5), depending on the location along the elevational gradient. Slow thermophilization will increase the "climatic debt" of forest communities, potentially reducing the ecosystem services they can provide and putting them at greater risk of collapse (52, 53), especially as compositional changes are driven by increased mortality of species along the lower portions of their ranges (i.e., range contractions).

Thermophilization is largely absent in the Amazon and highly variable in the Andes

Thermophilization rates in Andean forests were, on average, higher and more variable than in lowland Amazonian forests (Fig. 3, 4). These results indicate that tree community responses to climate warming are absent (in terms of thermophilization) in the Amazon, but slow and highly variable among plots in the Andes. Indeed, the signal appears to reflect more of a climatic disruption (via increased mortality rates) than a climatic migration (via increased recruitment rates). Although our study is one of the first to compare thermophilization between Amazonian and Andean tree communities based on plot census data, the findings broadly mirror those of a large-scale study using herbarium collection records (16). In their study, Feeley et al. (2020) found slower thermophilization rates in the lowland tropics compared to higher latitudes and elevations.

Several factors may explain the lack of thermophilization in Amazonian tree communities compared to Andean forests. First, compensatory changes in tree demographic rates (54) in the Amazonian forest may buffer population dynamics against temperature warming. Higher growth of individual trees can compensate for lower survival and recruitment rates, allowing for the persistence of Amazonian populations, though this depends critically on tree fecundity, whose response to climate change remains unknown in the tropics. For example, plots located in *floodplain* forests often showed negative thermophilization rates mainly driven by differential stem growth (Fig. 5, Supporting Information Table S2). Second, lowland Amazonian tree species may have greater tolerance to climate warming through local historical adaptation with persistence over time (21, 55). Also, it is possible that our characterization of thermal optima in Amazonian trees is inaccurate for species with truncated thermal niches (20). Finally, lowland species may be able to persist longer than predicted under increasing temperatures due to the lack of immigration from hotter areas and an absence of competition with species that are better adapted to the new conditions.

Positive rates of thermophilization in some lowland habitat types may also be counterbalanced by negative rates of thermophilization in other local habitat types. In Amazonian forests, physiographic differences between *floodplain* and *terra firme* forests may explain contrasting relationships between demographic processes and thermophilization. We found that thermophilization was positively correlated with tree mortality in 73 % of the *terra firme* plots. In contrast, thermophilization was negatively associated with growth in 50 % of the *floodplain* plots (Supporting Information, Fig. S9). This can be explained by the increase in tree mortality of wet-affiliated taxa (25) in *terra firme* forests. In addition, flooded areas could buffer the negative effects of droughts, decreasing tree mortality and increasing tree growth. Finally, multiple droughts in the last three decades are driving slow but directional shifts in species composition toward more drought-tolerant species across the Amazon (25). The lack of thermophilization in the Amazon suggests weak relationships between drought-tolerance traits and thermal-tolerance traits. Alternatively, these drought events could also promote longer periods of tree growth in *floodplain* forests because the roots will potentially be closer to the water table, extending the growing season. This current inertia of Amazonian tree communities in response to climate warming could lead to future lowland biotic attrition (56) if the thermal niches of the lowland species modeled here reflect likely climatic tolerances of species.

Thermophilization is driven primarily by differential tree mortality

Among the three demographic processes examined in our study (growth, mortality, recruitment), rates of thermophilization were most strongly determined by patterns of tree mortality and growth. There are several possible explanations for this result. First, mortality and recruitment could be decoupled in time, especially since we only considered trees with diameters ≥ 10 cm. Trees reaching the minimum measurable size of 10 cm d.b.h. can be decades to centuries old (57), having recruited in cooler than current temperatures. In this case, thermophilization resulting from growth may be a good indicator of future plant performance, particularly as mortality is a fast demographic process, while recruitment is inherently slower. If this is true, an examination of juvenile size classes (seedling and small saplings) should show accelerated thermophilization rates, with changes concentrated in recruitment as opposed to mortality. Second, our results suggest that warming may be driving elevated mortality of the cold-adapted less-thermophilic species compared to warm-adapted thermophilic species, consistent with findings from Colombia and Costa Rica (31, 32). High tree mortality, particularly in the Andes, can be explained by the incapability of species to persist in areas where temperatures increase exceed species' thermal tolerances, causing dieback along the lower hotter portions of species' ranges. Finally, the observed positive effect of tree growth on thermophilization may be due to the accelerated growth of warm-adapted species along the gradient.

Drought-induced tree mortality could also be causing shifts in species composition and function in Andean forests by disproportionally killing trees in the warmer (lower) portions of their ranges. This is supported by the fact that there have been three major drought events in the Amazon basin in the last two decades, increasing tree mortality and reshuffling species composition (25, 58, 59). In our study, the highest thermophilization rates were found around the cloud base (~1200-2000 m, Fig. 3a, b), where high tree mortality was reported (18). These results contrast with those of Fadrique *et al.* 2018, who reported negative thermophilization at elevations corresponding to the cloud base and suggested that the cloud base may be a barrier to species migrations. Our results suggest that the cloud base zone is shifting in species composition to greater relative abundances of more heat-tolerant species, potentially due to the interplay of drought events and heat stress increasing the potential for a future forest die-off in response to climate change (60) and, therefore to a high risk for biotic attrition.

In conclusion, slow thermophilization rates for Andean forests and the absence of thermophilization from lowland Amazonian forests indicate that they are likely to fall out of equilibrium with climate over the coming decades, if not sooner. As warming continues in tropical forests, long-term monitoring of growth, mortality, recruitment, and fecundity will be imperative for understanding the future population and community dynamics of Amazonian and Andean forests.

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Figure legends

Figure 1. (a) A map of the 66 permanent forest plots along the Amazon-to-Andes elevational gradient in Bolivia and Peru. The green circles represent the Amazonian forest plots (<500 m asl), and the orange triangles represent the Andean plots (≥500 m asl). (b) Temperature anomalies compared to 1980 in the Amazon (climate stations in Puerto Maldonado) and in the Andes (climate stations in Cusco) downloaded via Berkeley Earth Surface Temperature (http://berkeleyearth.org). Temperatures increased by ~1.17 (~0.0292 ºC y^{-1}) in Puerto Maldonado and by ~1.17 ºC (~0.0291 ºC y^{-1}) in Cusco since 1980.

Figure 2. The estimated community temperature index (CTI) anomaly for the 66 permanent forest plots. The CTI anomaly was calculated as the difference between a plot's CTI in year *i* and the plots' initial CTI along the Andes-to-Amazon elevational transects in Bolivia and Peru over 44 years (range of time intervals = 2 to 10 years per plot). Increases in CTI (i.e., positive CTI anomaly) indicate an increase in the relative abundance or basal area of more-thermophilic species from warmer climates over time-based on the (a) individual-weight CTI and (b) basal area-weighted CTI. The black horizontal line represents no change in CTI. Colored lines correspond to each plot at different time intervals along the elevational gradient.

Figure 3. The estimated plot-level thermophilization rates (TR) for the 66 Amazonian and Andean forests plots with multiple censuses based on the (a) individual-weighted community temperature index (CTI) and (b) basal area-weighted CTI. TR was calculated as the slope of the linear least-square regression between CTI and census year. Each circle (Amazon) or triangle

(Andes) represents one forest plot; solid green and orange colors represent positive TR and empty green, and orange colors represent negative TR. Error bars represent the 95% confidence intervals based on the linear least-square regressions of the CTI versus the census year of each plot. Circles and triangles with no error bars represent plots with one census interval. The dashed vertical line indicates the approximate transition from Amazonian to Andean forests at 500 m. The solid green line is the generalized additive model (GAM) fit using the smoothing function with 95% confidence limits. Vertical rectangles represent the approximate position of the cloud base along the gradient.

Figure 4. Violin plots showing variation in estimated plot-level thermophilization rates (TR) for the Amazonian (n = 17) and Andean (n = 49) forests plots based on the (a) individual-weighted community temperature index (CTI) and (b) basal area-weighted CTI.

Figure 5. Estimated changes in plot-evel thermophilization rates (TR_{plot}) due to tree mortality ($TR_{mortality}$), tree recruitment ($TR_{recruitment}$), and stem growth (TR_{growth}) along the Amazon-to-Andes elevational gradient. Forest plots are ordered from the low to high elevation. The dashed vertical lines indicate the approximate transition from Amazonian and Andean forests at 500 m. Positive changes (solid green and orange bars) indicate increased abundances of taxa from relatively warmer climates.

Figure 1

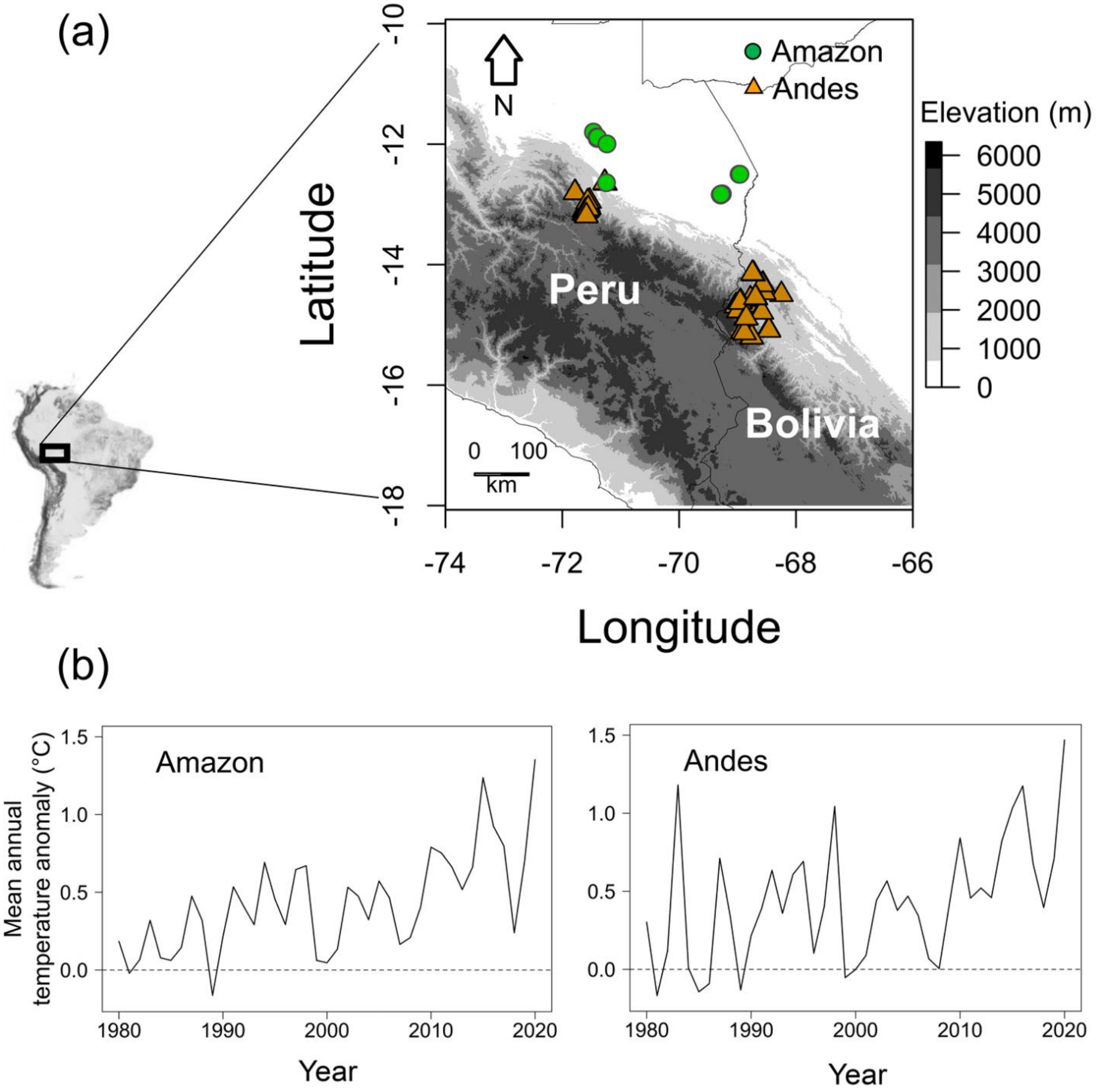

(a)
Amazon
Andes
N
Elevation (m)
6000
5000
4000
3000
2000
1000
0
Peru
Bolivia
0 100
km
Latitude
-10
-12
-14
-16
-18
Longitude
-74
-72
-70
-68
-66
(b)
Amazon
Andes
Mean annual temperature anomaly (°C)
1.5
1.0
0.5
0.0
1980
1990
2000
2010
2020
Year

Figure 2

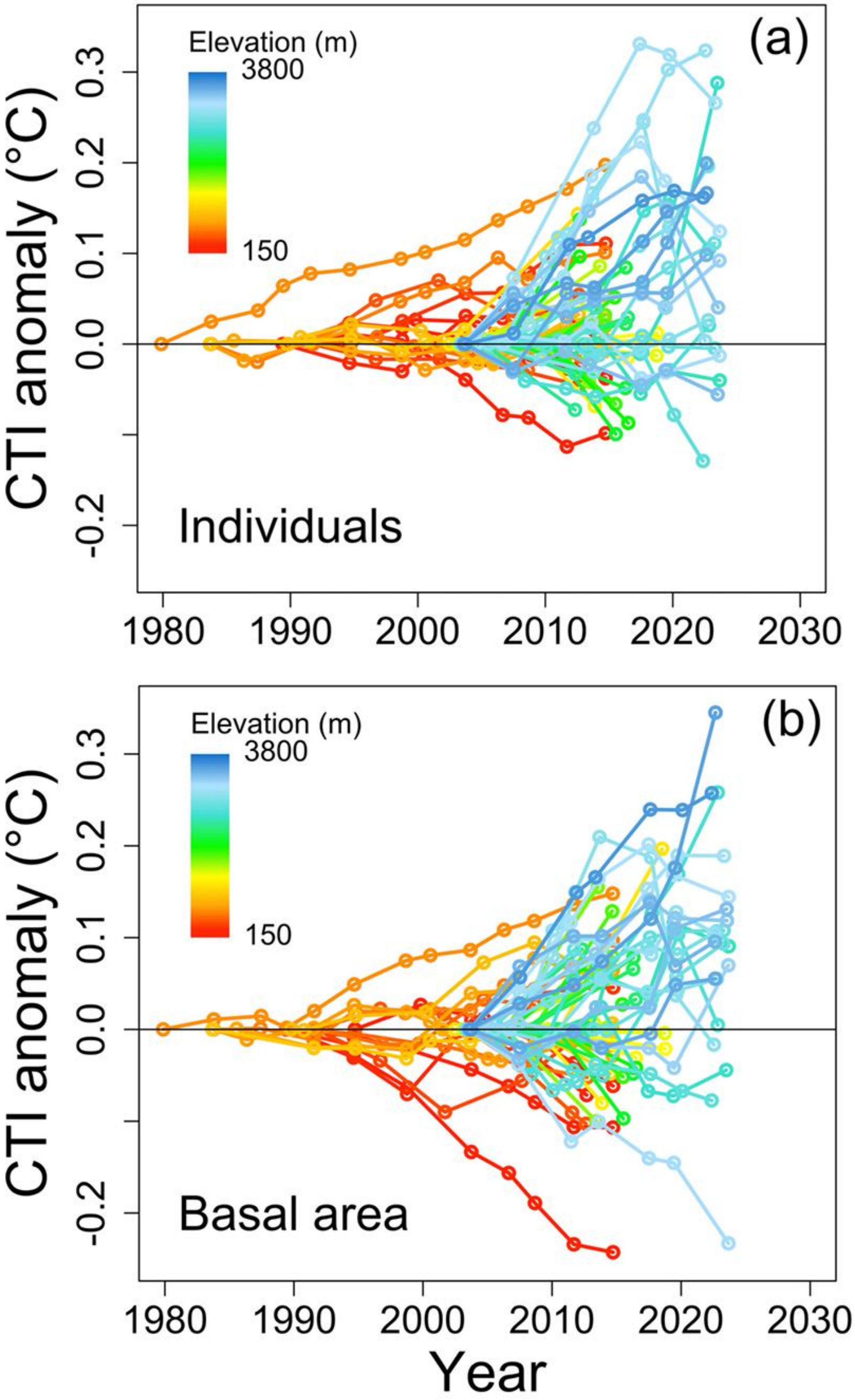

(a)
Elevation (m)
3800
150
Individuals
CTI anomaly (°C)
-0.2
0.0
0.1
0.2
0.3
1980
1990
2000
2010
2020
2030
(b)
Elevation (m)
3800
150
Basal area
CTI anomaly (°C)
-0.2
0.0
0.1
0.2
0.3
1980
1990
2000
2010
2020
2030
Year

Figure 3

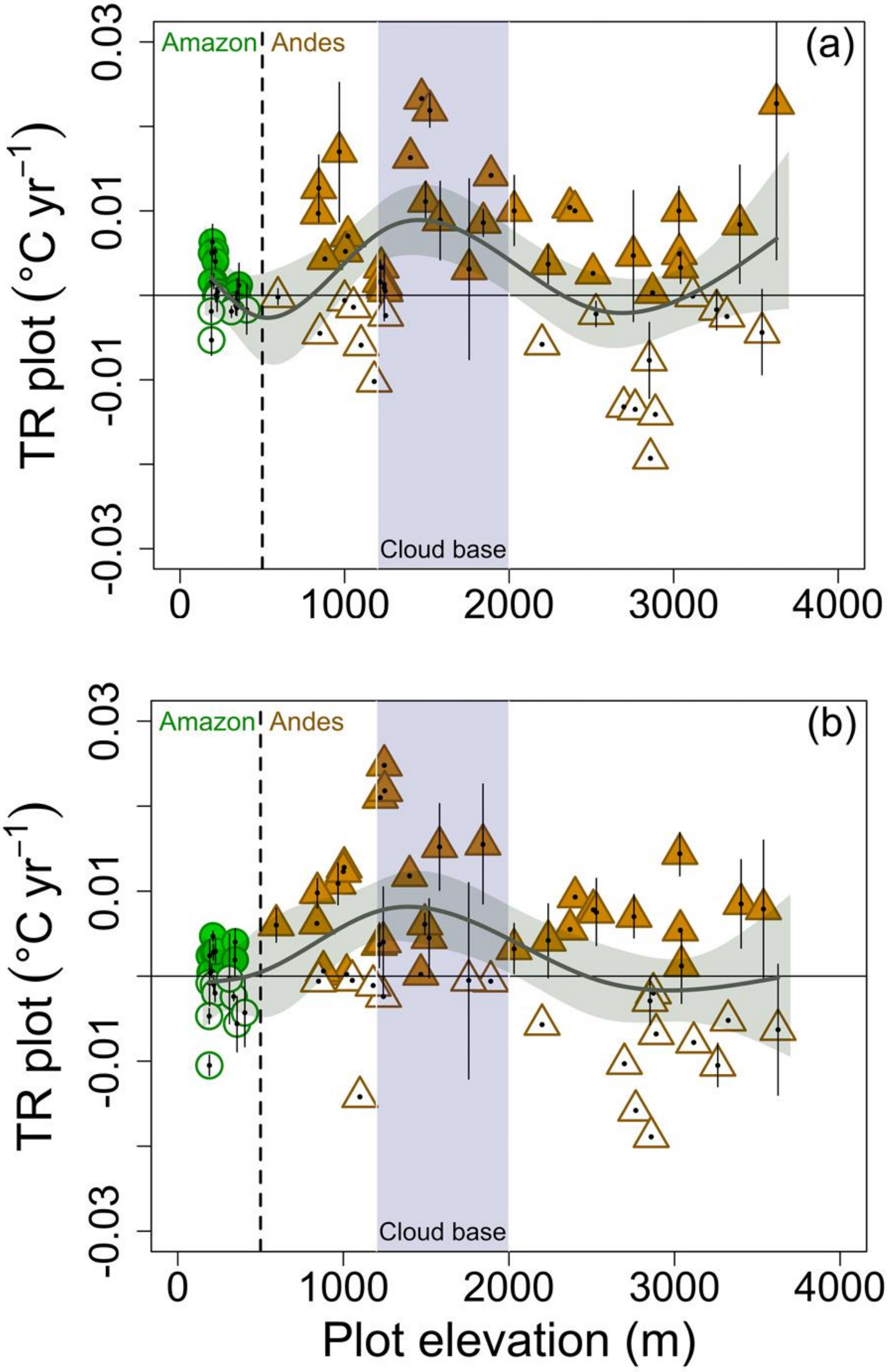

(a)
(b)
Amazon
Andes
Cloud base
TR plot (°C yr^{-1})
0.03
0.01
-0.01
-0.03
0
1000
2000
3000
4000
Plot elevation (m)

Figure 4

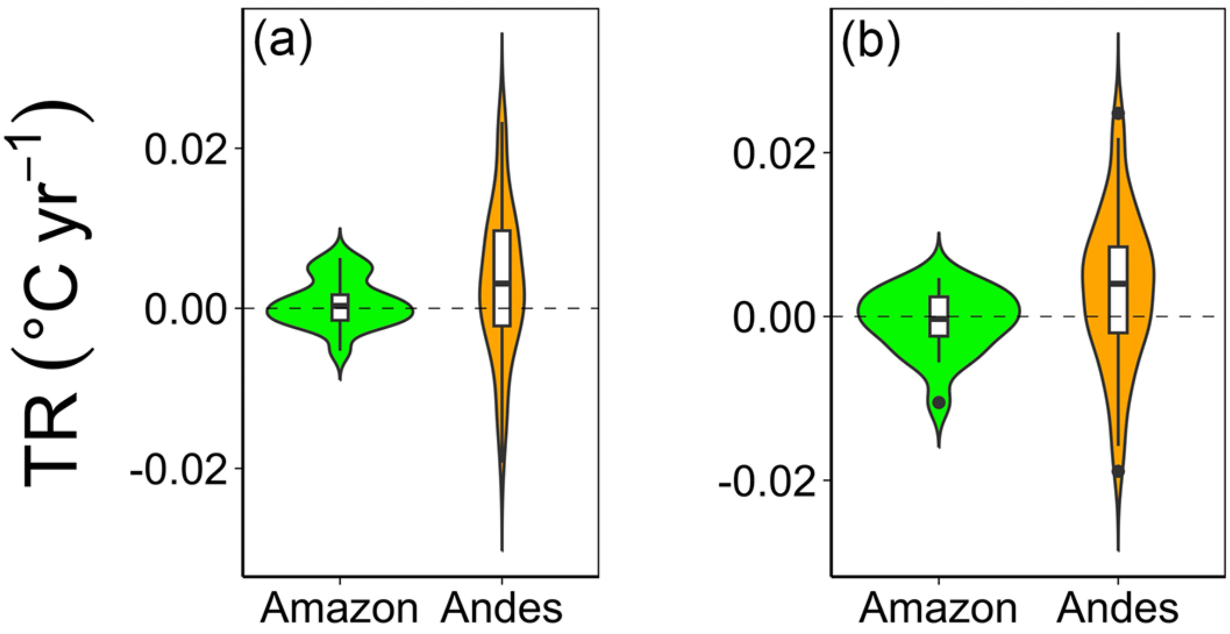
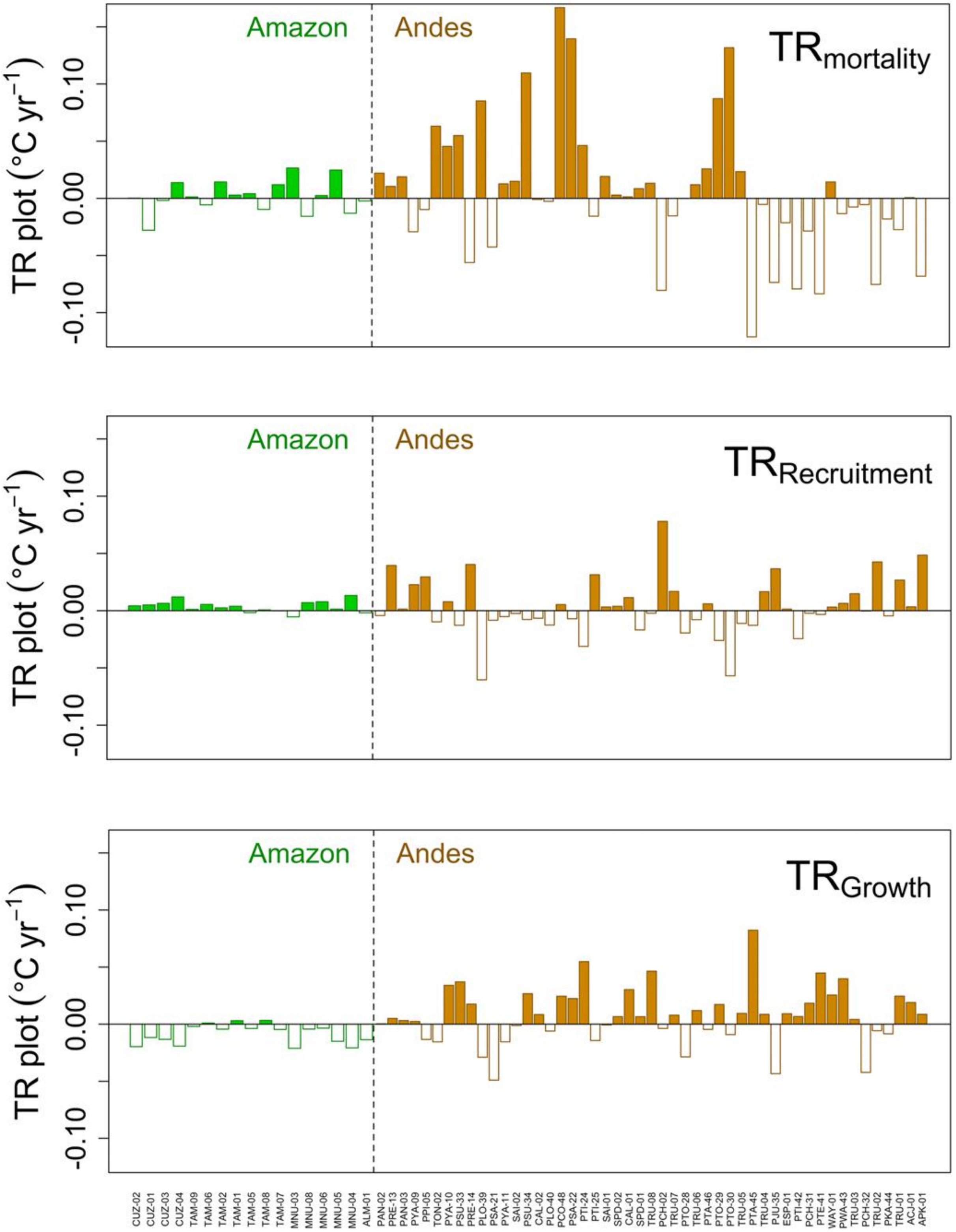


Figure 5


Amazon
Andes
$TR_{mortality}$
TR plot (°C yr^{-1})
0.10
0.00
-0.10
Amazon
Andes
$TR_{Recruitment}$
TR plot (°C yr^{-1})
0.10
0.00
-0.10
Amazon
Andes
TR_{Growth}
TR plot (°C yr^{-1})
0.10
0.00
-0.10
CUZ-02
CUZ-01
CUZ-03
CUZ-04
TAM-09
TAM-06
TAM-02
TAM-01
TAM-05
TAM-08
TAM-07
MNU-03
MNU-08
MNU-06
MNU-05
MNU-04
ALM-01
PAN-02
PRE-13
PAN-03
PYA-09
PPI-05
TON-02
PYA-10
PSU-33
PRE-14
PLO-39
PSA-21
PYA-11
SAI-02
PSU-34
CAL-02
PLO-40
PCO-48
PSA-22
PTI-24
PTI-25
SAI-01
SPD-02
CAL-01
SPD-01
TRU-08
PCH-02
TRU-07
PTO-28
TRU-06
PTA-46
PTO-29
PTO-30
TRU-05
PTA-45
TRU-04
PJU-35
ESP-01
PTI-42
PCH-31
PTE-41
WAY-01
PWA-43
TRU-03
PCH-32
TRU-02
PKA-44
TRU-01
ACJ-01
APK-01