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The importance of tropical tree-ring chronologies for global change research

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Abstract

Tropical forests and woodlands are key components of the global carbon and water cycles. Yet, how climate change affects these biogeochemical cycles is poorly understood because of scarce long-term observations of tropical tree growth. The recent rise in tropical tree-ring studies may help to fill this gap, but a large-scale quantitative analysis of their potential in global change research is missing.

We compiled a list of all tropical tree species known to form annual tree rings and built a network encompassing 492 tropical ring-width chronologies to evaluate the potential to generate insights on climate sensitivity of woody productivity and to build centuries-long reconstructions of climate variability. We assess chronology quality, length, and climatic representativeness and explore how these change along climatic gradients. Finally, we applied species-distribution modeling to identify regions with potential for tree-ring studies in ecological and climatic studies.

The number of tropical chronologies has rapidly increased, with ~400 added over the past two decades. Yet, tree-ring studies are biased towards high-elevation locations, with gaps in warmer and wetter climates, on the African continent, and for angiosperm species. The longest chronologies with strongest climate signals (i.e., synchronous growth variations among trees) are from cool regions. In wet regions, climate signals and precipitation sensitivity decrease. Most tropical regions harbor 5–15 (and up to 80) species with proven potential to generate chronologies. The potential for long climate reconstructions is particularly high in drier high elevation sites. Our findings support strategies to effectively expand tree-ring research in the tropics, by targeting specific species and regions. Tropical dendrochronology can importantly contribute to global change research by generating historical context of climate extremes, quantifying climate sensitivity of woody productivity and benchmarking vegetation models.

Keywords: Climate sensitivity, growth synchrony, pantropical tree growth, dendrochronology

Introduction

Tropical forested ecosystems are key components of the global carbon and water cycles. Forests and woodlands in the tropics and subtropics (herein defined based on latitude between 30 ^{0}S and 30 ^{0}N; Corlett, 2013) contribute substantially to carbon sequestration (Pan et al., 2024), drive the interannual variability in the land carbon sink (Fan et al., 2019; Friedlingstein et al., 2020), and generate rainfall through high transpiration rates at regional and sub-continental levels (Staal et al., 2018). These contributions depend critically on the productivity of tropical vegetation (Poulter et al., 2014), and is modulated by geographic location and climate variability (Wang et al., 2016; Humphrey et al., 2018).

Insights on this climate sensitivity of tropical vegetation are limited by the paucity of ecological field data and long-term climate data in the tropics (Menne et al., 2012). Compared to temperate and boreal zones, the density of meteorological stations, flux towers, permanent sampling plots, climate manipulation experiments, and tree-ring studies is much lower in the tropics (Babst et al., 2021; Crowther et al., 2015; Villarreal and Vargas, 2021; Zhao et al., 2019). In addition, the duration of tropical studies on climate-productivity relations is often much shorter compared to that of studies in other climate zones (Pastorello et al., 2020). This data scarcity limits options to calibrate and benchmark Dynamic Global Vegetation Models (DGVMs) for tropical ecosystems (Zuidema et al., 2018; Xu et al., 2024). In addition, the low density of meteorological stations and short duration of instrumental climate across much of the tropics impairs the accuracy of gridded climate data products and prevents climatologists to put current climate extremes into a long-term perspective (Menne et al., 2012).

Tree-ring analyses can contribute to filling these data gaps by providing long-term, annually resolved datasets on species-level woody productivity and by allowing climate reconstructions. Extra-tropical tree-ring studies have been used to reveal shifts in climate-growth relationships (Babst et al., 2019), to benchmark DGVMs (Barichivich et al., 2021), and to perform distribution-wide analyses of climate sensitivity (Klesse et al., 2020). At tropical and subtropical latitudes, the annual formation of tree rings has now been proven for approximately 500 tree species (Brienen et al., 2016; Locosselli et al., 2020; Schöngart et al., 2017), and almost 500 tree-ring chronologies – time series of common tree-ring width patterns within a population – have been published (Zuidema et al., 2022). These recent advances exemplify the large potential of tropical dendrochronology to reconstruct past climate variability, to improve our understanding of the effects of climate fluctuation on tropical woody productivity, and offer opportunities to benchmark and calibrate remote sensing products and DGVM output (Babst et al., 2014; Jeong et al., 2020). Yet, a pantropical assessment of the potential of tropical tree-ring data for global change studies is missing to date.

Here we leverage quantitatively review the quality, length, and climatic representativeness of tropical tree-ring chronologies, and by assessing the magnitude of climate sensitivity of tropical tree growth. We also evaluate the potential of current tropical dendrochronology to contribute to our understanding of climate sensitivity of woody productivity and to reconstruct climate variability over the past centuries. We conclude by identifying opportunities and difficulties for tropical tree-ring studies in hitherto underrepresented regions.

We address the following questions: (1) To what extent are tropical tree-ring chronologies geographically and climatically representative of tropical wooded ecosystems? (2) What is the strength of the climate sensitivity of tropical tree growth and does this sensitivity depend on mean climate and on the quality of meteorological data? (3) Which climatic conditions offer the best opportunities for climate reconstruction based on tropical tree-ring chronologies? (4) What is the pantropical distribution of the potential for tree-ring studies and climate reconstruction?

Methods

Assembling tree-ring chronologies

Our review is based on chronologies included in a recently established tropical tree-ring network (www.tropicaltreeringnetwork.org). We compiled published ring-width chronologies from naturally regenerating tree populations in tropical and subtropical latitudes (30°N to 30°S). Thus, we included chronologies based on geographical limits of the tropics in a broader sense and we did not select sites exclusively within the climatological definition of the tropics or exclusively in tropical biomes. This implies that several of the genera we include are commonly present in temperate regions (*Abies*, *Picea*, *Larix*, etc.).

We used raw ring-width data from two sources: (1) 242 chronologies from the International Tree-Ring Data Bank (ITRDB, https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) and (2) 250 chronologies from individual contributors. We thus included a total of 492 chronologies in the quantitative analyses, based on measurements of 10,936 individual trees and 20,915 radial series from 139 species (Appendix 1). Short or statistically "unsafe" chronologies are usually removed from studies that combine datasets. Yet, as our intent was to provide the widest possible perspective on tropical tree-ring studies, we included short chronologies (here, the minimum was 16 years) and those based on only a few individuals (minimum here = 4 trees). In our final dataset, 82.7% of the chronologies covered at least 35 years and included a minimum of 10 individuals.

Additionally, to explore the broader potential of using tree rings in the tropics, we also compiled a species list from studies that use tropical tree rings for other purposes than building chronologies. Several studies exist that have applied tree-ring data without building chronologies to answer questions related to forest ecology (Van der Sleen et al., 2015a), dynamics (Godoy-Veiga et al., 2018), isotope-based rainfall reconstructions (Woodborne et al., 2015), tree physiology (Garcia et al., 2022; Loader et al., 2011), anthropogenic disturbances (Caetano-Andrade et al., 2020), or forest management (Groenendijk et al., 2017). Many of these studies did not focus on climate-growth related questions *per se*, and hence did not seek to build chronologies. A large part of these studies therefore do provide proof of annuality of ring formation using radiocarbon dating, phenology observations, dendrometers, cambium wounds or ring counts in plantations of known age (Brienen et al., 2016). Although not producing chronologies, these studies reflect the potential of a broader set of species for tree-ring studies. This species list was created by complementing species lists from review papers (e.g., Brienen et al., 2016; Locosselli et al., 2020; Quesada-Román et al., 2022; Portal-Cahuana et al., 2023) with a literature search using the search terms "tropical tree rings" and "tropical dendrochronology". This was not intended to be an exhaustive search and we acknowledge that we have missed non-English publications (e.g., in Spanish; see Portal-Cahuana et al., 2023), but we believe it does provide a good representation of tropical tree species with potential to be used in global change studies.

Chronology construction

To allow for the comparison of results across sites, we redeveloped chronologies from the raw ring-width data. We applied a flexible 30-year cubic-spline detrending method (with a 50% frequency cut-off) to all individual raw ring-width series to remove low-frequency signals (i.e., trends in the growth series at frequencies of decades or centuries) and emphasizes the interannual variation in ring widths that was our main interest (Hughes et al., 2010). We developed mean site chronologies of a dimensionless ring-width index (RWI) from the detrended series using a bi-weight robust mean. We then used the most recent 50 years of each chronology (or less in case of short chronologies) for further analyses (e.g., of inter-series correlations (Rbar) or monthly climate correlations, etc.). We followed the Schulman convention in the development of all tree-ring series from the Southern Hemisphere (Schulman, 1956), except for chronologies in the Brazilian Caatinga biome, where the rainy season coincides with the Northern Hemisphere's growing season (Zuidema et al., 2022). We conducted detrending and chronology building using the dplR package (Bunn, 2008; Bunn et al., 2023) in R (R Core Team, 2023). We note that chronologies and further analyses presented here may slightly differ from those of the published chronologies, because of differences in detrending procedure and period covered in the study.

Climate data and distance to climate stations

We used two types of gridded climate data: (1) Worldclim version 2 (worldclim.org) to obtain mean annual precipitation (MAP) and temperature (MAT) between 1970-2000 at 1-km spatial resolution, and (2) CRU TS4.02 to obtain monthly maximum temperature (T_{max}) and monthly precipitation data for the most recent 50 years of each chronology, at a coarser spatial resolution of 0.5°. The quality of gridded climate data is a function of the local density of meteorological stations. A low density likely weakens the accuracy of the interpolation and, with that, also weakens the correlation between climate variability and ring width. To evaluate the impact of meteorological station density on the magnitude of climate-growth relationships we calculated the mean distance between each chronology location and its five nearest meteorological stations. We do not account for elevation differences between the climate stations and the study location as we assume that these changes will affect the absolute values of temperature and precipitation, but not so much the interannual variation in the data. We obtained locations of all stations within the (sub-)tropics from the Global Historical Climatology Network (Menne et al., 2012) and selected stations with at least 25 years of data. We then calculated the distance of each study location to the nearest stations per corresponding continent using 'Vincenty' (ellipsoid) great-circle distance estimations with the *distm* function of the *geosphere* R package (Hijmans, 2021). We then identified the five stations closest to each of the tree-ring sites and calculated their mean distance to the site. Finally, we checked for a statistical relationship between this mean distance and the strength of the climate-growth correlations obtained from the tree-ring data.

Climatic representativeness

We evaluated the climatic representativeness of our network (research question 1) by comparing the MAP and MAT distribution of the chronologies from our tree-ring study sites against MAP and MAT distributions from the entire tropical land areas supporting woody vegetation (i.e., with >10% tree cover). We used tree-cover data from the MODIS-derived MOD44B product (version 6; https://lpdaac.usgs.gov/products/mod44bv006/) to mask out areas with <10% tree cover from the Worldclim 2 data. We then calculated continent-level relative MAP and MAT distributions (i.e., the kernel density estimates) of the tropical land area with woody vegetation. To obtain corresponding density estimations for precipitation and temperature of the tree-ring network, we calculated these density estimates for the sites in the network using the same maximum, minimum and bin-size values as for the entire forested area. By dividing the scaled distribution values of the network by those of the forested land area per continent, we obtained a measure of biases in how the network represents the climatic envelope: values above 1 indicate “overrepresentation”, those below 1 “underrepresentation”. Thus, if a certain MAT bin contains 5% of the values of the tree-ring network but represents only 2% of the values of all tropical land area, this ratio would be 2.5 and an indication that the network is biased towards overrepresenting this MAT range. Note that this measure of representativeness tells how well a part of the climatic envelope is covered in relative terms but does not provide information on the absolute density of tree-rings sites (per unit area).

Climate correlations and growth synchronicity

To estimate the strength of climate signals embedded in tropical tree-ring chronologies (research question 2), we calculated simple Pearson’s correlation coefficients between Ring Width Index (RWI) and monthly T_{max} and precipitation data for a 24-month period that includes the year of growth (e.g., the peak of the growing season) and the previous year. For Northern Hemisphere and *Caatinga* sites, this period includes the full calendar year prior to the year of ring formation, plus the full calendar year during which the ring was formed. For Southern Hemisphere sites, it contains the 12-months July-June period preceding the onset of ring formation, and the following 12 months during which the ring was formed. For each climatic variable we then selected the highest monthly correlation coefficient of the 24 correlations. We do not present a more exhaustive analysis of climate responses, because our aim is to provide an indication of the maximum climate sensitivity of growth, which is relevant for climate reconstructions and studies quantifying climate effects on tree growth.

The quality of tree-ring chronologies is commonly indicated by a measure of growth synchronicity. As a measure of this synchronicity, we used the dendrochronological statistic 'Rbar': the mean correlation between all the ring-width series within a population (Hughes et al., 2010). Low Rbar-values may indicate poor dating quality, weak effects of common environmental drivers on growth, or both. We did not set a minimum Rbar criterion for this review, because we were interested in presenting the full scope of characteristics of tropical tree-ring chronologies.

Statistical analyses: climate correlations, Rbar, chronology length

To evaluate factors driving the degree of climate sensitivity (question 2), we performed a multiple regression of the strongest monthly climate correlation, which we expected to increase with site aridity (i.e., higher MAT and lower MAP) and to be reduced when meteorological stations are scarce (i.e., higher distance to the five nearest stations). A second regression assessed factors influencing the growth synchronicity (Rbar) of the chronologies, which needs to be high for climate reconstructions (question 3). Rbar is expected to be higher at low MAT (i.e., in colder, mountainous climates), at low MAP (i.e., where precipitation exerts a strong common limitation to the growth of co-occurring trees) and to increase with the strongest monthly correlation (i.e., a strong synchronicity is likely driven by a common climatic limitation). The third multiple regression analysis evaluated how the potential for climate reconstruction (question 3) in terms of chronology length (tree longevity) is associated with mean site climate. We expected longer chronologies at lower MAT and lower MAP, thus at sites at cold and/or dry limits of the species where its growth is restricted by climate.

For all multiple regressions, we used the “leaps” algorithm for model selection, an all-subset model comparison that is more robust than stepwise methods (Furnival and Wilson, 1974). We checked the Variance Inflation Factors (VIFs) of all models and found these to be lower than 2. Analyses were conducted in R using packages *leaps* (Lumley, 2020) and *bestglm* (McLeod et al., 2020).

Species distribution models

To identify geographic regions that harbor tree-ring forming species, and areas that are particularly suitable for building tropical tree-ring chronologies, we ran species distribution models (Maxent) based on occurrence data from Global Biodiversity Information Facility – GBIF – extracted using the *rgbif* R package (Chamberlain et al., 2023) – and Worldclim2 climate data. We ran these distribution models for the larger set of ring-forming species (i.e., the 513 species extracted from the literature) and the set of species for which chronologies have been built (i.e., the 139 species of which chronologies are included in the network). For each species, we ran distribution models only for the continent where the species occurs naturally. To reduce the effect of a high local density of occurrence data on model fits, we thinned observation data to a maximum of one observation per 0.5° grid cell. Additionally, we only conducted distribution models for species that had a minimum of 10 grid cells with observations, that is, for 450 (out of 513) species for the large set of ring-forming species, and for 122 (out of 139) species for the chronology-bearing species list. We summed the probability of occurrence of all species per cell to produce a map with estimates of the total number of ring-forming species and that of species with dendrochronological potential per grid cell.

We used a similar approach to quantify the potential length of the chronologies that can be built in each cell, using the species list for which chronologies exist. For grid cells with a probable species occurrence ($P>0.5$), we calculated the maximum length (90% of the maximum chronology length) of the chronologies for that species and averaged this across all species occurring in that cell. This yielded a map with estimates of the maximum chronology-length per grid cell, a proxy for the potential for climate reconstruction.

We note that values in the resulting maps should be interpreted cautiously because (1) the 0.5 probability cut-off for the species distribution model is rather arbitrary and probably does not represent well marginal sites where the most growth-limiting conditions for a species occur and thus where the longest and most climate-sensitive chronologies for that species can be built, (2) species occurrence in a certain grid cell does not necessarily imply its suitability for chronology construction at that local climate (Baker et al., 2017), (3) the quality and density of species-occurrence data may vary between continents (Meyer et al., 2016), which affects distribution modelling (Beck et al., 2014), (4) the maximum lifespan of a species changes along environmental gradients (Locosselli et al., 2020), which was not accounted for, and (5) distribution modelling based on climate data does not account for changes in species occurrence due to soil conditions (Zuquim et al., 2020) and effects of forest degradation on tree age (Feeley et al., 2012). Thus, the resulting maps provide a first representation of the geographic distribution of the potential for chronology building and climate constructions.

Results and Discussion

Geographic and taxonomic distribution of tropical tree-ring chronologies

The geographic distribution of tropical tree-ring chronologies is uneven (Fig 1A). Among the 492 chronologies included in this review, less than 10% are located on the African continent, whereas more than half are from the Americas. Dendrochronology studies are also biased towards the Northern hemisphere: most studies were performed in the Northern Hemisphere (~1.5 times more), while a larger proportion of land between 30ºS and 30ºN is in the Southern hemisphere (134% more land than the Northern Hemisphere). These geographic biases coincide with those of the global tree-ring databank (ITRDB), in which extra-tropical and Northern Hemisphere chronologies dominate (Zhao et al., 2019). These biases possibly arise from the nature of research funding (concentrated in the Global North) or the role of site selection close to home institutions. The number of tropical chronologies has increased rapidly over the past decades. Since the year 2000, close to 400 chronologies have been added at a rather steady rate of around 20 per year (Fig 1B); equivalent to an annual addition 8.3% for tropical chronologies to the ITRDB. About two thirds of the new additions (217 out of 378) are from lowland regions (<1500m a.s.l.) and the growth in the number of chronologies has been particularly steep in the Americas.

In total, our literature search identified 513 species belonging to 287 genera and 72 plant families. Our network encompasses chronologies for 139 tree species (Fig 1B-D), belonging to 88 genera and 35 plant families (Appendix 2). Our network thus includes about one quarter of the (sub)tropical tree species with known annual ring formation (139 out of a total of 513). The lower number of species covered in our network partly reflects chronologies that have not (yet) been included, but a much larger share represents species for which tree-ring studies did not include the construction of chronologies. The difference in species number also demonstrate the high potential to increase the number of species and chronologies for tropical trees. On the other hand, the rather high proportion of tree-ring studies without chronology building also likely reflects difficulties of constructing ring-width chronologies in the tropics. Ring boundaries are diverse and can be difficult to identify in tropical species (Fichtler and Worbes, 2010; Brienen et al., 2016).

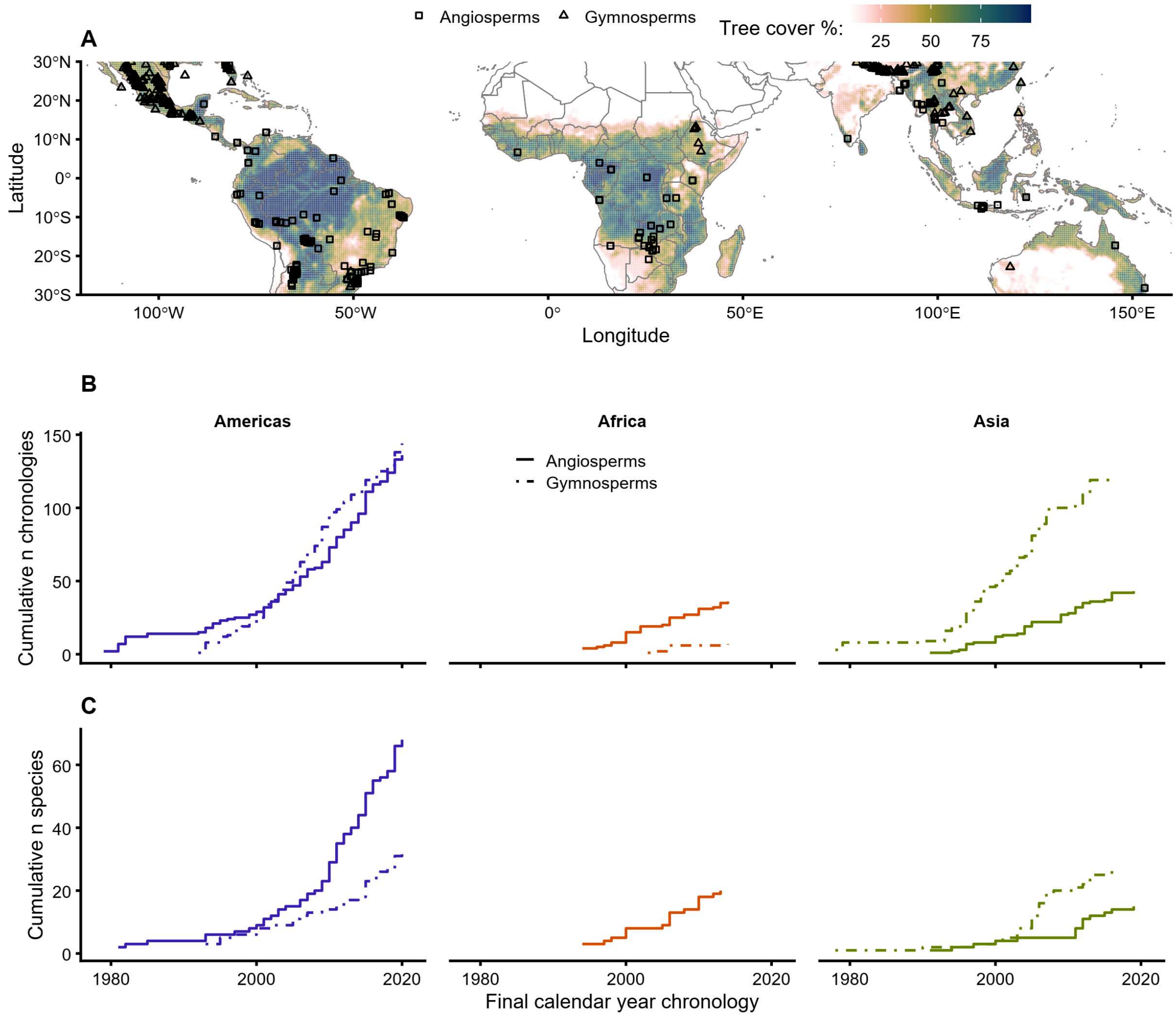

Figure 1. Pantropical distribution and recent increase in the number of tropical tree-ring chronologies. (A) Geographical distribution of 492 tropical tree-ring chronologies from angiosperms (black squares) and gymnosperms (triangles) included in this review. The map background is MODIS-based tree cover percentage. (B-C) Temporal change in the number of chronologies per continent (B) and the number of species for which chronologies have been constructed (C), grouped by gymnosperms and angiosperms and separated in columns per continent: Americas, Africa, Asia.

Tropical trees can also show irregular growth (e.g., fluted stems, buttress roots), form false rings, and partial cambial dormancy (Boninsegna et al., 2009). These difficulties increase the chances of accumulated measurement errors hampering crossdating further into the past (Black et al., 2016) and it is recommended to work with a large number of individuals, with cross-sectional discs or multiple radii collected per tree (Brienen & Zuidema, 2005; Groenendijk et al., 2014) and sampling above parts of the stem with irregular growth (Granato-Souza et al., 2019). Another difficulty in constructing chronologies may be the lack of a strong limiting climatic factor on growth (e.g., a pronounced dry season) (Groenendijk et al., 2014). Yet, this does not apply everywhere, because chronologies have been successfully built in a-seasonal, hyper-wet tropical forests (Giraldo et al., 2023). Additional barriers for chronology building include the difficulty to assess remote field areas for collection of additional samples, the low number of tree-ring researchers and laboratories, and difficulties to publish in English (Portal-Cahuana et al., 2023). National and international training programs can strongly boost tree-rings studies in a country (Portal-Cahuana et al., 2023) and are needed, especially in Africa where tree-ring analyses has a large but unfulfilled potential (Gebrekirstos et al., 2014). International projects should also foresee building laboratory and analytical infrastructure (increment borers, microtomes, polishing machines, measuring tables, scanners, software, etc.) and establish long-term collaborations and training to overcome these barriers in tropical dendrochronology and ensure a lasting legacy.

The taxonomic distribution of tree species with existing chronologies is strongly skewed, with 44% of chronologies stemming from pines (Pinaceae) and with gymnosperm taxa representing 55% of all chronologies. Yet, the dominance of gymnosperms in tropical chronologies is less pronounced than in the global ITRDB, where they represent >80% chronologies (Zhao et al., 2019). Among chronologies from angiosperm species, taxonomic diversity is particularly high, with 96 species represented belonging to 76 genera. The top-10 angiosperm families include Fabaceae (55 chronologies) and the typical tropical (lowland) families Meliaceae (53) and Bignoniaceae (9). During the past two decades, the number of species for which chronologies have been constructed increased by about 100 (Fig 1C). This growth has been particularly rapid in the Americas since 2010, where the number of species represented by chronologies has reached 100. The recent increase in the number of studied tree species producing rings and the number of chronologies built demonstrates the large and underexploited potential of dendrochronology in the tropics. This potential may even be larger, as many studies in the tropics are not published in peer-reviewed journals (remaining in grey literature, such as theses and reports; Portal-Cahuana et al., 2023), many studies are published in languages other than English (e.g., initial exploratory works in the 1930s and 1970s; Worbes, 2002), and many tropical chronologies are not added to global tree-ring networks. The rapid research advances in the tropical

Americas show no signs of leveling off. A likely factor responsible for this faster development of American dendrochronology is a higher number of tree-ring labs and trained professionals compared to Asia and Africa (Gebrekirstos et al., 2014; Pumijumnong, 2013). Yet, such potential is also likely to exist in Asia and Africa, given the abundance of ring-forming tree taxa and the availability of long-lived tree species (Gebrekirstos et al., 2014; Groenendijk et al., 2014; Pumijumnong, 2013), but the high diversity and abundance of dipterocarps that do not form rings may limit opportunities in the wet Asian tropics (especially in the 'Indo-Malayan Realm').

Climatic representativeness of tropical tree-ring chronologies: new frontiers

Tropical tree-ring chronologies have been constructed across a wide MAP range, from <200 to >5000mm and these chronologies thus represent precipitation regimes of the tropical woody land area well. Arid climates (with MAP <500 mm), that cover >15% of the tropical woody land area, are also somewhat underrepresented with ~5% of the chronologies. Sites with more semi-arid and seasonal climates (500-1500 mm MAP) are better represented than wetter regions (>2000 mm MAP), with the latter covering only 8% of all chronologies (n=39 sites). The chronologies at wetter sites and recent studies in extremely wet regions (Giraldo et al., 2023) illustrate the prospects to conduct tree-ring studies at the wettest extremes of the tropical rainfall distribution.

In contrast to the fairly good representation of precipitation regimes in tree-ring chronologies, their distribution rather poorly follows that in temperature. Half of the tropical tree-ring studies have been conducted in montane ecosystems (>1500 m a.s.l.), particularly studies with a focus on (long-lived) gymnosperm species in Asia and the Americas. These areas with low-temperature climates (<15°C MAT), which cover just 2% of the tropical land area with woody vegetation, are strongly overrepresented (Fig 2A-C) in our network. Conversely, warm tropical lowland ecosystems with a MAT >25°C, which cover 88% of wooded land in the tropics, are represented by only 15% of chronologies.

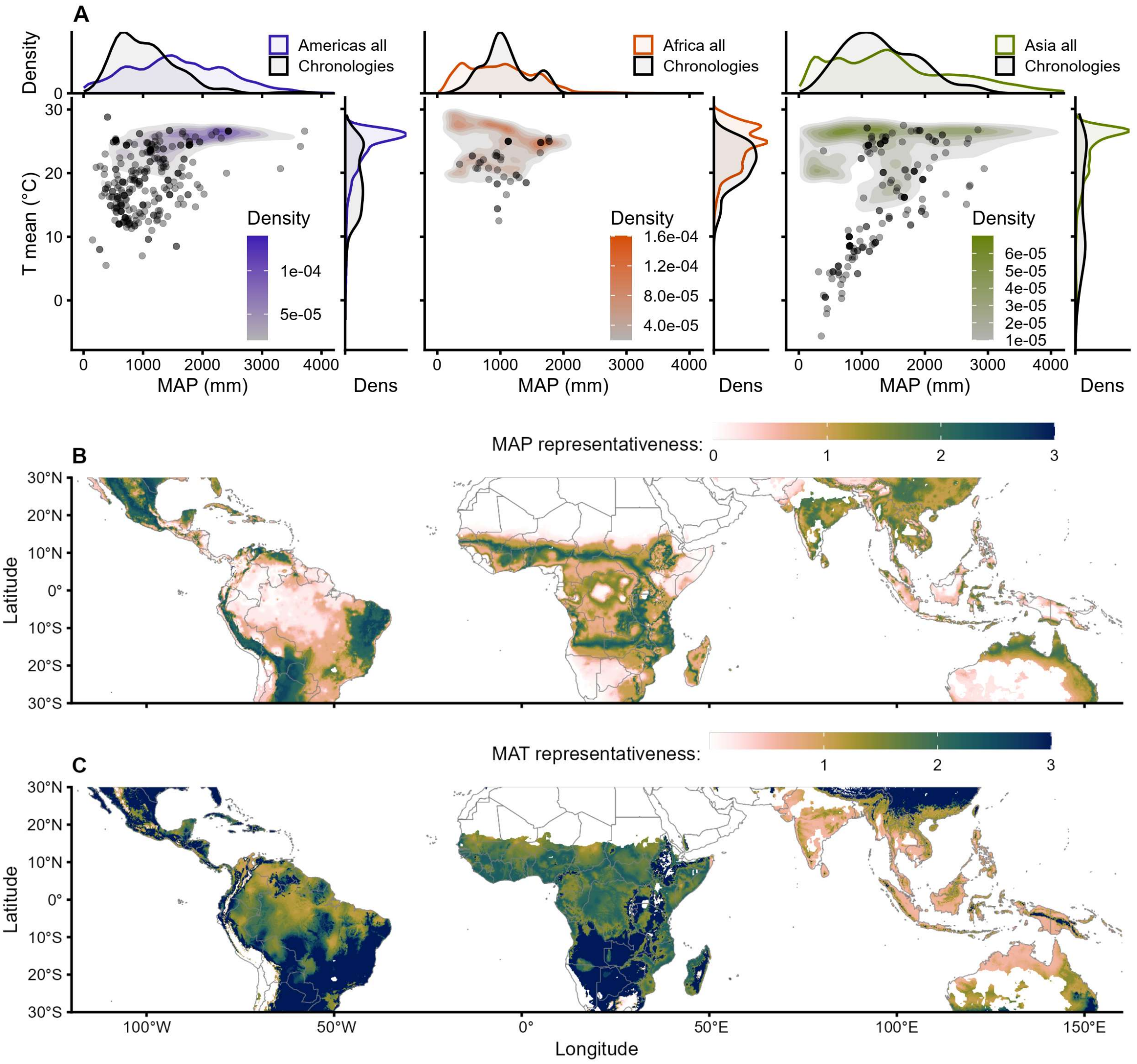

Figure 2. Climatic distribution and skewness of tropical tree-ring chronologies. (A-C) Continental-level relative kernel-density estimates of the mean annual precipitation (MAP) and temperature (MAT) envelope covered by the tree-ring chronologies ('Chronologies') and the tropical land area with woody vegetation (pixels with >10% tree cover; 'Continent all'). Spatial distribution of over- and underrepresentation of MAP (B) and MAT (C) of tropical tree-ring chronologies. Underrepresentation (values < 1) implies that – for a given climatic condition – the proportion of sites in the tree-ring network is smaller than that of the forested area. Values >3 were set to 3 to improve clarity.

We projected the climatic "representativeness" covered by tropical dendrochronological studies spatially, to identify regions that require more research attention or that are well represented climatologically (Fig 2D-E). In terms of precipitation, regions with seasonally dry climates (Central America, Northeastern Brazil, the Sahel, large areas in India) are more prominently represented in our network while the wet tropics (Amazon, Central Africa, Southeast Asia) are underrepresented. In terms of temperature, patterns are similar but show the prevalence of colder climates in the network. Regions that are overrepresented in terms of temperature include high-elevation areas in parts of Mexico and Asia, and – to a lesser extent – low-elevation subtropical regions in Southeast Brazil and subtropical China. We note that, independent of the climate-envelope coverage, the overall low number of tropical dendrochronology studies implies that the representation of tropical climates in tree-ring records is considerably lower (by a factor 5) than that of temperate and Mediterranean climates (Babst et al., 2019; Zhao et al., 2019). The interpretation of these maps should thus be cautious, especially for Africa, where the number of chronologies is low, and representation is poor across the full climatic gradients.

What does this climatic skewness in tropical chronologies imply for their use in global change studies? First, climatic over- and underrepresentation needs to be accounted for in regional or pantropical analyses by checking its influence on results or explicitly accounting for its influence using weighted statistical analyses (e.g., Zuidema et al., 2022). Second, published tropical tree-ring chronologies should be readily uploaded in databases such as the ITRDB, because this increases their representation in pantropical or global analyses. This also applies to chronologies with weak climate responses as this helps drawing a more complete picture of tropical and global tree responses to climatic variation. Additionally, ring-width data need to be archived correctly (e.g., TRiDaS format; Jansma et al., 2010), and supported by appropriate metadata (Zhao et al., 2019) and preferably also with ancillary tree-level data that currently not supported by the ITRDB (Rayback et al., 2020).

Third, our analyses of climatic representativeness provide guidance to identify priority regions for tree-ring sampling. Evidently, the highest priority is in collecting samples and building chronologies for African tree species, which are poorly represented. In addition, increased sampling efforts are needed in the wet and warm tropics, which cover a vast area but are poorly represented. Chronology building in the wet and warm tropics can be challenging, because interannual climatic variation is limited and common climate responses across trees can be concealed by the impacts of canopy dynamics (Giraldo et al., 2023; Groenendijk et al., 2014). Nevertheless, quantifying such subtle and variable responses of tree growth to climate variability in the wet and warm tropics is crucial to understanding and predicting climate-change effects on forest productivity. Broadly, the priority regions indicated here are consistent with those based on a global analysis of the ITRDB (Zhao et al., 2019), but the considerably larger number of tropical chronologies included here allowed us to provide more specific recommendations for tropical climates and biomes.

Potential of tropical tree-ring chronologies to reveal climate sensitivity of tree growth.

The potential of tree-ring chronologies to provide insight into the sensitivity of tropical tree growth to climate fluctuations depends on the strength of climate-growth correlations and the degree to which temporal variations in tree-ring width are similar across trees in a population (the interseries correlations, i.e., Rbar). We analyzed both factors for all chronologies. Tree-ring width may strongly respond to climatic conditions during one or more months in a year. Strong correlations between ring width and climate variables such as precipitation or maximum temperatures (T_{max}) during a particular month provide a first indication of the climate sensitivity of tree growth. We found these maximum correlations with monthly precipitation to be mostly positive (in 73.6% of chronologies) with a mean Pearson correlation coefficient of 0.39 (Fig 3A). By contrast, monthly correlations for T_{max} were mostly negative (66.5 %), and slightly stronger in magnitude (r=-0.40, Fig 3B). This distribution of prevailing positive precipitation and negative T_{max} sensitivities is consistent with those obtained in global and pantropical analyses (Babst et al., 2019; Zuidema et al., 2022). Across continents, stronger correlations were found for chronologies from the Americas, for both T_{max} (negative) and precipitation (positive) (Fig 1A).

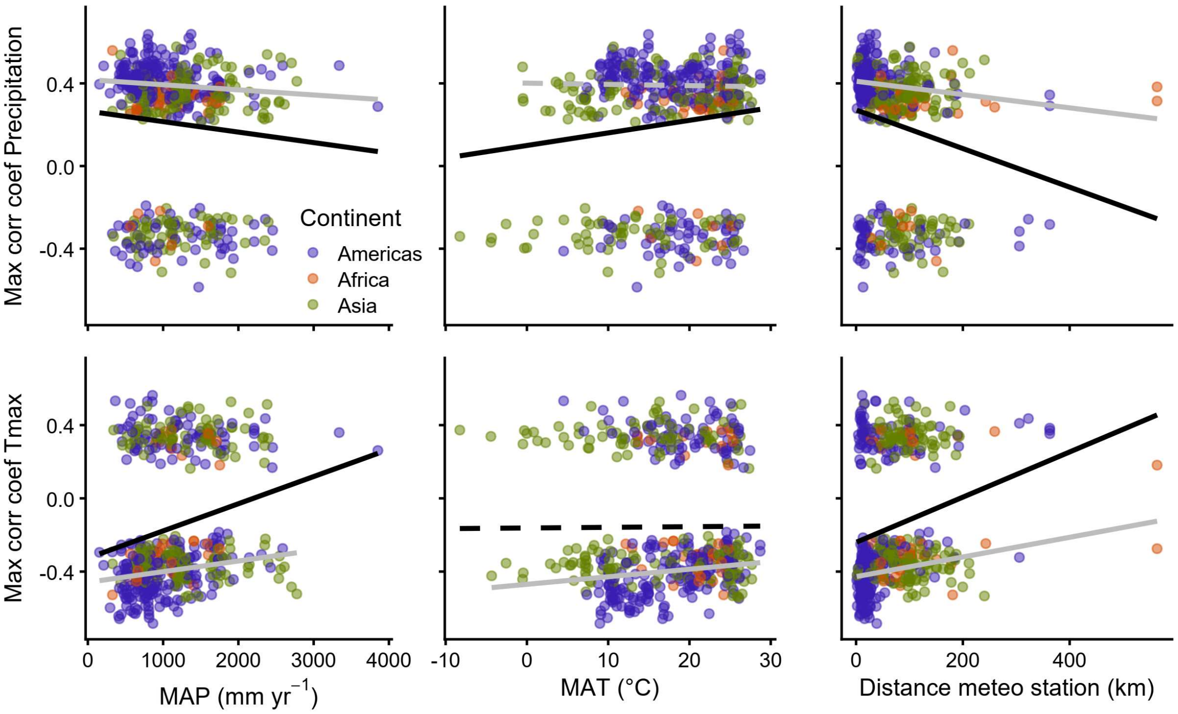

Figure 3. Climate sensitivity of tropical tree growth and its relation to mean climate and the quality of climate data. Maximum climate sensitivity is shown as the highest correlation coefficient between the tree-ring chronologies and monthly climate (precipitation or T_{max}) for 24 months including the year of ring formation and the preceding year. Multiple regression models were constructed, with explanatory variables MAP, MAT and distance to the nearest meteorological station (as a proxy for climate data quality). Lines represent predicted relations of the regression model (Table 1): black lines represent the results including all correlations, grey lines the results of modeling with only the prevailing correlations (positive correlations for Precipitation and negative for T_{max}), full lines represent significant and dashed lines non-significant correlations ($p< 0.05$).

For a subset of the prevailing correlations (positive for precipitation, negative for T_{max}) we tested associations of correlation coefficients with mean climate and with distance to the nearest meteorological station (viewed as a proxy for the representativeness and quality of climate data). Only a small portion of the variation in precipitation and temperature sensitivity across chronologies was explained by these variables (Table 1). Climate sensitivity of precipitation was stronger at drier sites, for both precipitation and temperature, suggesting a stronger water limitation during hot or dry years in more arid conditions. Negative effects of Tmax increased with decreasing MAP, but, contrary to our expectations reduced at warmer sites (i.e., less negative with increasing temperatures).

Table 1. Associations of climate sensitivity with mean climate and the quality of climate data. The proxy for climate sensitivity used is the maximum correlation between ring-width index (RWI) and monthly precipitation or T_{max}. Only prevailing correlations are used, so: positive correlations for precipitation and negative for T_{max}. Shown are estimates (Est, unscaled) of coefficients, significance levels and relative importance values (RI) per explanatory variable. N=number of chronologies. *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

	Precipitation sensitivity		**T_{max} sensitivity**	
Explanatory variables	Est	RI	Est	RI
Intercept	0.43***		-0.52***	
MAP (mm)	-0.000017*	0.23	0.000030**	0.24
MAT (°C)	NS	-	0.0034***	0.3
Distance to nearest meteorological station (km)	-0.00029***	0.77	0.00049***	0.46
R^2	0.07		0.19	
Degrees of freedom	361		326	

Climate sensitivity was weaker for chronologies situated at longer distances from meteorological stations. An increase in the distance to the nearest station of 100 km reduced the absolute correlation coefficient by 0.03 for precipitation and by 0.05 for T_{max}. Distances to the nearest station were smaller in South America, reflecting the higher density of stations. As a large share of tropical chronologies is obtained from sites at >100 km from the nearest station (~24%), this finding suggests that dendrochronological analyses underestimate the climate sensitivity of tropical tree growth. In addition, in mountainous areas elevational differences between tree-ring sites and climate stations may add additional uncertainties in the position of chronologies in our climate space based on interpolated data. Yet, a more detailed analysis of the effect of distance to climate station conducted for a smaller set of tropical chronologies (n=347) revealed limited sensitivity of climate correlations to proximity of climate stations (Zuidema et al., 2022).

The extent to which tree growth is synchronized depends on the degree to which climate exerts a dominant limitation on tree growth, compared to other factors such as canopy dynamics, disturbances, pests, and diseases. The Rbar of all series within a chronology varied strongly between chronologies, from -0.04 to 0.85, thus from no common growth signal to very strong synchronization among trees. The strength of growth synchronicity differed between continents and was considerably lower for African chronologies (mean=0.30) compared to American and Asian chronologies (0.50-0.52; Fig 4). We further assessed to what extent the variability in growth synchronicity can be explained by mean climate (MAT and MAP) and by information on the maximum climate sensitivity (i.e., the maximum climate correlation). As expected, we found a higher Rbar (i.e., stronger synchronicity) at more arid (low MAP) and cooler (low MAT) sites. At those sites, years with low water availability or low temperatures may impose strong limitations to tree growth. We also found growth synchronicity to be stronger for chronologies that exhibited stronger correlations with monthly climate (Fig. 4).

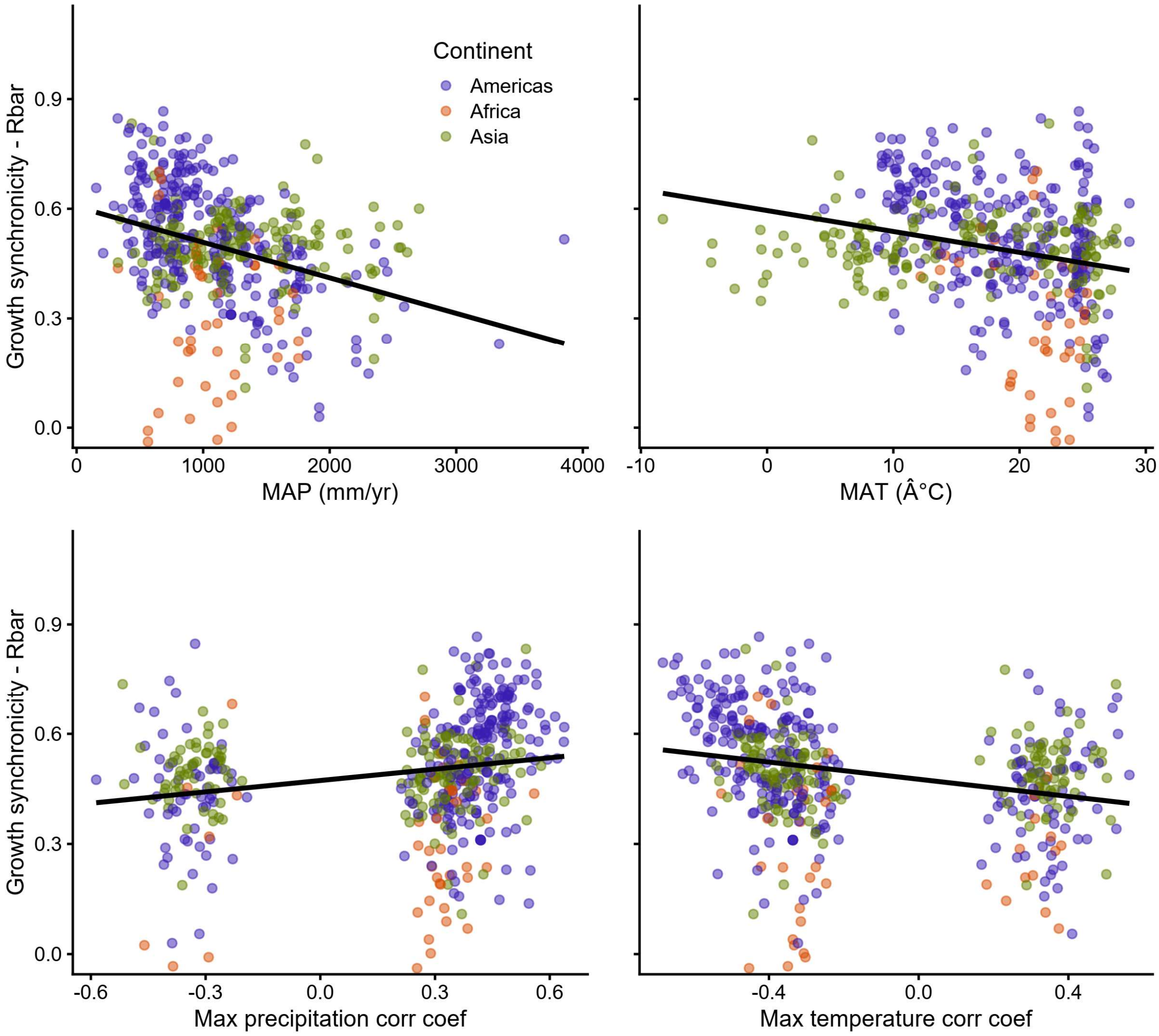

Figure 4. Growth synchronicity of tropical tree species as a function of mean climate and maximum climate sensitivity. Growth synchronicity is calculated as the mean of all correlation coefficients between individual tree-ring series within a chronology (Rbar). Lines represent predicted effects of Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and maximum

climate sensitivity (i.e., highest maximum monthly correlation) based on a multiple regression model (Table 1).

Our review of climate sensitivity shows that tropical tree-ring chronologies can be an important tool to assess climatic impacts on radial stem growth. This sensitivity can be evaluated at annual resolution for many species and sites. Another important virtue of tropical tree-ring chronologies is the ability to obtain tree growth data retrospectively and thus fill gaps in growth measurements in both space and time. We also found that the quality of some tropical tree-ring chronologies is rather poor, as they are based on few radial series or from few individuals only, resulting in low growth synchronicity and weak climate correlations. Part of the variability in growth synchrony and climate-signal strength in the chronologies from these limitations and from decision of individual researchers building chronologies (e.g., synchronization effort, number of trees in the dataset to select only the most sensitive, etc.). Such data limitations can be overcome by teaching, applying, and publishing best practices of (tropical) chronology construction (Black et al., 2016), but also by reporting on the failure to build chronologies (Aragão et al., 2022; Groenendijk et al., 2014). Assessing the quality of tree-ring chronologies is not straightforward, because low growth synchronicity can result from small sample sizes, poor quality of ring measurements and cross-dating, or from the lack of a common signal and complacent growth. No analyses tools are currently available to disentangle these causes in tree-ring datasets. Long-term annual monitoring of large permanent plots (Feeley et al., 2007) and studies using (automatic) high-resolution dendrometer measurements on species with varying strategies (Wagner et al., 2016) may help elucidating these causes.

An important limitation of the current set of tropical tree-ring chronologies is poor species replication. Among the 164 species included in the Network, 134 are represented by just 1-3 chronologies, and only 8 species are represented by 10 or more chronologies, mostly in montane climates. Proper replication is needed to assess and predict how climate sensitivity shifts across climate gradients within the distributional ranges of species (Babst et al., 2018; Klesse et al., 2020), and thus to assess its vulnerability to shifting climates (Heilman et al., 2022; Perret et al., 2024). At present, this is possible for only very few tropical tree species and genera (Aragão et al., 2022; Baker et al., 2015; Zuidema et al., 2020), with limited spatial replication and across limited climate ranges.

Potential of tropical tree-ring chronologies for climate reconstruction

An obvious prerequisite for tree-ring based climate reconstruction is the length of the chronology. Chronology length varied from 16 to 1237 years (Fig 5). Median chronology length was 203 years, but it was substantially higher for gymnosperms (median length of 288 years) than angiosperms (131 years). About half (n=249) of the chronologies had a length of >200 years. Given that instrumental climate data in tropical climate zones are sparse and short, these longer chronologies provide opportunities for climate reconstruction, provided that their climate signal is strong. Successful climate reconstructions based on tropical tree-ring data have been conducted on all tropical continents (Buckley et al., 2010; Granato-Souza et al., 2019; Heinrich et al., 2008; Stahle et al., 2011; Therrell et al., 2006) and have been used to establish continental-scale drought atlases, as well as analyses of major drought events (Cook et al., 2010; Morales et al., 2020; Stahle et al., 2016).

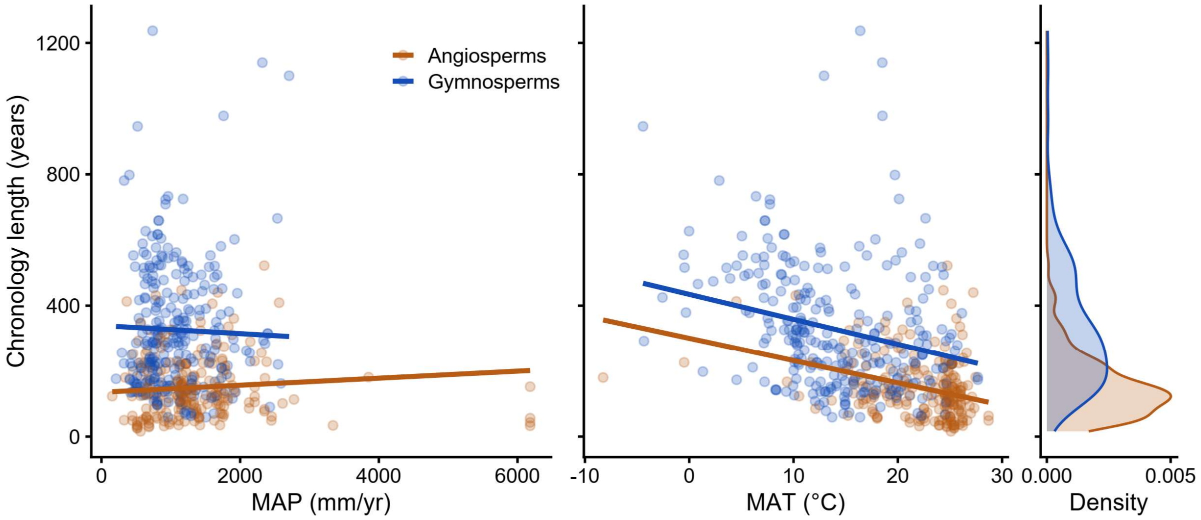

Figure 5. Potential for tree-ring based climate reconstruction and its relation to mean climate. Shown is the longevity of all reviewed chronologies – an important prerequisite for climate reconstruction – for gymnosperms and angiosperms separately. Lines represent predicted effects of MAP and MAT on chronology length based on a multiple regression model (Table 2).

The exploration of additional proxies of climate information (e.g., stable isotopes, wood anatomy) have also shown promising results (Van der Sleen et al., 2015b; Wils et al., 2010). We tested the extent to which mean climate is associated with chronology length and whether this relationship differs between gymnosperms and angiosperms. We found chronologies to be longer in cooler climates and for gymnosperms compared to angiosperms (Table 2). The temperature effects were quite strong: chronology length extended by almost 8 years for every degree decrease in MAT. While high-elevation sites and gymnosperm species dominated the subset of long tropical chronologies, about 29.5% of angiosperm chronologies from warm (>20 °C) and moist (>1200 mm yr^{-1}) tropical climate sites extended to >200 years (n=26 of 88). Some of these angiosperm chronologies have been used for climate reconstruction in lowland tropical forests, adding essential, century-scale climate records to the instrumental record (D'Arrigo et al., 2011; Granato-Souza et al., 2019; Lopez et al., 2017).

Table 2. Results of multiple regression models relating chronology characteristics with mean climate and climate sensitivity. Shown are estimates (Est, unscaled) of coefficients, significance levels and relative importance values (RI) per explanatory variable. Dashes (-) indicate variables not initially included in the model. N=number of chronologies. *=p<0.05, **=p<0.01 ,***=p<0.001.

	Growth synchronicity (Rbar)		**Chronology length (y)**	
Explanatory variables	Est	RI	Est	RI
Intercept	0.616***		295***	
MAT(°C)	-0.00427***	0.26	-7.78***	0.43
MAP (mm)	-0.0000621***	0.36	0.0191*	0.02
Highest T_{max} correlation	-0.0730*	0.22	-	-
Highest P correlation	0.0649***	0.16	-	-
Gymnosperms	-	-	134***	-
R^2	0.19		0.25	
Degrees of freedom	479		493	

The rapid rise of tree-ring studies and chronology construction in the Americas reveals the large potential for developing the field. But this rapid development likely also reflects recent increase in opportunities, funding, and interest in this field within the Americas, which may be slower in other continents. Main barriers to rapid development of tropical dendrochronology include limited laboratory infrastructure, experience, and funding for tree-ring analysis. In addition, factors such as low tree abundance in the forest, high wood density, poor taxonomic knowledge, and difficulties to anatomically identify ring boundaries may limit practical application of tree-ring studies on many tropical (angiosperm) tree species (e.g., Groenendijk et al., 2014). High-resolution X-ray CT scanning (De Mil et al., 2016) and pith-to-bark histological sections (Quintilhan et al., 2021) can aid in ring-boundary identification. Opportunities to overcome these barriers include capacity-building programs, North-to-Tropical skill transfer and support with laboratory equipment, intensified cross-continental tropical collaborations (e.g., in networks) and open science (access to data, data standards, scripts for analyses and publications).

Pantropical and continental-level gaps and opportunities for tree-ring analysis

To identify opportunities for tropical dendrochronology, we produced global maps of estimated number of species with proven annual tree-ring formation, of the number of species with published chronologies and of age estimates based on species distribution models (Fig 6). The maps show that across large parts of the woody tropical land area >20 tree species are expected to occur with known annual ring formation (Fig 6A), and >5 species with potential for chronology building (Fig 6B). Yet, large continental differences on these projections exist, with overall a greater apparent potential in regions in the Americas and Asia compared to Africa. In some areas – South-Eastern Brazil, Mesoamerica, and Southern China – more than 15 species with potential for chronology construction are expected to occur. The geographic distribution of species in these maps is a direct function of the total number of studied species per continent, because species distribution models are produced at continental level. As a result, the values for the African continent are low and should be interpreted with caution. Yet, this map does provide a first guidance to select target areas for future dendrochronological studies.

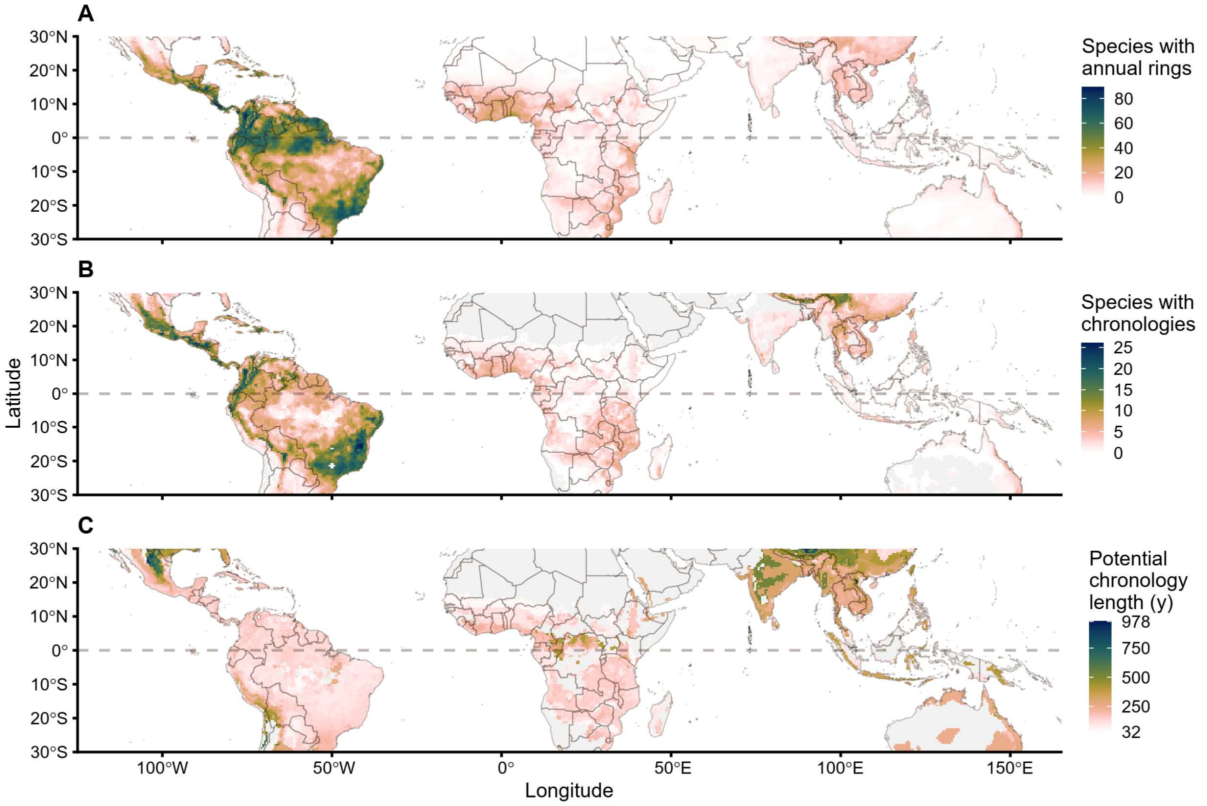

Figure 6. Pantropical distribution of tree species with potential for tree-ring studies, chronology building and climate reconstruction. Distribution of the estimated number of species for which (A) annual tree-ring formation has been proven and (B) ring-width chronologies have been constructed. Values were obtained by adding the probability of occurrence of all species distribution models per 0.5 × 0.5◦ pixel. Areas with <10% tree cover are masked (white). (B) Distribution of maximum chronology length for species with known potential for chronology building. Values are obtained using the maximum chronology length for species with likely occurrence per 0.5x0.5° pixel and averaging this across all species in a pixel.

We also evaluated the opportunity for centuries-long climate reconstruction using tropical tree-ring chronologies. We used the results of species distribution modeling to identify areas with the longest chronologies, based on species-specific maximum chronology lengths (Fig 6C). The resulting map provides a first indication of regions that are likely more suitable for constructing long chronologies. For a large part of the woody tropics, maximum chronology length is expected to be >200 years, whereas in some areas – northern Mexico, Central India, and southern China – chronology length can be 500 years or more. The importance of climate reconstructions is particularly large in regions where meteorological data are scarce or cover short periods. This is particularly the case for Africa, where a large proportion of the continent lacks long-term instrumental climate data.

Conclusions

How can tree-ring chronologies contribute to global change research in tropical ecosystems? We identify three primary opportunities. First, tropical tree-ring chronologies can generate much-needed historical climate data to understand past climate dynamics and provide necessary context for climate extremes. Tree-ring based climate reconstructions have been crucial in identifying historical megadroughts (Cook et al., 2022; Morales et al., 2020; Stahle et al., 2011), and putting recent drought events into a long historical perspective (Belmecheri et al., 2016; Morales et al., 2020; Williams et al., 2022). In addition, they can be used to evaluate the possible attribution of meteorological extremes to ongoing climate change (Williams et al., 2022). To realize this potential, the replication and length of tropical tree-ring chronologies need to be substantially increased.

Second, tropical tree-ring chronologies can help assess the sensitivity of woody net primary productivity (NPP) to climate fluctuations, adding a century-long perspective and complementing other approaches such as eddy covariance flux towers, permanent sampling plots, and remote sensing data. Understanding this sensitivity helps to quantify the woody component of NPP and to improve our understanding of the mechanisms driving climate-C-sink dynamics of tropical vegetation (Zuidema et al., 2018). This approach could be of particular interest to assess El Niño Southern Oscillation (ENSO) effects and drought/heat effects on the tropical carbon balance (Rifai et al., 2018). Tree-ring derived climate sensitivity may also help estimate the potential and risks of failure of forest-based natural climate solutions (Anderegg et al., 2020). This is particularly true as long-term carbon sequestration critically depends on wood formation, which can be affected by climate extremes (Anderegg et al., 2020).

Third, tree-ring chronologies can help improve the simulation of woody productivity in Dynamic Global Vegetation Models (DGVMs). DGVMs increasingly represent wood formation processes (Friend et al., 2022) and tree-ring derived data can be used to simulate individuals or cohorts (Fisher et al., 2018), for model benchmarking (Jeong et al., 2020; Xu et al., 2024) and for improving models by data assimilation in DGVMs (Barichivich et al., 2021). So far, tropical tree-ring data have hardly been used for these purposes. Yet, the potential contribution of tropical tree-ring data is large, because of the relatively low density and duration of tropical sampling plots, flux towers and global change experiments.

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Data availability

A large share of the raw tree-ring data (99 chronologies) have previously been uploaded to the International Tree-Ring Data Bank – ITRDB (www.ncei.noaa.gov/products/paleoclimatology/tree-ring) following Zuidema et al. 2022. We are processing the remaining datasets to also be uploaded to the ITRDB. Analysis scripts will be made available via the main author's Github page: https://github.com/groenendijk.

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Author contributions:

Conceptualization: PG, PAZ, FB, VT, ZXF, DGS, GML, MM, SP, NP; Data contribution: all co-authors except FB; Data analyses: PG, PAZ, FB; Writing – original draft: PG and PAZ, with important contributions from FB, VT, ZXF, DGS, GML, MM, SP, NP; Writing – review & editing: all coauthors.

Table 1. Associations of climate sensitivity with mean climate and the quality of climate data. The proxy for climate sensitivity used is the maximum correlation between ring-width index (RWI) and monthly precipitation or T_{max}. Only prevailing correlations are used, so: positive correlations for precipitation and negative for T_{max}. Shown are estimates (Est, unscaled) of coefficients, significance levels and relative importance values (RI) per explanatory variable. N=number of chronologies. *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

	Precipitation sensitivity		**T_{max} sensitivity**	
Explanatory variables	Est	RI	Est	RI
Intercept	0.43***		-0.52***	
MAP (mm)	-0.000017*	0.23	0.000030**	0.24
MAT (°C)	NS	-	0.0034***	0.3
Distance to nearest meteorological station (km)	-0.00029***	0.77	0.00049***	0.46
R^2	0.07		0.19	
Degrees of freedom	361		326	

Table 2. Results of multiple regression models relating chronology characteristics with mean climate and climate sensitivity. Shown are estimates (Est, unscaled) of coefficients, significance levels and relative importance values (RI) per explanatory variable. Dashes (-) indicate variables not initially included in the model. N=number of chronologies. *=$p<0.05$, **=$p<0.01$,***=$p<0.001$.

	Growth synchronicity (Rbar)		**Chronology length (y)**	
Explanatory variables	Est	RI	Est	RI
Intercept	0.616***		295***	
MAT(°C)	-0.00427***	0.26	-7.78***	0.43
MAP (mm)	-0.0000621***	0.36	0.0191*	0.02
Highest T_{max} correlation	-0.0730*	0.22	-	-
Highest P correlation	0.0649***	0.16	-	-
Gymnosperms	-	-	134***	-
R^2	0.19		0.25	
Degrees of freedom	479		493	

Appendices

Appendix 1 and 2 – Separate PDF

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