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Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature

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Main Text

Figures 1 to 4

Tables 1 to 2

Abstract

Forests are the largest terrestrial biomass pool, with over half of this biomass stored in the highly productive tropical lowland forests. The future evolution of forest biomass depends critically on the response of tree longevity and growth rates to future climate. We present the first analysis of the variation in tree longevity and growth rate using tree-ring data of 3,343 populations and 438 tree species and assess how climate controls growth and tree longevity across world biomes. Tropical trees grow on average two times faster compared to trees from temperate and boreal biomes and live significantly shorter, on average 186 ± 138 years compared to 322 ± 201 years outside the tropics. At the global-scale, growth rates and longevity covary strongly with temperature. Within the warm tropical lowlands, where broadleaf species dominate the vegetation, we find consistent decreases in tree longevity at dry sites, as well as, a pronounced reduction in longevity at mean annual temperatures above 25.4°C . These independent effects of temperature and water availability on tree longevity in the tropics are consistent with theoretical predictions of increases in evaporative demands at the leaf level under a warmer and drier climate, and could explain observed increases in tree mortality in tropical forests, including the Amazon, and shifts in forest composition in Western Africa. Our results suggest that conditions supporting only low tree longevity in the tropical lowlands are likely to expand under future drier and especially warmer climates.

Significance Statement

This study highlights previously unknown patterns of tree longevity and growth across the world. Tree-ring data reveal a large-scale trade-off between tree longevity and growth, following global patterns of increasing forest productivity and biomass turnover rate from temperate to tropical regions. The oldest known trees live under dry conditions in

temperate and boreal zones, while in the dry tropical lowlands, trees only reach relatively short lifespans. Longevity of tropical trees also sharply decreases above mean annual temperatures of 25.4°C. Thus, predicted future changes in moisture availability and increases in temperature have the potential to reduce tree longevity in tropical lowlands impacting carbon stocks.

Main Text

Introduction

Forests are the largest terrestrial organic carbon pools. Plants process approximately one fifth of the total amount of atmospheric CO₂ annually (1) through photosynthesis. Small changes in forest functioning may thus significantly affect atmospheric CO₂ levels, stressing the need to understand the sensitivity of forests to climate. Tree growth and tree longevity are key determinants of the amount of woody biomass a forest can hold (2, 3). Recent globally observed changes in the dynamics of forests indicate that these key determinants are changing, likely in response to atmospheric CO₂ and climate change (4, 5, 6, 7). This raises concerns on how much carbon these forests may hold in the future (8).

Tropical lowland forests are the most productive systems on Earth and are particularly important for the global carbon cycle (9). Their response to variation in temperature and precipitation significantly affects inter-annual variation of atmospheric CO₂ globally (10, 11). Tropical trees are thought to be especially sensitive to high temperatures, operating close to, or even above, the optimum temperature for photosynthesis, while elevated temperatures also increase respiration and alter other physiological processes (12, 13, 14). Precipitation anomalies have also been shown to exert strong controls on tropical tree mortality (15,16). Specifically, low soil moisture combined with high temperature causes an increase in the evaporative demand, which may lead to severe water stress in trees (17). This may, in turn, cause hydraulic failures that affect both their capacity to conduct water and their long-term survival (18,19). Thus, gaining a better understanding of tropical forest sensitivity to a changing climate is of paramount importance to predict its future.

While we have gained some insights on growth sensitivity of tropical forests and trees to climate variation from experiments (20, 21), forest monitoring (22), and tree-ring studies (23), our understanding of the controls of tree longevity remains very limited. In temperate regions tree-ring studies have provided a wealth of information on tree longevity (24), showing that cold and dry conditions can lead to extremely long lifespans in conifers (25). The application of similar tree-ring techniques to the tropics has lagged behind mostly because of issues related to annual formation of growth rings. While the existence of annual tree rings in the tropics has been disputed for a long time and the development of robust and long chronologies is still slow, multiple studies demonstrated, using various methods including radiocarbon dating or cross-dating, that tree rings are annual even in seemingly ever-wet regions (26, 27). Nonetheless, there is still significant debate on the maximum ages of tropical trees (e.g. 28, 29, 30), how they compare with temperate regions and how they vary with climate. Over recent decades, a large number of tree-ring studies has emerged in the tropics (27), allowing a large-scale assessment of the relationship between tree growth and longevity, and the sensitivity of these key characteristics to climate.

Here we present the first assessment of tropical tree longevity and growth using data from tree-ring studies, which confirmed directly or indirectly the annual growth of trees in more than 86% of the analyzed populations (see further details in the Material and Methods). To put tropical trees in a global context, we first evaluated patterns of tree longevity and growth rate across different biomes, from boreal to tropical lowlands, and across different taxa, from conifer to broadleaf species. We then developed a Bayesian mixed-effects model, that accounts for phylogenetic effects, to understand how longevity and growth rate of trees from tropical lowlands are influenced by changes in temperature and water

availability. We conclude that tree longevity significantly decreases under drier and warmer conditions in the tropics, probably affecting forest dynamics and its role as carbon stores.

Results and Discussion

Global patterns in tree longevity and growth rate

We find that longevity and growth of trees covary across the globe with consistently decreasing longevity and increasing growth rates when moving from higher latitudes towards the tropics (Figure 1a). The estimated mean longevity of trees in the tropics is 186 ± 138 years compared to 322 ± 200 years for all extratropical biomes (Figure 1b), and tropical trees grow on average two times faster, 4.70 ± 3.29 mm/yr, compared to trees outside the tropics, 2.30 ± 1.52 mm/yr (Figure 1c). We also observed an inverse relationship between longevity and growth rates of trees across biomes and species and find that conifers, on average, grow slower and live longer than broadleaf tree species (Fig. 2b).

These negative relationships between growth and longevity arising from our global tree-ring analysis are consistent with widely observed trade-offs between metabolism, productivity, and lifespan across both taxa (24, 31, 32, 33) and biomes globally (34). The causes of these trade-offs are still under debate (35), but various mechanisms have been proposed in literature. These vary from the “*rate of living*”-theory related to cell metabolism (32), to mechanisms invoking trade-offs between growth and mechanical stability (36), defenses (37) and hydraulic safety (38). Hydraulics is thought to play a particularly important role for both tree growth and survival with strong evidence for a trade-off between hydraulic efficiency and safety (39, 40). Higher hydraulic efficiency allows for

higher rates of photosynthesis and growth but at the expense of lower safety margins (41, 42), which in turn may reduce species' longevity. This hydraulic efficiency-safety dichotomy could explain the differences in tree longevity and growth between conifers and broadleaf (angiosperm) trees (Fig. 2b) as these groups have distinctly different hydraulic systems. Broadleaf trees have more efficient hydraulic systems which help supporting high growth rates, but at the cost of greater vulnerability (39, 43), which may explain their shorter longevity observed here (Fig. 2b).

The observed general increase in tree-ring growth along a gradient of temperature from higher latitude towards the tropics (Figure 2a, SI Appendix, Fig. S1, Table S1) is consistent with the global variation of ecosystem productivity and turnover rates (9, 44, 45). Temperature plays an important control on vegetation productivity (14) with low temperature restricting photosynthesis, cell division, and expansion, and thus limiting tree growth rate (35). The observed decrease in tree longevity (Fig. 2a, SI Appendix, Fig. S1, Table S1) is also consistent with predictions from modeling studies estimating higher turnover at higher temperatures in the tropics (45).

Effects of water availability on longevity and growth in the tropics

Having established the broad global patterns of tree longevity and tree-ring- derived growth rates and its climatic controls, we now focus on the tropical tree-ring data. We assess the controls of climate on sites within the wider tropics (i.e, all sites between 30°N and S, including high-altitudes) and those within the warm tropical lowlands (altitude < 1500m a.s.l., temperature $\geq 20^{\circ}\text{C}$) using a Bayesian statistical model of tree longevity and growth as a function of climate. This model accounts for the expected negative effects of human influence on tree longevity (Table 2). We disentangle below the effects of water

availability as estimated from precipitation, evapotranspiration and soil moisture (46), and also of mean annual temperature, on trees' longevity and growth.

We find that water availability exerts an important control on tree longevity in the tropics both in our analysis of the wider tropics as well as in the analysis restricted to the warm lowland sites. Mean tree longevity is 52% higher in moist compared to dry tropical biomes (Figure 2a, Table 1, SI Appendix, Fig. S2, S3, Table S1). The estimated coefficients of the Bayesian models for the effect of moisture availability in the driest three months of the year on tree longevity are almost two times higher for the warm lowland sites compared to the larger tropical dataset (one increase in the standard deviation of moisture index resulting in 31% vs. 16% longevity increase, respectively, Table 2, SI Appendix, Table S2). This greater control of moisture availability on tree longevity at warm lowland sites may reflect the rapid increase in the evaporative demand with temperature (19). It is consistent with previous observations of forest monitoring plots in the Amazon that show higher tree mortality and turnover-rates in dry compared to wet forests (47, 48).

In contrast to the effect of moisture on longevity, we find no significant effects of moisture availability on growth rate in both the wider tropics and the tropical lowland sites (SI Appendix, Fig. S2 and S3, Table 2). Since we control for the effect of soil types, as well as for species, in the model as random effects, this result suggests that for a given species and identical soil conditions, growth rate does not vary with moisture. This observed lack of an effect of moisture on trees growth rate in the tropical dataset seems in contradiction with previously reported increases in woody productivity of forests with water availability (49). However, reported stand level productivity increase with moisture could be the result of variation in tree density and/or forest composition (50) without changes in individual tree level growth. At wet sites, average tree growth rate may also not increase despite greater

water availability due to increased competition for light combined with lower initial growth rate usually reported for trees in the understory (51).

The lack of an effect of moisture on growth, but a positive association with longevity, seems to be at odds with the observed trade-off between tree longevity and growth rate across biomes and species. However, trees in the tropics are known to grow taller at wetter compared to drier sites (52), thus these trees reach their limiting size later in life which may explain the greater tree longevity observed here (SI Appendix, Fig. S2 and S3). In addition, trees growing in wet forests usually experience more intense competition for light, likely resulting in longer times spent in the understory (51). Recent reports of giant trees growing under various climate conditions in the tropics (53, 54) represent exceptions to the tree size and water availability relationship. Such populations of giants from specific tree species are likely to reach longer lifespans than expected given the local water availability. The fast-growing baobabs are one of these known exceptions. They can reach a massive size and proven very old ages in the water-limited and open formations of African savannas (55), probably due to their specific strategy to store large volumes of water in their succulent stems (56).

Effects of temperature on growth and longevity in the tropics

In our analysis for the wider tropics we find that growth increases by 12% every 7°C increase in mean annual temperature along latitudinal and altitudinal gradients (Table 2, Figure 3). In terms of carbon store, however, this observed increase in growth rate maybe be partially offset by an expected lower wood density in the fast-growing trees (Table 2). If we restrict our dataset to warm tropical lowlands (i.e., sites with $T \geq 20^{\circ}\text{C}$ and below 1500 m a.s.l.), the temperature effect on growth disappears, indicating that low temperature is no longer a limiting factor.

The mean annual temperature has no effect on longevity in the wider tropics. However, in the warm lowlands, tree longevity is strongly reduced above a threshold of 25.4°C (Figure 3, Table 2). This result is based on 190 populations in our dataset, and 3,170 trees, evenly distributed across tropical moist broadleaf forests (48% of the populations, SI Appendix, Fig. S4), savannas and dry forests (50%). According to our model, this threshold in the effect of temperature on tree longevity is independent of moisture availability, as it remains significant for any constant humidity subsets along a moisture gradient (Figure 3a, Table 2).

The observed reduction in tree longevity with increasing temperature and decreasing moisture availability is consistent with theoretical considerations of the effects of high temperature and low water availability on tree physiology which suggest overall a reduction in tree longevity and an increase in tree mortality rates (18). For instance, atmospheric vapor pressure deficit (VPD) increases exponentially with temperature, which likely increases the risk of hydraulic failure, especially under low relative humidity conditions (18). Trees may compensate for increased water losses under high temperature and low water availability by closing their stomata, but this will result in lower carbon assimilation rates and may kill trees through carbon starvation (18). Furthermore, carbon costs increase with respiration rates which tend to increase under warm conditions. Any structural adjustments to cope with these conditions, like the addition of new xylem tissue, are likely to add to respiratory costs (18). These failures may accumulate as trees grow bigger, reducing their life-spans.

The temperature-dependence of tropical tree longevity revealed by the present study could explain some of the observed increases in tropical tree mortality since 1980's (4). Particularly in the Amazon, strong increases in tree mortality occurred since 1980s leading

to a decrease in the Amazon carbon sink (6). In Western Africa recent drying and warming trends have been driving changes in tree species composition towards more drought-adapted vegetation (57), that according to our findings here only support shorter lifespans in the tropics (Figure 2a, Table 1). Finally, drying and warming trends are also likely the cause behind recent substantial increases in mortality rates of the oldest Baobab trees in the African savannahs (54).

Prospects on growth rate and longevity of tropical trees

The geographical patterns of tree longevity and growth reported by the present study are likely the result of a long history of shifts in vegetation cover, composition, and adaptations to past climate conditions on Earth. However, recent rates of tropical climate change and predictions for the future, in particular for temperature levels, are unprecedented in history (58) and are thus likely to affect tropical forest dynamics in a significantly shorter time-scale. Our results here suggest that temperature increases, together with water limitation, exert significant control over tree longevity. Even modest increases in mean annual temperature above 25.4°C are associated with decreases in tree longevity. The area in the tropics with temperature exceeding this threshold of 25.4°C is expected to increase from currently 37% of the total area to 60% by 2050, for Representative Concentration Pathway (RCP) 4.5 emissions scenario (Figure 4, SI Appendix, Fig. S5 for all other RCPs). Forested area that will likely exceed this temperature threshold by 2050 are mostly located at the southern edges of the Amazon basin, and over the entire Congo Basin in Africa (Figure 4). Temperature increases in the Congo Basin could have a particularly large impact driving up mortality rates, which only recently showed signs to be increasing in this African region (59), risking the sink capacity of the second largest expanse of tropical rainforest. Thus, one could expect tropical forest turnover rates to increase further in a

warming climate, driving-up tree mortality rates. As mortality rates are a key determinant of forest carbon stocks (60) one could thus expect tropical forest carbon stocks to decrease in a warmer world.

Materials and Methods

Data acquisition

We have compiled tree-ring datasets from the tropics and subtropics, defined here as the regions between 30 degrees north and 30 degrees south (61). We surveyed the literature, including master theses and dissertations, using Google Scholar, Science Direct, SCOPUS. We used the following search keywords: “tree rings”, “dendrochronology”, “dendroecology”, “tropics”, “sub-tropics”. We then looked for additional studies based on the reference list of each scientific paper or thesis we found.

Tropical tree-ring studies have severely lagged behind temperate regions due to a long-perceived misconception that most tropical trees grow continuously (26, 27) and do not form annual growth rings. However, studies showed tree rings to be annually formed even in ever-wet regions (26, 27). We carefully recorded for each evaluated study whether annual character of tree rings was established and by which method. More than 60% of populations (defined here as a group of trees of the same species growing at the same site) had their annual tree-ring formation proved in the study by internal cross-dating and correlation with climate, radiocarbon bomb peak dating, counting of tree rings of trees with known ages, cambium marking or cambium activity (SI Appendix, Fig. S6). A smaller portion (between 17% and 26% of the dataset) relied on secondary proof of annual ring formation for that particular species (i.e., from another study). Only a very small proportion (<14%) of the included tree species had no proof of annual ring formation of the observed distinct rings, but most of these (8% to 11%) grew in seasonal climates (i.e., distinct dry

season or a flood period). Unlike dendrochronological studies that requires fully dated tree-rings series, for the applications in climatology, forest dynamics, to name a few, age and growth estimations are significantly less sensitive to small deviations from some missing and false rings that may be common in the tropics (26).

Tree-ring derived data were obtained for each population analyzed in the present study. Here, we refer to the reported maximum number of tree rings counted in the oldest tree from a population as “estimated longevity”. We carefully avoided the underestimation of tree longevity by defining criteria for data inclusion. We excluded studies that only sampled younger individuals or studies that used only segments of the full tree-ring series. Nevertheless, we still expect a minor underestimation of real longevity because most studies have sampled living trees, samples were taken at breast height or higher, some increment cores may lack the pith, some trees may be hollow, or because some sample sites may be under the influence of selective logging. However, as the sampling procedures did not vary much among biomes and as our dataset includes a large number of records and a generally large number of trees per site, large-scale emerging longevity and growth rate patterns should not be affected. Population mean diameter growth rates were calculated from average tree-ring widths of all analyzed individual trees from the same population. Where either growth data or longevity data were not reported in a given the study, we contacted the authors to obtain the missing data.

Our final database for the tropics and subtropics includes data from a total of 209 studies with an additional 44 records from the International Tree-Ring Data Bank (ITRDB, 62) (SI Appendix, Table S3). This dataset is based on the previous tree-ring analyses of more than 17,000 individual tree records, distributed across 763 populations (average of 22 trees per population, SI Appendix, Fig. S7), including 284 species from 53 families (SI

Appendix, Table S3). To place the tropical dataset into a global perspective, we also included extratropical populations using ITRDB data from latitudes outside 30° N and 30° S. We calculated, for these populations, the maximum length of the tree-ring series and average diameter growth rate.

In contrast to the tropics, extratropical tree-ring chronologies often comprise tree-ring series from living and dead trees. Such records using long-dead trees were excluded from the analyses, to make the datasets from the tropics and extra-tropics comparable. To account for over- and under-estimation of tree longevity, only the populations with at least one individual tree-ring series with length equal or higher than 90% of the tree-ring chronology length, were included (SI Appendix, Fig. S8). For the extra-tropics, the dataset is represented by 161 species, and 2,580 populations based on the previous tree-ring analyses of more than 84,000 trees.

Data analysis

Global patterns of tree longevity and growth rate

We characterized the spatial variability of tree longevity and growth at a global scale by calculating descriptive statistics at the biome level (63), including only biomes with at least 10 populations. We further compared longevity and growth rate of trees by combining biomes according to temperature limitation and water availability: cold-dry (Temperate Deserts and Xeric Shrublands), cold-wet (Temperate Montane, Conifer Forests, Mixed Forests, Savannas, Boreal Forests, Tundra, Mediterranean Forests, Tropical Montane and Tropical Conifer Forests), warm-dry (Tropical Dry Forests, Tropical Savannas, Tropical Flooded Savannas, Tropical Deserts and Xeric Shrublands) and warm-wet

(Tropical Moist Broadleaved Forests). Differences in longevity and growth rate among biomes were tested using ANOVA and Tukey Test.

Mixed-effects models of longevity and growth rate in the tropics

To assess how longevity and growth rates are related with climate in the tropics, we applied a linear mixed model in a Bayesian framework (64) using a Markov-Chain Monte Carlo method for model parameter estimation (65). This approach allowed to estimate the covariance between the response variables: longevity and growth rate (log transformed); and predictors: regional climate (46, 66), 'human influence index' as a proxy of human accessibility to natural areas (67), and wood density at species level (68). We included in the model soil classes (69) and species identity as random effects, together with a phylogenetic distance matrix to deal with phylogenetic residual correlations.

Two different statistical models were developed to test for these relationships. The first model, here referred to as "wider tropics", used all 763 populations from the tropics and sub-tropics, including sites from higher altitudes. The second model includes only data from populations in the "warm tropical lowlands" with altitudes below 1500 m a.s.l. and mean annual temperature above 20°C, which are the main focus of this study (442 populations, more than 8,400 trees). For each model, we ran four Markov-Monte Carlo chains with two million iterations, discarding the first 10000 iterations, with a thinning interval of 200 resulting in 4950 iterations per chain. We checked the convergence of the chains using the Gelman-Rubin criterion (70).

We treated soil as a random effect because of the large number of classes, a total of 17 classes (71). We also added the phylogenetic distance to the random effects. For the phylogenetic distance, we constructed the phylogenetic tree using the Phylomatic

software (72) based on a revised vascular megatree (73). We estimated the ancestral values of longevity and growth at internal nodes using maximum likelihood under the assumption of Brownian motion for trait evolution (74, SI Appendix, Fig. S9). We also added species to account for the variability that has been caused by species-specific effects after removing the phylogenetic effect (64).

Since many of the predictors in the fixed effects considered initially for this study (around 40 variables) covary spatially, we identified the most independent predictor variables using the Ascendant Hierarchical Clustering method (75). The analysis identified 7 main clusters. For each of them, we chose the climate variable, which was the most closely correlated with the central synthetic variable of each cluster. The 7 variables are mean annual temperature, temperature seasonality (standard deviation of monthly data x 100), water-balance soil moisture index of the wettest quarter of the year (based on precipitation, evapotranspiration, soil type and soil water availability, 46), moisture index of the driest quarter, cloud cover, lowest weekly radiation, and human influence index. We checked once more for collinearity among the chosen variables during model implementation. We used these 7 variables in the mixed linear model with the dataset, including all populations within 30°N and S of latitude.

Although human influence tends to reduce tree longevity according to the results of the Bayesian model (Table 2, SI Appendix, Table S2), most of the studied tropical and extratropical populations are from areas with relatively low influence of human activities (SI Appendix, Fig. S10). As it is weakly associated with the main climate variables used in the implementation of this statistical model (SI Appendix, Fig. S11), the level of regional human influence is not expected to bias the results presented here for longevity and growth of tropical trees.

Based on the results of that model, we chose the two variables with the most substantial effects on longevity and growth, namely the mean annual temperature and moisture of the driest quarter, to further understand longevity and growth rate variability in warm tropical lowlands. Because of the non-linear relationship between the raw data and mean annual temperature (SI Appendix, Fig. S12), we parameterized the effect of temperature using a cubic function. Based on the results of this model, we plotted the spatial distribution of the populations in sites with the current mean annual temperature above 25.4°C, together with the predicted expansion of the area with the mean annual temperature above 25.4°C by 2050, using HadGEM2-ES model output (46, 76).

In order to check if the model outputs were affected by how the studies approached the issue of tree-ring annuality, we separately plotted subsets of the data with different degrees of confidence in annual ring formation onto the raw data (SI Appendix, Fig. S13 and S14). This shows no evidence for an apparent bias due to uncertainty with regard to the annual character of the rings of the used study. We further re-ran the models removing the datasets that include populations without proved annual tree-ring formation. SI Appendix, Fig. S15 shows no significant differences in the coefficient estimation among the models. We are therefore confident that our results are not an artefact of potentially misattributed ages of a subset of our dataset.

Data availability

The dataset of tropical trees is available at Figshare (DOI: 10.6084/m9.figshare.13119842) together with the R codes for the two models, their respective diagnostics and results. The dataset from extropical trees is available at the International Tree-Ring Data Bank (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>).

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Figures Legends

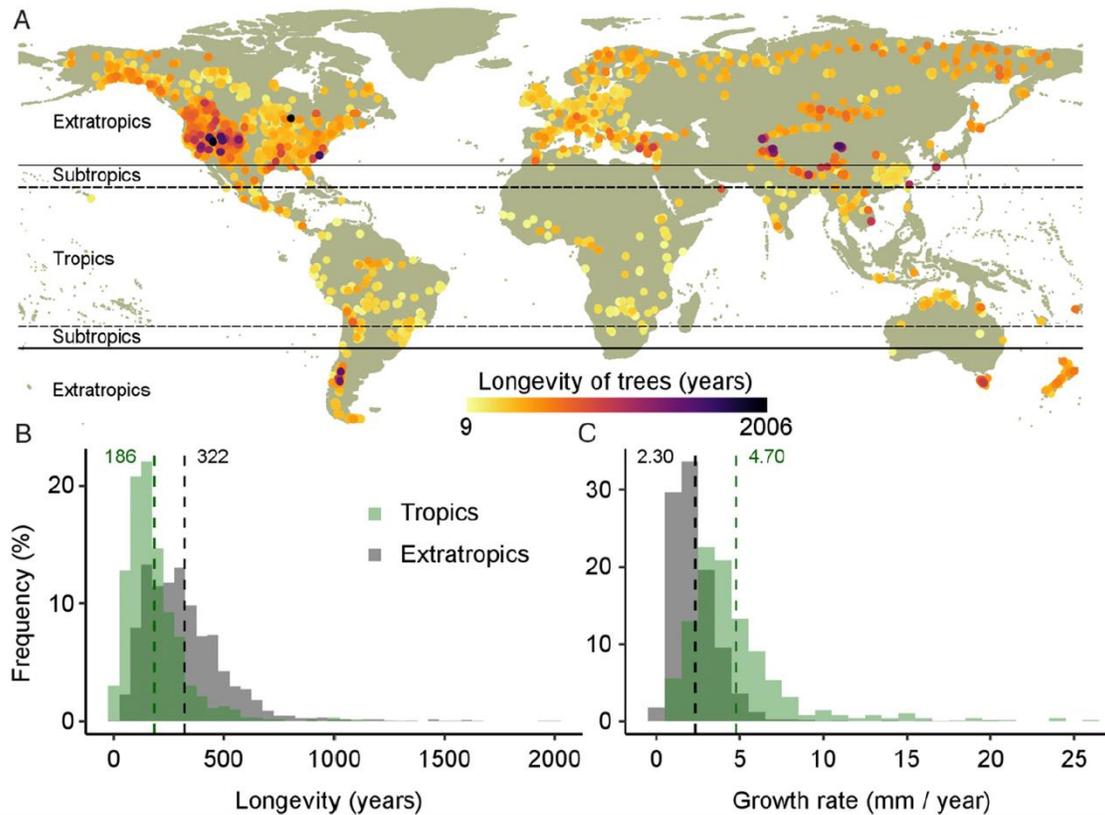


Figure 1. Longevity of trees based on tree-ring data. A) Geographical distribution of the maximum reported ages, here referred to as longevity, for 3343 populations in the World. Dashed lines indicate the limits of tropical zone (23.5° N to 23.5° S) and the continuous line indicate the limits of subtropics areas (23.5° to 30° N and S). Older populations were plotted over younger ones on the map to highlight the distribution of the oldest populations. Histograms show the distribution of tree B) longevity and C) growth rate of the populations from tropical biomes (green, between 30° N and S of latitude) and extratropics (grey).

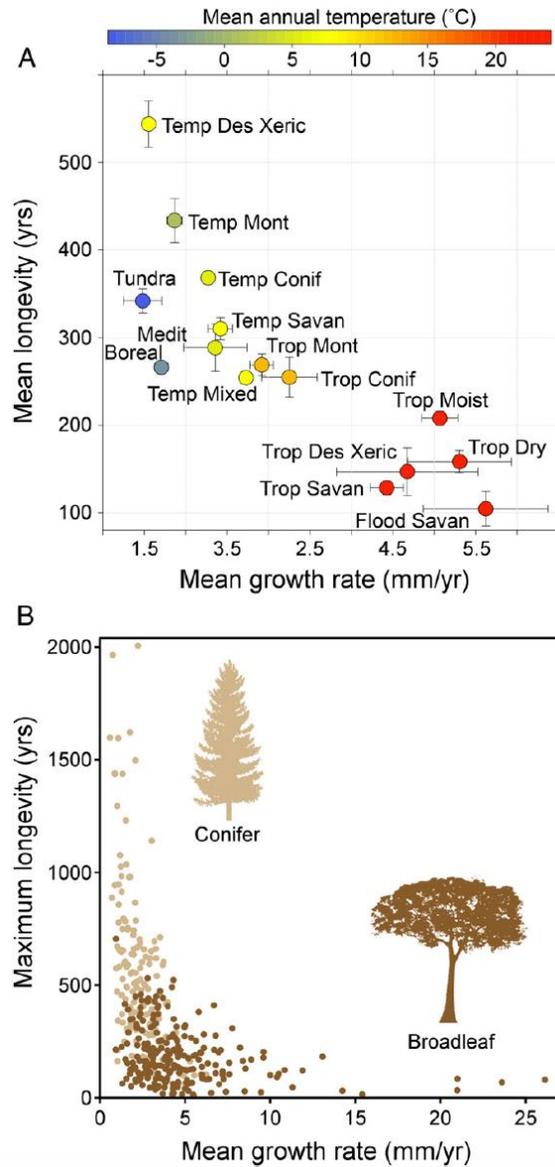


Figure 2. Comparison of longevity and growth rate of trees by biome of provenance and taxa. A) Average maximum age and growth rate for all biomes from tropics and extratropics based on the data from 3343 populations. The error bars account for the uncertainty of the mean estimation (95% interval). Color scale indicates the mean annual temperature of the sites in each biome. Montane (Mont) and Desert and Xeric Shrublands (Des Xeric) were the only biomes divided in tropical (Trop) and temperate (Temp) areas. B) Maximum reported longevity and mean annual growth rate for each one of the 438 species used in this study.

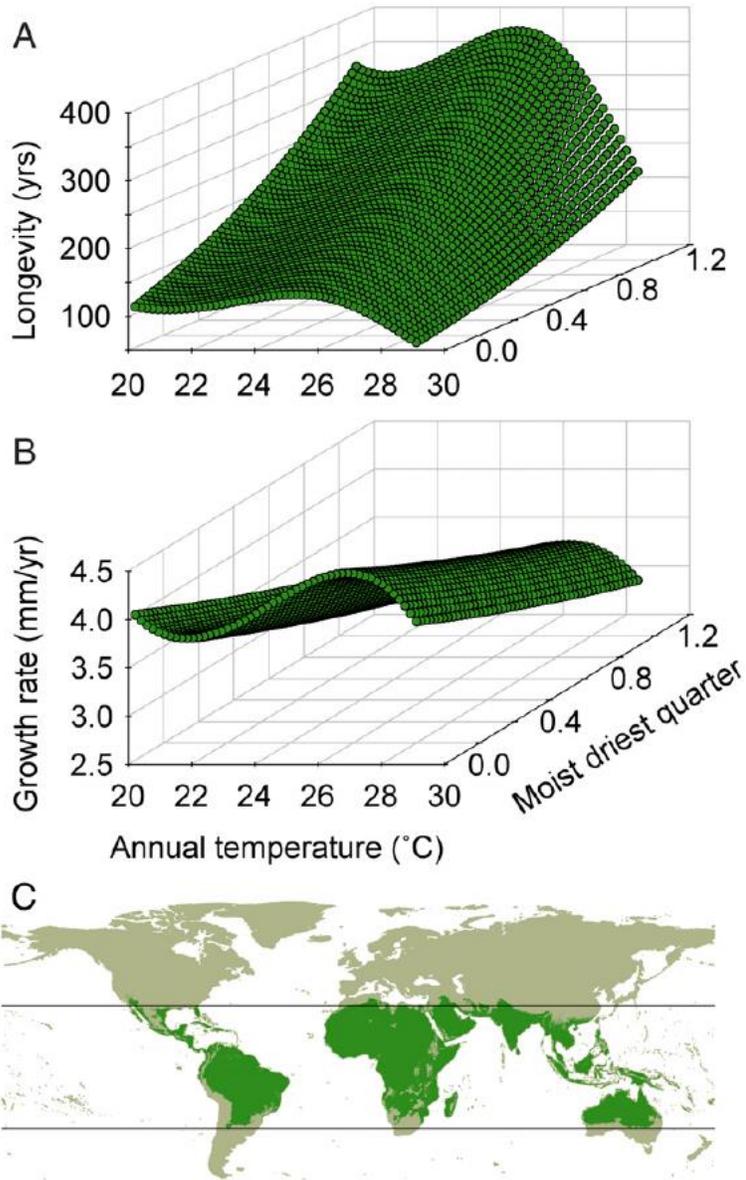


Figure 3. Model output for populations inhabiting warm tropical lowlands. The graphics represent the predicted curves of longevity and growth rate variability driven by independent effects of moisture index of the driest quarter and mean annual temperature. The map shows the spatial distribution of areas with mean annual temperature above 20°C (in green). The lines represent the subtropical limits (30°N and 30°S).

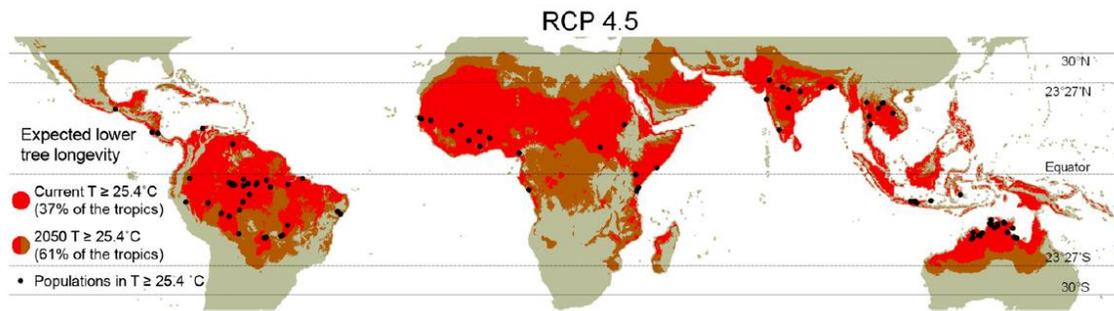


Figure 4. Geographical distribution of tropical areas with current mean annual temperature above the threshold of 25.4°C (red), and brown areas representing the spatial expansion by 2050 according to the Representative Concentration Pathway (RCP) 4.5, HadGEM2-ES. Black circles represent the tree-ring dataset from the populations of trees used in this study that support the threshold of 25.4°C , above which trees are expected to show significant lower tree longevity than in cooler areas.

Table 1. Comparison of longevity and growth rate of trees from four site conditions according to the temperature and water availability in the biomes: 1 – Cold - limited and Dry (Temperate Deserts and Xeric Shrublands), 2 – Cold - limited and Wet (Temperate Montane, Conifer Forests, Mixed Forests, Savannas, Boreal Forests, Tundra, Mediterranean Forests, Tropical Montane and Tropical Conifer Forests), 3 – Warm and Wet (Tropical Moist Broadleaved Forests), 4 – Warm and Dry (Tropical Dry Forests, Tropical Savannas, Tropical Flooded Savannas, Tropical Deserts and Xeric Shrublands). Results of the ANOVA and Tukey HSD are presented.

Biomes	Age (years)		ANOVA ($p < 0.01$)	Growth rate (mm/yr)		ANOVA ($p < 0.01$)
	Mean	SE	Tukey	Mean	SE	Tukey
Cold / Dry	544	26.23	A	1.55	0.07	A
Cold / Wet	309	3.62	B	2.35	0.03	B
Warm / Wet	208	5.07	C	5.07	0.22	C
Warm / Dry	137	4.72	D	4.72	0.21	C

Table 2. Effects of climate, and other variables on tree longevity and growth for the wider tropics and the warm lowlands. Results show the significant effects detected using bivariate Bayesian models. Full results are shown in Table S2. The first model explains 80% of the variability of longevity and 76% of growth rate of trees from all populations found within the latitudinal range between 30°N to 30°S. The second model only explains 82% of the variability of longevity and 72% of growth rate of trees from tropical lowlands with mean annual temperature above 20°C. Phylogeny and soil classes are controlled in the models. The values of posterior means (coefficient estimates) and p values of each predictor variables are given. The change in the posterior mean by increasing one standard deviation of the predictor values (% change, $e^{(\text{Post.mean}-1)} \times 100$) is also given for all significant variables.

Wider tropics (30°N to 30°S)				
Response	Predictors	Post.mean	p	% change
Longevity	Moisture driest Quarter	0.15	< 0.01	16%
	Lowest Weekly Radiation	-0.08	0.01	-8%
	Human Influence	-0.10	< 0.01	-10%
Growth rate	Temperature	0.11	< 0.01	12%
	Wood Density	-0.12	< 0.01	-11%
Tropical lowlands (altitude < 1500m a.s.l., temperature ≥ 20°C)				
Longevity	Moisture driest Quarter	0.27	< 0.01	31%
	Temperature ³	-1.99	0.02	-84%
Growth Rate	Moisture driest Quarter	-0.07	0.03	-7%