Small and slow is safe: on the drought tolerance of tropical tree species

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DR. JOANNÈS GUILLEMOT (Orcid ID : 0000-0003-4385-7656)

DR. XAVIER MORIN (Orcid ID : 0000-0003-1961-8700)

MR. PAULO L BITTENCOURT (Orcid ID : 0000-0002-1618-9077)

MS. COLINE BOONMAN (Orcid ID : 0000-0003-2417-1579)

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Joannès Guillemot[1,2,3,*], Nicolas K. Martin-StPaul[4], Leticia Bulascoschi[3], Lourens Poorter[5], Xavier Morin[6], Bruno X. Pinho[7,8], Guerric le Maire[1,2], Paulo Bittencourt[9], Rafael S. Oliveira[10], Frans Bongers[5], Rens Brouwer[5], Luciano Pereira[10,11], German Andrés Gonzalez Melo[12], Coline C. F. Boonman[13], Kerry A. Brown[14], Bruno E.L. Cerabolini[15], Ülo Niinemets[16], Yusuke Onoda[17], Julio V. Schneider[18,19], Serge Sheremetiev[20], Pedro H.S. Brancalion[3]

[1]CIRAD, UMR Eco&Sols, Piracicaba, SP 13418-900, Brazil
[2]Eco&Sols, Univ. Montpellier, CIRAD, INRAe, Institut Agro, IRD, Montpellier 34060, France
[3]Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, São Paulo 13418-900, Brazil
[4]URFM, INRAe, 84000, Avignon, France
[5]Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands
[6]CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France
[7]AMAP, Univ Montpellier, INRAe, CIRAD, CNRS, IRD, Montpellier, France

[8]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil
[9]College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4QE, UK

[10]Department of Plant Biology, Institute of Biology, CP 6109, University of Campinas – UNICAMP, Campinas SP 13083-970, Brazil
[11]Institute of Systematic Botany and Ecology, Ulm University, Albert-Einstein-Allee 11, 89081 Ulm, Germany.
[12]Biology Department, Faculty of Natural Sciences, Universidad del Rosario, Avenida carrera 24 # 63C-69. Bogotá, Colombia
[13]Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University, Nijmegen, The Netherlands

[14]Department of Geography, Geology and the Environment, Kingston University London, Kingston Upon Thames, KT1 4DW, UK

[15]Department of Biotechnologies and Life Sciences (DBSV) University of Insubria via J.H. Dunant, 3 - I-21100 Varese, Italy

[16]Estonian University of Life Sciences, Kreutzwaldi 1, 51006 Tartu, Estonia

[17]Graduate School of Agriculture, Kyoto University, Kyoto, 606-8502 Japan

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[18]Senckenberg Research Institute and Natural History Museum Frankfurt, Department of Botany and Molecular Evolution, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany

[19]Senckenberg Research Institute and Natural History Museum Frankfurt, Entomology III, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[20]Komarov Botanical Institute, St. Petersburg, Prof. Popov str., 2, 197376, Russia

[*]Correspondence to: J. Guillemot. University of São Paulo, "Luiz de Queiroz" College of Agriculture, Department of Forest Sciences, Avenida Pádua Dias, 11 - Piracicaba/SP - CEP 13418-900. Tel. +55 (19) 99130-9658; Email: joannes.guillemot@cirad.fr

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ABSTRACT

Understanding how evolutionary history and the coordination between trait trade-off axes shape the drought tolerance of trees is crucial to predict forest dynamics under climate change. Here, we compiled traits related to drought tolerance and the fast-slow and stature-recruitment trade-off axes in 601 tropical woody species to explore their covariations and phylogenetic signals. We found that xylem resistance to embolism (P50) determines the risk of hydraulic failure, while the functional significance of leaf turgor loss point (TLP) relies on its coordination with water use strategies. P50 and TLP exhibit weak phylogenetic signals and substantial variation within genera. TLP is closely associated with the fast-slow trait axis: slow species maintain leaf functioning under higher water stress. P50 is associated with both the fast-slow and stature-recruitment trait axes: slow and small species exhibit more resistant xylem. Lower leaf phosphorus concentration is associated with more resistant xylem, which suggests a (nutrient and drought) stress-tolerance syndrome in the tropics. Overall, our results imply that: 1) drought tolerance is under strong selective pressure in tropical forests, and TLP and P50 result from the repeated evolutionary adaptation of closely related taxa; and 2) drought tolerance is coordinated with the ecological strategies governing tropical forest demography. These findings provide a physiological basis to interpret the drought-induced shift toward slow-growing, smaller, denser-wooded trees observed in the tropics, with implications for forest restoration programmes.

Keywords: demography, drought, forest dynamics, hydraulic, life-history strategies, tree mortality, trait trade-off, water stress

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INTRODUCTION

The current increase in the intensity and frequency of drought events causes large-scale tree mortality and threatens the carbon (C) sink capacity of tropical forests (Aleixo et al., 2019; Hubau et al., 2020). Characterizing the drought tolerance of the vast diversity of tropical woody species is crucial to predict the future dynamics of tropical forests and promote resilient forest restoration as a nature-based solution to mitigate climate change (Poorter et al., 2019).

Functional trait-based approaches have proven relevant to identify the functional constraints and trade-offs underlying plant ecological strategies across species (Westoby et al., 2002). Trait trade-offs in woody species can be captured by two fundamental axes (Díaz et al., 2016). The first describes the “fast-slow” trade-off of resource acquisition and processing (Reich, 2014; Wright et al., 2004), which underlies the growth-survival trade-off observed in forests (Sterck et al., 2006; Wright et al., 2010). The second trait axis is related to the size of the whole plant and its parts (especially seed and leaf size) and describes a “stature-recruitment” trade-off, in which tall species tend to maximize growth and survival at the expense of recruitment (Kohyama, 1993; Rüger et al., 2018). These two fundamental trait axes have been shown to explain the demographic and compositional changes that occur with forest succession in the forest of Barro Colorado Island (Rüger et al., 2018, 2020). They may be relevant for many tropical forests (Bugmann, 2020).

In addition, functional traits can help predict the effects of drought on forest dynamics (Aguirre-Gutiérrez et al., 2019; Esquivel-Muelbert et al., 2019). Current knowledge suggests that drought-induced mortality is either caused by xylem hydraulic failure or by a combination of xylem hydraulic failure and reduced photosynthesis (i.e. C starvation; Adams et al., 2017). Hydraulic failure results from the formation of gas emboli in xylem conduits, as xylem water potential decreases in response to water deficit. During the first phase of drought (i.e. before massive xylem embolism has occurred), plants close their stomata to limit water loss and delay the decrease in xylem water potential (Bartlett et al., 2016; Choat et al., 2018). Although they differ, leaf water potential at stomatal closure correlates with the leaf water potential at turgor loss (turgor loss point, TLP) across plant species (Bartlett et al., 2016; Brodribb and Holbrook, 2003; Hinckley et al., 1980). Therefore, the risk of plant hydraulic failure during drought can be measured as the difference between TLP and the water potential that causes xylem dysfunction (commonly measured as the water potential causing 50% loss of hydraulic conductance, P50). This definition of a hydraulic safety margin (TLP-based HSM, where TLP-based HSM = TLP - P50) proved useful in predicting the risk of drought-

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induced tree mortality (Martin-StPaul et al., 2017; Powers et al., 2020; see the Methods for a further description of alternative HSM definitions).

P50 and TLP are key functional traits that determine species drought tolerance. However, while resistant xylem has been associated with a greater HSM and greater drought tolerance (Anderegg et al., 2016; Martin-StPaul et al., 2017; Nolan et al., 2021), the association between TLP and drought remains unclear. If we consider the HSM, greater drought tolerance should be found in species that close their stomata early during a drought (i.e. with *less negative* TLP), and exhibit more negative P50. However, TLP measures the ability of leaves to maintain turgor and operate under water stress, which means it is an indicator of drought tolerance. Indeed, species with *more negative* TLP are associated with dryer habitats (Bartlett et al., 2012; Kunert et al., 2021; Zhu et al., 2018). This apparent contradiction may result from a correlation between TLP and other key drought tolerance traits, but this trait coordination is not ubiquitous among woody species (Christoffersen et al., 2016; Laughlin et al., 2020). Alternatively, the tighter stomatal control in species with less negative TLP (Meinzer et al., 2016) may be associated with a decrease in photosynthesis earlier on during a drought. This could lead to the gradual competitive exclusion of these species due to C starvation or the difficulty of maintaining hydraulic functions (O'Brien et al., 2014; Skelton et al., 2015). It is also important to note that the importance of P50 and TLP in determining drought tolerance may vanish in deciduous tree species because leaf shedding decouples the plant significantly from the atmospheric water demand (Kunert et al., 2021; Oliveira et al., 2021). Exploring the covariation of drought tolerance traits among species may reveal their functional significance and improve our understanding of tree drought responses.

We know little about the coordination between drought tolerance and the trait trade-off axes that govern tropical forest demography (González-M et al., 2021; Oliveira et al., 2021). The efficiency of the xylem to transport water and its ability to resist embolism are both determined by xylem anatomical features, which means that trees may face a hydraulic safety-efficiency trade-off (e.g. larger - and more efficient - conduits and pit membrane pores are also more prone to embolism; Zimmermann, 2013). In such cases, P50 should be coordinated with the fast-slow axis, with resistant xylem found in slow, conservative species. However, evidence of the hydraulic safety-efficiency trade-off is not widespread in the literature (Gleason et al., 2016). In addition, it was recently suggested that stomatal function is also constrained by a safety-efficiency trade-off, where species with greater stomatal conductance (and thus greater C assimilation capacity) show greater sensitivity

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to closure during leaf dehydration (Henry et al., 2019). This implies that species with fast, acquisitive strategies tend to show tighter leaf stomatal control (and, therefore, less negative TLP) than slow strategy species. Consequently, the fundamental trade-off governing stomatal regulation may align TLP with the fast-slow axis. However, local studies that examined the degree of coordination between drought tolerance and the fast-slow axis revealed contrasting results, ranging from significant coordination (Aleixo et al., 2019; Maréchaux et al., 2016; Markesteijn et al., 2011) to weak coordination (Maréchaux et al., 2020), to no coordination (Maréchaux et al., 2015; Pineda-Garcia et al., 2013; Powell et al., 2017). Lastly, P50 may be negatively associated with tree height (Liu et al., 2019; Skelton et al., 2021), and, therefore, with the stature-recruitment axis. Indeed, large trees tend to be more affected by drought than smaller trees (Bennett et al., 2015) and are at greater risk of hydraulic failure (McDowell and Allen, 2015; Rowland et al., 2015).

The associations between functional traits may be shaped by evolutionary history (Cavender-Bares et al., 2016). Traits with strong phylogenetic signals are largely determined by ancestors' legacy and show a high degree of similarity between closely related species (Münkemüller et al., 2012). This may hide the fact that some traits seem to have evolved in a coordinated manner, either because of their independent responses to environmental selective pressure or because they co-evolved in response to functional or developmental constraints (Sanchez-Martinez et al., 2020). In such cases, trait coordination and species trait profiles can be interpreted in terms of ecological strategies (Reich et al., 2003). Identifying evolutionary convergences between drought tolerance and the other trait trade-off axes is crucial to understanding the drivers of the diversity of physiological functions found in woody species (Skelton et al., 2021).

Here, we explore the phylogenetic and ecological differentiation in the drought tolerance of tropical woody species. To do so, we compiled data for TLP, P50, leaf habit and 7 key traits linked to the fast-slow and stature-recruitment axes. We tested the following hypotheses: 1) TLP and P50 are coordinated across evergreen species, but not deciduous species. P50, and not TLP, is a primary determinant of TLP-based HSM. 2) Drought tolerance traits are under strong selective pressure, which has led to their evolutionary lability and a substantial variation between closely related taxa. 3) Drought tolerance is coordinated with the other ecological strategies governing tropical forest demography: P50 and TLP-based HSM are associated with the stature-recruitment axis, while TLP is associated with the fast-slow axis.

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MATERIAL AND METHODS

Data compilation

We screened the literature for data on P50 and TLP measured in woody species in tropical or sub-tropical forests. Much of the data was drawn from previous meta-analyses: Bartlett et al. (2012), Christoffersen et al. (2016), Choat et al. (2012), Liu et al. (2019) and Zhu et al. (2018). In addition, we included data from the works by Barros et al. (2019), Fontes et al. (2020), Kröber et al. (2014), Maréchaux et al. (2020), Oliveira et al. (2019), Powers et al. (2020), Santiago et al. (2018), Vinya et al. (2012) and Zhang et al. (2019). The forest type was determined, separating seasonally dry forests (hereafter referred to as “dry” forest type) from evergreen forests and rainforests (hereafter referred to as “moist’ forest type). We only selected P50 data that originated from branch xylem measurements (i.e. leaf P50 measurements were excluded to avoid potential bias related to hydraulic vulnerability segmentation; Levionnois et al., 2020). When available, the leaf habit (deciduous or evergreen) and the observed minimum water potential (Ψ_{min}, a measure of the water stress that trees experience in natural conditions) were collected from the same databases.

A variety of methods has been developed over the years to measure P50 (Cochard et al., 2013). The capacity of these methods to provide accurate across contrasting wood properties has been widely discussed, given that different artefacts have been shown to potentially affect P50 values, if procedures are not followed correctly (Cochard et al., 2013; Pereira et al., 2021; Sergent et al., 2020). In this study, we aimed to reduce the risk of collecting data affected by artefacts. To do so, we adopted the broadly held view that massive xylem embolism does not occur at very low levels of water stress, and only occurs when water stress exceeds the threshold that triggers stomatal closure (Bartlett et al., 2016; Choat et al., 2018). Therefore, we removed P50 data when the values exceeded those of TLP data for a given species (when both were available), as suggested in Sergent et al. (2020). We also excluded P50 data when values were greater than -0.5 MPa.

Subsequently, we screened global databases for seven key traits: leaf mass per area (LMA, g m^{-2}), leaf size (cm^2), leaf nitrogen concentration (leaf N, mg g^{-1}), leaf phosphorus concentration (leaf P, mg g^{-1}), wood density (g cm^{-3}), maximum height (m) and seed mass (g). These traits were found to describe two independent dimensions that crucially drive demography in tropical forests: the fast-

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slow and stature-recruitment axes (Kohyama, 1993; Poorter et al., 2006, 2005, Rüger et al., 2020, 2018). Higher LMA and wood density and lower leaf N and leaf P concentrations are a feature of slow strategy species. Higher maximum height, seed mass and leaf size characterize species that favour growth and long-term survival at the expense of recruitment.

To avoid mismatch between databases potentially caused by spelling errors in species name and species synonyms, the species names of all databases were first standardized using the *Taxonstand* R package (Cayuela et al., 2012). The explored databases included the TRY database (Kattge et al., 2020*,* for a full reference list of the TRY database data, see Supporting information 1), the BIEN database (Enquist et al., 2016) accessed using the *BIEN* R package (Maitner et al., 2018), the wdData database (Chave et al., 2009) accessed using the *BIOMASS* R package (Réjou-Méchain et al., 2017), and the database published by Liu et al. (2019). Trait values were averaged per species to account for multiple occurrences. For leaf habit, in cases where both deciduous and evergreen types occurred for the same species, we attributed the deciduous type. The final dataset contained 601 tropical woody species (including 393 evergreen species, 122 deciduous species and 86 species without specified leaf habit), from 340 genera, 107 families and 41 orders measured throughout the tropical and subtropical zones (Fig. S1).

Calculation of the Hydraulic Safety Margin

The HSM is the risk that a plant will experience hydraulic failure in the driest conditions it normally experiences. Two definitions of HSM are found in the literature: 1) *HSM as the difference between the water potential at stomatal closure and P50 (TLP-based HSM)*. This safety margin quantifies the extent to which early stomatal closure prevents the risk of hydraulic failure for a species (Martin-StPaul et al., 2017). Although stomatal closure occurs before leaf turgor loss during drought, TLP is an indicator of the water potential at stomatal closure across species (Bartlett et al., 2016; Brodribb and Holbrook, 2003; Hinckley et al., 1980). Therefore, using this definition, HSM is calculated as TLP - P50. 2) *HSM as the difference between* Ψ_{min} *and P50 (*Ψ_{min}*-based HSM)*. Ψ_{min} results from both the environmental conditions of water deficit and the different mechanisms that allow a plant to avoid water stress (Brodribb et al., 2020). Therefore, Ψ_{min}-based HSM, calculated as Ψ_{min} - P50, puts xylem resistance to embolism in the context of the actual water stress experienced by a species (i.e. drought exposure, Choat et al., 2012).

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Here, we used TLP-based HSM to explore how drought tolerance is associated with the other trait axes. This was because 1) Ψ_{min} was less abundant than TLP in our dataset (Table 1), 2) Ψ_{min} field data may be affected by sampling protocol (Martínez-Vilalta et al., 2021) and 3) TLP-based HSM recently proved to be highly indicative of observed drought-induced mortality rates (Martin-StPaul et al., 2017; Powers et al., 2020). However, we included Ψ_{min} and Ψ_{min}-based HSM in our exploration of how drought tolerance traits are coordinated.

Data imputation for multivariate analyses

Principal Components Analyses (PCAs) can only be performed on complete datasets. However, if we had restricted our dataset to species with no missing values, it would have been much smaller (to n=134) and we would have lost a great deal of information. Therefore, for PCA analyses only, missing values were imputed based on trait associations, using the R package *missMDA* ('PCA model', Josse and Husson, 2016). Thus, predicted values replaced 31% of the PCA dataset that was missing. The influence of data imputation on the result of the PCA was evaluated using a multiple imputation, based on a parametric bootstrap procedure provided by the *MIPCA* function. In addition, we evaluated potential methodological bias by performing imputation with an alternative model (based on linear regressions between traits) using the *mice* R package (Van Buuren and Groothuis-Oudshoorn, 2011). Finally, we tested the robustness of our results by performing additional imputation and PCA on a dataset, which excluded species with more than three missing trait values. This generated a dataset with 412 species and 10% missing values.

The data imputation was deemed satisfactory based on three lines of evidence (Supporting information 3). First, the multiple bootstrapped procedure indicated that the dataset successfully constrained the data imputation and allowed for reliable estimates of the PCA axes. Second, data imputation based on two different methods, i.e. using the *missMDA* R package and the *mice* R package, yielded comparable variable correlation plots (Figs. S3 and S5). This suggests that there was no methodological bias in the imputation of our dataset. Finally, performing the PCA on a smaller dataset (in which the proportion of missing values was reduced by a factor of three compared to the whole dataset), did not affect the results or any of our conclusions (Fig. S6).

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Data analyses

First, we set out to test the influence of evolutionary history on traits, by assessing the degree of trait similarity between closely related species. We identified phylogenetic relationships between the studied species, using the mega-tree “GBOTB.extended.tre” with the *V.PhyloMaker* R package (Jin and Qian, 2019), which provided the backbone. We subsequently determined the degree of phylogenetic signal using Blomberg’s K (Blomberg et al., 2003), by comparing the value obtained for each trait to 1000 values obtained for the same trait sampled randomly across the phylogeny. This was conducted using the *phytools* R package (Revell, 2012). A value of Blomberg’s K close to zero indicates phylogenetic independence and a value of one indicates that species’ traits are distributed as expected under Brownian motion. To determine how the total variance in TLP, P50 and TLP-based HSM was partitioned between taxonomic levels, we performed a linear mixed model with genus, family and order, treated as nested random effects on the intercept (Chave et al., 2006). Pairwise trait correlations were explored using Pearson correlations and phylogenetic correlations. The phylogenetic pairwise trait correlations, as well as the effects of forest type, leaf habit and their interaction on TLP, P50 and TLP-based HSM were explored using the *pglm* function of the *caper* R package (Orme et al., 2013). The relative contribution of TLP and P50 in determining TLP-based HSM was quantified using a multiple regression (TLP-based HSM ~ P50 + TLP, performed using the *pglm* function), by calculating the ratio between the sum of square (explained by each variable), and the total sum of square.

Phylogenetic PCA was used to describe the multivariate trait spectrum, using the *phyl.pca* function in the *phytools* R package (Revell, 2012). Leaf habit was not included as a variable in the PCA because it is categorical. TLP-based HSM was not included either because it was strongly correlated with P50 and presented a high proportion of missing data (Table 1), which prevented a reliable imputation of the dataset. In order to test how species drought tolerance was associated with the trait spectrum, we used linear models to test the significance of the association of P50, TLP, TLP-based HSM and leaf habit with the two main axes of the PCA. In addition, we aimed to evaluate the association between drought tolerance and composite variables summarizing the fast-slow and stature-recruitment axes. To accomplish this, we performed two phylogenetic PCAs with subsets of variables corresponding to the fast-slow axis, on the one hand, and the stature-recruitment axis, on the other hand (Table 1). We used the first axis of each PCA as composite variables summarizing trait trade-

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offs. We then evaluated the relationships of P50, TLP, TLP-based HSM and leaf habit with the fast-slow and stature-recruitment composite variables obtained from the PCA transformations.

To analyse the associations between the drought trait and the other trait axes, the dataset was natural log-transformed (using the absolute values of TLP and P50) to meet assumptions of normality and reduce the importance of outliers. All statistical analyses were performed with the R software v4.0.4 (R Core Team, 2021).

RESULTS

Effects of leaf habit and forest types on drought tolerance traits - On average across the whole dataset, Ψ_{min}, TLP and P50 were more negative in dry than in moist forests ($P<0.001$), while TLP-based HSM did not differ significantly between forest types ($P=0.26$, Fig. 1). The interaction between forest type and leaf habit was not significant ($P>0.3$) for Ψ_{min}, TLP, P50 and TLP-based HSM. However, evergreen species, rather than deciduous species ($P=0.06$ and $P>0.4$, respectively; Fig. S7), tended to exhibit more negative TLP and smaller TLP-based HSM in dry forests. By contrast, both evergreen and deciduous species had more negative P50 in dry forests than in moist forests.

[Figure 1]

Pairwise correlations: coordination between drought tolerance traits - P50 was positively associated with TLP across the studied species (Fig. 2a, $r=0.33$, $P<0.001$, $n=137$). More negative P50 values were closely correlated with greater TLP-based HSM (Fig. 2b, $r=0.92$, $P<0.001$, $n=137$), while TLP was not significantly correlated with TLP-based HSM (Fig. 2c, $r=0.08$, $P=0.6$, $n=137$). Similarly, a multiple regression revealed that the relative contribution of P50 in determining TLP-based HSM was much stronger (0.86) than the contribution of TLP (0.14). The relationships between TLP, P50 and TLP-based HSM did not vary with leaf habit (Fig. 2a-c, $P>0.3$). TLP (Fig. 2d, $r=0.59$, $P<0.001$, $n=158$) and P50 (Fig. 2e, $r=0.52$, $P<0.001$, $n=137$) were positively correlated with Ψ_{min}. The majority of the species with both, non-missing TLP and Ψ_{min} values had greater (less negative) Ψ_{min} than TLP ($n=121$, 76%), which indicates that these species remained in the range of water potential

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that allows leaves to function. The average difference between TLP and Ψ_{min} across species was 0.44 MPa. The TLP-based HSM and Ψ_{min}-based HSM were closely correlated (Fig. 2f, r=0.88, P<0.001, n=83), with an average difference of 0.39 MPa across species.

[Figure 2]

Trait phylogenetic signal - Except for leaf P concentration, the variance in the traits linked to the fast-slow and stature-recruitment axes was phylogenetically structured (Table 1). Seed mass was the trait with the highest phylogenetic signal (Blomberg's K=0.23, P<0.001), followed by wood density (Blomberg's K=0.11, P<0.001). The traits determining drought tolerance had weak phylogenetic signals: significant for P50 (Blomberg's K=0.07, P=0.003), non-significant for TLP (Blomberg's K=0.02, P=0.18), Ψ_{min} (Blomberg's K=0.04, P=0.12) and TLP-based HSM (Blomberg's K=0.07, P=0.75). The phylogenetic mapping qualitatively confirmed this result, showing substantial changes in P50 and TLP at the tips of the phylogeny (Fig. 3). The nested analysis of variance showed that 26% of the species-level TLP variation was explained at the genus level and 20% at the family level (Fig. S9). For P50, 20% of the variation was explained at the genus level and 11% at family level. The order level explained a small fraction (<2%) of the variance in TLP and P50. Despite substantial intra-family variation, we found significant differences between families for TLP and P50 (P<0.001, Fig. 4). The degree of phylogenetic signal found within a family was not correlated with the family's average trait value for TLP or P50 (P>0.5, Fig. 4). Among the genera represented by four or more species, the within-genus coefficients of variation (CV) of TLP ranged from 7% to 32%, with a mean of 20% (Fig. S10). For P50, CV ranged from 19% to 73% with a mean of 40% (Fig. S11).

[Figure 3]

[Figure 4]

[Table 1]

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Multivariate trait analysis: coordination of drought tolerance traits with the other trait axes - A phylogenetic PCA conducted with leaf N, leaf P, LMA, wood density, seed mass, leaf size and maximum height confirmed that these traits were coordinated along two independent dimensions corresponding to the fast-slow and stature-recruitment trait axes (Fig. S12). The first axis of this phylogenetic PCA (30% of explained variability) was coherent with the fast-slow trait axis, with LMA, wood density, leaf N and leaf P showing high absolute loadings. The second axis of the PCA (19% of explained variability) was coherent with the stature-recruitment trait axis, with leaf size, maximum height and seed mass showing high absolute loadings. When TLP and P50 were included in the PCA analysis along with the other traits examined, TLP appeared to be closely aligned with the fast-slow axis (Fig. 5A), with lower TLP found in slow strategy species. P50 significantly contributed to both the fast-slow and stature-recruitment axes (Fig. 5A), with lower P50 found in slow strategy species and in species favouring recruitment over stature. These correlations were confirmed by testing the relationships between the PCA scores and the drought tolerance trait values (Fig. 5B), and by testing the relationships of P50 and TLP with the fast-slow and stature-recruitment composite variables (Fig. S13). TLP-based HSM tended to behave as P50 and was significantly associated with the fast-slow and stature-recruitment axes of the PCA (Fig. 5B). However, the relationships between TLP-based HSM and the fast-slow and stature-recruitment composite variables were not significant ($P>0.2$, Fig. S13). Leaf habit was marginally associated with the fast-slow axis ($P=0.08$, Fig. 5), with evergreen species showing slower strategies than deciduous species. The variable correlation plots obtained from phylogenetic and non-phylogenetic PCAs were comparable (Figs. 5 and S3).

[Figure 5]

Pairwise correlations: coordination of drought tolerance traits with the other trait axes - TLP and P50 were significantly correlated to both fast-slow and stature-recruitment traits (Table 2, TLP and P50 are in absolute values): species with more negative TLP showed greater LMA ($r=0.39$, $P<0.001$, $n=347$) and smaller leaf size ($r=-0.17$, $P<0.001$, $n=227$); species with more negative P50 showed less leaf P ($r=-0.34$, $P<0.001$, $n=209$) and smaller leaf size ($r=-0.31$, $P<0.001$, $n=224$). Although the strongest associations indicated by the Pearson correlations were conserved when accounting for the effect of species evolutionary history (e.g. positive TLP-LMA association), Pearson

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and phylogenetic pairwise trait correlations yielded different results. In particular, the phylogenetic analysis revealed the significance of the P50-wood density (r=0.24, P<0.001, n=260), the P50-leaf P associations and the non-significance of the TLP-wood density association (r=0.12, P=0.06, n=252, Table 2).

[Table 2]

DISCUSSION

We compiled data for traits related to drought tolerance and to the fast-slow and stature-recruitment trade-off axes in order to explore their covariations and phylogenetic signals across 601 tropical and sub-tropical woody species. Our results demonstrate that: 1) Inter-species variation in xylem resistance to embolism (P50), and not leaf turgor loss point (TLP), determines the hydraulic safety margin (HSM) of tropical woody species; 2) P50 and TLP exhibit a weak phylogenetic signal and substantial variation within genera; and 3) TLP is strongly associated with the fast-slow trait axis (more negative in slow species), while P50 is associated with both the fast-slow and stature-recruitment trait axes (more negative in slow and small stature species). Therefore, our findings suggest that drought tolerance is coordinated with the ecological strategies governing tropical forest demography.

TLP and P50 are more negative in dry forests than moist forests, but they exhibit considerable variation within forest type

We found that TLP and P50 were on average more negative in dry forests than in moist forests (Fig. 1), which is further evidence to suggest that these traits contribute to species segregation along water availability gradients in tropical and sub-tropical zones (Kunert et al., 2021; Oliveira et al., 2019). However, both traits showed considerable variation within forest type. This variation reflects not only the range of water deficit conditions found in the tropics (Schwartz et al., 2020), but also the diversity of drought tolerance strategies between tropical species. Drought tolerance traits can be

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separated into two categories: those that allow plants to *resist* water stress (e.g. xylem resistance to embolism); and those that allow plants to *avoid* water stress, by preventing or delaying the decrease in plant water potential during drought (Choat et al., 2018). Drought avoidance traits reduce water loss (e.g. tighter stomatal control, drought-deciduousness) or provide access to greater stored water resources (e.g. high internal water storage, deep rooting). Recent studies suggest that species with different combinations of drought tolerance traits and contrasting strategies (e.g. low xylem resistance but access to deep soil water *versus* high xylem resistance and shallow rooting), can thrive in the same conditions of water deficit (Brum et al., 2019; Rutuja et al., 2021). As a result, species with contrasting xylem resistance to embolism and stringency in stomatal control (here indicated by TLP) coexist within a single community, even in tropical rainforests (Maréchaux et al., 2015; Oliveira et al., 2019).

P50 determines the hydraulic safety margin and TLP is associated with water use strategies

In this study, we defined the hydraulic safety margin as the extent to which early stomatal closure protects the xylem from dysfunction during drought (TLP-based HSM = TLP - P50, Martin-StPaul et al., 2017). In order to explore the significance of TLP, P50 and TLP-based HSM for drought tolerance in tropical species, we compared these traits to another definition for hydraulic safety margin proposed in the literature (Ψ_{min}-based HSM, Choat et al., 2012). The Ψ_{min}-based HSM (i.e. P50 - Ψ_{min}) puts xylem resistance in the context of the water stress actually experienced by a species. The diversity of drought strategies found in tropical species emphasizes the relevance of Ψ_{min}-based HSM, because Ψ_{min} is jointly determined by the local conditions of water deficit and the cumulative effect of the different avoidance strategies of a species (Brodribb et al., 2020). The differences between the two definitions of safety margin is expected to increase with water deficit because stomatal closure and the loss of leaf turgor occur at relatively low water stress, while Ψ_{min} may continue to decrease because of residual (leaf, bark) water loss (Martin-StPaul et al., 2017). Our findings show that in tropical forests, most species face leaf turgor loss at levels of water stress that are close to the seasonal maximum (i.e. at water potential close to Ψ_{min}). Consequently, Ψ_{min}-based HSM and TLP-based HSM are closely associated across species (Fig. 2f), which indicates that they quantify the same drought tolerance responses. This result parallels a recent study showing that both HSM definitions have comparable average values in an Australian tropical rainforest (Peters et al.,

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2021). Our results suggest that TLP-based HSM quantifies drought exposure and risk of drought-induced hydraulic failure in tropical species (Powers et al., 2020).

We found that P50, but not TLP, determines TLP-based HSM in tropical woody species. This is in line with the premise that tree species operate within a limited range of stomatal regulation, which means that P50 is a crucial determinant for TLP-based HSM and the risk of hydraulic failure (Martin-StPaul et al., 2017). Indeed, the 5.74 MPa range of P50 values in our dataset (-0.53 MPa to -6.27 MPa) was almost double the 3.3 MPa range of TLP values (-0.75 MPa to -4.08 MPa, Fig. 1). We confirm that xylem resistance to embolism is an essential trait for drought tolerance in tropical biomes (Anderegg et al., 2016; Oliveira et al., 2019).

The positive association between TLP and Ψ_{min} indicates that tropical trees coordinate different water use strategies to maintain water potential within a range that allows for leaf function (Zhu et al., 2018). Moreover, TLP was positively correlated with xylem resistance to embolism, which suggests an adaptive coevolution between leaf and wood drought tolerance traits (Méndez-Alonzo et al., 2012). Collectively, these results provide a plausible explanation for the relevance of TLP as an indicator of drought tolerance and species preference for dryer habitats in the tropics (Bartlett et al., 2012; Kunert et al., 2021). Further studies are needed to evaluate whether the relevance of TLP as an indicator of drought tolerance can also be explained by its correlation with the stringency of the stomatal control of photosynthesis (Meinzer et al., 2016), which may make it difficult to maintain hydraulic functions (O'Brien et al., 2014).

Since leaf shedding significantly decouples the plant and the atmospheric water demand, leaf habit is expected to affect the other drought tolerance strategies (Aguirre-Gutiérrez et al., 2019; Oliveira et al., 2021). In particular, coordination between leaf and wood drought tolerance traits and water deficit conditions was observed for tropical evergreen species, but not for deciduous species (Kunert et al., 2021; Méndez-Alonzo et al., 2012; Oliveira et al., 2021). These distinct responses between evergreen and deciduous species were not apparent in our study, although we report on marginal evidence that changes in TLP and TLP-based HSM between forest types were greater for evergreen species than for deciduous species (Fig. S7). The absence of a clear effect of leaf habit on drought trait coordination probably reflects the difficulty of measuring drought-deciduousness in the field because leaf shedding in tropical species varies quantitatively in time and space and is driven by various environmental cues (Williams et al., 2008).

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Drought tolerance exhibits weak phylogenetic signal and substantial variation within genera

In our global study, we found that P50 had a weak but significant phylogenetic signal, while TLP had no phylogenetic signal. Previous studies on the degree of phylogenetic signal in the xylem resistance of tropical trees have shown variable results (Laughlin et al., 2020; Maherali et al., 2004; Oliveira et al., 2019), which are probably due to variation in the studied lineages and environmental conditions. The degree of phylogenetic signal in a species pool tends to increase with the phylogenetic scale (i.e. how phylogenetically inclusive a study is), which is likely to correlate with the size of the sampled geographical zone (Losos, 2008). Therefore, large-scale studies are crucial to identify patterns of phylogenetic signal that are representative of evolutionary trends (Coelho de Souza et al., 2016). Previous studies showed that both TLP and P50 exhibit moderate phenotypic plasticity in response to changes in water deficit conditions (Bartlett et al., 2014; Bittencourt et al., 2020). This suggests that phenotypic plasticity is not responsible for the weak phylogenetic signal found in both traits (Burns and Strauss, 2012). Therefore, our findings support the view that although xylem resistance to embolism is shaped by evolutionary constraints, recent adaptation to contrasting environmental conditions has resulted in trait diversification in the tropics (Sanchez-Martinez et al., 2020). The weak phylogenetic signal of P50 in tropical trees, previously observed in a local study (Oliveira et al., 2019), may indicate that hydraulic traits are less phylogenetically constrained in tropical biomes than in temperate biomes. Overall, these results indicate that drought tolerance is under strong selective pressure in tropical forests. They also suggest that TLP and P50 are the result of repeated evolutionary adaptations of closely related taxa, which radiate to different habitats (Fig. 3, Oliveira et al., 2019).

A consequence of the evolutionary lability of TLP and P50 is that these traits exhibit substantial variation within orders, families and genera. This has been previously reported in local studies (Maréchaux et al., 2015; Oliveira et al., 2019). In our study, Fagaceae and Lauraceae, which were the two families with the highest average xylem resistance to embolism, exhibited a within-family standard deviation greater than 3MPa, which is more than half of the total amplitude of P50 observed in our dataset (Fig. 4). The same applies to Burseraceae and Fabaceae for TLP. Similarly, for both traits, less than a quarter of the total variation was explained by differences between genera. This indicates that drought tolerance substantially varies between species of the same genus. By

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contrast, Chave et al. (2006) showed that 74% of the variation in wood density between tree species from Central and South America could be explained at the genus level. Given the challenge of taxonomic identification in tropical forests, many ecological and phylogenetic trait-based studies have been conducted at the genus level (Coelho de Souza et al., 2016; Esquivel-Muelbert et al., 2019). Our results indicate that this approach has a limited potential for understanding drought tolerance responses in tropical woody species.

Overall, our findings suggest that taxonomy and phylogeny are of limited help when it comes to understanding and modelling drought tolerance in tropical forests. However, accounting for phylogeny revealed key pairwise correlations, for example, between P50 and wood density, and between P50 and leaf P concentration. Therefore, controlling for the effects of ancestors' legacy is required to interpret trait coordination and species trait profiles as ecological strategies in tropical forests (Reich et al., 2003).

Small and slow tropical tree species tend to be more drought tolerant

We show that drought tolerance is not an independent dimension in the ecological strategy of tropical woody species, but that it is highly coordinated with both the fast-slow and the stature-recruitment trade-off axes (Fig. 5). Specifically, TLP was strongly aligned with the fast-slow axis, with slow species maintaining leaf functioning under higher water stress. This suggests that the recently proposed safety-efficiency trade-off in stomatal control (Henry et al., 2019) is integral to the fast-slow axis in tropical woody species. The stomatal safety-efficiency trade-off states that species with greater stomatal conductance (and thus greater C assimilation capacity) show greater sensitivity to closure during drought. This variation in stomatal control is captured by TLP, whereby a more negative TLP indicates less sensitivity to closure during drought (Meinzer et al., 2016). Therefore, tropical woody species with fast strategies, usually associated with high growth and high mortality rate, tend to show tighter leaf stomatal control - and less negative TLP - than slow strategy species. In line with this, a previous study reported that less negative TLP was associated with higher maximum C assimilation across woody species (Zhu et al., 2018). We found that the highest pairwise correlation of TLP was with LMA (Table 2), which confirms that the ability to operating leaves under greater water stress is linked to increased leaf carbon investment (Zhu et al., 2018). One explanation for this is that high LMA may be associated with thicker cell walls and higher bulk elastic modulus

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(Onoda et al., 2017), which may, in turn, facilitate water uptake from drying soil and results in more negative TLP (Niinemets, 2001). Generally, our results reveal that the maintenance of leaf gas exchange under water stress is linked to key leaf and wood carbon economic traits, which determine the fundamental trade-off between growth and survival in tropical forests (Sterck et al., 2006; Wright et al., 2010).

Slow species tend to exhibit more resistant xylem. This may reflect the fact that, despite the wide range of safety-efficiency combinations observed in tree species, high resistance and high efficiency have not evolved in xylem (Gleason et al., 2016). The idea that the coordination of P50 with the fast-slow axis is driven by a trade-off between xylem traits is corroborated by the significant correlation between P50 and wood density (Table 2). This probably arises from the fact that wood density is an emergent property, which is influenced by the xylem's different anatomical traits (Ziemińska et al., 2013). Therefore, our results indicate that higher xylem resistance to embolism can explain why drought tolerant communities of tropical tree species tend to exhibit higher wood density (Liang et al., 2021; Poorter et al., 2019). However, the relationship between wood density and drought tolerance is ambiguous, because lower wood density allows higher stem water storage capacity, which can delay the effect of water stress and allow fast species to tolerate drought (Pineda-Garcia et al., 2013). The significance of this avoidance strategy for the drought tolerance of tropical woody species has yet to be quantified, but it may contribute to linking drought tolerance to the fast-slow axis. In any case, our results suggest that trade-offs between xylem traits mediate the relationship between xylem resistance to embolism and the fast-slow axis in the tropics.

Species with more resistant xylem also showed lower leaf P concentration. This result is in line with a recent study showing that woody species with more resistant xylem occur preferentially on P-poor soils in an Amazonian rainforest (Oliveira et al., 2019). A plausible explanation is that nutrient poor soils impose slow conservative strategies that enhance the efficacy of nutrient use and nutrient residence time in the tree. This is achieved by growing dense, long-lived wood (Heineman et al., 2016), which also tends to exhibit high xylem resistance to embolism (Laughlin et al., 2020). Soil P availability affects leaf P concentration in tropical tree species, as well as their distributions and functions (Hidaka and Kitayama, 2011; Turner et al., 2018). In addition to these documented effects, we suggest that soil P availability is positively associated with xylem resistance to embolism and drought tolerance in tropical forests. This implies the evolution of a pervasive (nutrient and drought) stress-tolerance syndrome in the tropics, which warrants further investigations (Oliveira et al., 2021).

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Xylem resistance to embolism was also associated with the stature-recruitment axis: more resistant species presented typical adaptations to a dry environment, i.e. small stature (Klein et al., 2015; Liu et al., 2019) and small leaf size (Kröber et al., 2014; Skelton et al., 2021). This is in line with previous evidence that large trees are at greater risk of hydraulic failure than small trees (McDowell and Allen, 2015; Rowland et al., 2015). Our findings complement previous studies (Liu et al., 2019; Olson et al., 2018; Skelton et al., 2021), by showing that the coordination of hydraulic functions with plant size is an important axis of variation in tropical species. This may have major implications for species distribution and responses to climate change.

Broader implications

Tropical forest restoration has received wide international attention as a crucial opportunity for mitigating climate change (Cook-Patton et al., 2020). When tree planting is used for forest restoration in drought-prone sites, the drought tolerance of the selected species will condition the capacity of the newly forested areas to cope with climate change and store C over time. In the absence of species-level information on drought tolerance, our results suggest that it is generally not good practice to base species selection on phylogeny or taxonomy. Moreover, although we found that small and slow tree species tended to be more drought tolerant, the pairwise correlations between easy-to-measure morphological traits and drought tolerance traits were weak. Therefore, they cannot be used in the design of species selection guidelines. Consequently, measuring drought tolerance traits remains crucial when it comes to designing tropical forest restoration programmes under climate change. Our finding that xylem resistance to embolism determines the risk of hydraulic failure in tropical trees under drought conditions makes this trait a priority for future research. More generally, the coordination between drought tolerance and the ecological strategies of tree species that we highlight here provides a physiological basis to interpret the current drought-induced shift toward slow-growing, smaller, denser-wooded trees observed in the tropics (Aleixo et al., 2019; Esquivel-Muelbert et al., 2019; Greenwood et al., 2017; McDowell et al., 2020).

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Figures and Tables

Figure 1. Effects of forest type on seasonal minimum water potential (a, Ψ_{min}), leaf turgor loss point (b, TLP), xylem resistance to embolism (c, P50) and hydraulic safety margin (d, HSM) in tropical and sub-tropical woody species. Circles are average, error bars are standard deviation.

Figure 2. Phylogenetic correlations between drought tolerance traits in tropical and sub-tropical woody species. Dash lines are 1:1 lines. Colours in (a), (b) and (c) indicate leaf habit: deciduous (yellow) or evergreen (green). Colours in (d), (e) and (f) indicate forest type: dry (red) or moist (blue).

Figure 3. Phylogenetic mapping of xylem resistance to embolism (P50, outer circle), leaf turgor loss point (TLP, intermediate circle) and leaf habit (inner circle) for 601 tropical and sub-tropical woody species. The Gymnosperms and the families of Angiosperms represented by four or more species are indicated.

Figure 4. Within-family phylogenetic signal and variation in leaf turgor loss point (a, TLP) and xylem resistance to embolism (b, P50). Symbols are averages and error bars are standard deviations. Triangles and circles indicate Blomberg's K significantly and non-significantly greater than zero (P=0.05), respectively. n indicates the number of species represented in each family.

Figure 5. Association of the drought tolerance traits with the fast-slow and stature-recruitment trait axes. Phylogenetic principal component analysis of nine functional traits across 601 tropical woody species (a). Significance of the relationships between drought tolerance traits and the fast-slow (b, PC1) and stature-recruitment (c, PC2) scores. *, °, ns indicates $P<0.05$, $P<0.1$ and non-significant associations, respectively. Arrow colours in A indicate trait category: fast-slow (red), stature-recruitment (green) and drought tolerance (blue). HSM is the difference between TLP and P50.

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Table 1. Description of the examined functional traits.

	Abbrev.	Cat.	Unit	Mean	SD	Min	Max	n	Blomberg's K
Leaf nitrogen concentration	Leaf_N	FS	mg g^{-1}	19.2	6.33	4.18	47	421	**0.07**
Leaf phosphorus concentration	Leaf_P	FS	mg g^{-1}	1.45	1.03	0.12	7.19	358	0.04
Leaf mass per area	LMA	FS	g m^{-2}	91.37	46.65	27.42	352.6	493	**0.07**
Wood density	Wood_density	FS	g cm^{-3}	0.58	0.15	0.18	1.04	421	**0.11**
Leaf size	leaf_size	SR	cm^2	116.49	335.78	0.5	5213	375	**0.08**
Maximum potential height	max_height	SR	m	16.22	10.74	0.73	80	497	**0.04**
Seed mass	Seed_mass	SR	g	1.74	7.68	1e-05	89	276	**0.23**
Hydraulic safety margin	HSM	DT	MPa	1.08	0.93	0.01	4.28	137	0.07
Xylem resistance to cavitation	P50	DT	MPa	-2.58	1.28	-6.3	-0.53	345	**0.07**
Leaf turgor loss point	TLP	DT	MPa	-1.78	0.53	-4.08	-0.75	393	0.02
Leaf minimum water potential	Ψmin	DT	MPa	-1.54	0.77	-6.07	-0.4	212	0.04
Leaf habit	leaf_habit	DT	D/E	-	-	-	-	515	-

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Note: Abbrev. is abbreviation, Cat. is trait category: fast-slow (FS), stature-recruitment (SR) and drought tolerance (DT). SD is standard deviation. Leaf habit is a categorical variable, where species are classified as deciduous (D) or evergreen (E). Blomberg's K characterises the strength of phylogenetic signal in the data. Blomberg's K values in bold were significantly different from 0, indicating significant phylogenetic signal ($P<0.05$). n is the number of observations (at species level). HSM is the difference between TLP and P50.

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Table 2. Pearson (upper diagonal) and phylogenetic (lower diagonal) correlations among functional traits for 601 tropical and subtropical woody species.

	Leaf N	Leaf P	LMA	Wood density	leaf size	Max. height	Seed mass	HSM	-P50	-TLP
Leaf N	■	**0.21**	**-0.41**	-0.01	0.07	**0.13**	-0.07	-0.02	**-0.15**	-0.03
Leaf P	**-0.28**	■	**-0.41**	**-0.25**	-0.02	-0.02	**-0.2**	0.00	-0.05	**-0.16**
LMA	-0.03	**-0.4**	■	**0.15**	0.05	**0.1**	**0.23**	0.04	0.07	**0.41**
Wood density	0.01	**-0.15**	0.03	■	**-0.22**	0.03	**0.23**	0.02	0.1	**0.37**
leaf size	-0.03	**0.28**	0.06	**-0.22**	■	**0.11**	0.02	-0.18	**-0.29**	-0.12
Max. height	**0.27**	**0.19**	0.03	**-0.11**	**0.13**	■	**0.23**	0.03	0.03	-0.06
Seed mass	**0.13**	**-0.17**	**0.17**	0.08	**0.24**	0.07	■	-0.17	-0.05	**0.32**
HSM	**0.25**	0.14	-0.03	0.03	0.01	-0.03	-0.11	■	**0.81**	0.09
-P50	**0.16**	**-0.34**	0.00	**0.24**	**-0.31**	**-0.13**	-0.06	**0.83**	■	**0.53**
-TLP	-0.06	**-0.13**	**0.39**	0.12	**-0.17**	0.03	0.11	-0.02	**0.43**	■

Note: All trait values were natural log-transformed. Significant correlations (P<0.05) are indicated in bold. HSM is the difference between TLP and P50.

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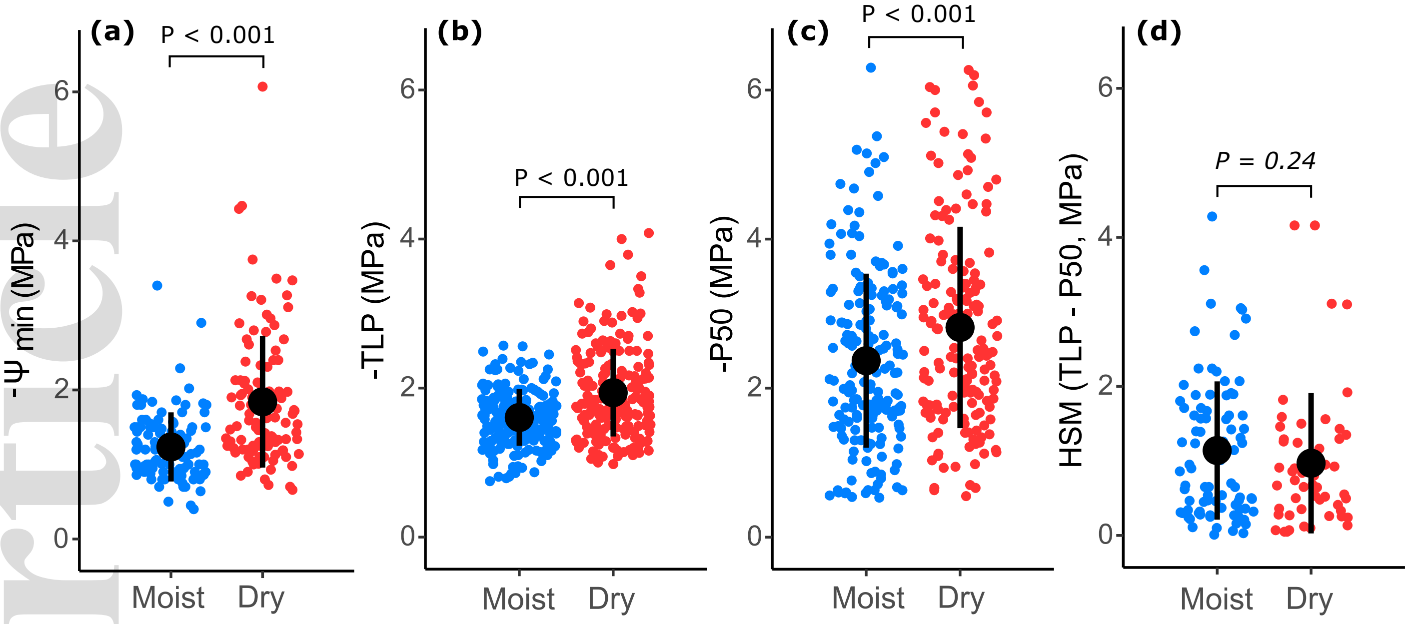

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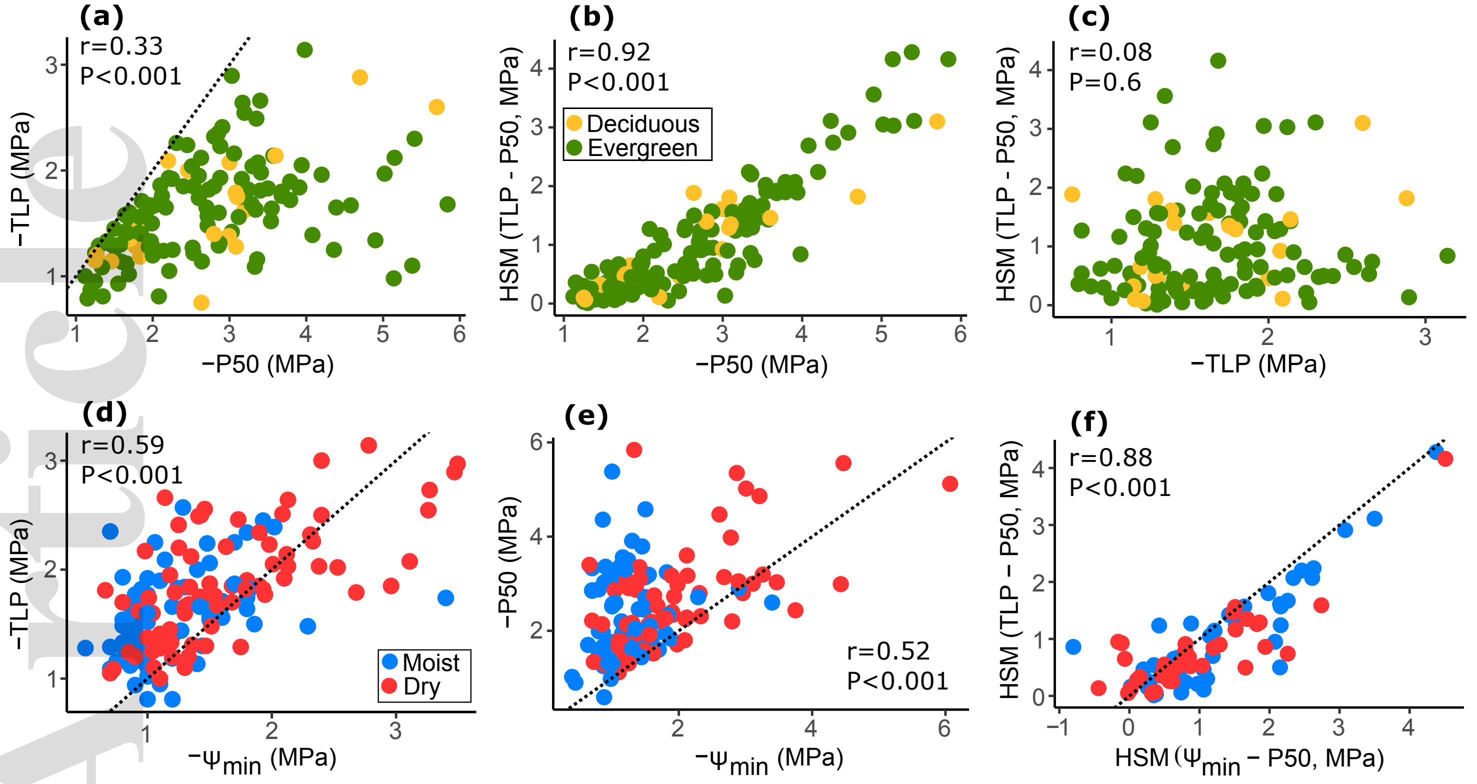

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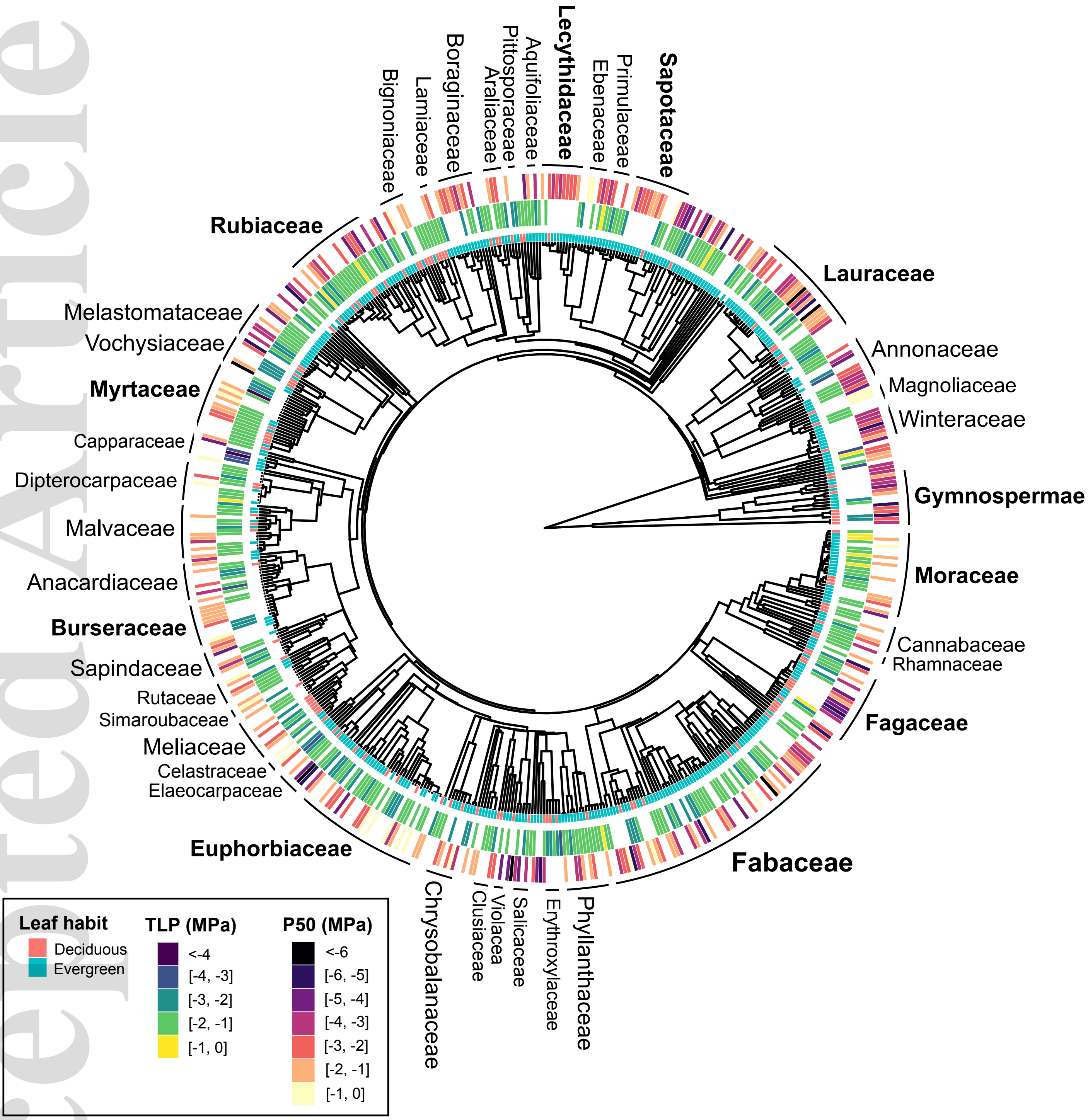

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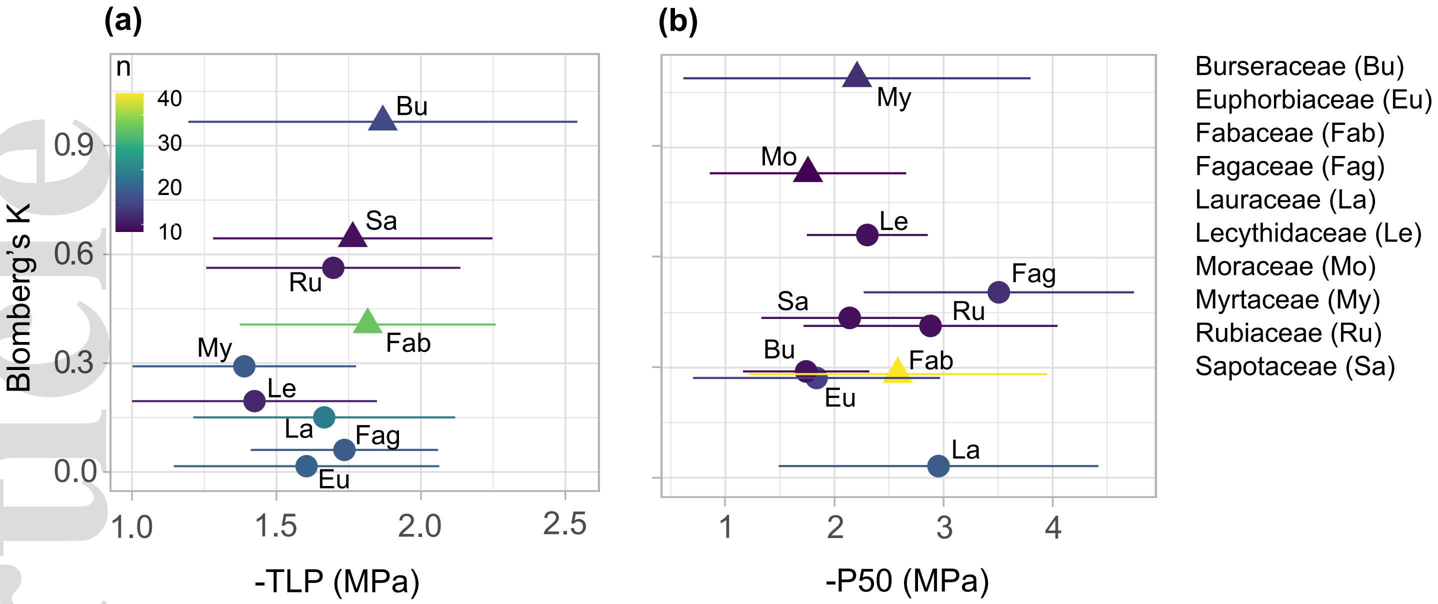

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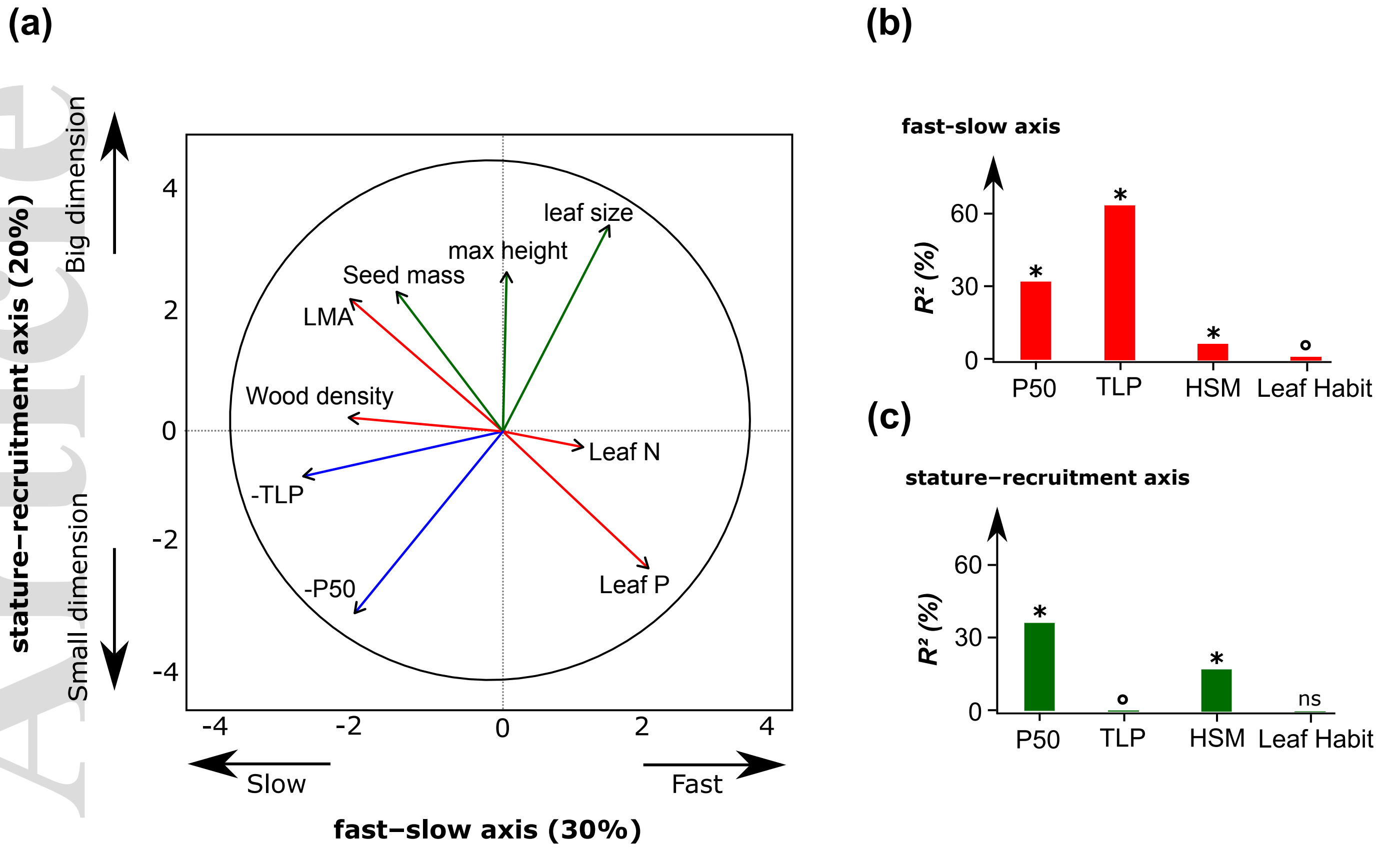

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