

Growth rings in tropical trees: role of functional traits, environment, and phylogeny

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Abstract

Key message Subjective and anatomy-based quantitative indices of distinctness of growth rings in tropical trees were related to deciduousness, species maximum height, and also potentially to local topography, independent of phylogenetic relationships.

Abstract Most tropical tree species do not produce distinct growth rings, and the causes of this phenomenon have not received sufficient quantitative study. It has been shown that rainfall seasonality influences the formation of growth rings in some deciduous taxa. However, the numerous exceptions observed call for an examination of additional drivers of the phenomenon. We therefore hypothesized that in addition to seasonal climatic stress, functional and phylogenetic constraints may determine growth-ring distinctness. Ten potentially influential factors were examined in 38 Indian tropical tree species. Distinctness of growth rings was quantitatively assessed based on both subjective visual criteria and objective measures of anatomical characters. Multivariate and phylogenetically constrained

analyses were used to test for functional, environmental, and phylogenetic effects. First, subjective scores of growth-ring distinctness correlated with objective anatomical measurements of vessel size and porosity related to water conductance, but also with additional anatomical characteristics unrelated to water dynamics. Second, ring distinctness variables were primarily related to deciduousness and species maximum height, and also weakly influenced by the topographic slope. A phylogenetic signal was detected in wood specific gravity values, the climatic variable of dry season rainfall, and the subjective distinctness score of growth rings, but accounting for phylogenetic structure did not significantly improve the prediction of ring distinctness. Thus, there was no evidence of an evolutionary constraint on the relationship in our sample of species. Our study thus demonstrates how distinctness of growth rings in tropical trees can be objectively represented on a continuous scale, and provides a quantitative explanation for its variability.

Keywords Angiosperm · Distinctness of growth rings · Deciduousness · Drought stress · Phylogenetic constraint · South India

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Introduction

The formation of growth rings is common and well-studied in numerous temperate tree species, whereas among tropical angiosperm dicot trees relatively few species are known to produce distinct growth rings (Wheeler et al. 2007). The internationally accepted standard set of “Features for hardwood identification” (IAWA Committee 1989) suggests that tropical species’ growth rings can be described as “Distinct”, “Indistinct”, or “Absent”,

indicating that growth rings in this part of the world vary widely in terms of visibility and clarity. However, as there are no objective or quantitative standards currently available to define precisely the limits of usage of these terms, there is likely to be much subjectivity in the detection and assignment of growth-ring boundaries by different researchers. The obvious question of why all tropical species do not produce distinct growth rings has been studied previously (Détienne 1989; Alves and Angyalossy-Alfonso 2000; Callado et al. 2001; Marcati et al. 2006; Lisi et al. 2008), but a fine-scale understanding of the biological mechanisms yielding such observed variations is still lacking and this needs to be acknowledged when classifying tropical tree rings (for example, Carlquist 1988; Worbes 1989), especially if they vary substantially within species. A better knowledge of the mechanisms underlying the formation and distinctness of growth rings is also critical for tropical dendrochronological studies (Stahle 1999; Worbes 2002).

Growth rings are likely to be formed when diameter growth reduces substantially or ceases for short intervals of time due to reduction or ending of cambial activity after a growth interval (Alvim 1964; Carlquist 1988; Détienne 1989; Worbes 2002; Lisi et al. 2008; Rozendaal and Zuidema 2011; Mariaux 2016). Thus, a first approach to understanding the determinants of distinctness of tree rings across and within species is to identify different circumstances under which growth ceases long enough to cause ring formation in the wood. Formation of growth rings is expected in ecosystems with seasonally varying environments that produce cyclical plant growth (Creber and Chaloner 1984; Stahle 1999). A common proximate mechanism that causes diameter growth to stop is leaf shedding (deciduousness), which could be triggered by seasonal environmental stress (Alvim 1964; Borchert 1999) and has been clearly linked with dormancy of the cambial meristem in Indian tropical species (Dave and Rao 1982; Rao and Rajput 1999). Crossdating studies have also confirmed that ring formation in some tropical tree species may be related to annual cycles of reduced cambial activity during summer drought (Worbes 1999; Brienen and Zuidema 2005), wet season floods (Worbes 1989; Schöngart et al. 2002), and salinity peaks (i.e., in mangrove swamps; Menezes et al. 2003; Verheyden et al. 2004). These events are experienced by plants as either physical or physiological drought, which shuts down diameter growth and induces ring formation (e.g., floods and salinity may render soils temporarily anoxic, thereby inhibiting root activity and preventing water uptake despite the roots being surrounded by water). From these results, we hypothesize that the seasonality and intensity of water shortage (resulting from local climatic and topographic factors) are positively related to the formation of distinct rings, and also that

tropical deciduous tree species, having evolved to shed leaves in response to water shortage, are more likely to cease growing during the hot dry season and form distinct growth rings compared to evergreen species at the same site. It is possible that the latter also may be vulnerable to reduced cambial activity (or cease cambial activity without shedding leaves) and thus also produce growth rings in the dry season, but this mechanism has not been established clearly in evergreen trees. Consequently, the observation of some evergreen species producing growth rings (Carlquist 1988; Callado et al. 2001; Marcati et al. 2006) has prevented generalization from studies that suggest that leaf shedding is required for growth cessation and ring formation. These observations raise the possibility that endogenous factors (i.e., based on internal rather than external factors, *sensu* Tomlinson and Longman 1981) may also contribute to the formation of growth rings in addition to external environmental stress.

The wood economics spectrum (Chave et al. 2009) and earlier theories of life history strategies (Pianka 1970; Grime 1977) suggest several axes of potential covariation among wood traits depending on environmental variation. Yet, a theory of formation of growth rings has not been developed in response to the recognition of this spectrum, and the status of growth rings in a more comprehensive characterization of ecological strategies is still pending. Resource-demanding early successional and fast-growing trees, which are under selection to maximize biomass growth during the favourable growing season (Pianka 1970; Grime 1977), should be expected to possess large vessel size, high porosity of wood (and thus less dense wood), and large leaves to profit from increased resource availability early in the growing season (Poorter et al. 2010; Reich 2014). As large vessels are vulnerable to embolism, such species would also be expected to produce smaller vessels under low water availability at the end of the growing season (Baas 1982; Carlquist 1988) and/or shut down growth, perhaps via leaf shedding. In fact, ring porous and semi-ring porous species (cf. IAWA Committee 1989) are known to produce narrow vessels at the end of the growing period that are similar to those of arid region species, indicating that hydraulic safety is more important than water conduction efficiency towards the end of a growing season (Carlquist 1988). Occurrence of co-evolved or coordinated syndromes of traits for fast growth, such as large leaves and low wood density (Wright et al. 2006; Chave et al. 2009; Reich 2014), would also make such species more vulnerable to higher evapotranspiration and reduced growth under low soil water and drought conditions compared to conservative and slow-growing species (Ouédraogo et al. 2013), leading to a slowing or cessation of growth during the latter part of a growing season. According to this hypothesis, species with traits

adapted for a fast growth strategy thus may be more likely to show greater vessel size variability across a growth ring, ring porosity, and formation of distinct growth rings under periodic growth cycles enforced by climatic seasonality.

Tree size and growth form are also related to different life history or resource use strategies, which may influence growth cessation and ring formation. For example, in the Brazilian cerrado six tall tree species were observed to produce well-defined and distinct growth rings, and they included both deciduous and evergreen species (Marcati et al. 2006). Studies in tropical evergreen and deciduous forests of India and elsewhere have previously suggested that taller or larger trees may be more vulnerable than smaller trees to the impact of water shortage due to higher exposure and greater demand on stored water (Pélissier and Pascal 2000; Nath et al. 2006; Poorter et al. 2010). We suggest that this is a possible mechanism by which larger trees can be expected to produce more distinct growth rings under drought conditions than smaller trees.

Interactions between intrinsic functional traits and environmental factors may also serve to modulate the physiological stress experienced by different species. Further studies are required to address this possibility, as the likelihood of deciduous or tall trees producing distinct rings may be amplified or reduced depending on the local climatic seasonality regime. Previous studies have also hypothesized that climatic factors, such as temperature, photoperiod, and precipitation, as well as endogenous factors may be responsible for producing growth rings (Tomlinson and Longman 1981; Fahn et al. 1981). In addition, growth-ring patterns appear more complex and diverse in tropical than temperate trees, perhaps due to the continuum of different types existing between cyclic and acyclic growth. In this context, a lacuna in tropical wood anatomy studies has been a lack of systematic investigations into variations in the formation of growth rings across functional types and environments (Sonsin et al. 2012).

In the present work, we addressed the influence of four functional traits on distinctness of growth rings, and hypothesized that their influence is based on species' sensitivity to seasonal drought stress and on their relative position within the fast–slow growth strategy continuum. For ring distinctness assessment, we considered both subjective visual indices of ring distinctness and quantitative indices of anatomical variation between earlywood and latewood (average vessel area and total porosity ratios, explained below). The functional traits used as predictors of these indices were: (1) leaf phenology (evergreen versus deciduous), as deciduous trees obligatorily cease cambial activity during the dry season (Borchert 1999), ring porosity is strongly associated with deciduousness (Boura and De Franceschi 2007), and previous studies have

suggested that deciduous species are more likely to produce distinct growth rings (Stahle 1999; Worbes 1999; Marcati et al. 2006; Nath et al. 2012); (2) species stature (i.e., maximum potential height per species), as tall species tend to be fast growing (King et al. 2006), taller and larger trees have been associated with greater reductions in growth rate during low rainfall years compared to smaller trees (Pélissier and Pascal 2000; Nath et al. 2006) and also appear to be most sensitive to dry season water shortage (Poorter et al. 2010); (3) average leaf length, as longer leaves are associated with species that occur in environments with higher rainfall (McDonald et al. 2003), and larger leaves are associated with faster growth (Wright et al. 2006) and may increase drought vulnerability due to higher evapotranspiration rates than small leaves (Smith 1978; we assume that leaf length, which we measured, is correlated with leaf area, as it was not within the scope of this study to obtain values for the latter); and (4) wood specific gravity, as lighter woods are associated with fast growth, larger vessel size, and greater vulnerability to cavitation during drought (King et al. 2005; Chave et al. 2009). To our knowledge, this is the first study to quantitatively test the influence of multiple functional traits on the formation and distinctness of tropical tree rings.

These ecological and functional attributes are the result of evolutionary processes, and a further issue is whether closely related taxa display common inherited patterns of formation of growth rings, or if convergence has occurred among distant lineages under the influence of common selective forces. As evolutionary processes are known to have driven the diversification of anatomical characters among distinct clades (Schweingruber et al. 2007), we might expect the distribution of growth-ring types across a phylogeny to reflect the imprint of these processes. It has been suggested that evolutionary relationships may constrain the formation of growth rings in tropical trees at the level of genus (Détienne 1989), but there is also evidence of growth-ring anatomical variation within genera (Heimlich and Wetmore 1939; Chowdhury 1953; Marcati et al. 2006). If growth rings in tropical trees are assumed parsimoniously to be produced by similar physiological mechanisms as in temperate trees, cessation of cambial activity (which results in the formation of growth rings) that has evolved as a strategy in temperate trees facing low winter temperatures and frost damage may be physiologically analogous to similar reduction of cambial activity that has evolved to help tropical trees avoid seasonal drought stress and damage related to embolisms, regardless of taxonomic affiliation. This could potentially lead to evolutionary convergence of growth cessation and ring formation traits across distant clades. In fact, many previous multi-species studies on climatic stress and formation of growth rings in

tropical trees have not addressed phylogenetic constraints (Alves and Angyalossy-Alfonso 2000; Lisi et al. 2008; Marcati et al. 2006; Sonsin et al. 2012). It remains to be established whether climatic factors and functional traits are more widely influential than phylogenetic constraints in tropical growth-ring development and distinctness, as well as whether there are any phylogenetic constraints on the covariation of growth-ring traits and the hypothesized predictors. A better understanding of the respective influences of ecological and evolutionary processes is thus needed, which would benefit or complement palaeobotanical and palaeoclimatological research on past ecosystems. Therefore, our current objective is to address how wood anatomical features associated with the formation of growth rings vary across Indian tropical trees, in relation to functional traits, environmental conditions, and phylogenetic affinities, making this the first study to examine the joint effects of these factors on tropical tree-ring formation.

We tested the following main hypotheses, of which the first relates to the development of appropriate methodology and the last two relate to the ecological aspects of the study:

H1: Distinctness of growth rings in tropical tree species can be objectively quantified in terms of measurable anatomical features, which agree with subjective (visual) assessments.

H2: Intrinsic functional traits that increase a species' drought sensitivity are associated with distinct growth rings, and are independent of phylogenetic effects. In particular, we hypothesized that the traits of deciduousness, species stature, leaf length, and the inverse of wood specific gravity would be associated with more distinct rings.

H3: The variability and influence of environmental factors (i.e., the topographic variables of elevation, slope, and topographic wetness index, as well as the climatic variables of dry season rainfall and potential evapotranspiration) in determining the formation of growth rings are independent of phylogenetic effects.

Methods

Study area and data collection

The study area was Kodagu district (approximately 11°55'–12°49'N and 75°22'–76°10'E, Fig. 1) in the Western Ghats of India, a global biodiversity hotspot (Myers et al. 2000). The region is strongly influenced by heavy rainfall annually during the monsoon period (approximately June–October), which alternates with 3–5 months of dry season (i.e., during November–March when the monthly precipitation is <100 mm). The dry season is more intense in the

eastern and northern side and is characterized by water shortage, high temperature, and high evaporative demand (Pascal 1988). The altitude declines from west to east, with a rainfall gradient from 5000 to 800 mm year⁻¹ in the same direction (Fig. 1). The landscape is hilly in the west and undulating in the east (Fig. 1), and dominated by traditional coffee plantations in which native trees have been retained to shade the coffee bushes, and these are interspersed with private and government-owned forest fragments. The natural vegetation includes wet evergreen forests on the western side grading into moist or semi-evergreen forest in the central region and dry deciduous forests in the east, with the driest vegetation types in the northeast (Pascal 1988; Elouard 2000).

Small cylindrical wood samples, with a diameter of approximately 1.5 cm and length of 2 cm, were obtained using a wood punch at a height of approximately 1–1.5 m on the main trunk of trees. The sampled trees belonged to 38 locally common angiosperm dicot species belonging to 24 families. One-to-four species were sampled per family (Appendix Table 5), with one-to-two trees sampled per species depending on availability (three replicate individuals were used for one species due to high intraspecific variability in the vessel area ratio measure). Eleven families had at least two species sampled, while 13 families had one species sampled. Twenty-nine species had more than one tree (replicate) sampled, and a total of 68 trees were used for this study. In species that had more than one replicate sampled, for 23 species, the individual trees were sampled from separate sites approximately 5–57 km apart, while six species had two replicates sampled at different locations on the same site (<1 km apart). Thus, replicate trees per species were obtained from an average distance of 12.9 km apart, and for the majority of species, the replicates provided intraspecific spatial variability. Sampled trees ranged in girth at breast height (“gbh”, circumference measured at 1.3 m above the ground) from 34 to 348 cm (average = 130 cm) and were in good health. The minimum tree size targeted was 30 cm girth, as juvenile trees are sometimes less likely to show tree-ring formation (Détienne 1989; Groenendijk et al. 2014; Mariaux 2016). Wood samples were extracted from locations on the stem that were free of knots, buttresses, and injuries.

Due to legal restrictions over extraction of wood samples from Government-administered forests in Karnataka, our study focused on privately owned shade-coffee plantations (agroforests) or forest patches subject to permission from the landowners, which limited the extent of our sampling design. Most of the wood samples were obtained from 15 traditional multi-species shade-coffee plantations, and eight samples were obtained from two private forest fragments without coffee (i.e., a total of 17 sites, Fig. 1). The plantation sites largely corresponded with those in

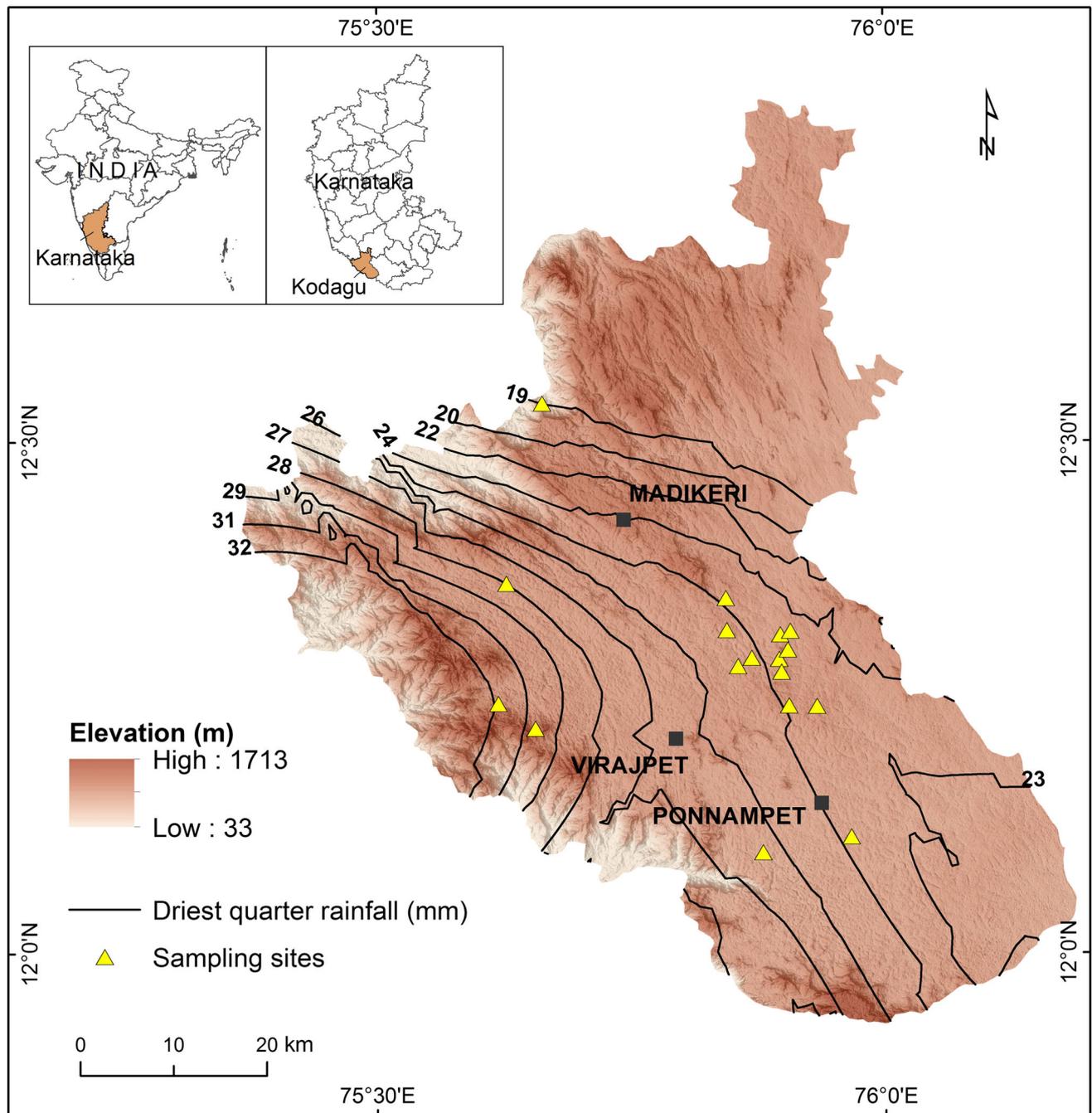


Fig. 1 Map of the study area Kodagu, Western Ghats of India, showing topographic relief, 17 sampling sites, and rainfall (mm) isoclines during the driest quarter. The topographic map was downloaded from the ASTER GDEM website ([https://asterweb.jpl.](https://asterweb.jpl.nasa.gov/gdem.asp)

[nasa.gov/gdem.asp](https://asterweb.jpl.nasa.gov/gdem.asp)), and rainfall isoclines were calculated by simple kriging using site-based dry season rainfall data downloaded from the WorldClim database (<http://www.worldclim.org>, Hijmans et al. 2005)

which previous tree growth studies were carried out (Nath et al. 2011, 2012), and trees of 38 relatively common species were sought throughout the plantations with the help of local staff. The plantation and forest sites were situated at a distance of 1.1–57.3 km apart from each other (Fig. 1).

Tree identification was confirmed using field guides, photo documentation, and consultation with botanical experts at the French Institute of Pondicherry. Species nomenclature follows that used by Mabberley (2005) and the Herbarium of the French Institute of Pondicherry (HIFP, <http://www.ifpindia.org/content/herbarium>).

Measurement of growth-ring variables

Microscope slides were prepared from 68 wood samples by obtaining sections approximately 20–30 μm thick using a GSL-1 sledge microtome and staining with safranin (Gärtner and Schweingruber 2013). Very hard woods were softened by placement of samples under negative pressure using a vacuum pump (which released trapped air bubbles from within the vessels) and heat (75° C water bath) for several days, and, in a few extreme cases, by soaking for a few days in $\leq 2.5\%$ sodium hydroxide solution. The resulting microslides were compared against anatomical details available in the published literature and online sources (Gamble 1922; Pearson and Brown 1932; Purkayastha 1999; InsideWood website: inside-wood.lib.ncsu.edu/) to confirm similarity of anatomical features and reduce the possibility of obtaining false negative results (i.e., failure to detect rings that had been detected by others). If species were described to have “distinct” or “fairly distinct” growth rings by others but found to have a lower degree of distinctness in our sample, a second replicate collected from a different tree of the same species (if available) was used to prepare a fresh microscope section to confirm the level of distinctness. The anatomical measurements were then averaged across replicates to give a single value per species. In general, our microscopic sections matched or exceeded the level of distinctness of growth rings described in the literature. In *Santalum album* (only one replicate available), our sample showed no rings, whereas it was earlier described as having distinct rings (Gamble 1922) or with the possibility of absent rings at some locations due to intraspecific variation depending on the environmental context (Pearson and Brown 1932). The results were not significantly different if *S. album* was deleted during analyses, and therefore, it was included in the results reported below.

Quantitative measures of growth-ring occurrence and distinctness were developed, which involved the use of subjective and objective techniques as well as incorporated different biological properties (overall visual assessment versus average vessel size and total porosity). Two subjective variables were developed based on visual characterisation of the overall distinctness of growth rings in microscope slides of wood anatomy as follows: (1) the overall level of “Visual distinctness” was scored according to the observed clarity of growth rings observed (i.e., distinct = 1, less distinct = 0.5, absent = 0) and (2) several growth-ring features were evaluated and combined to create a “Cumulative or composite score” representing overall ring distinctness. For the cumulative score, nine variables were selected based on recommendations from previous studies (IAWA Committee 1989; Nath et al. 2012). These features were:

1. Porosity type (ring porous, semi-ring porous, or diffuse porous).
2. Presence of a visible smooth continuous line (i.e., the growth-ring boundary line) separating the earlywood (EW) of a new annual growth season from the latewood (LW) of the previous season.
3. Vessel size differences between EW and LW across a common growth-ring boundary.
4. Vessel group size differences between EW and LW (i.e., solitary vs. grouped vessels).
5. Presence of marginal parenchyma at the growth-ring boundary (i.e., initial or final parenchyma).
6. Fibre density difference between EW and LW.
7. Parenchyma type difference between EW and LW.
8. Flattened row(s) of cells at the growth-ring boundary.
9. Fibre zone or band containing no (or very few) vessels, at the ring boundary in EW or in LW.

Qualitative scores were assigned per growth-ring image, for each of the above features by subjective observation of growth rings and assigning a score of 1 (feature is clearly visible), 0.5 (feature is not clearly visible or rudimentarily formed), or 0 (feature is absent). In the case of Porosity type, ring porous species were assigned a score of 1, semi-ring porous species were scored as 0.5, and diffuse porous species were scored as 0. From these values, a total cumulative score per tree-ring image “Cumulative distinctness score” was obtained by summing the values across all nine features. A single representative cumulative score was then obtained per species by averaging across the respective replicates.

Two objective quantitative measures of distinctness of growth rings were also obtained in terms of average vessel size and total vessel area (i.e., “porosity”), as vessel size and number are among the most reliable environmentally responsive wood traits (Baas 1982; Boura and De Franceschi 2007; Wheeler et al. 2007). We expected these objective continuous measures of distinctness of growth rings to reflect this sensitivity and variability along environmental gradients. Growth rings, when present, were analyzed quantitatively using the image analysis software ImageJ (Schneider et al. 2012) to obtain data on average vessel size and total vessel area in EW and LW on opposite sides of a growth-ring boundary line. To obtain quantitative values, a rectangular section of the image, having similar dimensions on opposite sides of a growth-ring boundary, was extracted from the EW and LW areas, respectively. Whenever possible, attempts were made to randomly select the location of these sample windows across the wood section, but this was restricted to areas with flat and unambiguous growth-ring boundaries, sufficient distance between two consecutive ring boundaries for distinguishing earlywood and latewood, and absence of tears or

deformities in the anatomical section. The width of the rectangles corresponded approximately to the height of the largest vessel next to the boundary in EW. In general, one image was measured per individual tree, but in eight species with growth rings, which had only one replicate individual per species, a second image was obtained from a different location on the microslides produced from the same wood sample. Two objective quantitative variables were then calculated as follows:

1. Average vessel area ratio (i.e., average vessel lumen area (μm^2) in EW divided by the corresponding value from the LW section across a common ring boundary). Depending on vessel sizes and the extracted image area, the number of vessels measured per image in EW ranged from 1 to 59 (average = 8.6) and in LW it ranged from 1 to 35 (average = 9.5).
2. Total porosity ratio (i.e., the total lumen area of vessel tissue divided by total observed area, and calculated as a ratio of this value in EW versus in LW).

Functional, environmental, and phylogenetic predictors

Functional trait data

Functional traits of species were collected from various published and online sources and included data on species' leaf phenological strategy (deciduous versus evergreen), species stature (<http://www.biotik.org>; Gamble 1935; Nazma et al. 1981; Pascal 1988; Murthy and Yoganarasimhan 1990; Rani et al. 2011; see Appendix Table 5), and wood specific gravity (Chave et al. 2009; Zanne et al. 2009). Although deciduous species generally increase in frequency as rainfall decreases, we sampled co-occurring deciduous and evergreen species at many sites that spanned a range of rainfall conditions, in order to check for effects of deciduousness that were independent of the local climatic conditions. Deciduousness was not significantly related to climatic variables in our data set (Appendix Table 6). Average leaf length was obtained by measuring five leaves per species from preserved herbarium specimens (HIFP) that were collected at different locations in the Western Ghats. We acknowledge that there may be some underestimation of size due to shrinkage, especially for small-leaved species (Queenborough and Porras 2014), but do not expect it to significantly change the hierarchy of leaf length across species.

Environmental data

The geographical coordinates were recorded per coffee plantation or forest fragment during sample collection

using a GPS receiver (Trimble Juno SB). In a few cases where GPS data were missing, the approximate coordinates were obtained from Google Earth. The corresponding climate and elevation data were downloaded from the WorldClim Global Climate Data website (<http://www.worldclim.org>, Hijmans et al. 2005) at 1 km resolution and used to calculate potential evapotranspiration index values per site (PET) from the Thornthwaite and Hargreaves equations, using the R package 'SPEI' (<https://cran.r-project.org/>). The average PET value for the driest quarter (January to March, assuming that drought stress effects are likely to be most extreme during this period) was calculated per site and used in the analyses. The Bioclim variable # 17 (total rainfall during the driest quarter, <http://www.worldclim.org/bioclim>) was also included in our models. As the sites were separated by >1 km from all others (Fig. 1), they corresponded to different cells within the Bioclim data set, at 1×1 km resolution. As the species were also generally sampled at two sites that were on average 12.9 km apart, the climatic data averaged across these two replicates provided a unique climatic value per species. In the case of 15 species, the climatic data were shared by a few sets of two-to-five species that happened to be sampled at exactly the same sites.

In addition, for each site, we calculated the values of mean slope (i.e., topographic incline) and a steady-state wetness index or Topographic Wetness Index (TWI, also known as Compound Topographic Index or CTI, Gessler et al. 1995; Moore et al. 1993). The TWI indicates potential moisture accumulation in relation to the slope and upstream contributing area per-unit width orthogonal to the flow direction (i.e., a quantification of catenary topographic convergence) that was calculated as

$$\text{TWI} = \ln(\alpha(\tan\ominus))$$

where α = catchment area [(flow accumulation + 1) \times (pixel area in m^2)], and \ominus = slope angle in radians. Catchment area, flow accumulation, and slope values were calculated with ArcGIS (<http://www.arcgis.com>) from the ASTER Global Digital Elevation Model (NASA LP DAAC 2011).

Phylogenetic classification

Plant families followed the APG III classification system (The Angiosperm Phylogeny Group 2009). The phylogeny of families was extracted from the phylogenetic website (phylodiversity.net/phyloomatic/) using the R package 'taxize' (R20120829 version of the family tree), and the species were added at the end of the branches. The resulting phylogeny of species was ultrametric.

Data analysis

The dependent variables representing qualitative and quantitative measures of formation of growth rings and distinctness were the following (Table 1):

1. Qualitative (subjective, ordinal) scores: visual distinctness (scored as 0, 0.5, or 1).
2. Quantitative (subjective) scale: cumulative distinctness score (range 0–6.75).
3. Quantitative (objective) measures: average vessel area ratio and Total porosity ratio (range 0.59–11.4 and 0.29–6.36, respectively).

We tested for significant associations between subjectively and objectively obtained ring distinctness scores, and for possible grouping of species along principal axes of variation, by multivariate ordination of the four variables related to distinctness of growth rings. We used the Hill and Smith (1976) method to accommodate both categorical and quantitative indexes, using the *dudi.hillsmith* function in the R package ‘ade4’ (Dray and Dufour 2007).

We then investigated the influence of the following hypothesized drivers on the dependent variables (Table 1):

1. Life history and functional traits (species level): leaf phenological type (evergreen/deciduous), species stature, average leaf length, and wood specific gravity.
2. Environmental variables (associated with site coordinates): the three topographic variables of elevation, slope and topographic wetness index (TWI), and the three climatic variables of rainfall during the driest

quarter and two potential evapotranspiration indices (Thornthwaite and Hargreaves PET Indices).

3. Phylogeny: phylogenetic tree imported and analyzed using the R package ‘ape’ (Paradis et al. 2004).

First, we tested whether the growth-ring features and their hypothesized predictors were more similar among close relatives in the phylogeny (phylogenetic signal, Blomberg and Garland 2002). For this, we compared the variance of phylogenetically independent contrasts (PICs) to a null expectation, for all the dependent and independent variables using species’ average values (Blomberg and Garland 2002; Blomberg et al. 2003). The null expectation was obtained by shuffling the tips of the phylogenetic tree (*phylosignal* function in the R package ‘picante’, Kembel et al. 2010) and randomly resolving the polytomies (i.e., nodes with more than two lineages descended from a single ancestral lineage) into dichotomies within the tree. These results were repeated with 1000 iterations of random selection of individuals from among the available replicates per species. This randomisation test helped to assess if significant values obtained using species average values were robust in the presence of intraspecific variation.

We then performed Phylogenetic Generalized Least-Squares regressions (pGLS) to relate each of the three quantitative growth-ring variables to the hypothesized functional and environmental predictors (*gls* function in R package ‘nlme’, Pinheiro et al. 2016), while considering a phylogeny-dependent correlation structure. This correlation structure was based on a Brownian motion model of trait evolution and we performed ANOVA of the models to

Table 1 Basic statistics of the functional, topographic, climatic and distinctness variables used in the study

Variable type	Average	Median	Standard error	Minimum	Maximum
Independent variables					
Leaf phenological type	0.58	1.00	0.08	0.00	1.00
Species stature (m)	28.05	30.00	1.80	8.00	50.00
Avg. leaf length (cm)	12.40	13.41	0.84	1.06	23.66
Wood specific gravity	0.65	0.65	0.03	0.40	1.08
Altitude (m)	914.83	932.00	14.98	487.00	1048.50
Slope (°)	10.37	9.74	0.82	3.41	30.53
Topographic wetness index (TWI)	7.94	7.47	0.23	5.83	11.99
Dry season rainfall (mm)	24.99	24.00	0.36	19.00	32.00
Thornthwaite PET index	89.13	88.35	0.79	82.93	113.02
Hargreaves PET index	134.52	135.43	0.42	127.31	140.88
Dependent variables					
Visual distinctness	0.58	0.50	0.06	0.00	1.00
Cumulative score	2.88	2.88	0.28	0.00	6.75
Average vessel area ratio	2.41	1.64	0.37	0.59	11.38
Total porosity ratio	1.88	1.62	0.20	0.29	6.36

test the contributions of functional and abiotic predictors, as well as to test the importance of adding phylogenetic information. The full model with ten predictor variables was tested with (pGLS) and without (GLS) phylogenetic structure, and the better model per quantitative growth-ring variable was selected based on reduction of the Akaike Information Criterion (AIC) value. This test was also checked for robustness with 10,000 iterations of random selection of a single replicate per species.

Finally, after testing if the phylogenetic structure contributed to the relationship, we expected to retain or remove it from the final model of growth-ring distinctness when testing the contributions of each predictor. We obtained the most parsimonious model for each of the three quantitative growth-ring variables, by starting with an initial full GLS model comprising all the ten independent variables. In some cases, the dependent variable was transformed to meet the assumption of normality of residuals, and for two models, a single independent variable had to be deleted from the initial full model to avoid multicollinearity (details provided in Table 4). To test for multicollinearity, the final reduced models were tested for variance inflation factor values (VIF) using the *vif* function in the R package ‘car’ (Fox and Weisberg 2011). A backward stepwise (model reduction) procedure was implemented (using the *stepAIC* function in the R package ‘MASS’, Venables and Ripley 2002) on this initial model to remove less important predictors, and model selection was based on reduction of the Akaike Information Criterion (AIC) value. Jackknife support for the final parsimonious model was obtained through iterations of the stepwise deletion process (with a different species excluded in every iteration), to establish the robustness of the final parsimonious model using different subsets of species. For the final model that was supported by the highest number of iterations, the jackknife results were used to obtain a confidence range (minimum and maximum, rather than 95 % confidence intervals, due to low sample size) for each estimated coefficient in the model. All analyses were carried out using R, version 3.2.3 (R Development Core Team 2015).

Results

Quantifying distinctness of rings

Among the 38 species examined, 11 species were classified as having distinct growth rings (29 %), 21 species as having rings with generally variable to low distinctness (55 %), and the remaining six as having no detectable rings (16 %, Appendix Table 5). All species with ring porous or semi-ring porous wood (i.e., vessel size, and sometimes also frequency, being many times greater in EW than in LW across a growth-ring boundary) had growth rings that

were distinct and clearly detectable. In the case of a few diffuse porous woods also, distinct rings could be observed due to the presence of detectable vessel size differences, extreme fibre density differences, or marginal parenchyma rows that clearly marked the growth-ring boundary (Fig. 2). The six species with absent rings (scored as zero for visual distinctness and cumulative score) were exclusively evergreen. The proportion of deciduous species increased with increasing visual distinctness of rings, and only one of the 11 species with distinct growth rings was evergreen (*Michelia champaca*, Magnoliaceae).

The two subjective scores of distinctness of growth rings were significantly correlated between themselves (Spearman Rho (ρ) = 0.89, p value < 0.0001), the two objective ratio measures were also significantly correlated between themselves (Spearman ρ = 0.59, p < 0.0001), and each of the subjective scores was significantly correlated with the two objective measures (lowest Spearman ρ = 0.42, all values p < 0.01). This indicates that there was consistency between subjective and objective scores, and the qualitative concept of distinctness of growth rings has a logical basis that can be reliably represented by quantitative methods. Ordination of the four growth-ring variables in Hill–Smith analysis captured 88.5 % of overall variation with the first two axes. All four growth-ring variables were negatively correlated with the first axis (accounting for 73.6 % of total variation), which is indicative of a consistent underlying gradient of ring distinctness in the data. However, the subjective and objective variables were correlated in opposite directions with the second axis (accounting for 15.4 % of total variation) (Fig. 3). This suggests that the two objective variables, vessel size and porosity ratio, may be able to quantify distinctness of growth rings adequately for some species (especially those with ring porous and semi-ring porous anatomy), but may be inadequate for other species in which the growth ring is characterized by alternative anatomical features, such as fibre differentiation, marginal parenchyma, fibre zones, etc. These additional features were incorporated implicitly or explicitly within the subjective scores.

Phylogenetic effects

Significant phylogenetic signal was established in only two of the nine explanatory variables tested (wood specific gravity and dry season rainfall), and in one of the quantitative growth-ring variables (cumulative distinctness score, Table 2). To test the robustness of these results, we reclassified two species, *Phyllanthus emblica* and *Bischofia javanica*, within the family Phyllanthaceae, in order to align our original classification with that of The Plant List (<http://www.theplantlist.org/>). The results were similar when using the new classification and the

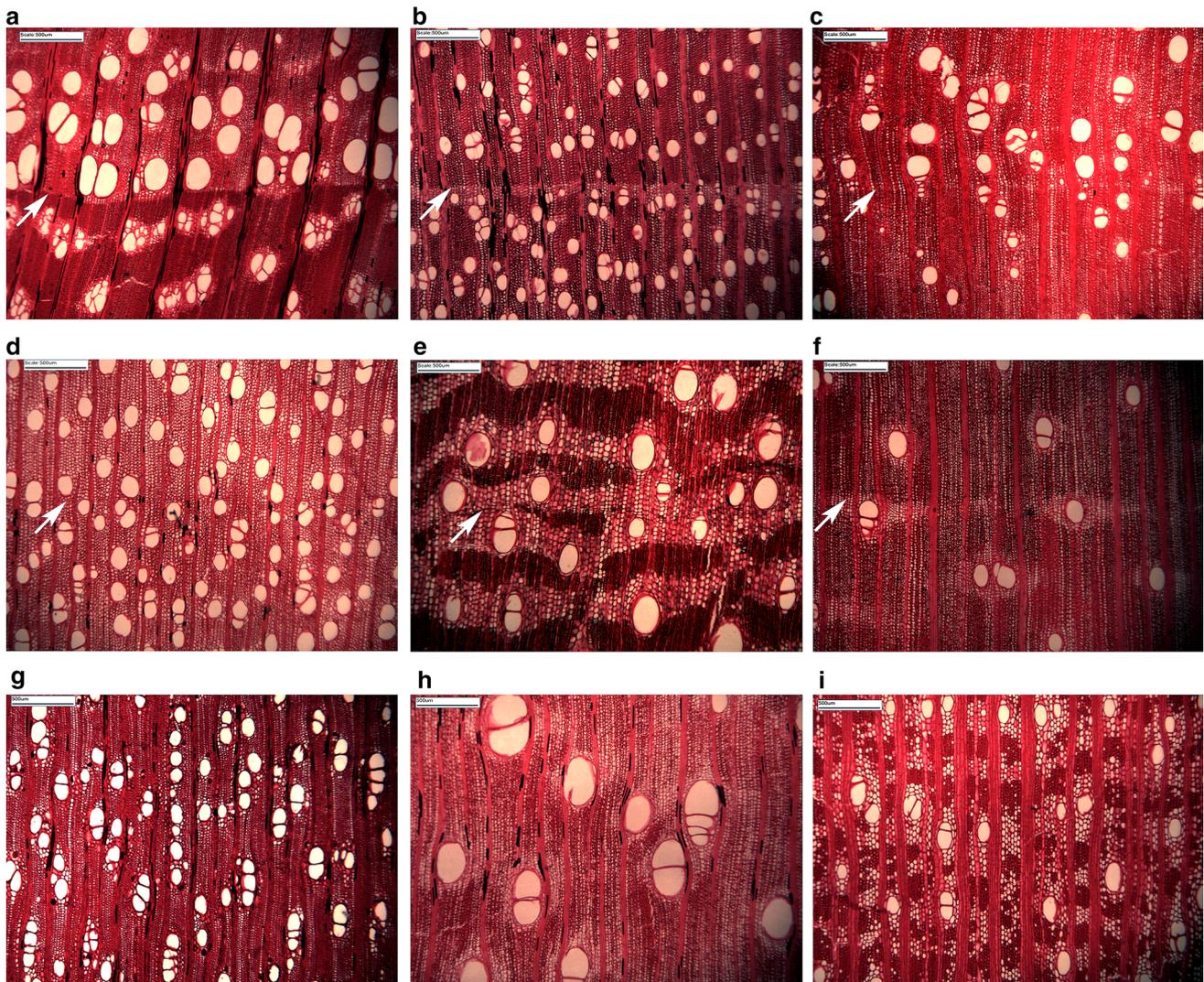


Fig. 2 Wood anatomy of nine tropical Indian tree species showing different levels of distinctness of growth rings, from easily recognisable distinct rings to less distinct and absent rings. In the first six images, earlywood is above and latewood is below the horizontal growth-ring boundary (indicated by arrows). Species shown are: **a** *Celtis tetrandra* (Ulmaceae, distinct ring), **b** *Michelia champaca* (Magnoliaceae, distinct), **c** *Gmelina arborea* (Verbenaceae, distinct),

d *Persea macrantha* (Lauraceae, less distinct), **e** *Terminalia bellirica* (Combretaceae, less distinct), **f** *Artocarpus heterophyllus* (Moraceae, less distinct), **g** *Cinnamomum malabatum* (Lauraceae, absent), **h** *Artocarpus hirsutus* (Moraceae, absent), and **i** *Garcinia cambogia* (Clusiaceae, absent). Scale bar at top left of each photo represents 500 μm (colour figure online)

same two explanatory variables as above had significant phylogenetic signal, but none of the quantitative dependent variables had significant results. The lack of phylogenetic signal in most of the explanatory and independent variables was further supported by an iterative procedure that randomly selected one of the two available replicate values per species and repeated the statistical test 1000 times. The randomization procedure produced a significant phylogenetic signal in 100 % of iterations only for wood specific gravity, whereas a significant phylogenetic signal was produced in a relatively small proportion of iterations for two additional variables: dry season rainfall

(33 %) and cumulative distinctness score (31 %). This indicates that the significant PIC result obtained initially with average species values was not robust in the latter two variables (Table 2; the same result was obtained when tested with the new classification of species). When plotted on the phylogenetic tree to illustrate phylogenetic constraint (Fig. 4), almost all of the dependent and independent variables in this study showed no patterning at a deep phylogenetic level. In other words, the traits vary broadly within higher taxa. Therefore, the phylogenetic signal, when significant (as in the case of wood specific gravity), may be related to trait conservatism at a finer

Fig. 3 Species scores plotted on the first two principal axes representing maximum variation in the data, which was obtained by Hill-Smith ordination of four variables that included subjective assessment of growth-ring distinctness (Visual distinctness score and Cumulative distinctness score; *top left*) and objective assessment of growth-ring distinctness (Vessel area ratio and Porosity ratio; *bottom left*). Numbered squares represent different species, whose growth-ring distinctness values were averaged across replicates. Inset panel shows eigenvalues of the four ordination axes. The *scale* of the graph is indicated by the *grid*, and the size of which is given in the upper right corner (here, the length of each *grid square* is one unit)

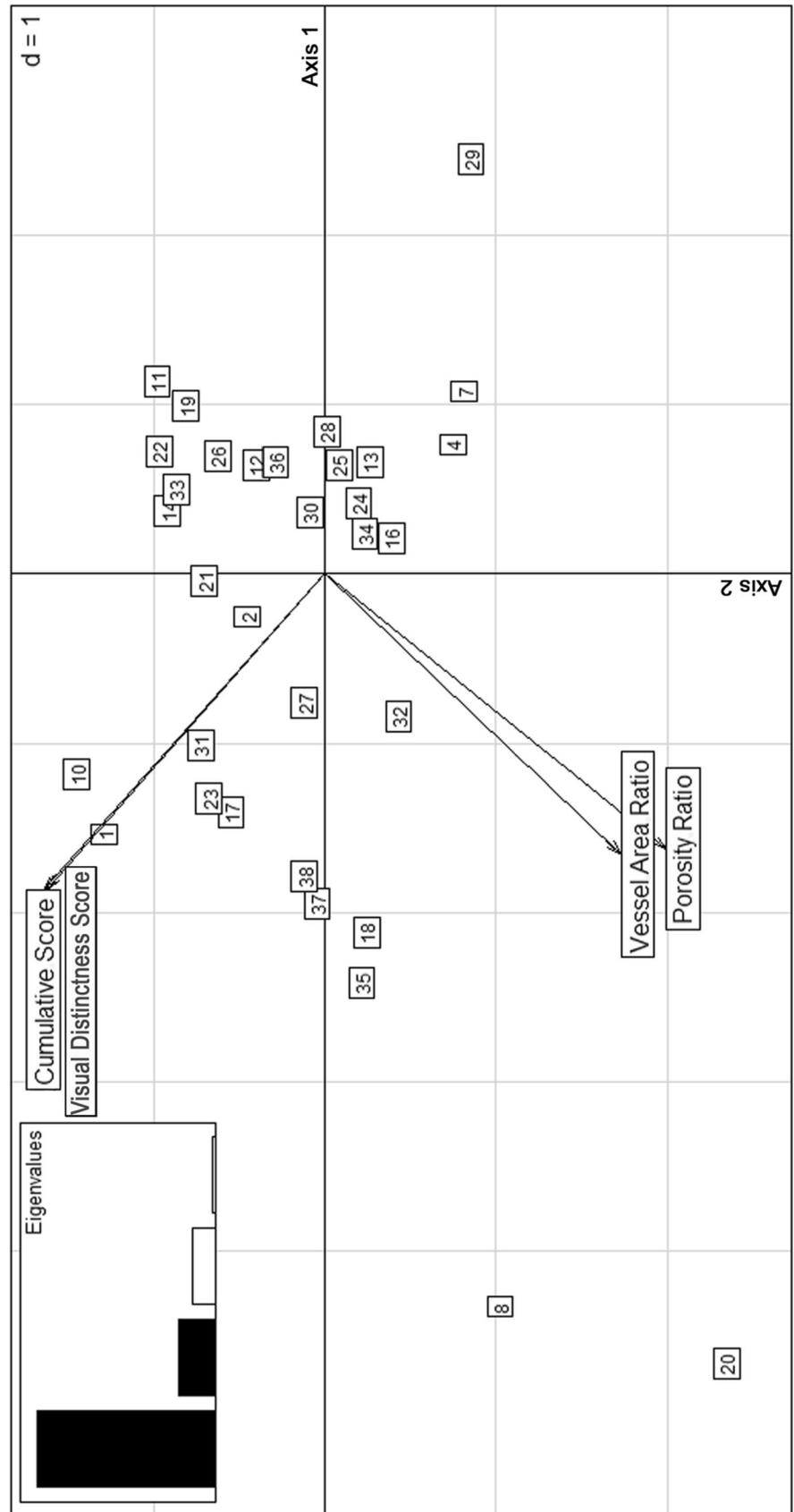


Table 2 Results of testing for phylogenetic signal (via phylogenetic independent contrasts, PIC) in nine independent functional and environmental variables and in three dependent growth-ring variables

Variable, type	K-statistic (rand-value)	PIC var. <i>p</i> (rand-value)	Prop iter. <i>p</i> < 0.05 (%)	PIC Z-score (rand-value)
<i>Independent variables</i>				
<i>Functional traits</i>				
Species stature (m)	0.09 (0.09)	0.34 (0.36)	0	−0.43 (−0.39)
Avg. leaf length (cm)	0.10 (0.10)	0.20 (0.18)	0	−0.90 (−0.92)
Wood specific gravity	0.12 (0.12)	0.03* (0.03*)	100	−1.79 (−1.79)
<i>Environmental: topography</i>				
Altitude (m)	0.08 (0.08)	0.49 (0.53)	0	0.14 (0.11)
Slope (°)	0.07 (0.08)	0.59 (0.43)	1	0.24 (−0.21)
Topographic Wetness Index (TWI)	0.07 (0.08)	0.77 (0.59)	0.1	0.83 (0.29)
<i>Environmental: climate</i>				
Dry season rainfall (mm)	0.12 (0.11)	0.04* (0.22)	33.4	−1.70 (−1.09)
Thornthwaite PET index	0.08 (0.08)	0.52 (0.57)	0	0.30 (0.28)
Hargreaves PET index	0.11 (0.10)	0.06 (0.22)	20.6	−1.52 (−0.98)
<i>Dependent variables (growth-ring distinctness)</i>				
<i>Subjective quantitative</i>				
Cumulative score	0.12 (0.11)	0.04* (0.10)	30.7	−1.58 (−1.38)
<i>Objective quantitative</i>				
Average vessel area ratio	0.08 (0.08)	0.43 (0.44)	0	−0.12 (−0.14)
Total porosity ratio	0.07 (0.07)	0.81 (0.76)	0	0.97 (0.82)

The values in parentheses are the average values obtained after 1000 iterations of random selection of replicates per species (*rand-value*). The proportion of randomized iterations in which the PIC variance *p* value was <0.05 is provided in the fourth column for each variable (*Prop iter. p* < 0.05). The ordinal variable, visual distinctness score, and binary variable, leaf phenological type, were not tested here

Statistical significance: * *p* < 0.05

taxonomic level within families (i.e., more conserved at the genus level).

Ordination of the four variables related to distinctness of growth rings together with Hill–Smith analysis at the level of families showed that 11 families, in which more than one species was sampled, had overlapping scores on the first two ordination axes. Such overlaps were inconsistent with the expected relationships observed in a dated family phylogenetic tree (Fig. 5), which is further indicative of a lack of phylogenetic signal. This also suggests that distinctness of growth rings may not be constrained over long evolutionary time frames and possibly is an evolutionarily labile trait.

Phylogenetically constrained linear models of distinctness of growth rings, which included all four functional traits and six abiotic predictor variables together, did not show improved fit to the data compared to null models with no phylogenetic correlation structure (AIC of cumulative distinctness score model with phylogenetic structure = 178 and without phylogenetic structure (null) = 171; AIC of vessel area ratio model with phylogenetic structure = 213 and null = 195; and AIC of

porosity ratio model with phylogenetic structure = 176 and null = 165). The lack of improved fit was fully supported by the test with randomized selection of replicates per species using 10,000 iterations for all three dependent variables (these results were confirmed after reclassifying *P. emblica* and *B. javanica* within Phyllanthaceae, according to The Plant List's classification of species). This indicates that there was no significant influence of phylogeny, and hence no evolutionary constraint, in the dependence of growth-ring variables on their functional and environmental predictors.

Correlation of explanatory factors with distinctness of growth rings

As there were no phylogenetic effects, we checked for empirical relationships between the explanatory variables and each of the variables related to distinctness of growth rings, using non-parametric correlations (except in the case of the binary variable leaf phenological type, for which a Mann–Whitney *U* test was used). Among the ten variables tested, leaf phenological type and species stature were

Fig. 4 Independent predictors and dependent variables of growth-ring distinctness plotted on the phylogeny of species (*GR* growth ring). Data are centered, and the means are, therefore, zero. *Black solid circles* depict positive values, and *white circles* depict negative values. *Circle size* is proportional to the absolute values

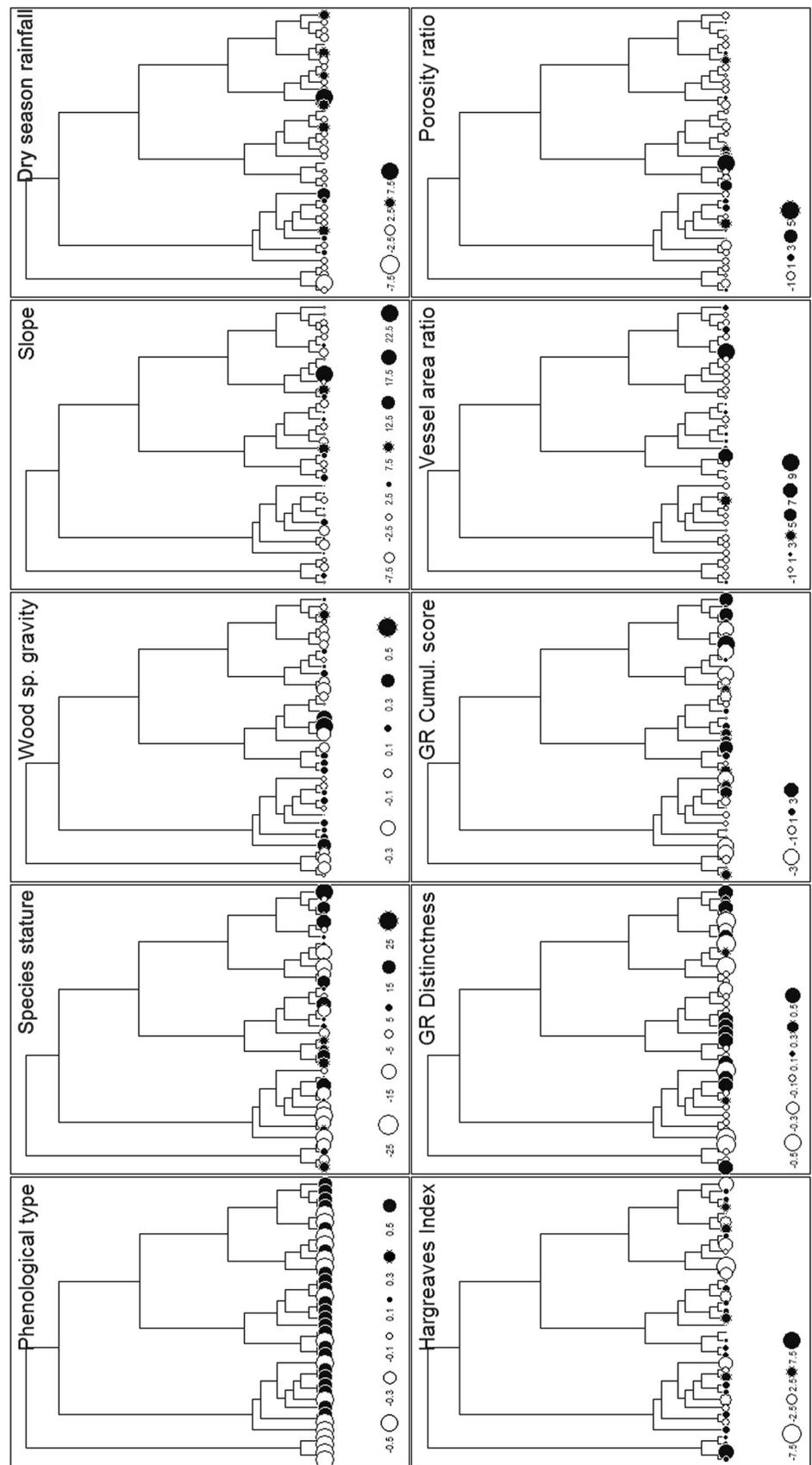
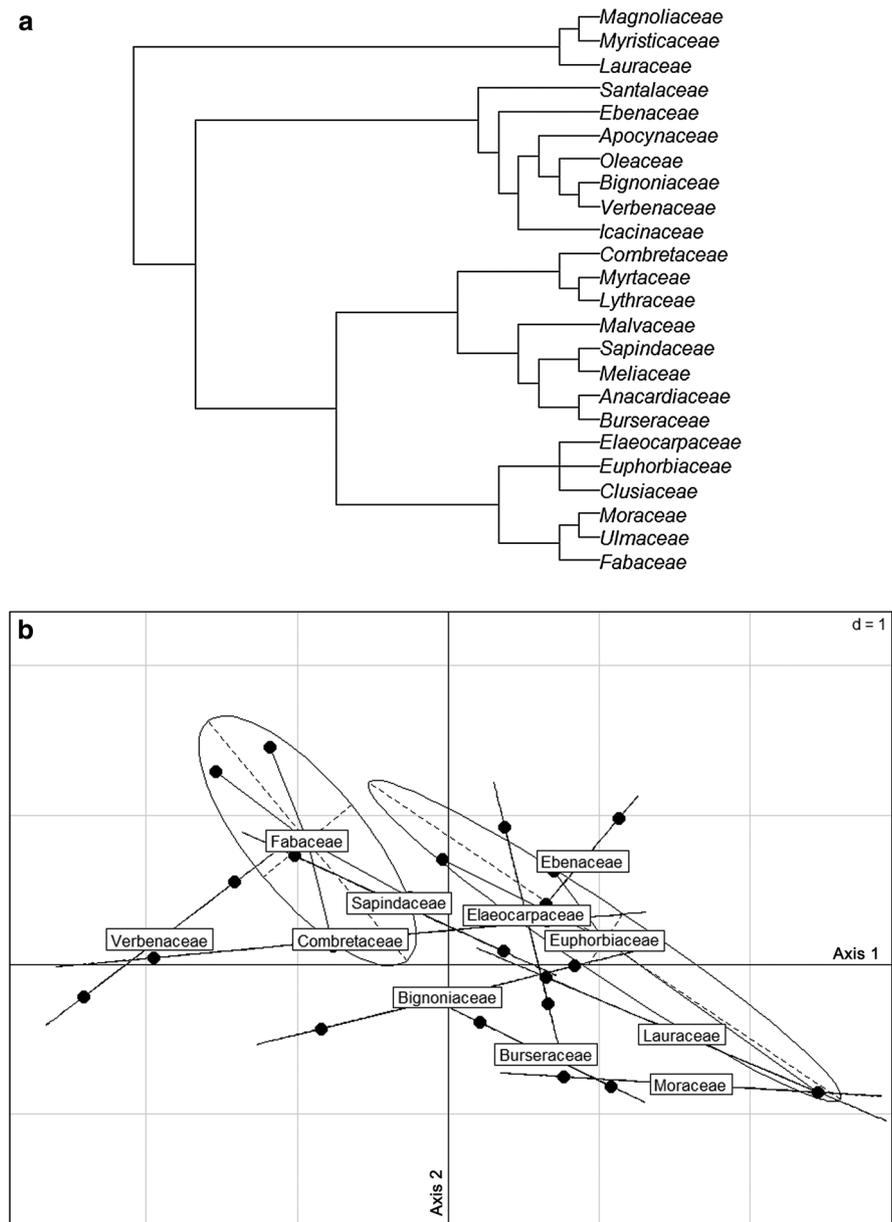


Fig. 5 Evidence that suggests evolutionary lability of distinctness of growth rings across and within families of tropical angiosperm dicot trees in the Western Ghats, India: **a** Phylogenetic relationships between the 24 sampled families according to the APG III classification system. **b** Ordination of four variables associated with distinctness of growth rings, showing differences in growth-ring distinctness scores between and within 11 families, in which at least two species were sampled. The *black dots* represent species, and the lines and ellipses represent 1.5 times the standard deviation of family scores on the axes. The *scale* of the graph is indicated by the *grid*, and the *length* of each *grid square* is one unit



significantly correlated with three of the four growth-ring distinctness variables (Table 3).

Effects of climate and functional traits

Stepwise deletion of less important variables in GLS models without phylogenetic structure resulted in the final parsimonious models that retained only one or two important predictors associated with each of the three quantitative growth-ring distinctness variables (Table 4). Each growth-ring variable had a different set of predictors,

which concurs with the earlier observation that the subjective and objective growth-ring indices are partly consistent but also reflect complementary aspects of growth-ring patterns (Fig. 3).

The growth-ring cumulative distinctness score was significantly influenced by leaf phenological type and species stature. Thus, growth rings were generally more distinct in deciduous species and taller trees. Vessel area ratio was influenced significantly by leaf phenological type and non-significantly by slope, whereas porosity ratio was influenced significantly only by leaf phenological type

Table 3 Non-parametric Spearman rank correlation estimates (ρ) of four functional traits and six environmental variables, with four growth-ring distinctness variables (visual distinctness, cumulative distinctness score, vessel area ratio, and porosity ratio)

Independent variables	Visual distinctness	Cumulative score	Vessel area ratio	Porosity ratio
Functional traits				
Leaf phenological type	0.34, 0.75 (0.0005***)	1.77, 3.83 (0.0004***)	1.21, 3.28 (0.00007***)	1.38, 2.25 (0.05)
Species stature (m)	0.38 (0.02*)	0.52 (0.0008***)	0.29 (0.08)	0.01 (0.93)
Avg. leaf length (cm)	−0.06 (0.74)	−0.04 (0.80)	0.00 (0.98)	−0.05 (0.78)
Wood specific gravity	0.00 (0.98)	−0.01 (0.97)	−0.05 (0.75)	−0.17 (0.30)
Environmental variables				
Altitude (m)	−0.10 (0.55)	−0.12 (0.48)	−0.25 (0.13)	−0.13 (0.45)
Slope (°)	−0.01 (0.95)	0.00 (0.99)	−0.22 (0.17)	−0.02 (0.88)
TWI	0.18 (0.27)	0.22 (0.18)	0.23 (0.16)	−0.03 (0.87)
Dry season rain (mm)	−0.20 (0.22)	−0.11 (0.50)	−0.22 (0.18)	−0.03 (0.87)
Thornthwaite PET index	0.11 (0.50)	0.12 (0.47)	0.27 (0.10)	0.14 (0.40)
Hargreaves PET index	0.19 (0.26)	0.10 (0.57)	0.23 (0.16)	0.07 (0.69)

p values are provided in parenthesis. In the case of the binary variable “Leaf phenological type”, the values reported are averages of each dependent variable for evergreen and deciduous species, respectively, along with p value significance (in parentheses) according to the Mann–Whitney U test

Statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 4 Functional traits and environmental predictor variables that were retained in parsimonious GLS models of three quantitative variables associated with distinctness of growth rings (cumulative score, vessel area ratio, and porosity ratio)

Predictor variables	Cumulative score ^a	Vessel area ratio ^b	Porosity ratio ^c
Functional traits			
Leaf phenological type	1.69 (0.0005***) [1.42, 2.12]	0.85 (0.0000***) [0.74, 0.92]	0.28 (0.03*) [0.19, 0.40]
Species stature (m)	0.06 (0.007**) [0.05, 0.07]		
Environmental variables			
Slope (°)		−0.03 (0.097) [−0.04, −0.02]	
Jackknife support	92 %	82 %	68 %

Cell values indicate the estimated coefficient, p value of the estimate (in parentheses), and jackknife estimated range (minimum and maximum, within square brackets). The last row provides the jackknife support per model (percentage of iterations that returned the same final model)

Statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

^a Altitude not included in the full model due to variance inflation

^b Dependent variable was natural-log transformed; wood specific gravity not included in the full model to increase Jackknife support for final model (without increasing AIC)

^c Dependent variable was square-root transformed

(Table 4). These parsimonious models were supported by 68 to 92 % of jackknife iterations. The final models obtained for the first two independent variables (cumulative score and vessel area ratio) were tested again with the two retained explanatory variables plus their corresponding interaction term to check for interactive effects using

backward stepwise reduction as before, but the interaction term was not retained in both cases.

Leaf phenological type (deciduousness) emerged as the strongest and most consistent predictor that positively influenced all three growth-ring distinctness variables, with significant positive coefficient values ranging from 0.28 to

1.69. Species maximum height or stature was significant but weakly associated with the cumulative distinctness score, with a positive coefficient of 0.06 (Table 4). The non-significant effect of topographic slope on vessel area ratio was weak and negative (-0.03), suggesting that trees on sites with lower slopes had greater growth-ring distinctness. Perhaps this is due to the weak negative correlation between topographic slope and potential evapotranspiration as well as its positive association with dry season rainfall in our study area (Appendix Table 6; Fig. 1).

Discussion

Objective quantification versus subjective visual classification of distinctness of growth rings

Our study has provided a method to complement the conventional qualitative and visual categorization of distinctness of growth rings with quantitative scores and measures reflecting anatomical variation. The results suggest that subjective visual recognition of ring distinctness is the result of cumulative integration of a large number of anatomical features across a growth-ring boundary, as demonstrated by the strong relationship between the two subjective scores. The influence of multiple anatomical features was also mentioned by Mariaux (2016). Previous studies have revealed functional plasticity of wood anatomy in some highly responsive species that produce rings with different porosity types according to the external environment (Chowdhury 1953; Carlquist 1988). However, the significance of gradation in ring distinctness across species has generally been overlooked in previous studies.

The two subjective visual indices provided similar information on distinctness of growth rings across multiple species and ring types. In addition, quantitative support and validation of the subjective scores were provided by the objective measurement of vessel size and porosity ratios across growth-ring boundaries, which were calculated by the image analysis software and found to be significantly correlated with qualitative indicators of ring distinctness. With these results, the subjective concept of “distinctness of growth rings” is shown to have a logical quantitative basis in well-recognised and measurable growth-ring features related to average vessel size and total extent of porosity across a growth-ring boundary. Future studies could also examine the opportunity of objective quantification of complementary anatomical features contributing to wood structural heterogeneity, such as differences observed in parenchyma and fibres across growth-ring

boundaries. Thus, the concept of distinctness of growth rings in tropical trees can be successfully studied using quantitative methods.

Causes of variation in growth-ring distinctness in tropical trees

This study provided a plausible and quantitative explanation for why distinctness of growth rings varies widely across tree species in the tropics. The main proximal factors significantly influencing the formation of distinct growth rings in the tropical tree species studied here were leaf phenology (the most common trait that is closely related to seasonal drought effects) and species stature. There was also a weak (non-significant) effect of slope, which may be related to dry season soil moisture stress. The additional functional traits and environmental variables related to topography, rainfall, and potential evapotranspiration did not influence distinctness of growth rings in this study. The results also suggest that phylogenetic similarity of distinctness of growth rings may be limited to the fine taxonomic levels (among genera within families), as has been suggested for tree species in tropical Africa and South America (Détienne 1989). Although a robust phylogenetic signal was detected for wood specific gravity, accounting for phylogenetic correlations did not improve our GLS models, and therefore, evolutionary constraints did not contribute to explaining the influence of environmental and functional predictors on the formation of growth rings and their distinctness.

At the interspecific level, the distinctness of growth rings may be an evolutionarily labile trait influenced by multiple factors. Chowdhury (1964) suggested that growth-ring porosity types may be highly conserved in some families, genera, and species, but highly variable in others. In this context, we examined descriptions of tree-ring distinctness provided by Pearson and Brown (1932) for 122 species belonging to 28 families (the family names were assigned based on information available at The Plant List website, <http://www.theplantlist.org/>, and they include 20 families that were represented in our study). The species' descriptions were based on microscope slides prepared from at least two replicate samples per species (average = 2.3 replicates per species, range = 2–8 replicates) collected from different forest divisions across the Indian subcontinent and stored at the Forest Research Institute, Dehradun, India (Gamble 1922; Pearson and Brown 1932). Among these, 11 families had only one level of growth-ring distinctness each (in these families, one-to-six species were described, averaging 2.3 species described per family), while nine families showed at least two levels of

distinctness each (including Meliaceae, with one-to-15 species/family, averaging 4.2 species described per family) and eight families showed all three levels of distinctness across their species (three-to-17 species/family, averaging 7.4 species described per family). This suggests that interspecific variation in tree-ring distinctness within families may increase with the number of species examined (or evolved) per family, which appears to support our finding that tree-ring distinctness is generally labile at the family level. However, there were also a few families exhibiting some level of growth-ring conservatism, wherein only one growth-ring type was observed across ≥ 5 species (e.g., families with numerous species showing distinct rings were: Combretaceae, Verbenaceae, Lauraceae, Fabaceae, Lythraceae, and Meliaceae), which supports the prediction of Chowdhury (1964). Increased sampling effort at a lower taxonomic level (i.e., within genera) in the future could allow further assessment of the nature of fine-scale phylogenetic constraint.

At the intraspecific level also, the distinctness of growth rings may be a labile trait. Intraspecific variation in growth-ring distinctness or porosity type has been reported previously in some species (e.g., Chowdhury 1953, 1964; Fichtler and Worbes 2012). The potential for plasticity in growth-ring distinctness, as observed elsewhere, may help explain why conflicting observations of growth-ring type and porous nature (i.e., whether ring porous, semi-ring porous, or diffuse porous) have been reported for common and widespread species (Chowdhury 1953; Boura and De Franceschi 2007). The growth-ring descriptions of 122 species (Pearson and Brown 1932) examined by us revealed intraspecific variation of distinctness categories in 27 % of the species (this value is 30 % if we consider only the 23 species in which more than two replicate samples were used for preparing microscope slides). This suggests that for a large proportion of Indian species (at least 70 %), the growth-ring distinctness category does not vary across different geographic locations. This information also supports our results by indicating that the one or two samples collected by us per species is in fact a meaningful data set relative to the known variability within species, and as a first approximation, our conclusions are likely to be robust to the assumption that our sampling captures representative species-level values.

Ring distinctness is not exclusively based on vessel size and porosity properties alone, but may be related in some species to additional anatomical features that were assessed implicitly or explicitly by the subjective scores. This suggests that distinct ring formation in some tropical south Indian trees may be caused by factors unrelated to water

dynamics. For example, low light availability due to heavy cloud cover during the peak monsoon season (July–August) may inhibit growth in species persisting in shade close to the light compensation point for whole-plant growth. In addition, certain phenophases associated with extensive flower or fruit set may inhibit vegetative growth independent of water availability (Callado et al. 2001). The signature in growth-ring boundaries associated with such causes of growth cessation may be marked by anatomical features other than vessel and porosity variations, such as parenchyma or fibre density variations and marginal parenchyma bands. This also agrees with the previous studies suggesting that growth may be stopped and rings produced in wood due to cambial dormancy caused by external abiotic factors (i.e., environment) or internal rhythms (reproductive phenophases, multiannual leaf flushing, etc.) that are sometimes referred to as “endogenous factors” (Tomlinson and Longman 1981; Fahn et al. 1981; Callado et al. 2001).

This information is useful for tropical dendrochronologists who can in the future focus on the functional traits of deciduousness and species stature, to quickly identify locations and tree species that are most likely to produce distinct growth rings (i.e., forests with deciduous and/or tall trees). Our results concur with and complement the strategies suggested by Stahle (1999) for identifying tropical species for dendrochronology. Due to a lack of understanding of formation of growth rings across habitats, taxa, and strategies of trees, most tropical dendrochronological studies have been restricted to using a few species with well-established dendrochronological performance records. For example, tropical dendroclimatological studies from India have utilised generally common and widespread species with reliable formation of growth rings and ring porous to semi-ring porous wood, such as *Tectona grandis* and *Toona ciliata*. Only a few other species have been tested for their dendrochronological potential (Bhattacharyya and Shah 2009; Bhattacharyya et al. 2012). Given the high species richness of tropical forests, there is scope for larger numbers of species to be selected efficiently in the field based on the traits suggested above, for further dendrochronological evaluation and testing in the lab.

Functional and evolutionary significance of distinctness of growth rings

The hypothesis that the formation of distinct growth rings would be associated with a fast growth strategy, characterized by traits, such as short-lived leaves that are seasonally shed via deciduousness, was supported by this

study. This result allows the phenomenon of distinctness of tropical growth rings to be tentatively located within the hypothesized slow-fast life history continuum that is expected to be characterized by co-evolved coordinated traits along plant growth economics spectra (Wright et al. 2006; Chave et al. 2009; Reich 2014). It also suggests a potentially greater sensitivity of fast-growing deciduous species to drought stress (cf. Ouédraogo et al. 2013). However, given the wide variation in leaf phenological types and kinds of adaptation to drought (Borchert 1999; Eckstein 2004; Worbes et al. 2013; Pivovarov et al. 2015), it would be interesting to examine the relative effects of drought tolerance versus drought avoidance strategies on the formation of growth rings. Moreover, a few exceptional deciduous species were observed to produce distinct rings despite being relatively slow growing (*Dalbergia latifolia*, *Terminalia alata*, and *Schleichera oleosa*, unpublished data). In these cases, perhaps deciduousness and/or tall stature were the key factors influencing ring distinctness, and growth rate was less relevant. The relevance of deciduousness is underlined by its highly significant influence on vessel area ratio (Table 4). This anatomical feature reflects the porous nature of species (i.e., ring porous or semi-ring porous), which has been previously linked with deciduousness (Boura and De Franceschi 2007). In addition, taller trees have been associated with faster growth rates and/or greater competitive ability (King et al. 2006; Westoby 1998), and species stature was strongly associated with the cumulative growth-ring index in our study (Table 4). Thus, the tall evergreen species, *Michelia champaca*, produced distinct growth rings without complete leaf shedding. This supports our hypothesis that taller trees may be more likely to show increased distinctness of growth rings, possibly due to drought-related hydraulic constraints and their generally competitive strategy.

Leaf length was not a significant predictor of distinctness of growth rings, although it was expected to be indirectly associated with a fast growth strategy (through leaf area). This requires further investigation, preferably with the use of fresh leaves (cf. Queenborough and Porras 2014). Future studies should measure leaf area or specific leaf area, which are considered more conventionally as functional traits that are linked with life history strategies, rather than leaf length (cf. Wright et al. 2006; Reich 2014). Similarly, wood specific gravity was not a significant predictor of growth-ring distinctness, perhaps due to unaccounted variability across and within species. For example, some tall trees may belong to long-lived slow-growing species, and wood specific gravity variations may be affected by factors other than fast versus slow growth

strategies, such as architecture and soil properties (Tida et al. 2012; Fortunel et al. 2014). In addition, wood specific gravity values should be obtained from the field sites if possible, rather than from literature sources, to reduce the effects of intraspecific and spatial variability.

As distinctness of growth rings was significantly related to the functional traits of leaf phenological strategy and species stature (and potentially also to topographic slope), while the relationship was not influenced by phylogenetic relationships, the evolution of distinctness of growth rings across species does not appear to be evolutionarily constrained. Thus, the rate of change in distinctness of growth rings over time may be independent of general rates of evolution within a clade and may be capable of increasing relatively fast or reversing in response to environmental and endogenous variations. Such information is useful when reconstructing paleoecological conditions, including palaeo-climates and the state of functional traits (Baas 1982; Carlquist 1988). A lack of distinctness of growth rings in fossil angiosperm dicotyledonous woods obtained from tropical regions could, therefore, be interpreted as indicating an evergreen phenological strategy and/or short plant stature. Similarly, a high vessel area ratio across a growth-ring boundary (indicating ring porous nature) would suggest a high likelihood of deciduousness. Due to the variability of distinctness of growth rings within families, these traits should not be used to infer phylogenetic relationships above the genus level.

If indeed the distinctness of tropical tree growth rings is a relatively labile trait, as suggested by our results, then the proximate cause of distinctness at different locations may vary depending on local environmental conditions and functional trait values. In the Western Ghats, dry season deciduousness appears to be a key factor influencing distinctness of tree rings, and tall trees appear to produce more distinct rings than shorter trees. However, in the case of flooded or mangrove habitats, alternative functional trait variables (for example, absence/presence of pneumatophores and salt excretion mechanisms) that enhance or diminish the effects of the main seasonal stress factor of soil hypoxia or salinity in those environments (Menezes et al. 2003) may be associated with distinctness of growth rings. It is hoped that our results will stimulate similar quantitative studies on the multiple factors that appear to influence the distinctness of growth rings in tropical and subtropical regions elsewhere.

Limitations of our analysis

In this paper, we described a unique approach towards understanding the relationship between functional or

environmental factors and growth-ring distinctness in tropical trees. To assess the generalisability of these results across other tropical regions, the potential limitations of our study are described below, as well as reasons why we expect the conclusions to be robust. We acknowledge that lack of field data on key environmental features, such as soil texture and local moisture availability, or individual features, such as specific leaf area and wood density, may be responsible for the absence of statistical significance in some of the factors tested. Variations in cambial activity that could influence growth-ring formation have been previously linked with variations in local climate (Rao and Rajput 1999). However, in our study, the variation in dry season rainfall across the sampled sites may have been insufficient to produce marked variations in growth-ring formation within species, or alternatively, this may be related to local management practices that partially limit drought effects in the managed coffee plantations. Due to the possibility of intraspecific functional plasticity under different environmental regimes (which may occur in some species), a prospective future approach would be to design more specific sampling of widespread species to address in greater detail the potential for intraspecific variation in growth-ring distinctness across habitat types and climatic regimes.

We have discussed previously why increased sampling of species per family or individuals per species is unlikely to change our conclusion that there is no general phylogenetic constraint on growth-ring formation at the family level. Additional support for our analytical result was provided by randomization tests, use of a modified species classification, and secondary information (Pearson and Brown 1932). We thus expect that additional intra-individual variation in ring distinctness will not modify our results, due to the following reasons: first, this is unlikely to be relevant for species classified as having distinct rings (e.g., *Tectona grandis*, *Lagerstroemia microcarpa*, *Toona ciliata*, *Terminalia alata*, *Gmelina arborea*, *Acrocarpus fraxinifolius*, and *Dalbergia latifolia*), as they have been classified similarly by previous studies and successfully crossdated using narrow core samples from arbitrary locations around a stem (Chowdhury 1953; Bhattacharyya and Shah 2009; Nath et al. 2012). Second, our sampling and processing methods have minimised the effects of intra-individual variations that may characterise species with less distinct rings. Faint or absent rings have been recorded in juvenile wood near the pith (Détienne 1989; Worbes 2002; Groenendijk et al. 2014; Mariaux 2016), and less commonly species have been reported to show reduced

distinctness of growth rings in the outer wood region (Worbes 2002; Groenendijk et al. 2014) or variations in distinctness in the tangential direction (Krepkowski et al. 2012). In addition, the detection of rings may be difficult when observing polished wood in the light-coloured sapwood region due to a lack of contrast under the light microscope. However, we have minimised such limitations by sampling the outer part of stems, selecting trees that were >30 cm in girth (i.e., those likely to have completed the juvenile stage), sampling at least two individuals in most species, and using stained microscope slides to detect and characterise the growth rings, thus improving detectability of less distinct rings. Also, among the four different indicators of growth-ring distinctness used by us, the two subjective indexes were based on examination of all available rings per microscope slide (sometimes more than five rings per individual). Thus, our subjective characterization of ring distinctness was based on an integrated evaluation of multiple rings per species and may be less sensitive to intra-individual variability. We therefore suggest that future studies could focus on testing different families that were not tested here, including better representation of bioclimatic niches per species and selecting widespread taxa to enhance the evidence base for testing the hypotheses addressed in this paper.

Author contribution statement CDN and RP initiated the project; CDN, RP, and DFRPB planned the initial data collection and analyses; CDN carried out field and lab work; CDN, FM, and GM carried out analyses; all authors contributed to manuscript preparation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

See Tables 5 and 6.

Table 5 Details of 38 south Indian tropical angiosperm dicot tree species (arranged alphabetically by family) that were used for the analysis of distinctness of growth rings

Family	Scientific name	Phenological type	Species stature (m)	Visual distinctness
Anacardiaceae	<i>Mangifera indica</i> L.	E	45	0.5
Apocynaceae	<i>Tabernaemontana heyneana</i> Wall. ^a	D	8	0.5
Bignoniaceae	<i>Radermachera xylocarpa</i> K.Schum. ^a	D	15	0.5
	<i>Stereospermum colais</i> (Dillwyn) Mabb.	D	30	0.75
Burseraceae	<i>Canarium strictum</i> Roxb.	D	30	0.25
	<i>Garuga pinnata</i> Roxb. ^a	D	25	0.5
Clusiaceae	<i>Garcinia cambogia</i> Desr.	E	12	0
Combretaceae	<i>Terminalia bellirica</i> (Gaertner) Roxb.	D	40	0.5
	<i>Terminalia alata</i> Roth	D	37	1
Ebenaceae	<i>Diospyros montana</i> Roxb. ^a	D	15	0.5
	<i>Diospyros sylvatica</i> Roxb.	E	35	0.5
Elaeocarpaceae	<i>Elaeocarpus serratus</i> L.	E	18	0.5
	<i>Elaeocarpus tuberculatus</i> Roxb.	D	40	0.5
Euphorbiaceae	<i>Bischofia javanica</i> Blume	E	30	0
	<i>Mallotus philippensis</i> (Lam.) Muell.Arg.	E	12	0.75
	<i>Phyllanthus emblica</i> L. ^a	D	30	0.5
Fabaceae	<i>Acrocarpus fraxinifolius</i> Arn.	D	50	1
	<i>Albizia odoratissima</i> (L.f.) Benth.	D	25	0.75
	<i>Dalbergia latifolia</i> Roxb.	D	40	1
	<i>Pterocarpus marsupium</i> Roxb.	D	30	0.75
Icacinaceae	<i>Apodytes dimidiata</i> E.Meyer ex Arn.	E	25	0
Lauraceae	<i>Cinnamomum malabatum</i> J.Presl	E	15	0
	<i>Persea macrantha</i> (Nees) Kosterm.	E	33	0.5
Lythraceae	<i>Lagerstroemia microcarpa</i> Wight	D	35	1
Magnoliaceae	<i>Michelia champaca</i> L.	E	36	1
Malvaceae	<i>Grewia tiliifolia</i> Vahl	D	20	1
Meliaceae	<i>Toona ciliata</i> M.Roemer ^a	D	32	1
Moraceae	<i>Artocarpus heterophyllus</i> Lam.	E	25	0.25
	<i>Artocarpus hirsutus</i> Lam.	E	45	0
Myristicaceae	<i>Knema attenuata</i> Warb. ^a	E	20	0.5
Myrtaceae	<i>Syzygium cumini</i> (L.) Skeels	E	35	0.5
Oleaceae	<i>Olea dioica</i> Roxb.	E	15	0.5
Santalaceae	<i>Santalum album</i> L. ^a	E	10	0
Sapindaceae	<i>Sapindus laurifolius</i> Vahl	D	18	0.5
	<i>Schleichera oleosa</i> (Lour.) Oken	D	30	1
Ulmaceae	<i>Celtis tetrandra</i> Roxb. ^a	D	30	1
Verbenaceae	<i>Gmelina arborea</i> Roxb.	D	30	1
	<i>Tectona grandis</i> L.f.	D	45	1

Plant families follow the APG III classification system, and species' scientific names are based on Mabberley (2005) and the herbarium of the French Institute of Pondicherry (HIFP, <http://www.ifpindia.org/content/herbarium>)

Phenological-type classification: *E* evergreen, *D* deciduous

Species stature information was obtained from the following sources: <http://www.biotik.org>, Gamble (1935), Nazma et al. (1981), Pascal (1988), Murthy and Yoganarasimhan (1990), Rani et al. (2011)

Visual distinctness scores were assigned per replicate as follows: 1 = growth-ring boundary visually distinct, 0.5 = growth-ring boundary less distinct, 0 = growth-ring boundary absent. Scores were averaged across replicates per species

^a Only one replicate individual available per species

Table 6 Spearman non-parametric rank correlations (ρ) between all dependent and independent variables, whose values were averaged per species ($N = 38$)

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Leaf Phenol.													
2. Max height	[0.30]												
3. Leaf length	[0.10]	0.16											
4. Wood Dens.	[0.42]	-0.06	-0.16										
5. Altitude	[0.24]	-0.20	-0.03	-0.01									
6. Slope	[0.71]	-0.16	-0.11	-0.13	0.56***								
7. TWI	[0.69]	0.14	0.23	0.17	-0.20	-0.10							
8. Dry seas. rainfall	[0.11]	0.06	0.17	-0.06	0.33*	0.33*	-0.08						
9. Thor. PET	[0.22]	0.18	0.03	0.02	-0.99***	-0.55***	0.20	-0.39*					
10. Harg. PET	[0.10]	-0.01	-0.10	0.11	-0.46**	-0.28	0.19	-0.89***	0.53***				
11. GR vis. dist.	[0.00]***	0.38*	-0.06	0.00	-0.10	-0.01	0.18	-0.20	0.11	0.19			
12. Cumul. score	[0.00]***	0.52***	-0.04	-0.01	-0.12	0.00	0.22	-0.11	0.12	0.10	0.92***		
13. Ves. area ratio	[0.00]***	0.29	0.00	-0.05	-0.25	-0.22	0.23	-0.22	0.27	0.23	0.65***	0.59***	
14. Por. ratio	[0.05]	0.01	-0.05	-0.17	-0.13	-0.02	-0.03	-0.03	0.14	0.07	0.64***	0.44*	0.59***

In the case of the binary variable, leaf phenological type (first column), the entries show p values obtained with the Mann–Whitney U test (or Wilcoxon test)

Statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

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