



Review

Tropical and subtropical dendrochronology: Approaches, applications, and prospects

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ABSTRACT

Tropical and subtropical forests cover only 7 % of the Earth's land surface. Yet, they host nearly half of global tree density with a high species number (~40,000 species), store up to 25 % of global terrestrial carbon and represent one-third of net primary productivity on Earth. Over the last four decades, the study of tree growth in the tropics has gained substantial momentum, not least because of the increasing application in tropical and subtropical climatology, ecology, geomorphology, and archaeology. So far, various tropical and subtropical species have been shown to form growth rings with a regular, sometimes annual, layering that is driven by the species' sensitivity to climatic, ecological, or geodynamic variations. Here, we provide a detailed review of dendrochronology studies in the tropics indicating their (i) tree growth patterns, (ii) most common regions that have been studied preferentially and the families and genera of trees that have been employed most frequently, so as to provide an overview on the most suitable species, (iii) common approaches and techniques used in tropical and subtropical dendrochronology, (iv) different applications, and (v) limitations inherent to tree-ring research in the tropics. The paper concludes with a call for further research in this still understudied environment and provides potential perspectives for future work in the most biodiverse region of the world.

1. Introduction

Dendrochronology is the science of identifying and quantifying environmental processes through the dating of annual growth layers (or rings) in woody plants including perennial herbs, shrubs, lianas, and trees (Fritts, 1971; Schweingruber, 1996; Speer, 2010; Brandes et al., 2022). By doing so, dendrochronology represents a powerful tool to yield detailed insights into diverse fields of ecological, climatic and Earth sciences (Schweingruber, 1996). Among various other fields, dendrochronology has helped to critically advance our understanding of climatology (Hughes, 2002; Esper et al., 2016), ecology (Fritts and Swetnam, 1989; Amoroso et al., 2017), geomorphology (Stoffel et al., 2010; Stoffel and Corona, 2014; Ballesteros-Cánovas et al., 2015), and archaeology (Kuniholm, 2002; Sass-Klaassen, 2002). For more than a century now, tree-ring research has covered all continents except Antarctica and deserts, with chronologies being developed mostly in the

mid to high latitudes of the Northern Hemisphere (Zhao et al., 2019). This geographic focus is somehow the result between the availability of trees to record climate and environmental changes (Esper et al., 2016) and the extended/preferred use of forest regions with long-lived trees (Pearl et al., 2020; Anchukaitis, 2017).

Tropical forests cover just 7 % of the Earth's land surface, but they store an estimated 25 % of global terrestrial carbon and account for one-third of global net primary productivity (Amoroso et al., 2017). Tropical and subtropical forests sum the 56 % of all forest's areas worldwide (FAO, 2020). Tropical and subtropical forests encompass nearly half of the tree density at the global scale (Crowther et al., 2015). Tropical regions exhibit seasonal hydric variations which explain the main paradigm for tropical tree ring formation (Hubbell, 2013; Brienen et al., 2016; Locosselli et al., 2017; Schöngart et al., 2017; Worbes et al., 2017; Giraldo et al., 2020). Indeed, dendrochronology in the tropics is much more complex than in temperate regions because of the larger number of

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species, variety of habitats, variable cambial activity, and the complex phenology over the year in absence of well-defined seasons (Silva et al., 2019). Nonetheless, various tropical and subtropical species develop growth rings with a certain cyclicity different than annually.

According to Worbes (2002) and Rozendaal and Zuidema (2011), the first studies in the tropics were conducted by Sir D. Brandis (1898) who proposed the use of tree-rings for forest management. Moreover, Moll and Janssonius (1906-1926), Geiger (1915), and Coster (1927, 1928) described the presence of tree-ring boundaries in broadleaf tropical species in the Indonesian archipelago. In addition, Berlage (1931) constructed the first tree-ring chronology in Java and the tropics, opening the application of tree-ring chronologies for climatic comparisons. Later, Schulman (1944, 1956) published the first tree-ring chronologies from northwestern Mexico (*Abies durangensis*, *Pinus* sp., *Pseudotsuga menziesii*) and south of Mexico City (*Abies religiosa*; Schöngart et al., 2017). Many multi-centennial chronologies have been published since in the subtropics of North America, a region that is nowadays representing an outstanding network of dendroclimatic chronologies covering the southern United States and Mexico for the past 600 years (Stahle et al., 2016). Since the 1980 s, the scope and breadth of tropical and subtropical dendrochronology has increased steadily thanks to the study of growth rings to other regions and the expansion of research to tropical and subtropical tree species. Likewise, the breadth of fields within the environmental sciences has expanded exponentially (Worbes, 2002). Even if the focus of tree-ring research today still is on temperate and cold region environments, tropical and subtropical species have become more frequently studied as they have been shown repeatedly to form growth zones with an annual layering, with the latter being driven by the species' sensitivity to climate, ecological, and/or geodynamic variations (Worbes, 1989; Schöngart et al., 2017).

Over recent decades, tropical and subtropical dendrochronology has become an integral research field including ecology, climatology, and geomorphology approaches (Worbes, 2002), thereby contributing substantially to the broadening of current knowledge of tropical and subtropical forest ecosystem functioning (Worbes, 2010). Even if the plethora of studies and web platforms published on tropical trees and the nature of growth periodicity has provided invaluable insights into growth-climate relations, or the impact of drought and fire histories on tree growth and forest dynamics (e.g., Boninsegna et al. 2009; Rozendaal and Zuidema, 2011; Fichtler, 2017), many research questions remains. Which common families and species show annual ring formation along the tropics? Tropical and subtropical wood anatomy is been studied enough considering with its biodiversity and complexity? Are we considering enough alternative methods to determine annual growth rings? On one hand, more species need to be studied to explore the dendrochronology potential of tropical and subtropical species fully (Hayden, 2008; Zuidema et al., 2022). Thus, the growth rings of various tropical and subtropical species show greater variations and complexity than those already investigated – and much more so than those growing outside the tropics –, underlining the huge diversity of species in the often pristine, tropical and subtropical environments (Roig, 2000; Locosselli et al., 2020). On the other hand, the lesser identification accuracy that remains inherent to many of these underexplored tree species (Silva et al., 2019) call for a more detailed investigations of wood-anatomical structures (Worbes, 1995).

Tropical and subtropical dendrochronology has a vast potential to yield environmental and climatic information for a major ecotone of Earth for which systematic records are generally scarce and short, if not missing completely for times extending back beyond the start of satellite imagery. The necessity to fill large geographic gaps with dendrochronological data has propelled the realization of tree-ring analysis in the tropics and the rapid development of a network of previously unstudied species (Pearl et al., 2020). The recent increase of dendrochronology studies in tropics helps in closing the breach of regions without sufficient tree-ring chronologies and thereby support Earth-System sciences (Babst et al., 2017), although more tree-ring studies in these latitudes are still

needed to fill the spatial gap (Zuidema et al., 2012).

Here, we review the current state of tree-ring research in the tropics and assess the contribution of dendrochronological analyses to an improved understanding of environmental as well as climatic processes and drivers. To this end, we present an overview on the main suitable tree species used today and describe the main analytical approaches and fields of applications, but also remaining limitations. Based on this review, we provide a series of prospects of tree-ring analysis in the tropics. The review on tropical and subtropical dendrochronology was based initially on more than 1000 sources but then limited to the 459 reviewed contributions (i.e. peer-reviewed papers published in ISI indexed journals, MSc or PhD theses) available in Scopus and Google Scholar. We filtered only dendrochronology papers, with clear location, and the usage of growth rings. The Internet search has been restricted to the keywords “tropical”, “dendrochronology” and “tree rings” (using these keywords in English, French, Spanish, and Portuguese, and to a lesser extent in Chinese, Indonesian and Hindi). The search was realized between November 2019 and December 2021. From the 459 papers (see [Supplementary Material](#)), we extracted bibliometric indicators as well as quantitative and qualitative information, including geographic coordinates, elevation, methods used, number of samples, species, genera, and families. We removed all the studies outside 30° North and South to concentrate our analysis to tropical latitudes and species. In addition, we assessed chronology lengths (years), and information on how individual tree-ring series have been cross-dated (in terms of intercorrelation, mean sensitivity, autocorrelation, and Expressed Population Signals).

On this basis and following a brief appraisal of dendrochronology in the tropics and subtropics, this paper (i) highlights tree growth patterns at low latitudes, (ii) determines the studied geographical regions as well as the most known suitable tree families, genera and species, (iii) describe and discuss most common approaches in tropical dendrochronology so far, (iv) illustrates different applications and present current limitations, and (vi) concludes with a call for future work by presenting possible research perspectives. Our work is important due to the enormous biodiversity in the tropics and subtropics, its scarce dendrochronology knowledge because of its extended endemism, and the limitation of local specialized research groups. Therefore, this review can expand previous analyses in and out low latitudes (e.g. Worbes, 2002; Worbes and Fichtler, 2010; Rozendaal and Zuidema, 2011; Pearl et al., 2020; Pompa-García and Camarero, 2020) providing new key information for dendrochronology in the tropics and subtropics.

2. Growth ring formation in the tropics and subtropics

Growth rings are defined as changes in the structure of the secondary xylem of perennial plants; they are the result of seasonal variations of climatic conditions exerting control on growth conditions of plants, thereby producing areas with contrasting tissues (Schweingruber, 1996). Growth rings or more commonly tree rings can be found in trees, shrubs, lianas, and perennial herbs, such that the term ‘growth ring’ will be used here as it has greater generality (Silva et al., 2019). In temperate and warm-temperate environments, the contrasting tissues that are formed during the growing season (or vegetation period) of plants are commonly called ‘earlywood’ and ‘latewood’, with the aim to differentiate the two most prominent, annual growth periods (Fritts, 1971). Wood formed in the first weeks (to months) of the growing season is composed of cells with large diameters and thin cell walls (Fig. 1a). Later on, cells gradually become smaller with thicker cell walls. The process of earlywood and latewood formation – or the frequency of cambial cell division, enlargement of newly formed xylem cells and cell wall thickening in other words – is controlled by plant hormones (Buttò et al., 2020). Such differentiation is not equally straightforward in tropical and subtropical species where clearly defined earlywood and latewood tissues are either lacking or difficult to detect macroscopically (Fichtler and Worbes, 2012). In these cases, anatomical identification of growth rings needs to be based on the presence of analogous tissues resembling

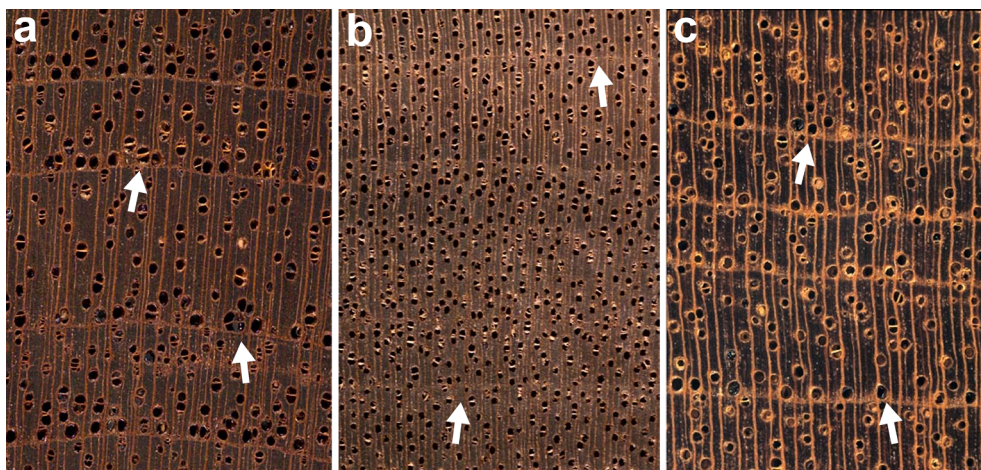


Fig. 1. Macroscopical pictures of growth rings from tree species growing in contrasting tropical and subtropical ecoregions: a) *Cedrela odorata*: growth ring boundaries distinct, wood ring porous or semi ring porous, fibers very thin walled (10 x). b) *Carapa guianensis*: Growth ring boundaries distinct, wood diffuse porous, fibers of medium wall thickness, axial parenchyma present and banded. c) *Toona ciliata*: growth ring boundaries distinct; vessels, axial parenchyma, and distended rays present. Arrows indicate tree-rings. Source: Richter and Dallwitz (2019).

early and latewood patterns (Fig. 1b). Therefore, one of the major continuing challenges in tropical and subtropical dendrochronology is inherent to the identification of growth rings, as objective anatomical parameters for the definition of growth ring boundaries is still lacking for many species today (Fig. 1c; Tarelkin et al., 2016).

Growth rings in tropical and subtropical species that have been classified as distinct by tropical wood anatomists would possibly be described as indistinct or absent by anatomists working on temperate species (Silva et al., 2019). In addition, the degree of distinction of individual growth rings may also vary with the magnification at which the wood is observed. Overall, in those species for which growth rings are well defined macroscopically, it may become difficult to identify the same rings microscopically – and vice versa (Worbes, 2010). Moreover, tangential discontinuities of growth rings are common in tropical and subtropical species, thereby inducing the tangential interruption of rings as a consequence of the lack of a complete reactivation of the cambium along the growing stem (Worbes and Fichtler, 2010). This phenomenon – known also in some temperate species – is commonly referred to as false rings (also known as tangential discontinuities). False rings have been ascribed to local differences around a stem in terms of competition for nutrients and/or light (Hallé et al., 2012).

As the clear identification of anatomical markers of ring boundaries renders the recognition of growth rings less arbitrary (Silva et al., 2017), a suite of common anatomical markers has been developed and employed in tropical and subtropical dendrochronology to identify growth rings and growth ring boundaries (Worbes, 1989, 1995, 2002; Worbes & Fichtler, 2010; Nath et al., 2016). Whereas the wood anatomy

of tree rings in conifers is very similar between those formed in (sub-) tropical and those present in boreal and temperate climate trees (Schöngart et al., 2017), tropical and subtropical broadleaved species present some distinct differences with respect to their extratropical counterparts (Worbes, 1989). Luckily and despite the vast diversity of tropical angiosperms, their wood anatomical features can be summarized with four basic types that have first been described by Coster (1927, 1928) for Java. The four basic types have since been adopted for tropical and subtropical species in more general terms (Fig. 2a; Worbes, 2002; Schöngart et al., 2017), and the classification has been expanded recently by Silva et al. (2019) to seven anatomical markers that should be taken into consideration when it comes to identifying growth rings in tropical and subtropical species: (1) thick-walled and/or radially flattened latewood tracheids; (2) thick-walled and/or radially flattened latewood fibers; (3) semi-ring-porous or (4) ring-porous structures in growth rings; as well as the presence of (5) marginal parenchyma; (6) fiber zone; or (7) distended rays (Fig. 2b). The same authors also propose that growth rings should be classified individually according to the presence of anatomical markers, rather than using combinations of markers (Fig. 2c; Silva et al., 2019).

The combination of periods that are favorable and unfavorable to growth may vary over the year depending on locality and species. In the tropics, and even in subtropical regions, species growing in the same habitat may form growth rings at different rates (Cherubini et al., 2003). This behavior is expected to be the result of the emergence of growth rings due to complex relationships between environmental factors (including ecological relationships among individuals of the same or

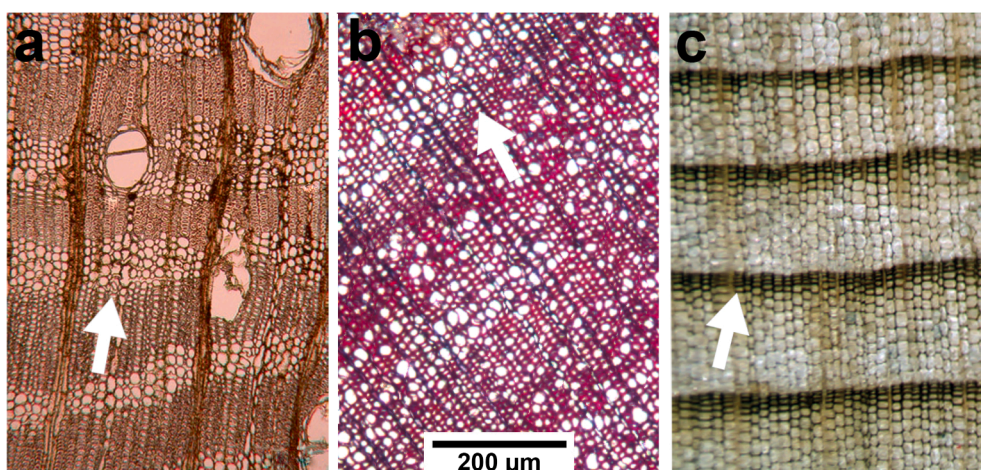


Fig. 2. Microscopical pictures of growth rings from tree species growing in contrasting tropical and subtropical ecoregions: a) *Erismacalcaratum* from the Igapó flooded Amazonian Forest with axial parenchyma, paratracheal bands, and diffuse pores (Worbes and Fichtler, 2010). b) *Hypericum irazuense*, an endemic shrub from highland páramo in Costa Rica with porous but distinct rings (Quesada-Román et al., 2020b). c) *Abies guatemalensis* from highland conifer forests of Guatemala shows annual rings with a xylem morphology and micro pores (Anchukaitis et al., 2013). Arrows indicate tree-rings. Figures use permission granted by the journals.

different species) and specific characteristics that are intrinsic to the species or an individual tree (e.g., genetic factors, ecophysiological, phenological and morphological traits; De Micco et al., 2016; Baker et al., 2017; Silva et al., 2021). Primary environmental factors that can directly affect plant growth include light (intensity, quality, duration), water (availability in the soil, humidity), carbon dioxide, oxygen, nutrient content, and availability in the soil, as well as temperature and toxins (e.g., heavy metals and salinity) (Worbes, 2002; Zuidema et al., 2022). Any alteration in one or more of these environmental factors which affects the levels needed for the normal functioning of plants can have negative consequences on growth (Silva et al., 2019). Sensitivity to environmental variations will depend on the interaction between the environmental parameter in question and on how susceptible the species/individual is, thus creating a complex relationship (DeMicco et al., 2016). Interestingly, however, correlations between deciduousness of species and the formation of growth rings does not seem to prevail in tropical and subtropical trees, neither do all deciduous trees form growth rings nor do evergreen tree species systematically lack growth rings (Borchert, 1999; Ferrero et al., 2014; Chen et al., 2015; Giraldo et al., 2020).

Tropical and subtropical trees can form annual growth rings if unfavorable environmental conditions regularly occur in one period of the year, thereby causing cambial dormancy (Worbes, 2002; Rozendaal and Zuidema, 2011). In tropical and subtropical regions, where air temperature is constant across the seasons, rainfall may become the main factor modulating the cyclic growth of trees (Jacoby, 1989; Brienen et al., 2016; Zuidema et al., 2022). Small variations in water availability for species adapted to wet habitats can be comparable to the major privations from which species would suffer in arid environments. Over vast regions of the tropics and subtropics, rainfall seasonality is known to be quite distinct, with an impact on annual growth rhythm and, by consequence, the formation of annual rings (Worbes, 1999; Dünisch et al., 2003; Volland-Voigt et al., 2011; Underwood et al., 2014; Schöngart et al., 2017). Rainfall and its seasonality have repeatedly been demonstrated to have a great impact on annual ring growth (Fichtler, 2017; Zuidema et al., 2022), and to be effective in controlling the layering of growth zones and growth periodicity, even if dry periods were very short (i.e., as short as 10 to 21 days; Silva et al., 2019). It has been shown that an annual dry season with a length of only 2 to 3 months with less than 60 mm monthly precipitation can suffice to induce annual rings to form in tropical trees (Worbes, 1995), thus resulting in a positive relation between precipitation totals and ring widths in many species in different parts of low latitudes (Worbes, 2002). Consistently, drier, and warmer years will result in reduced tree growth (Brienen et al., 2016). Likewise, the El Niño-Southern Oscillation (ENSO) has been shown to both limit and enhance ring growth in the tropics and subtropics (Anchukaitis et al., 2013; Alfaro-Sánchez et al., 2017; Quesada-Román et al., 2020b; Rodriguez-Morata et al., 2020). Thus, the seasonality of growth may reflect the effects of predictable, moderately long periods without rain during the “dry season” in tropical/subtropical forests, thus making these growth layers annual rings (Fichtler et al., 2003). Moreover, numerous species growing at higher elevations have been shown to form annual rings thanks to the existence of a climate with a slightly more marked seasonal contrast (García-Cervigón et al., 2020).

The seasonality of rainfall also has a distinct impact on runoff in catchments of large tropical rivers with monomodal flood pulses in their vast floodplains (Junk et al., 1989). These flood pulses control the annual growth rhythm of trees (Worbes, 1986; Schöngart et al., 2005; Herrera and del Valle, 2011; Montanher, 2012). Affected trees will shed their leaves until the flood waters recede and therefore fall into a phase of cambial dormancy (Schöngart, 2002; Schöngart et al., 2017). In mangrove species, the rainy season seems to reduce soil water salinity because of more abundant freshwater input, thereby triggering the formation of annual rings (Robert et al., 2011). As one moves to higher latitudes and altitudes, both photoperiod and air temperature seem to

control the onset and cessation of cambial activity (Oliveira et al., 2009; Blagitz et al., 2019; Marcati et al., 2016).

3. Methods to study growth rhythms in tropics and subtropics

Besides field-based studies, a suite of independent approaches has been applied to proof the annual nature of growth-ring formation in tropical/subtropical plants (Worbes, 1995). One of the approaches includes the monitoring of stem diameter variations with dendrometers (either through the use of bands or high-resolution, automated measurements) during consecutive years (Détienne, 1989; Schöngart et al., 2002; Spann et al., 2016). Other approaches included the measurement of cambial activity with electrical resistance (Worbes, 1995) or through wood anatomical analysis of cambium tissues sampled at monthly or seasonal intervals, thereby covering different (dry and wet) periods of a year (Lisi et al., 2008a; Volland-Voigt et al., 2011; Nicolini et al., 2012; Worbes and Raschke, 2012; Morel et al., 2015; Marcati et al., 2016). Alternatively, the wounding of cambial tissues (Mariaux, 1967) was employed to obtain scars that can be dated exactly in the wood and linked to phases of plant growth and/or dormancy (Détienne, 1989; Lisi et al., 2008b; Locosselli et al., 2013).

However, not all trees growing in tropical/subtropical environments form clearly distinctive, annual rings. Based on the systematic analysis of tree species, Alves and Angyalossy-Alfonso (2000) showed that roughly half of the 491 species belonging to 133 genera and 22 families growing in different Brazilian biomes formed distinct growth rings. Whereas a higher ratio was found for the Brazilian Atlantic forests (Silva et al., 2017), only 30 % and 35 % of the species analyzed in the Peruvian rainforest (Beltrán-Gutiérrez and Valencia-Ramos, 2013) and in the dry forests of Mexico (Roig et al., 2005) showed distinct tree rings. Moreover, Worbes (2002) showed that the distinctiveness of annual rings can vary between life stages of a tree: some trees form clear growth rings in the adult phases, but absent or vague ring structures in the juvenile phases, or vice versa. As such, and especially in the case of low-latitude dendrochronology, research is still facing long-standing challenges including irregular or indistinct growth patterns, complex morphology, and short-ring series (Pearl et al., 2020). Consequently, Silva et al. (2019) recently stressed the importance for more theoretical discussions to develop a clear, robust, and universal concept of growth rings, which would ultimately facilitate the study of tropical species further. The overwhelming number of tropical/subtropical woody species at first sight is a potential benefit to study dendrochronology in tropical and subtropical species. However, especially in the humid tropics, large aggregations of the same species do not easily form in relatively proximity (Fedorov, 1966).

Tropical/subtropical regions are more diverse in terms of the factors driving plant growth as well. Considering that species have different adaptation and evolutionary strategies to cope with environmental stresses, which in general are less acute in tropical and subtropical than in temperate regions (Scatena and Lugo, 1995), a variety of distinct patterns can be encountered in the tropics/subtropics. This is one of the reasons why growth rings of tropical/subtropical plants are more diverse than their temperate climate counterparts, both in terms of anatomical markers and their degree of distinction, tangential continuity, and periodicity (Silva et al., 2019). Worbes et al. (2017) even considered that the structure of growth rings is genetically fixed, but that the presence or absence of a triggering factor will determine whether they are expressed or not.

4. Longevity of tropical and subtropical trees and drivers of tree mortality

Tropical and subtropical trees take a minimum of 60 years to reach the canopy, and generally ~200 years for individuals to recruit in shady conditions (Metcalfe et al., 2009). As a result, tropical trees show “bathtub” mortality rates, where very small or old trees have bigger

possibilities to die, but where life expectancy peaks at surprisingly low sizes, often at ~5 cm diameter at breast height (DBH). At the same time, however, life expectancy is high for medium age trees. Age determination derived through the direct counting of annual rings and/or estimations in the case of hollow trees (by measuring growth rates and diameters) often result in ages between 400 and 500 years, without, however, exceeding 600 years for larger trunks (Worbes and Junk,

1999). Growth-ring studies indicate that the lifespan of tropical/sub-tropical tree species average c. 200 years and that only few species live for >500 years (Brienen et al., 2016). Some examples are species such as *Fokienia hodginsii* (758 yr), *Pinus hartwegii* (552 yr), or *Hymenolobium mesoamericanum* (530 yr) (Fichtler et al., 2003; Buckley et al., 2010; Cerano-Paredes et al., 2021). These estimates are consistent with tropical and subtropical tree ages as found through the systematic research

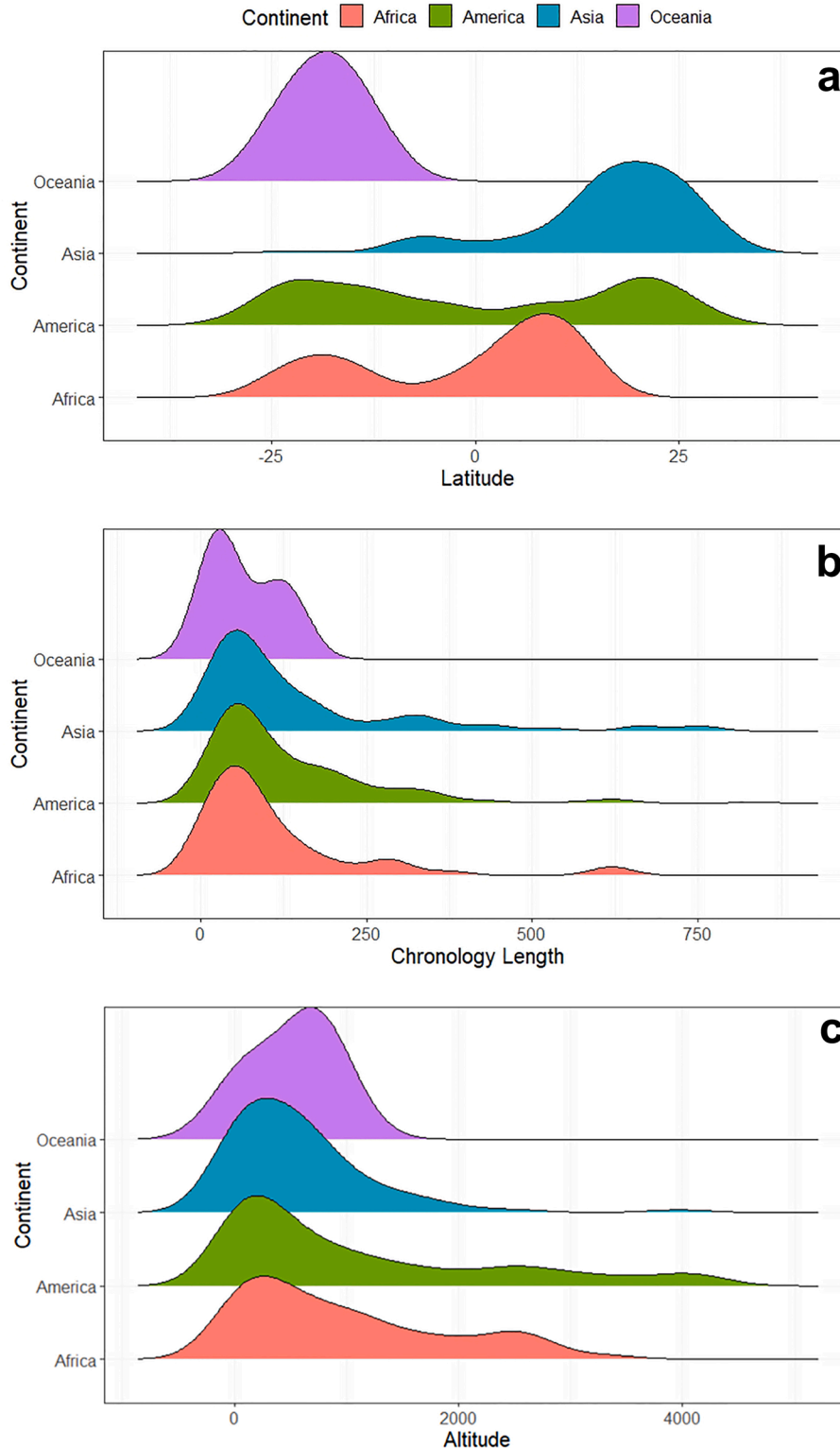


Fig. 3. Density ridgeline plot showing the relation between latitude in degrees (a), chronology length in years (b), and altitude in meters above sea level (c) for all continents with (sub-) tropical/subtropical climates. Produced using *ggplot* function in R software.

of growth-ring data in this review. In fact, our survey of tropical and subtropical trees yields a mean age across low latitudes of 139.92 ± 177.2 years ($n_{\text{obs}} = 365$), with marked differences between regions within the tropics: whereas for the Americas and Africa, trees reach comparable ages with 132.49 ± 129.32 ($n_{\text{obs}} = 218$) and 130.55 ± 185.91 years ($n_{\text{obs}} = 54$), ages are markedly higher in tropical Asia with 168.31 ± 257.18 years ($n_{\text{obs}} = 88$), but substantially lower in tropical Oceania with 65.4 ± 48.56 years. Note that for the latter, the number of observations is, however, extremely small ($n_{\text{obs}} = 5$) and probably not representative. Accordingly, most tropical/subtropical growth-ring chronologies do not exceed 300 years. Interestingly, Fig. 3b suggests that chronology lengths tend to increase slightly with increasing distance from the Equator.

The process of tree mortality has dimensions of intensity, spatial, and temporal scales that reflect the characteristics of endogenic processes (i. e., senescence, embolism) and exogenic disturbances in terms of their severity, frequency, duration, or spatial scale, as well as points of interaction with the ecosystem (Lugo and Scatena, 1996). Little is known about the drivers of tree mortality in tropical as well as subtropical forests due to the limited availability of long-term observational data (Brienen et al., 2015). Aleixo et al. (2019) reported that drought (during El Niño years), storms and/or extremely wet years tend to increase tree mortality for at least two years following the disturbance event in the tropics/subtropics. According to Lugo and Scatena (1996), the presence of old trees in the tropics and subtropics therefore also means that: (i) not all trees die at once in a catastrophic event, (ii) differential mortality exists among species, (iii) vegetation turnover differs between distinct geomorphic settings because of different disturbance regimes (Scatena and Lugo 1995), and that (iv) in the absence of disturbances, different stages of the life cycle can exhibit differential survival rates.

Forest turnover is likely to be in the order of at least hundreds of years, with negative implications for rates of carbon absorption (Metcalfe et al., 2009). In that context, Groenendijk et al. (2015) not only reported decreasing growth rates over time in wet tropical forests of Bolivia, Cameroon and Thailand, but also concluded that elevated ambient carbon dioxide (CO_2) did not directly lead to higher tree growth. Increasing mortality rates were associated with rising temperature and vapor pressure deficit, liana abundance, drought, wind events, or fires and – possibly – CO_2 fertilization-induced increases in stand thinning or an acceleration of trees reaching larger, more vulnerable heights (Brienen et al., 2015). These results were lately proved by Locoselli et al. (2020) indicating that growth rates and longevity are strongly correlated with temperature. Recently, Zuidema et al. (2022) demonstrated that future global warming will provoke drier conditions with a negative effect on annual tropical vegetation productivity. A vast majority of these mortality drivers may kill trees in part through carbon starvation and/or hydraulic failure, the relative importance of each driver remains, however, unknown (McDowell et al., 2018). Besides, vessel traits in angiosperms seem to be another key factor in tropical environments mortality (Fonti et al., 2010; Islam et al., 2018) as wider vessels will prioritize water conductivity at the expense of high risk of embolism during droughts (Rahman et al., 2019; Wu et al., 2020). In addition, long-term plasticity in vessel safety and low hydraulic efficiency have been shown to be compromised further by deforestation and climate change (Rodríguez-Ramírez and Luna-Vega, 2020). Therefore, predicted ongoing and future climate change will likely lead to higher tree mortality rates, especially in short-lived species, sadly common in the tropics and subtropics (Brienen et al., 2015).

5. Tropical and subtropical regions: diverse, rich in species and understudied

Compared to temperate regions, tropical and subtropical flora is extremely rich in species, even more so in terms of trees (Hallé et al., 2012), estimated to approximately 40,000 species (Slik et al., 2015).

Tropical rainforests have a remarkably complete and uninterrupted series of taxa with many entire plant families with very large genera but often confined within the limits of the same region (Fedorov, 1966). Despite the immense number of tropical tree species and related families and genera diversity and the limited number of dendrochronological studies existing around low latitudes, approximately 230 species have been reported to form annual rings in these regions (Brienen et al., 2016; Schöngart et al., 2017).

A vast majority of dendrochronological studies in tropical and subtropical regions have been realized in the Americas (59 %), and much less studies exist today for Asia (24 %), Africa (15 %), and Oceania (2 %). The fact that a clear majority of tropical tree-ring studies are centered in the Americas is presumably the result of the vast tropical forest area existing in these regions (Hansen et al., 2013). This is especially true for the state of Sao Paulo and the Amazon, for forests of the northern Mexico, trans-Mexican Volcanic Belt and Central Mexico, Guatemala, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and northernmost Argentina.

Major gaps in terms of dendrochronological research persist today in extreme tropical environments (the moist ever-wet forest and deserts). Similar gaps can, however, also be recognized in the more biodiverse regions of the Caribbean, Southern Mexico, Central America, Africa (in general), South Asia, Southeast Asia, and tropical Oceania (Fig. 4). So far, African dendrochronology has focused essentially on the dry forests of Ethiopia, with some additional, yet scattered studies undertaken in Kenya, Cameroon, or the Democratic Republic of Congo, and thus in quite different tropical forest types. Dendrochronological hotspots in Southeast Asia are clearly centered on India, Thailand, Malaysia, and Indonesia, but the potential for more research is still huge as it is for tropical Oceania (see Fig. 5).

Table 1 provides a summary of the families and genera that are most used in tropical and subtropical dendrochronology. Members of the *Fabaceae* family are present in America, Africa, and Asia, especially in Tropical and Subtropical Moist Broadleaf Forests. This family occurs in very diverse altitudinal and latitudinal tropical settings, with more common occurrences in America and Africa (Table 1; Fig. 4). Members of the *Pinaceae* family have been used widely as well, primarily above 14° N and 14° S, and in environments where Tropical and Subtropical Coniferous Forests are common. Tree-ring studies using *Pinaceae* are particularly widespread in Florida (United States), Mexico, Guatemala, Dominican Republic, India, and Thailand (see Table 2).

More than half of all studies realized on tropical dendrochronology focused on species of the *Meliaceae*, *Boraginaceae* and *Anacardiaceae* families, and were realized at latitudes up to 15° N and S, mostly in America and Asia. Studies using *Verbenaceae* are frequent as well, and sites investigated reach latitudes of up to 20° N, majorly in Asia, whereas members of the *Cupressaceae* and *Malvaceae* families have been used in tropical growth-ring research in different ecoregions beyond 14° latitude, mostly in Africa and America.

Representatives of the *Pinus* genus are abundantly present in studies realized at latitudes above 12° in both hemispheres, in the Tropical and Subtropical Coniferous, Dry Broadleaf and Moist Broadleaf Forests of Guatemala, Mexico, Brazil, Thailand, India, China and Australia. The most used species of the *Pinus* genus are *Pinus hartwegii* (Villanueva-Díaz et al., 2000; Villanueva-Díaz et al., 2015), *P. elliottii* (Tucker et al., 2018), *P. merkusii* (Hua et al., 2004), and *P. kesiya* (Ho et al., 2019). Representatives of the *Cedrela* genus have been studied mostly in the Dry and Moist Broadleaf Forests of Ecuador, Peru, Bolivia, Argentina, and Brazil. Here, the species that were most frequently used in dendrochronology so far include *Cedrela odorata* and *C. fissilis* (Venegas-González et al., 2018).

Growth-ring studies using species of the *Tectona* genus were performed at latitudes exceeding 10° (mostly N) in the Moist Broadleaf Forests of India, Thailand, and Myanmar (Pumijumnong, 2012). Research focused primarily on *Tectona grandis*, a species that has also been introduced for commercial purposes in Latin America, Asia, Africa, and Oceania (Gaitán-Alvarez et al., 2019). The genus *Acacia* is typical

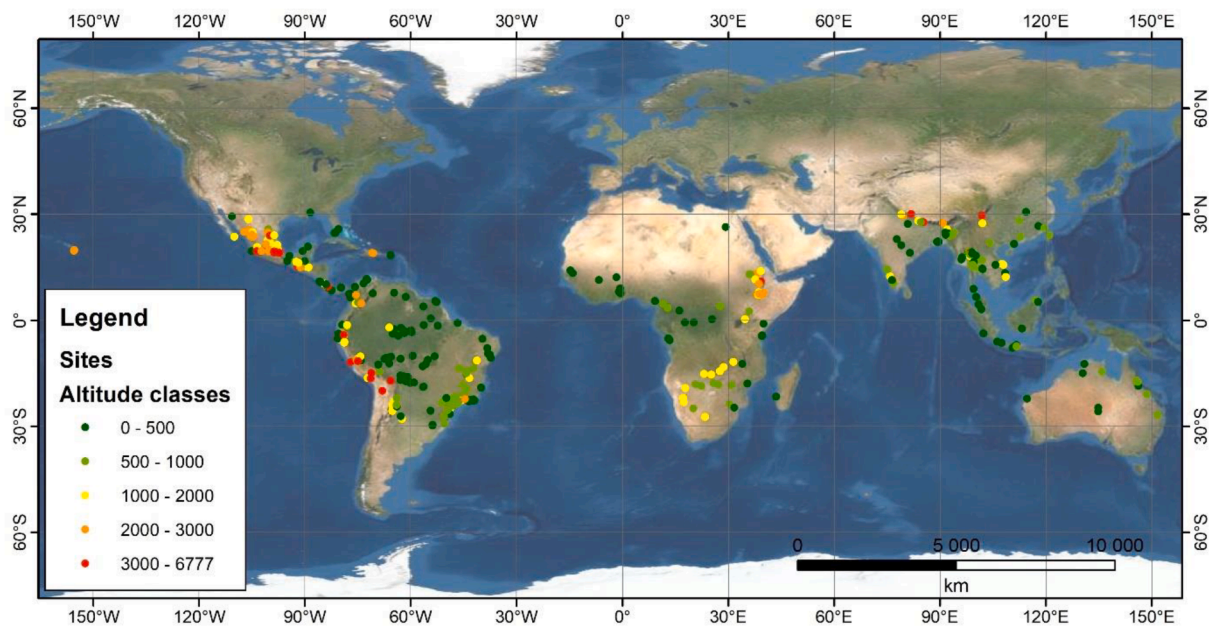


Fig. 4. Distribution of tropical and subtropical dendrochronological studies realized in the past. Dots indicate works published for study sites located between 30° N and 30° S. The total number of studies illustrated is 459. For details see Supplementary Material.

for latitudes below 10° in Tropical and Subtropical Grasslands, Savannas and Shrublands of Africa and Southeast Asia, and was employed in growth-ring research through the study of its species *Acacia mearnsii*, *A. tortilis*, *A. seyal*, and *A. mangium* (Gebrekirstos et al., 2008). The *Abies* genus is restricted to 14–24° N in the Tropical and Subtropical Coniferous Forests of Guatemala in Mexico and research was so far based mostly on *Abies religiosa* (Franco-Ramos et al., 2016) and *A. guatemalensis* (Anchukaitis et al., 2013).

The genus *Toona* and its most abundant species *Toona ciliata* (Rahman et al., 2017) occur in the Dry Broadleaf Forests at latitudes comprised between 14 and 24° N in Asia and around 21° S in Oceania, whereas the species of the *Hymenaea* genus used in dendrochronology was restricted to the Moist Broadleaf Forests of the neotropics, and particularly South America. Its most common representatives are *Hymenaea courbaril* and *H. stigonocarpa* (Locosselli et al., 2013). Growth-ring studies studying species of the *Juniperus* genus have been restricted so far to the Montane Grasslands, Shrublands or Coniferous Forests of Africa (mostly Ethiopia) and high elevation sites of Mexico, with research utilizing primarily *Juniperus procera* (Wils et al., 2011) and *J. monticola* (Villanueva-Díaz et al., 2016). Tree-ring studies realized with *Rhizophora* are common in Mangrove Forests of Africa and America using *Rhizophora mangle* (del Valle et al., 2012) and *R. mucronata* (Verheyden et al., 2005).

Fig. 3a illustrates that localities of dendrochronological studies tend to increase slightly with decreasing latitude. Most research on tropical and subtropical growth rings and their ecological interpretation has been realized at altitudes (well) below 2,000 m a.s.l (Fig. 3c). The Americas are somehow the exception to the rule, but the higher numbers can be explained by the fact that several studies have been realized in the trans-Mexican Volcanic Belt, thereby extending the altitudinal range of tropical and subtropical study sites in the Americas considerably. In addition, this cluster also contains the Andean tree-ring series, i.e., the highest chronologies collected so far in the tropics/subtropics. In Africa, the high-elevation Ethiopian chronologies are responsible for the outliers found in the altitudinal range of the African continent.

Interestingly, despite having the highest mountain ranges in the world, maximum altitudes of Asian growth-ring chronologies so far only exhibit a mean elevation of study sites that is slightly exceeding 1500 m a.s.l. The limited number of chronologies reported for Oceania prevents

any statistical analysis; in this region, we can only observe that most sites analyzed so far were located below 1000 m a.s.l. Studies realized at altitudes exceeding 2000 m a.s.l. were utilizing most often species from the genera *Podocarpus* (Krepkowski et al., 2013) and *Juniperus* (Mokria et al., 2015) in Africa, and *Pinus* (Pompa-García et al., 2015), *Abies* (Pacheco et al., 2020), *Juniperus* (Villanueva et al., 2016) and *Polylepis* (Gunderson, 2019) in the Americas, whereas research at higher elevations was restricted to *Pinus* in Asia (D'Arrigo et al., 1997).

6. Dendrochronological approaches applied to tropical and subtropical trees

A dendrochronological study typically starts with a field campaign during which samples are acquired from the trunks, stems, or roots of woody plants, depending on the goals of the study and the research questions. Sampling can be non-destructive through the extraction of increment cores (Fritts, 1971; usually 5.5 mm in diameter, but thicker borers with inner diameters of up to 12 mm exist and are primarily used in density and isotope analysis) or destructive (Worbes, 1995) in the case that cross sections or wedges are taken with a saw (Fig. 6). Sample depth – i.e., the number of samples selected – will depend primarily on the question to be answered and to the potential of trees to cross-date. According to the literature review, studies have reported between 1 sample using cosmogenic methods (Harada et al., 2014) and 600 samples (Groenendijk et al., 2014). On average, published papers rely on 77.7 ± 113.98 ($n_{\text{obs}} = 402$) samples; fewest samples are used in studies with a focus on geomorphology and climatology, whereas research on ecology and climatology typically relies on the largest sample sizes (Solíz et al., 2009; Bovi et al., 2018; Brandes et al., 2020). Sample depth of tropical and subtropical tree-ring studies are thus not fundamentally different from what is normally analyzed in extratropical work, with the exception maybe of large dendroclimatological or dendroecological tree-ring networks as they are used primarily in work spanning the northern hemisphere (St George, 2014; Stoffel et al., 2015; Anchukaitis et al., 2017).

Most dendrochronological studies realized in the tropics/subtropics so far relied on macroscopic applications (Fig. 7), i.e., on approaches where growth rings are analyzed, and ring boundaries distinguished at simple sight or with the aid of a stereomicroscope (Schweingruber,

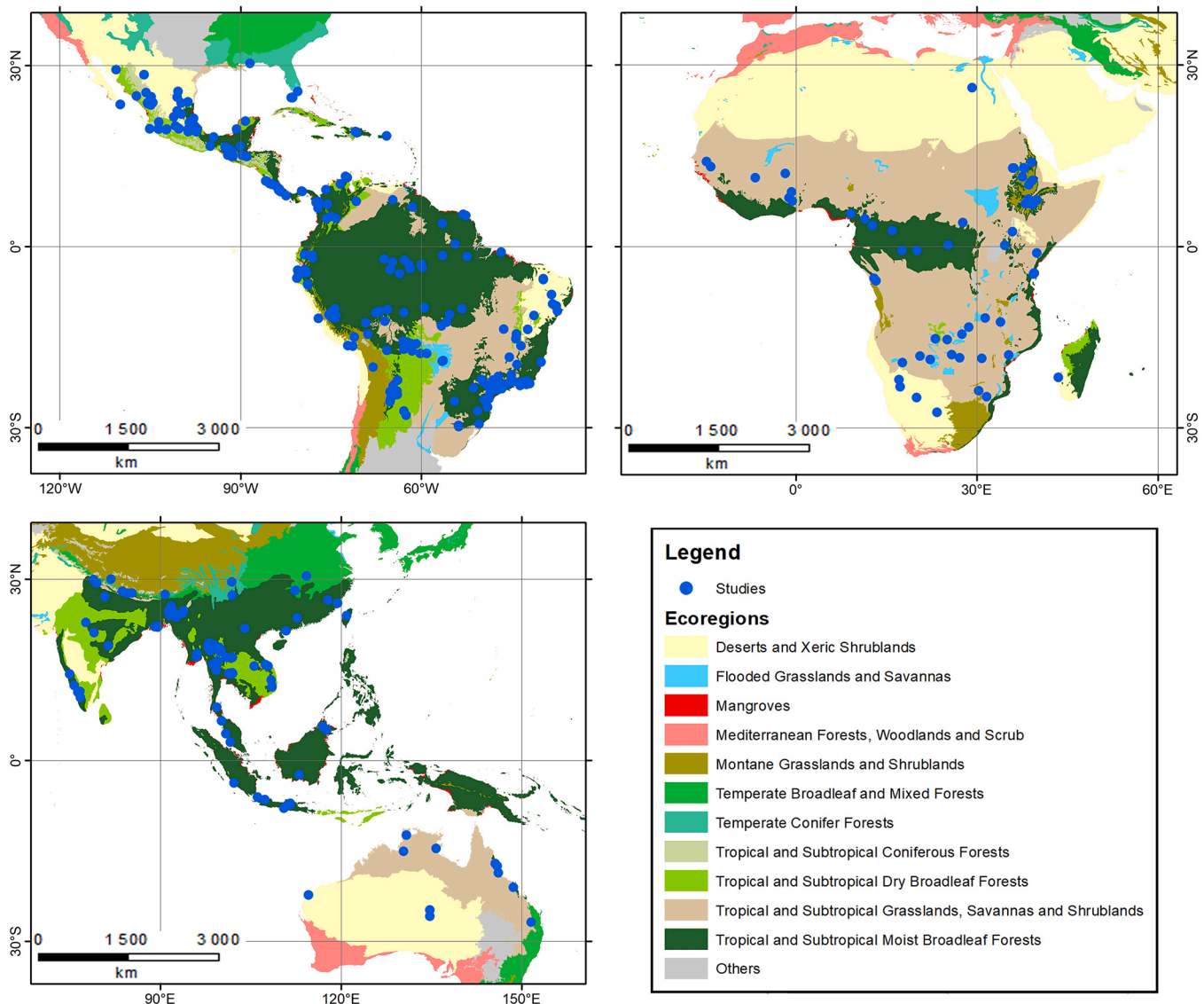


Fig. 5. Spatial representation of dendrochronological studies realized in different tropical and subtropical ecoregions (*sensu* Olson et al., 2001) comprised between 30° N and 30° S.

1996). We found 274 scientific papers (60 %) in which analyses were based solely on macroscopic ring analyses. 56 papers (12 %) focused on a microscopic assessment and interpretation of growth rings – especially since the early 2000 s – whereas 55 contributions (11 %) combined both macroscopic and microscopic analyses (Fig. 8). More recently, ^{14}C , ^{13}C and ^{18}O isotopes have been employed to corroborate results of macroscopic (56 studies; 13 %) and microscopic (18 studies; 4 %) analyses.

As in temperate and boreal climates, tropical dendrochronology also relies on a suite of statistical routines and tools facilitating crossdating, climate reconstructions, as well as ecological and biological response modeling (Speer, 2010). Statistical approaches typically include the assessment of intercorrelation between series, analysis of mean sensitivity of trees, expressed population signal (EPS; Fig. 8) of chronologies, as well as autocorrelation analyses (Fritts, 1976; Cook and Kairiukstis, 1990).

In terms of dendroecological potential and dendroclimatic signal strength, studies generally report more robust cross-dating results – expressed in terms of mean sensitivity and/or EPS – at altitudes below 1000 m a.s.l. and across all tropical/subtropical ecoregions on all continents. Consistently, series with the highest intercorrelation and autocorrelation values are also located below 2500 m a.s.l. Average values of

intercorrelation in tropical/subtropical studies are 0.45 ± 0.16 ($n_{\text{obs}} = 198$), mean sensitivity of records is 0.42 ± 0.15 ($n_{\text{obs}} = 161$), and studies reporting EPS values reach 0.84 ± 0.09 ($n_{\text{obs}} = 127$) on average, whereas autocorrelation values are given at 0.38 ± 0.22 ($n_{\text{obs}} = 97$) on average. The genera with by far the largest amount of intercorrelation series described are *Pinus*, with tree-ring data collected mostly above 1200 m a.s.l. In terms of mean sensitivity, *Chukrasia*, *Toona*, *Cedrela* and *Hymenaea* have the highest values (over 0.5); here, all samples were collected below 1000 m a.s.l. Among those studies reporting EPS, *Pinus*, *Cedrela* and *Tectona* had the highest overall values. *Pinus* and *Cedrela* (usually sampled above 1000 m a.s.l.) as well as *Toona*, *Chukrasia* and *Tectona* (below 1000 m a.s.l.) are most frequently published with data on autocorrelation series.

7. Applications based on tropical dendrochronology

Tropical and subtropical dendrochronological studies have started to increase almost exponentially at the beginning of the 21st century, with notable differences, however, between different applications or sub-disciplines. Most frequently, research focused on dendroclimatology (51 %) and dendroecology (45 %), encompassing a stunning 96 % of all

Table 1

Overview of woody species of the tropics and subtropics with confirmed annual growth rings (between 30° North and 30° South). A complete list of references can be found in the Supplementary Material.

Families	Species	References
Acanthaceae	<i>Avicennia marina</i>	Schmitz et al., 2007; Santini et al., 2013
Anacardiaceae	<i>Schinopsis brasiliensis</i> , <i>Schinopsis lorentzii</i>	López and Villalba, 2016; de Carvalho Nogueira et al., 2018; Bravo et al., 2008; Ferrero and Villalba, 2009; Ferrero et al., 2013, 2015
Apocynaceae	<i>Aspidosperma polyneuron</i> , <i>Pentalinon andrieuxii</i>	Briceño et al., 2018; Godoy-Veiga et al., 2018; Hiebert-Giesbrecht et al., 2018; Blagitz et al., 2019
Araucariaceae	<i>Agathis robusta</i> , <i>Araucaria angustifolia</i> , <i>Araucaria bidwillii</i> , <i>Araucaria columnaris</i> , <i>Araucaria cunninghamii</i>	Lisi et al., 2001; Medeiros et al., 2008 ; Oliveira et al., 2009 ; Boysen et al., 2014; Santos et al., 2015; Haines et al., 2018; Brandes et al., 2019
Asteraceae	<i>Moquiniastrum polymorphum</i>	Grau et al., 2003; Paolini et al., 2005 ; Ferrero et al., 2013; Armijos-Montaño et al., 2018
Betulaceae	<i>Alnus acuminata</i>	Volland-Voigt et al., 2011
Bignoniaceae	<i>Tabebuia chrysantha</i>	Devall et al., 1995; Enquist and Leffler, 2001; Hayden et al., 2010; Briceño et al., 2016
Boraginaceae	<i>Cordia alliodora</i>	Devall et al., 1995; Enquist and Leffler, 2001; Hayden et al., 2010; Briceño et al., 2016
Burseraceae	<i>Boswellia papyrifera</i> , <i>Bursera graveolens</i>	Rodríguez et al., 2005; Rodríguez et al., 2005; Feyissa, 2013; Tolera et al., 2013; Pucha-Cofrep et al., 2015
Capparaceae	<i>Capparis odoratissima</i>	Ramírez and del Valle, 2011; del Valle et al., 2012
Clusiaceae	<i>Chrysochlamys colombiana</i> , <i>Chrysochlamys dependens</i>	Ayala-Usuma et al., 2019
Combretaceae	<i>Laguncularia racemosa</i>	Estrada et al., 2008
Cupressaceae	<i>Callitris columellaris</i> , <i>Callitris endlicheri</i> , <i>Callitris glaucophylla</i> , <i>Callitris intratropica</i> , <i>Cupressus lusitanica</i> , <i>Callitris macleayana</i> , <i>Callitris preissii</i> , <i>Callitris rhomboidea</i> , <i>Fokienia hodginsii</i> , <i>Juniperus monticola</i> , <i>Juniperus procera</i> , <i>Taxodium ascendens</i> , <i>Taxodium distichum</i> , <i>Taxodium mucronatum</i>	Anderson et al., 2005; Couralet et al., 2005; Sass-Klaassen et al., 2008; Wils et al., 2009 ; Wils et al., 2010; Bowman et al., 2011; Pearson et al., 2011; Wils et al., 2011 ; David et al., 2014; Mokria et al., 2015; Villanueva-Díaz et al., 2016 ; Pompa-García et al., 2017; David et al., 2018; Gebregeorgis et al., 2018; Sano et al., 2009; Buckley et al., 2010; Sano et al., 2012; Buckley et al., 2017; Alcalá-Reygosa et al., 2018; Buckley et al., 2018; Franco-Ramos et al., 2018; Villanueva-Díaz et al., 2020
Dilleniaceae	<i>Dillenia indica</i>	Venugopal and Liangkuwang, 2007
Dipterocarpaceae	<i>Dryobalanops sumatrensis</i> , <i>Hopea odorata</i> , <i>Shorea leprosula</i> , <i>Shorea robusta</i> , <i>Shorea superba</i>	Sass et al., 1995; Ogata and Fujita, 2005; Azim et al., 2014; Ohashi et al., 2014
Euphorbiaceae	<i>Alchornea lojaensis</i>	Spannl et al., 2016
Fabaceae	<i>Acacia erioloba</i> , <i>Acacia tortilis</i> , <i>Azelia xylocarpa</i> , <i>Amburana cearensis</i> , <i>Baikiaea plurijuga</i> , <i>Brachystegia floribunda</i> , <i>Brachystegia spiciformis</i> , <i>Burkea africana</i> , <i>Centrolobium microchaete</i> , <i>Centrolobium robustum</i> , <i>Copaifera langsdorffii</i> , <i>Copaifera lucens</i> , <i>Dalbergia cochinchinensis</i> , <i>Dalbergia nigra</i> , <i>Dalbergia frutescens</i> ,	Boninsegna et al., 1989; Wyant and Reid, 1992; Enquist and Leffler, 2001; Lisi et al., 2001; Tarhule and Leavitt, 2004; Fichtler et al., 2004; Brien and Zuidema, 2005; Rodríguez et al., 2005; Schöngart et al., 2005; Brien and Zuidema, 2006; Brien et al., 2006; Grundy, 2006; Schöngart et al., 2006; Trouet et al., 2006; Westbrook

Table 1 (continued)

Families	Species	References
	<i>Daniellia oliveri</i> , <i>Dichrostachys cinerea</i> , <i>Dipteryx magnifica</i> , <i>Enterolobium maximum</i> , <i>Faidherbia albida</i> , <i>Hymenaea courbaril</i> , <i>Hymenaea stigonocarpa</i> , <i>Hymenolobium petraeum</i> , <i>Isobertinia angolensis</i> , <i>Isobertinia doka</i> , <i>Julbernardia paniculata</i> , <i>Machaerium scleroxylon</i> , <i>Macrolobium acaciifolium</i> , <i>Milletia stuhlmannii</i> , <i>Mimosa acantholoba</i> , <i>Mimosa tenuiflora</i> , <i>Parkia nitida</i> , <i>Parkia velutina</i> , <i>Parkinsonia praecox</i> , <i>Paubrasilia echinata</i> , <i>Pericopsis elata</i> , <i>Piptadenia adiantoides</i> , <i>Piptadenia micracantha</i> , <i>Poincianella pyramidalis</i> , <i>Prioria copaifera</i> , <i>Prosopis pallida</i> , <i>Pterocarpus angolensis</i> , <i>Pterocarpus macrocarpus</i> , <i>Pterocarpus rohrii</i> , <i>Pterogyne nitens</i> , <i>Schizolobium parahyba</i> , <i>Senegalia mellifera</i> , <i>Senna multijuga</i> , <i>Sindora siamensis</i> , <i>Sophora chrysophylla</i> , <i>Tamarindus indica</i> , <i>Xylocarpus xylocarpa</i>	et al., 2006; Brien and Zuidema, 2007; Bravo et al., 2008; Steenkamp et al., 2008; Gebrekirstos et al., 2008; Marcati et al., 2008; Ohashi et al., 2009; Brien et al., 2010; Hayden et al., 2010; Syampungani et al., 2010; Trouet et al., 2010; Brandes et al., 2011; Brien et al., 2011; Calzón and Giménez, 2011; Giraldo-Jiménez and del Valle-Arango, 2011; Herrera and del Valle, 2011; López et al., 2011; Nicolini et al., 2012 ; del Valle et al., 2012; López et al., 2012; Ramírez and del Valle, 2012; Locosselli et al., 2013 ; López et al., 2013; Mbow et al., 2013; Mendivelso et al., 2013; Paredes-Villanueva et al., 2013; Southworth et al., 2013; David et al., 2014; De Ridder et al., 2014; Gebrekirstos et al., 2014 ; Groenendijk et al., 2014; Kumaran et al., 2014; Mendivelso et al., 2014; Ohashi et al., 2014; Vlam et al., 2014; Vlam, 2014; Alves-Pagotto et al., 2015; Baker et al., 2015; Costa et al., 2015; Francisco et al., 2015; Groenendijk et al., 2015 ; Hietz et al., 2015; Morel et al., 2015 ; Paredes-Villanueva et al., 2015; Boakye et al., 2016; de Vasconcellos et al., 2016; Locosselli et al., 2016; Shimamoto et al., 2016; López et al., 2017; Herrera-Ramírez et al., 2017; Köhl et al., 2017; Linares et al., 2017; Ngoma et al., 2017; Barbosa et al., 2018; Batista and Schöngart, 2018; Bovi et al., 2018; David et al., 2018; de Carvalho et al., 2018; de Miranda et al., 2018; Fontana et al., 2018; Mattos et al., 2018; Nakai et al., 2018; Batista and Schöngart, 2018; Zacharias et al., 2018; Granato-Souza et al., 2019; Locosselli et al., 2019; López et al., 2019; Rahman et al., 2019 ; Macedo et al., 2020; Shikangalah et al., 2020
Fagaceae	<i>Fagus grandifolia</i>	Rodríguez-Ramírez et al., 2018
Hypericaceae	<i>Hypericum irazuense</i>	Kerr et al., 2018; Quesada-Román et al., 2020b
Juglandaceae	<i>Juglans neotropica</i>	Villalba et al., 1985; Villalba et al., 1992; Villalba et al., 1998; Arabe et al., 2011; Ferrero et al., 2013; Ferrero et al., 2015; Inga and del Valle, 2017; Armijos-Montaño et al., 2018
Lamiaceae	<i>Peronema canescens</i>	Azim et al., 2014; Harada et al., 2014
Lauraceae	<i>Cinnamomum amoenum</i> , <i>Nectandra maegapotamica</i> , <i>Nectandra oppositifolia</i> , <i>Ocotea pulchella</i>	Spathelf et al., 2010; Reis-Avila and Oliviera, 2017; Granato-Souza et al., 2019
Lecythidaceae		Brien and Zuidema, 2005; Brien and Zuidema, 2006;

(continued on next page)

Table 1 (continued)

Families	Species	References
	<i>Bertholletia excelsa</i> , <i>Cariniana estrellensis</i> , <i>Cariniana pyriformis</i>	Baker et al., 2015; Andrade et al., 2019
Lythraceae	<i>Sonneratia alba</i> , <i>Sonneratia apetala</i>	Chowdhury et al., 2008; Rahman et al., 2020
Magnoliaceae	<i>Magnolia champaca</i> , <i>Magnolia schiedeana</i> , <i>Magnolia vovidesii</i>	Rodríguez-Ramírez et al., 2020; Rahman et al., 2021
Malvaceae	<i>Adansonia grandidieri</i> , <i>Ceiba speciosa</i> , <i>Heritiera fomes</i> , <i>Heritiera littoralis</i>	Chowdhury et al., 2008; Robert et al., 2011; Patrut et al., 2015; Chowdhury et al., 2016; Barbosa et al., 2018; Maxwell et al., 2018; de Vasconcellos et al., 2019
Meliaceae	<i>Azadirachta excelsa</i> , <i>Cedrela fissilis</i> , <i>Cedrela lilloi</i> , <i>Cedrela montana</i> , <i>Cedrela nebulosa</i> , <i>Cedrela odorata</i> , <i>Chukrasia tabularis</i> , <i>Lagerstroemia speciosa</i> , <i>Melia azedarach</i> , <i>Neolitsea obtusifolia</i> , <i>Swietenia macrophylla</i> , <i>Toona ciliata</i> , <i>Vitex peduncularis</i>	Villalba et al., 1985; Boninsegna et al., 1989; Villalba et al., 1992; Villalba et al., 1998; Grau, 2000; Dünisch et al., 2003; Brienen and Zuidema, 2005; Hietz et al., 2005; Brienen and Zuidema, 2006; Brienen et al., 2006; Heinrich and Banks, 2006; Brienen and Zuidema, 2007; Bräuning et al., 2009; Rozendaal et al., 2010; Nock et al., 2011; Ferrero et al., 2013; López et al., 2013; Pumijumnong and Buajan, 2013; Tinco et al., 2013; Wang et al., 2013; Azim et al., 2014; Ohashi et al., 2014; Pereyra-Espinoza et al., 2014; Vlam et al., 2014; Baker et al., 2015; Ferrero et al., 2015; Hietz et al., 2015; Arêdes-dos-Reis et al., 2016; Martínez-Prera, 2016; Paredes-Villanueva et al., 2016; Susatya and Yansen, 2016; Baker et al., 2017; Köhl et al., 2017; Inga and del Valle, 2017; Rahman et al., 2017; Armijos-Montaño et al., 2018; Barbosa et al., 2018; Dünisch and Latorraca, 2018; Islam et al., 2018; Layme-Huaman et al., 2018; Venegas-González et al., 2018; Pereira et al., 2018; Rahman et al., 2018; Blagitz et al., 2019; Carlosama-Mejía and Herrera-Carrión, 2019; Granato-Souza et al., 2019; Hammerschlag et al., 2019; Marcelo-Peña et al., 2019; Rahman et al., 2019
Myrtaceae	<i>Eucalyptus nesophila</i> , <i>Eucalyptus miniata</i> , <i>Eucalyptus tetradonta</i> , <i>Melaleuca minutifolia</i> , <i>Melaleuca quinquenervia</i> , <i>Melaleuca viridiflora</i>	Mucha, 1979; Sharp and Bowman, 2004; David et al., 2014; Ohashi et al., 2014; David et al., 2018; Nakai et al., 2018; Adame et al., 2019; Rahman et al., 2019
Pinaceae	<i>Abies durangensis</i> , <i>Abies guatemalensis</i> , <i>Abies religiosa</i> , <i>Cedrus deodara</i> , <i>Picea chihuahuana</i> , <i>Pinus ayacahuite</i> , <i>Pinus cembroides</i> , <i>Pinus cooperi</i> , <i>Pinus elliotii</i> , <i>Pinus engelmannii</i> , <i>Pinus hartwegii</i> , <i>Pinus jeffreyi</i> , <i>Pinus kesiya</i> , <i>Pinus lagunae</i> , <i>Pinus leiophylla</i> , <i>Pinus lumholtzii</i> , <i>Pinus massoniana</i> , <i>Pinus merkusii</i> , <i>Pinus occidentalis</i> , <i>Pinus oocarpa</i> , <i>Pinus patula</i> , <i>Pinus pseudostrobus</i> , <i>Pinus</i>	Schulman, 1944; Johnson, 1980; Bhattacharyya and Yadav, 1990; Huante et al., 1991; D'Arrigo et al., 1997; Biondi and Fessenden, 1999; Biondi, 2001; Díaz et al., 2001; Díaz et al., 2002; Biondi et al., 2003; Brito-Castillo et al., 2003; Stephens et al., 2003; Hua et al., 2004; Speer et al., 2004; Buckley et al., 2005; González-Elizondo et al., 2005; Martin and Fahey, 2006; Pumijumnong and

Table 1 (continued)

Families	Species	References
	<i>teocote</i> , <i>Pinus wallichiana</i> , <i>Pseudotsuga menziesii</i>	Wanyaphet, 2006; Ricker et al., 2007; Palakit and Duangsathaporn, 2008; Zimmer and Baker, 2009; Harley et al., 2011; Krepkowski et al., 2011; Szejner, 2011; Harley et al., 2012; Anchukaitis et al., 2013; Franco-Ramos et al., 2013; Cardoza-Martínez et al., 2014; Pompa-García and Jurado, 2014; Anchukaitis et al., 2015; Pompa-García et al., 2015; Venegas-González et al., 2015; Belay, 2016; Carlón-Allende et al., 2016; Franco-Ramos et al., 2016; Singh et al., 2016; Trouet et al., 2016; Astudillo-Sánchez et al., 2017; Cabral-Alemán et al., 2017; Franco-Ramos et al., 2017; González-Elizondo et al., 2017; López-Sánchez et al., 2017; Luo et al., 2017; Pompa-García et al., 2017; Venegas-González et al., 2017; Beramendi-Orosco et al., 2018; Carlón-Allende et al., 2018; Carlón-Allende et al., 2018; Anderson et al., 2018; Franco-Ramos et al., 2018; López-Hernández et al., 2018; Rebenack et al., 2018; Tucker et al., 2018; Villanueva-Díaz et al., 2018; Astudillo-Sánchez et al., 2019; Correa-Díaz et al., 2019; Gu et al., 2019; Ho et al., 2019; Alfaro-Sánchez et al., 2020; Brandes et al., 2020; Carlón-Allende et al., 2020; Hua et al., 2020; Pacheco et al., 2020
Podocarpaceae	<i>Podocarpus falcatus</i> , <i>Podocarpus lambertii</i>	Poussart et al., 2004; Krepkowski et al., 2011; Krepkowski et al., 2012; Krepkowski et al., 2013; Locosselli et al., 2016
Rhizophoraceae	<i>Rhizophora mangle</i> , <i>Rhizophora mucronata</i>	Menezes et al., 2003; Verheyden et al., 2004; Verheyden et al., 2005; Schmitz et al., 2006; Ramírez-Correa et al., 2010; del Valle et al., 2012; Kumaran et al., 2014; Souza et al., 2016
Rosaceae	<i>Polylepis species</i> , <i>Polylepis pepeii</i> , <i>Polylepis subsericans</i> , <i>Polylepis rodolfo-vasquezii</i> , <i>Polylepis rugulosa</i> , <i>Polylepis tarapacana</i>	Solfz et al., 2009; Jomelli et al., 2012; Roig et al., 2013; Baker et al., 2015; Gunderson, 2019
Rubiaceae	<i>Breonadia salicina</i> , <i>Cordia concolor</i>	Gillespie et al., 1998; Norström et al., 2008; de Lara et al., 2017
Rutaceae	<i>Esenbeckia cornuta</i> , <i>Esenbeckia leiocarpa</i>	Bovi et al., 2019; Marcelo-Peña et al., 2019
Santalaceae	<i>Santalum paniculatum</i>	Constantz et al., 2021
Sapotaceae	<i>Pouteria orinocoensis</i> , <i>Pouteria</i> sp., <i>Vitellaria paradoxa</i>	Dezzeno et al., 2003; Anchukaitis and Evans, 2010; Armijos-Montaño et al., 2018
Verbenaceae	<i>Tectona grandis</i>	Pumijumnong et al., 1995; Murphy et al., 1997; Priya and Bhat, 1998; Poussart et al., 2004; Buckley et al., 2005; D'Arrigo et al., 2006; Shah et al., 2007; Wannasri et al., 2007; Ram et al., 2008; Ohashi

(continued on next page)

Table 1 (continued)

Families	Species	References
		et al., 2009; Deepak et al., 2010; Managave et al., 2010; D'Arrigo et al., 2011; Palakit et al., 2012; Pumijumnong, 2012; Palakit et al., 2015; Venegas-González et al., 2015; Buajan et al., 2016; Auykim et al., 2017; Managave et al., 2017; Venegas-González et al., 2017; Lumyai and Duangsathaporn, 2018; Gaitan-Alvarez et al., 2019; Khantawan et al., 2019; Pumijumnong et al., 2019; Rahman et al., 2019
Vochysiaceae	<i>Vochysia divergens</i>	Fortes et al., 2018

Table 2

Absolute and relative numbers of publications on tropical and tropical dendrochronology by ecoregion (*sensu* Olson et al., 2001).

Ecoregion	Studies (nb)	Percentage
Tropical and Subtropical Moist Broadleaf Forests	213	47.97
Tropical and Subtropical Dry Broadleaf Forests	62	13.96
Tropical and Subtropical Grasslands, Savannas and Shrublands	51	11.48
Deserts and Xeric Shrublands	40	7.65
Tropical and Subtropical Coniferous Forests	48	10.81
Flooded Grasslands and Savannas	6	1.35
Montane Grasslands and Shrublands	13	2.92
Mangroves	13	2.92
Temperate Conifer Forests	1	0.22
Temperate Broadleaf and Mixed Forests	3	0.67
Mediterranean Forests, Woodlands, and Scrub	1	0.29

work realized in the tropics/subtropics, with only scarce and scattered work on dendrogeomorphology (16 studies) in Latin America and dendroarchaeology in Southeast Asia. Dendroclimatological work is most common in America (57 %), but less frequently used in Asia (29 %), Africa (12 %), and Oceania (2 %). The focus very often is on climate-growth relationships (Fig. 9), regional or local climatic reconstructions as well as on relations between precipitation and tree growth, especially in the case of species used in the timber industry. Moreover, climatic variability, the response of trees to drought as well as the relationship between tree growth and the state of the El Niño Southern Oscillation (ENSO) are current topics in tropical dendroclimatology as well. Multiple chronologies have been constructed lately to better understand climatic variability and climate-growth response both in mountainous and lowland settings (Fichtler, 2017). As such, and by studying the signals recorded by different species in contrasting biomes along the tropics/subtropics, dendroclimatology can help to improve our understanding of tree and forest responses to modes of climate variability (e. g., ENSO) and climatic changes (Rozendaal and Zuidema, 2011), as well as to, tropical cyclones and droughts further (Boninsegna et al., 2009). Moreover, long-term trends in water use and growth can be obtained from measurements of stable isotopes and tree-ring widths, such that data can be retrieved on physiological changes that would, in turn, most likely be linked to rising CO₂ (Brienen et al., 2016). Woody plants also respond to certain external stressors that can change because of climate change in the tropics. The response of mangrove species to salinity and sea level changes can, for instance, not only improve our understanding of the process itself, but also illustrate how these fragile ecosystems will likely react to further warming and associated changes (Robert et al., 2011). Another topic of increasing relevance is related to wildfires, both in ecological terms but also in terms of ongoing and anticipated future climate change (Lindbladh et al., 2013).

Dendroecological studies were most frequently realized in the Americas (58 %), followed by Africa (20 %), Asia (19 %) and Oceania (3 %). Research here has been devoted primarily to cambial, vessel and xylem anatomy, phenological responses, timber-yield projections for commercial species, potential growth rhythms, wood traits, the impact of lianas on tree growth, water use efficiency as well as forest succession.

This clear focus on dendroclimatology and dendroecology (*sensu stricto*) is also reflected in the selection of journals in which researchers have published their papers. Indeed, most of these journals are devoted to ecology and climatology. Regarding the others field comprised within dendroecology (*sensu lato*), dendrogeomorphic research has been restricted largely to the neotropics, with a clear geographic focus on mass-movement processes in volcanic environments of Mexico (Figueroa-García et al., 2021; Franco-Ramos et al., 2022), erosional processes in Brazil (Bovi et al., 2022), floods in Costa Rica (Quesada-Román et al., 2022) and, again, mass-movement processes in northernmost Argentina (Paolini et al., 2005). With the ongoing climate warming and intensification of rainfall events, weathering rates have been observed to increase across the tropics/subtropics. The process has been exacerbated further by the fact that tropical regions also are hotspots of tectonic activity, and changing land use, resulting in an intensification of erosional processes and the formation of natural disasters. Growth rings in trees and roots have been applied repeatedly to quantify erosion (and the evolution of erosion rates in extratropical settings; Ballesteros-Cánovas et al., 2013; Stoffel et al., 2013), and have just lately been applied to tropical species as well (Bovi et al., 2019). Other approaches in the field of dendrogeomorphology have proven their potential in dating past disasters and in providing spatio-temporal records on the frequency and magnitude of past hydro-geomorphic and geological mass-movement events (Stoffel and Bollschweiler, 2008). Interestingly, however, they have only rarely been applied so far in the tropics and mainly to study peak discharges of recent floods (Quesada-Román et al., 2020a) or lahar events (Franco-Ramos et al., 2020) following extreme rainfall episodes. The potential of dendrogeomorphology in the tropics seems huge if one bears in mind that ~ 40 % of the world's population resides in developing, tropical countries facing the increasing impacts of disasters, both in terms of economic losses and in death tolls (Alcántara-Ayala, 2002; Carrión-Mero et al., 2021; Pinos and Quesada-Román, 2021).

Likewise, much more research could still be realized in dendroarchaeology, an approach that has made substantial advances over recent decades and through the inclusion of isotopic and chemical extraction approaches which will ultimately help to remove the historical limitations for dendroprovenance studies. Wood from archeological sites, if preserved, could be combined with growth-ring data from global-scale ecological and climatological studies to overcome the environmental restrictions and to elucidate direct anthropogenic disturbances of ancient communities in the tropics/subtropics (Pearl et al., 2020). As such, and in view of the persisting limitations in growth-ring research in fields other than climatology and ecology, any expansion of innovative multi- and *trans*-disciplinary approaches to growth-ring studies would enhance our knowledge of these biodiverse regions further (Zuidema et al., 2022). Conformingly, tropical and subtropical countries could develop their own laboratories and expand international collaboration to explore well-known as well as endemic and non-traditional species, with the goal to enhance the knowledge and to improve the protection and conservation of the most biodiverse region of the world.

8. Limitations and prospects

Despite being the most biodiverse, productive, and understudied environments, tropical and subtropical regions have long been avoided by dendrochronologists because of the often-inconsistent growth patterns in tropical trees, sampling difficulties, complex wood anatomy, and/or the lack of physiological knowledge of local wood species (Pearl

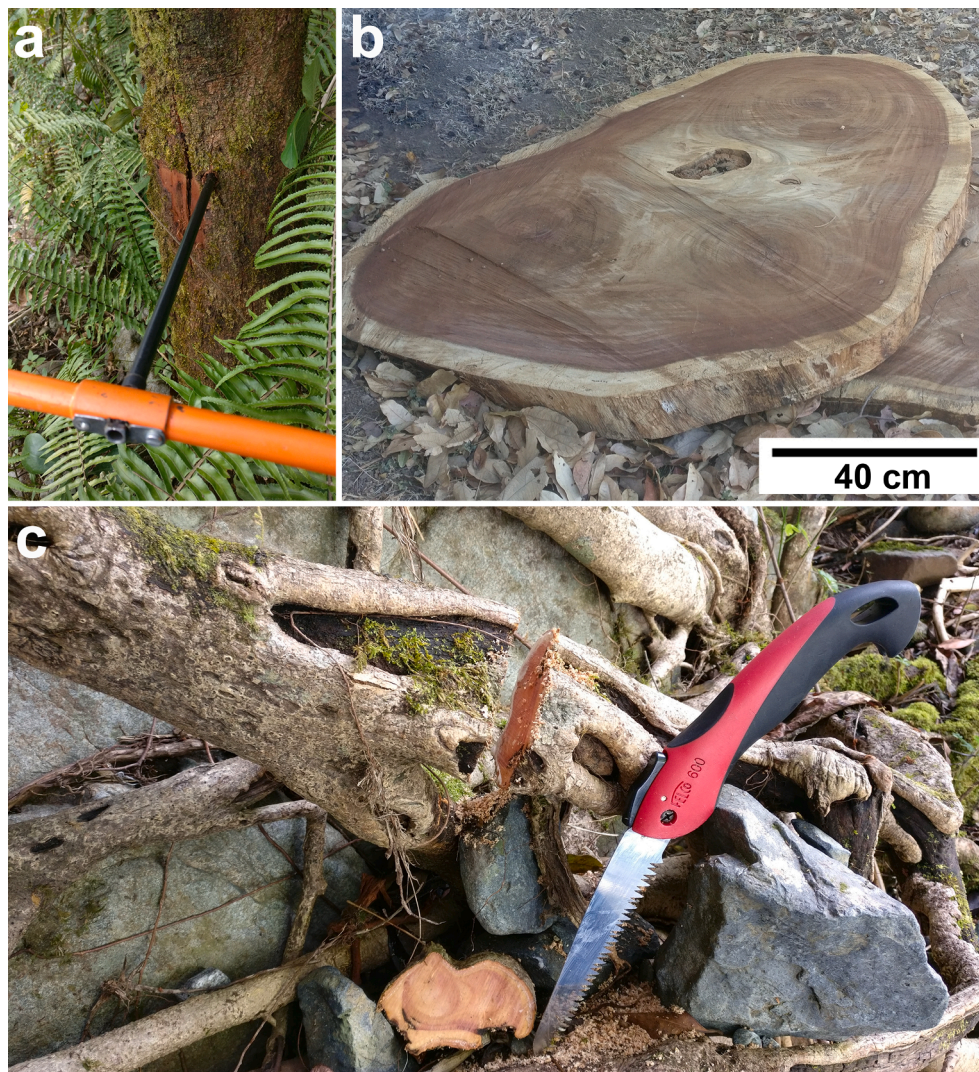


Fig. 6. Impressions from dendrochronological field campaigns: (a) Sampling of a *Sapindus saponaria* tree with an increment borer, Buenavista River, Costa Rica, (b) Cross section of a *Enterolobium cyclocarpum* tree, Guanacaste National Park, Costa Rica, (c), root cross-section taken from a *Zygia longifolia* tree with a handsaw, General River, Costa Rica.

et al., 2020). This review has shown that a multitude of approaches exists and that several hundreds of species have already been shown to be suitable for dendrochronological research. Nonetheless, this paper also showed that much remains to be done, and we thus repeat the call for a further development of approaches and techniques aimed at disentangling the climatic and ecological information contained in tropical/subtropical trees (Worbes, 2002). The recent, yet still emerging fields of chemical and physical wood analyses, substantial progress in improving the sampling design, statistical analyses, and tree-growth modeling are first steps toward the future of tropical and subtropical dendrochronology (Zuidema et al., 2013).

We observe a recently growing number of chronologies from South America and New Zealand, but also recognize that there still is a substantial lack of chronologies from Africa and the tropics in more general terms (Speer, 2010). Zhao et al. (2019) have quantified important limitations and biases as well as the alarming lack of information from Africa and the persistently low representation of tropical habitats, particularly in Asia, Central and South America, and Oceania in publications available in the International Tree-Ring Database (ITRDB; <http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>). So far, research on the response of tropical forests to global change focused primarily on the analyses of leaves and forest

communities, at the cost of studies addressing individual tree and population level reactions for which important gaps in knowledge still persist (Zuidema et al., 2013). In addition, a vast majority of tropical and subtropical regions are located primarily in emerging countries, where development and environmental concerns are often synonymous as a result of the constant impact that humans have on agribusiness, wood, and mineral extraction; at the same time, the regions are also among those most susceptible to the negative effects of climatic change (Lawrence and Vandecar, 2015). Moreover, old growth stands are becoming increasingly rare in the tropics/subtropics and, even when left standing, are becoming subject to decomposition, leaving their trunks hollow (Poussart et al., 2004).

Growth-ring studies of tropical/subtropical trees offer important insights into global change effects in tropical environments and forests. They have the potential to provide much more information on climate-forest interactions and climate reconstructions as new techniques become available and research efforts will hopefully intensify in regions that have been less studied so far and where a huge potential exists to improve local collaboration (Brienen et al., 2016). Many tropical species do not mark simple sight rings and need further anatomical assessments that require extra efforts and expensive lab equipment. This point is key as a vast majority of tree-ring laboratories and dendrochronologists are

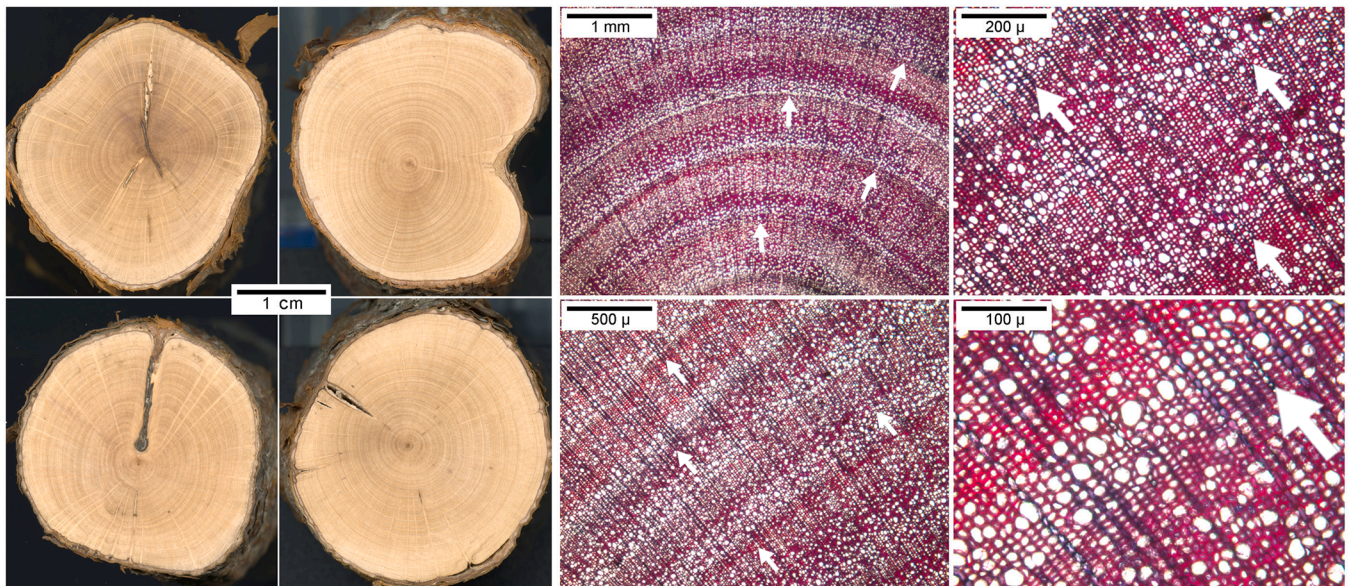


Fig. 7. Macroscopic (left panels) and microscopic (right panels) views of neotropical *Hypericum irazuense* growth rings. Wedging and micro rings, with a radially aligned band, with thick-walled latewood fibers, flattened along the ring boundary. Arrows indicate tree-rings.

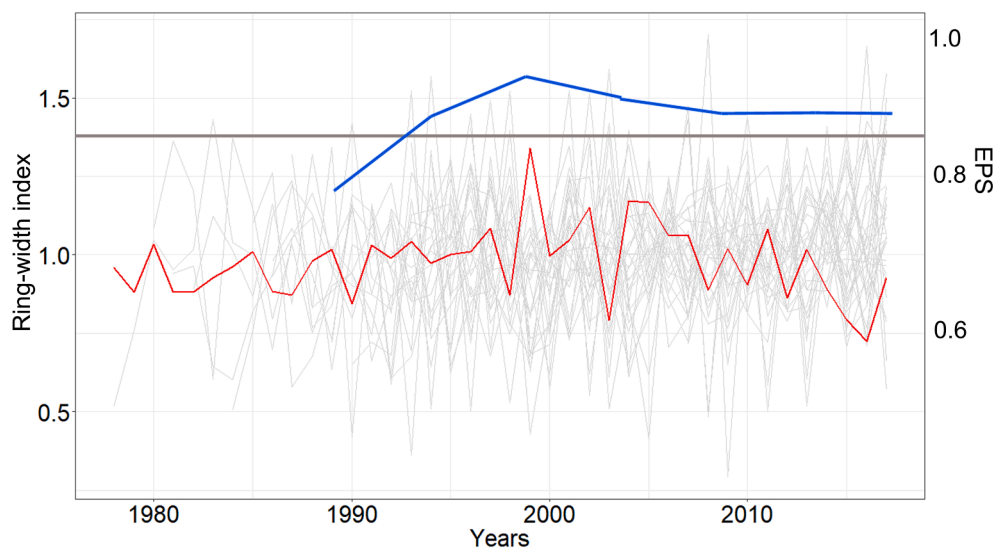


Fig. 8. Idealized statistical analysis applied to tropical and subtropical trees. The graph provides the ring-width index (RWI; light grey lines) as well as a residual chronology (red line) and their changes over time. The bold blue line denotes the running expressed population signal (EPS), whereas the bold grey line indicates the threshold limit of the EPS at 0.85. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

residing and working outside the tropics. Within tropical/subtropical environments, we are aware of only a limited number of tree-ring laboratories or individual researchers located in Argentina, Bolivia, Brazil, Colombia, Costa Rica, India, Indonesia, Malaysia, and Thailand. Due to the lack of large labs and high-end infrastructure, the efforts and implementation of cutting edge (and costly) techniques – including quantitative wood anatomy and/or isotopic analyses – have been restricted to labs in the United States and Europe so far.

Over the past three decades, tropical growth-ring research has overcome challenges of infancy (e.g., limited number of suitable species, limited spatial coverage, shortness of series) to become an important and increasingly growing branch of dendrochronology. Yet, further developments, both methodological and geographic, are still critically needed to bring the science of tropical and subtropical dendrochronology to an adult stage. The lack of ring formation in some tropical species can often be solved by favoring studies focusing on chemical or

stable isotopic signals in tropical/subtropical woods and by examining the wood anatomy of species to unveil annual ring formation (Speer, 2010). Progress can also be expected by simply developing multiproxy approaches relying on the detection and utilization of stable isotopes, radioactive isotopes, genetic information, wood chemistry, and wood anatomical structures in the annual rings (Pearl et al., 2020). In this way, one can expect that dendroecology will likely contribute to solving some of the remaining challenges in tropical forestry, ecological research and the applications of techniques that rely on growth rings as well but would contribute to the understanding of tropical/subtropical geomorphology, archaeology and chemistry (Worbes, 2002; Schöngart et al., 2017; Pompa-García and Camarero, 2020).

To extend the understanding of annual ring formation in tropical and subtropical trees further, it will be critical to develop (a) catalogue(s) of species of known dendrochronological potential, to better apprehend their wood anatomical features, and to diversify the suite of different

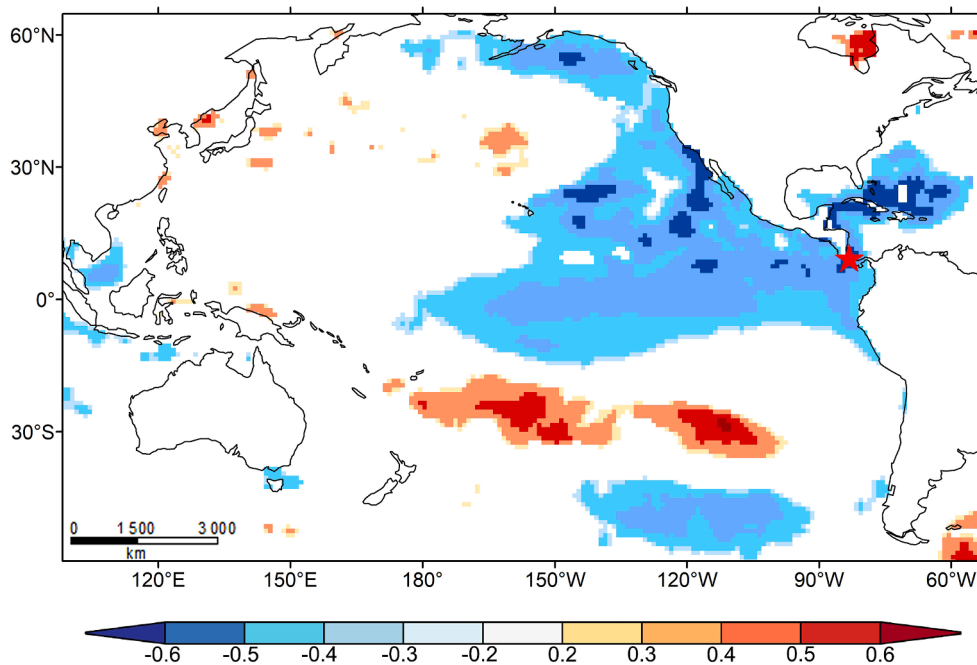


Fig. 9. Example of spatial correlation between a residual ring width index (RWI) chronology and December Sea Surface Temperature (SST). Here, growth rings can be used to reconstruct La Niña events. The red star indicates the study site from which the chronology was built (Modified from Quesada-Román et al., 2020b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analysis and approaches used to study growth rings in tropical trees. Furthermore, we call for a more systematic use of dendrometers and the continuous measurement of diameter growth and tree cambial activity (Worbes, 1995) as these tools could help in the major task of improving the understanding of growth ring formation in tropical trees further and would allow comparison of dendrometer results with high-resolution climatic data, thereby providing information on growth rhythms in trees. Another way to increase our understanding of growth patterns in growth rings is by realizing experiments in planted trees, by controlling rainfall and drought events so as to simulate dissimilar conditions that would induce anatomical responses under normal conditions along the year (Van Camp et al., 2018; Hayden et al., 2019). Despite the pernicious effects of non-native species in tropical as well as subtropical environments, they can play a non-negligible role in regional species richness and have a quite direct effect on conservation goals and ecosystem services (Schlaepfer, 2018). In terms of dendrochronology, non-native species can be valuable candidates when it comes to enhance our understanding of climatic, ecological, and geomorphic signals contained in growth rings that may not have been easily recognized in the annual growth rings of tropical and subtropical chronologies.

Endemism is higher in the tropics than in any other region of the world, especially in the wet tropics where tropical rainforests are found (Hobohm, 2014). This vast reservoir of wet tropical vegetation still waits to be exploited by dendrochronologists. Here, one would need to clearly change the common mentality of using only common or well-known species; instead, we as a community will challenge the discipline and to go ahead for new endeavors that are likely to yield interesting results from an environment that is increasingly threatened by climate change and human exploitation (Hobohm, 2014). To date, many of these regions with high endemism remain in critically understudied regions (Zhao et al., 2019), both in lowlands but especially also in the mountain systems (such as cordilleras and volcanic areas) of Southern Mexico, Central America, the Caribbean and the South American Andes (Pompa-García and Camarero, 2020), but also in the Himalayas, the Indian Ghats, the Pegu Range of Myanmar or the Central Mountain Range of Taiwan (Bhattacharyya and Shah, 2009; Pumijumngong, 2013). In Africa, high mountains and volcanic regions remain largely unexplored as

well, and research yet has to be realized along the African Rift and Cameroon Volcanic Line (Gebrekirstos et al., 2014). In Oceania, the New Guinean Highlands and the many islands of Hawaii remain white dots in terms of tropical and subtropical dendrochronology. By expanding the geographic scope of tropical dendrochronology and by enlarging the thematic fields of research, much more information will become available on how climate has changed at these latitudes, how vegetation has responded (and still is responding) to these changes and how humans have both lived in these pristine regions and changed it through their presence, sometimes even contributing to disasters. Tropical and subtropical dendrochronology can gain in importance further if barriers between disciplines are removed – but even more so also if labs and institutions within the tropics are given the means to develop high-end research locally.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109506>.

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