

**Lianas in tropical dry seasonal forests have a high hydraulic efficiency but not
always a higher embolism resistance than lianas in rainforests**

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Abstract

Background and Aims Lianas have higher relative abundance and biomass in drier seasonal forests than rainforests, but whether this difference is associated with their hydraulic strategies is unclear. Here, we investigate whether lianas of seasonally dry forests are safer and more efficient in water transport than rainforest ones, explaining liana abundance patterns.

Methods We measured hydraulic traits on five pairs of congeneric lianas of the tribe Bignonieae in two contrasting forest sites: the wet 'Dense Ombrophilous Forest' in the Central Amazonia (~ 2 dry months) and the drier 'Semideciduous Seasonal Forest' in the inland Atlantic Forest (~6 dry months). We also gathered a broader database, including 197 trees and 58 liana species from different tropical forests, to compare hydraulic safety between habits and forest types.

Key Results Bignonieae lianas from both forests had high and similar hydraulic efficiency and exhibited variability in resistance to embolism across forest types when phylogenetic relationships are taken into account. Three genera had higher hydraulic safety in the seasonal forest than in the rainforest, but species across both forests had similar positive hydraulic safety margin despite lower predawn water potential values of seasonal forest' lianas. We did not find the safety-efficiency trade-off. Merging our results with previously published data evidenced a high variability of resistance to embolism in both trees and lianas, independent of forest types.

Conclusions The high hydraulic efficiency of lianas detected here probably favors their rapid growth across tropical forests, but differences in hydraulic safety highlight that some species are highly vulnerable and may rely on other mechanisms to cope with drought. Future research on the lethal dehydration threshold and the connection between hydraulic resistance strategies and liana abundance could offer further insights into tropical forest dynamics under climatic threats.

Key Words: climbing plant, drought vulnerability, forest resilience, hydraulic safety margin, P50, safety-efficiency trade-off.

INTRODUCTION

Over the last decades, climatic seasonality intensified due to increased temperature and reduced precipitation in many tropical forests, increasing extreme drought events (Williams *et al.*, 2007; Phillips *et al.*, 2010; Sherwood and Fu, 2014; Esteban *et al.*, 2020). For plants to succeed in these new climatic conditions, they must resist drought and continue growing despite the drought effects. Although across tropical forests, there has been an increase in drought-induced mortality of tree species associated with the failure of the hydraulic transport system (Allen *et al.*, 2010; Anderegg *et al.*, 2016; Choat *et al.*, 2018), we know much less about this process for the diversity of liana species. At the same time, liana density is high in tropical forests with lower annual rainfall and long dry seasons (DeWalt *et al.*, 2015; Schnitzer, 2018; Schnitzer and van der Heijden, 2019; Medina-Vega *et al.*, 2021). It has been hypothesized that the high liana density in seasonally dry tropical forests may derive from advantages associated with their hydraulic traits (Allen *et al.*, 2010; Anderegg *et al.*, 2016; Choat *et al.*, 2018). Therefore, it is fundamental to investigate the hydraulic features of lianas in forests with contrasting hydrological regimes and understand how this compares to the variation of lianas and other angiosperm growth forms across tropical forests.

Plant resilience to drought varies among environments and plant lineages and can be related to xylem embolism resistance (Anderegg *et al.*, 2016). Drought induces more negative xylem water potentials, which may lead to the formation of air bubbles inside conductive cells and further propagation through “air-seeding” to neighboring conduits, decreasing the capacity to transport water and potentially leading to complete hydraulic failure (Tyree and Ewers, 1991; Tyree and Zimmermann, 2002). Xylem embolism resistance is commonly evaluated through the water potential values at which the plant loses 50% (P50) or 88% (P88) of its conductive capacity by embolism (Tyree and Ewers, 1991; Anderegg *et al.*, 2016). This hydraulic trait describes the lethal threshold of dehydration in many plants and their susceptibility to hydraulic failure, with implications for productivity and survival in different ecosystems (Brodribb, 2009; Choat *et al.*, 2012; Urli *et al.*,

2013). P50 is positively associated with the plant's minimum water potential throughout the day in the field, usually at midday and in the driest season (P_{\min}). Species that grow in drier environments attain more negative minimum water potentials in the xylem and are generally more resistant to drought-induced embolism than species that grow in moist environments (Choat *et al.*, 2012; Delzon and Cochard, 2014; Oliveira *et al.*, 2019). The P_{\min} associated with P50 or P88 is a threshold for calculating the hydraulic safety margin ($HSM = P_{\min} - P50$), indicating how much embolism the plant experiences in the field (Tyree and Ewers, 1991; Tyree *et al.*, 1994; Meinzer *et al.*, 2009). Based on a global meta-analysis, there is evidence of a worldwide convergence in the hydraulic safety margin of angiosperm and gymnosperm trees, indicating a similar narrow HSM value (<1MPa) for tropical seasonally dry forests and tropical rainforests (Choat *et al.*, 2012). However, these hydraulic safety values come from different methods, and currently, we know that some earlier P50 data may be overestimated by measurement artifacts (Cochard *et al.*, 2013; Wheeler *et al.*, 2013; Torres-Ruiz *et al.*, 2014), reducing the hydraulic safety margin. Recent evidence showed a broad variation in P50 and HSM in Neotropical forests (Smith-Martin *et al.*, 2023) and that angiosperm trees in central and eastern Amazon forests operated far from their hydraulic limits when exposed to extreme natural drought, thereby exhibiting a hydraulic conservative strategy (Brum *et al.*, 2019; Garcia *et al.*, 2021).

In previous studies on embolism resistance, lianas from seasonally dry and wet tropical forests in Panama and China have similar or higher hydraulic vulnerability compared to co-occurring tree species (Zhu and Cao, 2009; De Guzman *et al.*, 2017; Zhu *et al.*, 2017; Van der Sande *et al.*, 2019). If so, lianas in drier environments would likely have avoidance strategies to deal with water scarcity, such as greater stomatal control or increased leaf-shedding to reduce water loss and/or access to deep water sources through deep roots (Schnitzer 2018; Mantova *et al.*, 2021). On the other hand, liana species that grow in drier climates, such as semi-arid areas in Brazil (Carvalho *et al.*, 2016), were shown to have higher hydraulic safety than lianas of wet tropical forests in China and Panama (Zhu and Cao, 2009; Van der Sande *et al.*, 2013, 2019; Medina-Vega *et al.*, 2021), although there is also a notable interspecific difference. It might, therefore, be expected that seasonally dry

tropical forests with lower availability of water may have liana species that are more embolism resistant than liana species from wet rainforests, as has been shown for many tree species (Trueba *et al.*, 2017; Guillemot *et al.*, 2022; but see Garcia *et al.*, 2023 for factors beyond climate controlling hydraulic resistance). Consequently, if liana species from wet rainforests show reduced hydraulic safety and safety margin, they should be more vulnerable and prone to drought-induced mortality than lianas from seasonally dry forests or rely on other strategies to endure or escape drought.

Hydraulic safety is weakly related to xylem hydraulic efficiency in lianas, trees, and shrubs (Zhu and Cao, 2009; Gleason *et al.*, 2016; Van der Sande *et al.*, 2013, 2019, but see Wheeler *et al.*, 2005). Xylem hydraulic efficiency, measured as potential xylem-specific hydraulic conductivity, has been reported as a xylem space-use efficiency property (Bittencourt *et al.*, 2016). For a given stem diameter and length, a high hydraulic efficiency can supply a large leaf area at a lower energy cost if compartmentalization is ignored (Bittencourt *et al.*, 2016). Regardless of the environment, there is extensive evidence that lianas have higher conductive efficiency and lower mechanical demand for support compared to trees (Zhu and Cao, 2009; Zhu *et al.*, 2017; Van der Sande *et al.*, 2019; Medina-Vega *et al.*, 2021). The anatomical features of conducting cells of most lianas include a combination of wide and long vessels with narrow and short vessels and tracheids (Carlquist, 1991; Tyree and Ewers, 1991; Angyalossy *et al.*, 2012, 2015), favoring higher xylem space-use efficiency and hydraulic conductivity compared to trees (Ellmore and Ewers, 1985; Ewers and Fisher, 1989; Tyree and Zimmermann, 2002; Gerolamo and Angyalossy, 2017). High hydraulic efficiency can be considered an essential feature of the liana's success since greater conductivity increases the delivery of water to plant tissues and may favor photosynthesis and, consequently, the stem and leaf area growth (Zhu and Cao, 2009; Van der Sande *et al.*, 2013, 2019). Therefore, a higher xylem hydraulic efficiency could contribute to higher liana growth in drier forests, potentially leading to the higher abundance observed in those environments compared to wet forests.

Hydraulic safety and efficiency integrate critical aspects of plant physiology, structure, and their interaction with the microclimate and soil (Choat *et al.*, 2012; Delzon and Cochard, 2014; Skelton *et al.*, 2015; Fontes *et al.*, 2020). These hydraulic features are associated with niche differentiation across environmental gradients (Engelbrecht *et al.*, 2007; Brodribb, 2017; Brum *et al.*, 2019; Garcia *et al.*, 2023) and are rarely explored on liana assemblages across contrasting forest types (Medina-Vega *et al.*, 2021). Therefore, in this study, we investigated the hydraulic safety and efficiency of five pairs of congeneric liana species of the tribe Bignonieae distributed in two distinct Neotropical Forest types: the wet 'Dense Ombrophilous Forest' in the Central Amazonia (~ 2 dry months), and drier 'Semideciduous Seasonal Forest' in the inland Atlantic Forest (~ 6 dry months). The tribe Bignonieae (Bignoniaceae) is the most diverse lineage of lianas in the Neotropics (Gentry, 1991; Lohmann *et al.*, 2013), and the most parsimonious interpretation of the biogeographic history of this group indicates that the crown node of Bignonieae originated in South American rainforests, diversifying in the lowland Amazon forest, and more recently spread to seasonally drier forests and savannas (Lohmann *et al.*, 2013). For lianas to have survived in seasonally dry forests, they must resist drought. After and along this period, a high conductive efficiency would favor their growth, but survivorship would depend on hydraulic resistance. In this context, the main question that emerges is whether liana species of seasonally dry forests are safer and more efficient in transporting water than those of wet rainforests. We hypothesized that: (H1) Bignonieae liana species of seasonally dry forest cope with lower availability of water and consequently have a higher hydraulic safety compared to liana species of wet rainforest, minimizing the risk of hydraulic failure under drought; (H2) Bignonieae liana species of seasonally dry forest have a more efficient xylem hydraulic transport than liana species of wet rainforest, not supporting the safety-efficiency trade-off. If the safety-efficiency pattern is recurrent among genera of the two forest types, this would indicate a consistent adaptation strategy to drier conditions after this group invaded the dry belt. Furthermore, by combining a large plant hydraulic safety dataset, we can evaluate the variation in hydraulic safety of lianas concerning different families, plant habits, and forest types within a broader context and test

(H3) if liana species of seasonally dry forests have higher hydraulic safety than trees, shrubs, and lianas from other tropical forests. Addressing these hypotheses and understanding how hydraulic safety and efficiency changes in lianas from different tropical forests allow us to provide a valuable framework for mechanistic models of plant hydraulics under the intensification of climate change.

MATERIALS AND METHODS

Study site and climate

The study was carried out in two contrasting forest types marked by the differentiation of the water regimes according to the classification conducted by the Brazilian Institute of Geography and Statistics (IBGE, 2012). The first one was the 'Dense Ombrophilous Forest,' encompassing the continuously green, non-flooded Amazon Forest, located at Ducke Reserve, a 10,000 ha reserve situated in the central region of the Amazon basin, Manaus, Brazil (02°55'S, 59°58'W). In contrast, the second was the 'Semideciduous Seasonal Forest' that includes the inland Atlantic Forest, located at Santa Genebra Reserve, a 250-ha reserve in the Atlantic Forest domain in São Paulo, Brazil (22°45' S, 47°33'W). The distinction between 'Ombrophilous' (hereafter called rainforest) and 'Seasonal' (hereafter called seasonal forest) forests lies in their climatic conditions, with the former occurring in regions experiencing less than four months of a dry season, while the latter is found in areas with more extended periods of dry season (IBGE, 2012).

According to the Koppen-Geiger climate classification, the Ducke Reserve experiences a tropical 'Am' climate, with dry and rainy seasons ruled by monsoons (Peel *et al.*, 2007). Annual rainfall and average maximum temperature in the 2018 collection were 2147 mm and 32 °C, respectively, with August being one of the driest months with 86 mm of precipitation (Supplementary data Fig. S1 - Climate diagram; data obtained from the Station of Ducke Reserve, Laboratory of Climatic Modeling of National Institute for Amazonian Research - INPA - managed by

Dr. Luiz A. Candido). The vegetation of the Ducke Reserve was an old-growth perennial rainforest with a high diversity of tree and liana species. The forest has a 30-37 m closed canopy and emerging trees reaching 45 m (Guillaumet and Kahn, 1982; Ribeiro *et al.*, 1999; Rocha *et al.*, 2022). The topography was heterogeneous, with elevations ranging from 40 to 140 m above sea level (Ribeiro *et al.*, 1999). Soils form a continuum of clayey oxisols on plateaus, with increasing sand on the slopes, until they become pure sand at the bottom of the valleys, forming small floodplains (Chauvel *et al.*, 1987; Mertens, 2004).

According to the Koeppen-Geiger climate classification, Santa Genebra Reserve experiences a tropical 'Cwa' climate (Peel *et al.*, 2007). Annual rainfall and average maximum temperature in 2020 were 871 mm and 40 °C, respectively, with September being a dry month at the end of the dry season with 18 mm of precipitation (Supplementary data Fig. S1; data obtained from the <http://clima.iac.sp.gov.br/> in Campinas station). The vegetation of the Santa Genebra Reserve was a semideciduous seasonal forest, occupying 85% of the reserve, with a high diversity of tree and lianas species and an almost continuous canopy at about 15 m in height with emerging trees reaching 30 m (Morellato, 1991; Morellato and Leitaó-Filho, 1996). The topography was homogeneous, with elevations ranging from 580 to 610 m above sea level, and soils were typical dystrophic red argisol (Mendes *et al.*, 2013).

Species collection and design

We selected five abundant species of Bignoniaceae lianas in the rainforest site (Ducke Reserve) and the other five in the seasonal forest site (Santa Genebra Reserve), totaling ten species (Supplementary data Table S1). These species were chosen for being congeneric species pairs across forest types. Congeneric species pairs were used to assess whether habitat-associated drought traits repeatedly occurred in different phylogenetic lineages. An exception was the genus *Fridericia*. Due

to the existence of a species complex within *F. triplinervia*, in this specific case, we treated the two geographically disjunct and morphologically distinct populations of this species as congeneric pairs in the subsequent analyses comparing both forest types. All species included were abundant in these forests (Morellato, 1991; Morellato and Leitao-Filho, 1996; Rocha *et al.*, 2020, 2022; Gerolamo *et al.*, 2022). In our sampling, we included only mature individuals, i.e., plants that reached the forest canopy and had a stem diameter >1 cm at 1.30 m from the rooting point. Six to eight individuals were marked and sampled for each species. Each liana was located more than 10 meters from each other without any stem connection with other lianas to avoid clonal plants (Schnitzer 2006). The distribution of marked individuals/species in each forest varied according to the habitat. At Ducke Reserve, we found *Anemopaegma robustum* and *Bignonia aequinoctiales* predominantly distributed in the valleys near the watercourse. The other three species, *Adenocalymma validum*, *Fridericia triplinervia*, and *Tynanthus fasciculatus*, were predominantly distributed on the plateaus and slopes (Gerolamo *et al.*, 2022). At Santa Genebra Reserve, the five species occurred in the plateaus and close to the main trails in clearing areas. The liana species of wet rainforest and seasonal forest were collected in the dry season in 2018 and 2020, respectively (Supplementary data Fig. S1). After field collection, the branches were taken to the laboratory to estimate the vulnerability to embolism, as described below. A voucher for each species was deposited at the Herbarium of the University of São Paulo (SPF; the acronym of (Thiers, 2017); Supplementary data Table S1).

Vulnerability to xylem embolism

We collected a branch (ca. 2 m in length) of six to eight individuals longer than the maximum vessel length for each species. The maximum vessel lengths were measured using an air-injection method in at least three individuals per species (Greenidge, 1952; Ewers and Fisher, 1989; Jacobsen *et al.*, 2012), and values were 56-92 cm. We collected about three branches daily in the early morning between 5:30 am and 7:30 am local time (Manaus and São Paulo, Brazil) to avoid artificial

embolism propagation by cutting stems with rather negative xylem water potentials. All branches were cut from the canopy, and each branch was sprayed with water, placed inside dark plastic bags with moistened paper towels, and the cut ends were immersed in a beaker with water to prevent desiccation. We transported the branches to the laboratory within ca. 35 min. They were kept under dark plastic bags with moistened paper towels for at least one hour before starting the vulnerability curves. The hydraulic vulnerability curves were constructed using the manual pneumatic method (Pereira *et al.*, 2016; Bittencourt *et al.*, 2018; Zhang *et al.*, 2018). The total air-discharging tube volume of 3.915 ml was calculated from the tubing datasheets, in which each rigid tubing (Cole-Parmer, USA) had 1.304 ml (for details, see Bittencourt *et al.*, 2018). The air volume was estimated from the amount of gas extracted over 2.5 min from the cut end of the branch after applying a partial vacuum (~ 50 kPa absolute pressure). The measurements were carried out before the development of an automated pneumatic apparatus (Pereira *et al.*, 2020) and the estimation of the best extraction duration (Paligi *et al.*, 2021; Yang *et al.*, 2023), but we expect a relatively low error for the P50 estimation considering the agreement between the manual pneumatic method and other methods (Brum *et al.*, 2023).

Branches were bench dehydrated, and the xylem water potential was measured using a pressure chamber (PMS 1000; PMS Instruments Co., Albany, OR, USA; Scholander *et al.*, 1965). The branches were bagged for 30 min to 1 hour to balance the leaf and xylem water potential, and then two leaves from each branch were used to estimate the average xylem water potential in each measurement. About 8 to 10 measurements were conducted on each branch. The last measure was taken when the percentage of air discharge had stabilized, the leaves were completely dehydrated, and/or the xylem water potential exceeded -8 to -9 MPa. We pooled the data for each branch and fitted a sigmoidal curve to the data, relating the percentage of gas discharged (PAD) to the xylem water potential. In the sigmoidal curve, P50 and slope (b) were the fitted parameters (Pammenter and Willigen, 1998), and P88 was predicted from the fitted model: $PAD = 100 / \{1 + \exp [b (\Psi - P50)]\}$. We fitted the curves at the individual level and then pooled individuals' curves by species.

P50 and P88 were the xylem water potential at which 50% and 88% of the maximum gas amount were discharged, respectively. We used P50 and P88 as indicators of xylem resistance to hydraulic failure.

Predawn and midday water potential

Leaf water potential (MPa) was measured at predawn and midday and during the peak of the dry season in each forest (August-September; Supplementary data Fig. S1) using a pressure chamber. About three to six individuals of each species were selected (the same individuals used for the vulnerability curves), and leaves of two to three individuals per day were measured. For each chosen liana, three fully developed mature canopy leaves per individual were collected between 5:30 am and 7:00 am (P_{predawn}). Another three leaves were collected between 11:30 am and 2:00 pm (P_{midday}). The leaf water potential was measured immediately after collecting the leaves in the field. At the whole-plant level, the leaves were more exposed to the low water potentials of the atmosphere and consequently experienced more negative water potentials than those found in the stem (Tyree, 1988; Guan *et al.*, 2021). Due to the stem-leaf transition of the water potential gradient, if the stomata were not closed, we selected the most positive value of the three leaves measured in P_{midday} as a reference to represent the minimum water potential of the stem xylem (P_{min}). The xylem hydraulic safety margin (HSM) was calculated as $\text{HSM} = P_{\text{min}} - P50$, where P_{min} was the minimum seasonal leaf water potential measured in the field during the dry season (August-September, Supplementary data Fig. S1).

Anatomical measurements

To establish a standard for the distance from the apex, which was necessary for the comparison of the vessel diameter (Gasson and Baas, 1983; Rosell and Olson, 2014), we sectioned samples from the base of the stem (about 1 meter from the apex) from the same branches that were

used for the vulnerability curves to perform the anatomical procedures. Each stem sample was fixed in FAA (formaldehyde, acetic acid, and 50% ethanol, Johansen, 1940) and stored in 70% ethanol. The samples, composed of bark (secondary phloem and periderm) and secondary xylem, were embedded in polyethylene glycol 1500 (PEG-1500) (Rupp, 1964). Each sample's transverse, longitudinal, radial, and tangential sections were made with a sliding microtome, following Barbosa *et al.*, (2010). Sections were stained in 1% astra blue, and 1% safranin (Bukatsch, 1972; Kraus and Arduin, 1997), and permanent slides were mounted for anatomical analyses. We photographed each histological slide with a photomicroscope (Leica DML and camera DFC 310FX) to estimate vessel diameter, frequency, and theoretical specific hydraulic conductivity. The images were analyzed using ImageJ version 1.45d software (National Institutes of Health, Bethesda, MD, USA; <http://rsb.info.nih.gov/ij/>). We used the procedures established by (Scholz *et al.*, 2013), measuring at least 100 vessels per stem sample to characterize vessel diameter and counting the number of vessels in four areas of 1 mm² to estimate the vessel frequency per sample. All anatomical measurements were accomplished in the interwedge regions, i.e., stem portions with regular secondary growth in Bignoniaceae lianas (Gerolamo and Angyalossy, 2017).

Specific hydraulic conductivity

Theoretical specific hydraulic conductivity (K_s ; $\text{Kg} \cdot \text{m}^{-1} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$) was indirectly used to describe water transport efficiency. Using vessel diameter and vessel frequency of each individual, we calculated the K_s (Equation 1) following Hagen–Poiseuille's law (Tyree and Ewers, 1991; Poorter *et al.*, 2010), as

$$\text{(Eq. 1)} \quad K_s = \left(\frac{\pi p w}{128 \eta} \right) \cdot F v \cdot D_h^4$$

where ρ_w was the density of water at 20°C (998.2 kg.m⁻³), η was the water viscosity at 20 °C (1.002 10⁻⁹ MPa.s), F_v was the vessel frequency per mm², and D_h was the hydraulic vessel diameter (m).

We calculated D_h (Equation 2) considering both wide and narrow vessels as

$$\text{(Eq. 2)} \quad D_h = \left[\left(\frac{1}{n} \right) \sum_{i=1}^n d^4 \right]^{1/4}$$

where n was the number of vessels and d was the vessel diameter.

Narrow vessels could be misinterpreted as tracheids (Carlquist, 1985). However, we analyzed the dissociated xylem cells in macerated tissue and found no tracheid in all liana species sampled. K_s was assumed to be higher than actual conductivity values because of the resistance of the end walls of vessels (Gibson *et al.*, 1985; Sperry *et al.*, 2008), and embolized vessels were not taken into account. Here, we assumed that these additional resistances did not change the relative differences found in K_s between species since K_s would scale positively with actual conductivity values (Ewers *et al.*, 1989; Tyree and Zimmermann, 2002).

Data analysis

Following the first hypothesis (H1), we expected that Bignoniaceae liana species from the drier seasonal forest would cope with lower availability of water (lower P_{predawn} and P_{min}) and consequently have a higher hydraulic safety (lower P50) compared to liana species of rainforest, minimizing the risk of hydraulic failure (HSM) under drought. To evaluate our H1, we assessed the effect of forest type and genus (predictor variables) on predawn water potential (P_{predawn}), minimum seasonal water potential (P_{min}), hydraulic safety (P50), and safety margin (HSM) (response variables), using a model selection approach for each response variable (Legendre and Legendre, 1998), described below. We built linear mixed models (LMM) with Gaussian error distribution for each response variable,

considering the forest type, genus, and interaction term as fixed factors and the species nested within a genus as a random variable on the intercept. The structure of random variables was defined to account for the nonindependence of individuals nested in species and species nested by genus following our sampling design.

Following the second hypothesis (H2), we expected that Bignoniaceae liana species of the drier seasonal forest had a more efficient xylem hydraulic transport (K_s) than liana species of rainforest, not supporting the safety-efficiency trade-off. To evaluate our H2, we used the same model selection approach, evaluating the effect of forest type, genus, and the interaction term on the theoretical specific hydraulic conductivity (K_s). Also, we tested the relationship between theoretical specific hydraulic conductivity and hydraulic safety (P50) to investigate the safety-efficiency trade-off across plants directly. We included the random term in the models above to describe the nested structure of our sampling design. Data of K_s were log-transformed before analysis to achieve normality.

In all cases above, we evaluated the most suitable minimal model from a set of models that included a null model (only intercept without forest type, genus, and the interaction term between both). The minimum suitable model had the lowest Akaike information criterion (AIC) value, and models with $\Delta AIC < 2$ were considered plausibly similar. We validated the selected models by visually verifying the homogeneity of variance and normality of the residuals. For all statistical analyses, we used R v.3.3.0 (R Core Team, 2020) with base packages and the lmer function of lme4 (Bates, 2010).

To contextualize the variation in the hydraulic safety of lianas in a broader framework and test the third hypothesis (H3) that liana species of drier seasonal forests were hydraulically safer than shrubs, trees, and lianas from other tropical forests, we combined a large dataset with average hydraulic safety (P50) for angiosperm species, including trees, shrubs, succulents, herbs, and lianas from different families and forest sites (Zhu and Cao, 2009; Choat *et al.*, 2012; Carvalho *et al.*, 2016; Chen *et al.*, 2017, 2021; Oliveira *et al.*, 2019; Tan *et al.*, 2020; De Guzman *et al.*, 2021; Medina-Vega

et al., 2021; Smith-Martin *et al.*, 2022). Data on the number of species per habit included in each study can be viewed in Supplementary Data Table S2. We did not include studies that used air injection and centrifugation techniques to estimate P50 because we know that these techniques can overestimate P50 values due to effervescence (Yin and Cai, 2018) and open-vessel artifacts (Cochard *et al.*, 2013; Wheeler *et al.*, 2013; Torres-Ruiz *et al.*, 2014; Pereira *et al.*, 2021). Data on tree, shrub, and liana species in tropical rainforests and seasonal tropical forests were separated for analysis. We compared the hydraulic safety range (P50 max – P50 min) of lianas in the seasonal forest with the rainforest and trees and shrubs of other tropical forests. The difference in P50 values was tested using t-tests and $\alpha = 0.05$.

RESULTS

Hydraulic safety and efficiency in lianas

Liana species of the seasonal forest had lower (more negative) predawn water potential (P_{predawn}) values than congeneric liana species of the rainforest (Table 1; Fig. 1A; Model 1 in Table 2). In the rainforest and seasonal forest, most species reached P_{predawn} close to zero, but *Adenocalymma* and *Bignonia* in the seasonal forest reached values close to -2.5 MPa (Fig. 1A; Table 1). The minimum seasonal water potential (P_{min}) of liana species of the seasonal forest was 1.4 to 4.8 times more negative than congeneric rainforest lianas, except for *Tynanthus* (Fig. 1B; Table 1). However, the differences in the P_{min} averages between liana species of rainforest and seasonal forest were genus-dependent (Model 6 in Table 2). Two genera (*Adenocalymma* and *Bignonia*) had more negative P_{min} values in the seasonal forest (Supplementary data Table S3). In contrast, the other three genera had similar P_{min} values between the forest types.

The hydraulic safety (P50) of liana species of the seasonal forest was 1.7 to 3.2 times more negative than liana species of the rainforest, although this difference was genus-dependent (Fig. 1C;

Table 1; Model 11 in Table 2). Three congeneric pairs of Bignonieae lianas from the seasonal forest had higher hydraulic safety values (more negative P50) than the paired liana species of the rainforest (Supplementary data Table S3). In contrast, the other two congeneric pairs, *Fridericia* and *Tynanthus*, had similar hydraulic safety values between the two forest types (Fig. 1C). The genus-dependent effect of forest type on hydraulic safety indicated that the higher hydraulic safety found in liana species of seasonal forest compared to liana species of rainforest repeatedly occurred at least in three different phylogenetic lineages within the tribe Bignonieae. The hydraulic safety margin ($P_{\min} - P50$) was similar between liana species from the rainforest and seasonal forest (Model 16 in Table 2; Fig. 1D). The hydraulic safety margin ranged from -0.2 to 2 MPa in liana species of the rainforest, and from -0.2 to 1.5 MPa in liana species of the seasonal forest (Table 1; Fig. 1D).

The hydraulic efficiency, as quantified by the theoretical specific conductivity (Ks), was high and similar between liana species from the rainforest and seasonal forest (Model 21 in Table 2; Fig. 1E). Also, Ks was not related to hydraulic safety (P50) (Model 26 in Table 2, Fig. 2).

Hydraulic safety of trees, shrubs, and lianas in tropical forests

Using the combined dataset (i.e., our data and literature review), there was no difference in xylem resistance to embolism between liana species of seasonal forests (36 liana species of 13 families) and rainforest (22 liana species of 8 families) (t-test = -0.05; $P = 0.95$; Fig. 3). Similarly, there was no significant difference in P50 between Bignonieae lianas from the rainforest and the global average for tree and shrub angiosperms from the tropical rainforest (Fig. 3; t-test = -0.81; $P = 0.41$). The average P50 of Bignonieae lianas from the seasonal forest was 21% more negative than the global average for tree and shrub angiosperms from the seasonal tropical forest (-2.58 MPa) (Fig. 3), but this difference also was not significant (t-test = 1.69; $P = 0.09$). The local variation in P50 for Bignonieae lianas (-3.18 and -2.86 MPa ranges in the rainforest and seasonal forest, respectively)

covered about 30 % of the global variation in P50 for angiosperms (-10.9 MPa, ranging from -0.1 to -11 MPa, dataset indicated in the M&M section, Fig. 3). The variation in P50 for all lianas (-3.82 and -4.5 MPa for rainforest and seasonal forest, respectively) covered about 42% of the global variation in P50 for angiosperms (Fig. 3).

DISCUSSION

We investigated the hydraulic performance of lianas in Neotropical forests, specifically, whether pairs of congeneric species from the tribe Bignoniaceae have differences in safety and efficiency of water transport associated with climate seasonality. The first hypothesis was partially supported: Bignoniaceae lianas of the seasonally dry forest cope with lower water availability, with 3 of 5 genera having a higher hydraulic safety that can minimize the risk of hydraulic failure (positive HSM) under drought. The increased hydraulic safety of seasonally dry forest' lianas appeared at least three times within Bignoniaceae. In contrast, the field data did not support our second hypothesis: lianas species of both forest types invest in equally highly efficient xylem in water transport rather than only the seasonal forest ones. Therefore, we did not detect the hydraulic safety-efficiency trade-off. Lastly, our third hypothesis was not supported by the dataset available from the literature: lianas of seasonal forests in the Neotropics do not show higher embolism resistance, and in general, hydraulic safety is similar among lianas, shrubs and trees from wet and seasonal tropical forests. This pattern reveals the similarity in hydraulic traits among different tropical plant groups, especially within the same forest site, probably due to abiotic variations (e.g., edaphic features) within each tropical site associated with multiple hydraulic strategies.

High hydraulic efficiency but not always a higher embolism resistance

Plants from drier environments cope with lower water availability, reaching more negative seasonal minimum water potentials (Choat *et al.*, 2012, 2018; Mantova *et al.*, 2021; Oliveira *et al.*, 2021), as observed in our seasonal forest species. The establishment and survival of plants in seasonally dry environments are related to drought resistance mechanisms (Choat *et al.*, 2008, 2010; Trifilò *et al.*, 2014; Santiago *et al.*, 2016), allowing plants to operate at more negative xylem water potential with reduced levels of embolism (Gleason *et al.*, 2016). We found a wide variation in hydraulic safety in both forests and a higher embolism resistance (more negative P50) in three lineages of Bignoniaceae lianas from seasonal forests compared to rainforests. These findings emphasize the crucial role of increased xylem resistance as one of the mechanisms to cope with water scarcity in drier environments across life-forms (Anderegg *et al.*, 2016; Barros *et al.*, 2019).

The higher hydraulic safety of lianas was not universal across genera in lineages of Bignoniaceae from seasonal forest compared to rainforest. Two lineages of Bignoniaceae had similar hydraulic safety between the seasonal forest and rainforest. The *Tynanthus* lineage had above-average hydraulic safety values, even if this did not differ among forest types, indicating that they have a hydraulic structure with high resistance to embolism independent of the forest type. On the other hand, the hydraulic safety of the *Fridericia* lineage was similar between forests, but the seasonal forest species were below average for this forest. In this case, the low hydraulic safety in *Fridericia* species could indicate that these plants invest more in drought avoidance mechanisms, as observed in *Frideria caudigera*, *Fridericia dispar*, and *Frideria chica* (Carvalho *et al.*, 2016). These *Fridericia* species have rapid stomatal control and/or leaf shedding during drought, reducing water loss and embolism risk under drought conditions (Carvalho *et al.*, 2016; Chen *et al.*, 2017). Also, some species can have deep roots accessing water from deeper soil layers (Holbrook and Putz, 1996; Restom and Nepstad, 2001; Brum *et al.*, 2019). However, data on deep root systems in lianas is scarce (De Deurwaerder *et al.*, 2018; Smith-Martin *et al.*, 2019), and *Fridericia* and other liana

species have commonly thin roots in the superficial soil layers (Andrade *et al.*, 2005; Carvalho *et al.*, 2016; Putz, 2023), hardly reducing water limitation during droughts. Finally, some liana species could have a multifocal growing strategy with hydraulic redistribution and higher water storage (Morris *et al.*, 2016; de Azevedo Amorim *et al.*, 2018) that should be further investigated for Bignoniaceae species. Therefore, some seasonal tropical forest species with lower hydraulic safety may invest in avoidance rather than tolerance strategies to ensure survival (Oliveira *et al.*, 2021). Still, we are unsure which combined functional traits could be associated with the avoidance strategy in lianas of seasonal forests.

Given the high total annual rainfall and the short dry season, water availability tends to be high in the Amazon rainforest. Consequently, the less negative values of P_{min} and P50 found here for three lineages were expected for the entire liana assemblage. However, we found that the xylem resistance to embolism was highly variable across Bignoniaceae lianas at the small spatial scale of a single Amazon rainforest site. This high variability of P50 may be due to local differences in soil water availability along the hydro-edaphic gradient that was already associated with differences in hydraulic resistance across tree species (Oliveira *et al.*, 2019; Garcia *et al.*, 2023). Similarly, we found the liana species with greater resistance to embolism farther away from water courses (e.g., *Tynanthus*, *Fridericia* and *Adenocalymma* species), i.e., in relatively drier conditions compared to those species located in stream valleys (e.g., *Anemopaegma* and *Bignonia* species), clear evidence of habitat partitioning associated with hydraulic features (Cosme *et al.*, 2017; Oliveira *et al.*, 2019). The higher hydraulic vulnerability of tree and liana species associated with valleys may be counterbalanced by the valley's wetter conditions, where groundwater supplies plants all the time during 'standard' climatic years. However, these species may be at particular risk if the water-table level deepens during extreme droughts (Costa *et al.*, 2023).

The average positive hydraulic safety margin (HSM) across forest types indicates that their xylem does not experience a high risk of embolism formation, similar to findings for central and

eastern rainforest trees (Brum *et al.*, 2019; Garcia *et al.*, 2021). However, at least some species have a greater risk of hydraulic failure due to the large variation in HSM between lianas within each forest type. Damage to the xylem system with increased water stress reduces the conductive capacity, but can be relieved by producing new vascular tissue and/or tissue rehydration (Brodersen and McElrone, 2013; Knipfer *et al.*, 2016). Some studies suggested that lianas have efficient mechanisms to recover embolized vessels during the day (Van der Sande *et al.*, 2013; Johnson *et al.*, 2013), although the frequency and mechanism of refilling remain unresolved (Brodersen *et al.*, 2010; Delzon and Cochard, 2014; Trifilò *et al.*, 2014). There is evidence of cambial activity producing new vascular tissues during the wet season and early dry season in lianas of Bignoniaceae (Lima *et al.*, 2010; Angyalossy *et al.*, 2015) and Fabaceae (Brandes *et al.*, 2011) and throughout the year in Sapindaceae (León-Gómez and Monroy-Ata, 2005; Brandes *et al.*, 2022). Even if the damage to the hydraulic system is severe for some liana species, the small area of non-embolized xylem and water reserves in the parenchymal tissue must be enough to supply the young branches and leaves with water, avoiding desiccation and apical branches deaths (Morris, 2016; Mantova *et al.*, 2021).

The highly efficient water transport system in lianas has been shown in many studies (Carlquist, 1985; Ewers and Fisher, 1989; Ewers *et al.*, 1990) and could reach ten times more efficiency than trees and shrubs (Gartner *et al.*, 1990; Gerolamo and Angyalossy, 2017; Zhu *et al.*, 2017). In agreement with this pattern, we detected a high and constant theoretical specific conductivity for lianas' stems across forest types, similar to 16 other species from dry and wet forests (Medina-Vega *et al.*, 2021). Also, we did not find a negative relationship between transport efficiency and hydraulic safety, as predicted by the safety-efficiency trade-off, and other lianas from different tropical forests did not follow this trade-off (Zhu and Cao, 2009; Van der Sande *et al.*, 2019; Medina-Vega *et al.*, 2021). This decoupling of hydraulic efficiency from safety has recently been advocated based on a three-dimensional pit membrane model (Kaack *et al.*, 2021; Lens *et al.*, 2022).

Could embolism resistance be viewed as an adaptation for restrictive hydric conditions?

Drought survival strategies, such as hydraulic safety, may vary among populations, species, and lineages (Sperry and Saliedra, 1994; Lens *et al.*, 2013; Anderegg *et al.*, 2016; Dias *et al.*, 2019) as a result of repeated evolutionary adaptation under similar environments (Fontes *et al.*, 2020; Guillemot *et al.*, 2022) or phylogenetic conservatism (Losos 2008; Skelton *et al.*, 2021). We had higher hydraulic safety in three genera independent in Bignoniaceae under similar environments (seasonal forest). Nonetheless, this simple correlation does not explain why particular features are favored in specific habitats, and additional evidence is needed to support a non-stochastic mechanism for convergent evolution (Losos, 2008; Stayton, 2015). The biogeographic history of Bignoniaceae highlights more recent migrations of lianas of various lineages from wet rainforests to dry forests and savannas (Lohmann *et al.*, 2013). This historical scenario and our functional evidence for hydraulic safety indicate that hydric selective pressures could lead to similar tolerance strategies in some Bignoniaceae lineages in seasonal forests. Additional evidence of hydraulic safety from more species across plant lineages is needed to support the hypothesis that adaptive convergence occurred in some genera within Bignoniaceae in the transition to drier seasonal forests. However, the appearance of other strategies in the drier seasonal forest may help explain the success of some Bignoniaceae lineages, as discussed above.

Embolism resistance in a broader context

There was a high variability of resistance to xylem embolism and no difference between drier seasonal and rainforest lianas in the combined dataset of eighteen families across the Neotropics. Indeed, some Bignoniaceae (our study), Sapindaceae, Malpigiaceae, Convolvulaceae, Phytolaccaceae and Combretaceae liana species had high drought tolerance with more negative P50 values (< -3MPa) in drier seasonal forests as well some Bignoniaceae, Polygonaceae and Olacaceae species in rainforests (Chen *et al.*, 2021; Smith-Martin *et al.*, 2022). Also, on average, the liana hydraulic safety was similar to that found for trees and shrubs in rainforests and drier seasonal

forests (Fig. 3). If these hydraulic safety values are not overestimated by technical artifacts as open-vessels for plants with long vessels (Wheeler *et al.*, 2013; Torres-Ruiz *et al.*, 2014; 2017; Pereira *et al.*, 2021), these results reinforce that drought tolerance is only one of the potential strategies of lianas to deal with drought (Schnitzer *et al.*, 2018; Smith-Martin *et al.*, 2022). At the same time, the absence of a consistent pattern of embolism resistance among forests with the same climate may also arise due to differences in other factors, namely soil fertility and water table depth, which can vary within climates and strongly filter hydraulic traits (Garcia *et al.*, 2023).

Conclusion

Dry seasonal forests commonly exhibit a high abundance of lianas. This abundance is dictated by dominant species showing rapid growth, attributed to their efficient hydraulic and photosynthesis, continuous vascular tissue production, and diverse drought resistance strategies. In our study, the hydraulic efficiency of lianas of the tribe Bignoniaceae was similar across tropical forests, probably favoring their rapid growth broadly. In addition, they have multiple drought resistance strategies, in which some lineages were optimized to drier seasonal forests by enhancing hydraulic safety, and others more vulnerable have probably other mechanisms to cope with drought. Together, our results highlight that the higher density of lianas in seasonal forests may be a temporary occurrence in response to current conditions. If drought intensity rises, these fast-growing plants' mortality risk could also increase, similarly to other plant groups (e.g., Oliveira *et al.*, 2021). Also, the local environmental gradients (e.g., soil features) could shape plant hydraulic strategies within each forest type (Costa *et al.*, 2023). This pattern should be further investigated and considered in climate change scenarios where extreme droughts are anticipated to be more frequent. Future research on the lethal dehydration threshold and the connection between hydraulic resistance strategies and liana abundance could offer further insights into tropical forest dynamics under climatic threats.

ACKNOWLEDGEMENTS

We thank Rafael Oliveira, Ellen Carvalho, and Nara Vogado for their helpful suggestions. We acknowledge the invaluable help of Guilherme Antar, Valdiek Menezes, Elisangela Rocha, Lorena Bueno, Marília Quinalha, Carlos Roberto, and José Raimundo in the field and INPA's (DSER) Department of Reserves for Logistical Support. This work was only possible due to 20 years of research conducted under the Brazilian LTER, funded by national (CAPES, CNPq) and regional (FAPEAM) Brazilian Science Foundations, including the latter: - CHAMADA PÚBLICA Nº 021/2020 - PELD/CNPq/FAPEAM.

AUTHOR CONTRIBUTIONS

CSG, AN, and VA designed research. CSG collected the hydraulics data. CSG, AN, FRCC, LP, and SJ analyzed the hydraulics data. CSG and AN wrote the first version of the manuscript with substantial input from FRCC, LP SJ, and VA; all authors contributed to revisions.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

FUNDING

This work was supported by the São Paulo Research Foundation (FAPESP) [2013/10679-0, 2018/06917-7], Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) [grant number 88882.333016/2019-01 to CSG], Brazilian Long-Term Ecological Research Program (PELD-CNPq) [grant number 403764/2012- 2], and funded by national (CAPES, CNPq) and regional (FAPEAM) Brazilian Science Foundations, including the latter: - CHAMADA PÚBLICA Nº 021/2020 - PELD/CNPq/FAPEAM.

DATA AVAILABILITY

The average species trait data are available upon reasonable request from the authors.

Accepted Manuscript

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Tables

Table 1. Mean value (\pm SD) of theoretical specific hydraulic conductivity (Ks), xylem pressure at which 50% and 88% of maximum gas amount was discharged (P50 and P88), predawn water potential (P_{predawn}), minimum seasonal water potential (P_{min}), hydraulic safety margin (HSM = $P_{\text{min}} - P50$) and, for congeneric liana species of Bignoniaceae occurring in two contrasting forests (rainforest and seasonal forest).

	Ks					
	($\text{Kg.m}^{-1}.\text{MPa}^{-1}.\text{s}^{-1}$)	P50 (MPa)	P88 (MPa)	P_{predawn} (MPa)	P_{min} (MPa)	HSM (MPa)
<i>Adenocalymma validum</i> ¹	36.42 (\pm 25.99)	-3.13 (\pm 0.63)	-4.36 (\pm 1.1)	-0.06 (\pm 0.02)	-2.50 (\pm 0.61)	0.79 (\pm 0.8)
<i>Adenocalymma bracteatum</i> ²	16.65 (\pm 7.41)	-4.7 (\pm 0.68)	-7.04 (\pm 0.62)	-2.33 (\pm 1.86)	-4.46 (\pm 0.38)	0.24 (\pm 0.44)
<i>Anemopaegma robustum</i> ³	24.45 (\pm 16.05)	-1.08 (\pm 0.33)	-1.34 (\pm 0.57)	-0.14 (\pm 0.09)	-0.81 (\pm 0.07)	0.15 (\pm 0.11)
<i>Anemopaegma chamberlyni</i> ⁴	26.68 (\pm 12.85)	-1.84 (\pm 0.44)	-2.89 (\pm 0.61)	-0.61 (\pm 0.26)	-1.72 (\pm 0.45)	0.29 (\pm 0.30)
<i>Bignonia aequinoctiales</i> ⁵	23.04 (\pm 29.15)	-1.48 (\pm 0.69)	-2.01 (\pm 1.01)	-0.05 (\pm 0.01)	-0.80 (\pm 0.17)	0.74 (\pm 0.77)
<i>Bignonia campanulata</i> ⁶	16.67 (\pm 9.16)	-4.23 (\pm 1.24)	-6.82 (\pm 0.71)	-2.82 (\pm 1.15)	-3.91 (\pm 0.68)	0.94 (\pm 0.48)
<i>Fridericia triplinervia</i> ⁷	27.76 (\pm 30.91)	-2.88 (\pm 0.45)	-4.44 (\pm 0.82)	-0.13 (\pm 0.14)	-1.54 (\pm 0.58)	1.39 (\pm 0.80)
<i>Fridericia triplinervia</i> ⁸	38.5 (\pm 30.35)	-2.29 (\pm 0.39)	-3.39 (\pm 0.53)	-0.22 (\pm 0.15)	-2.11 (\pm 0.31)	0.16 (\pm 0.16)
<i>Tynanthus panurensis</i> ⁹	10.55 (\pm 5.8)0	-4.1 (\pm 0.46)	-6.3 (\pm 1.09)	-0.09 (\pm 0.03)	-3.35 (\pm 0.48)	1.06 (\pm 0.36)
<i>Tynanthus fasciculatus</i> ¹⁰	18.35 (\pm 11.12)	-3.3 (\pm 0.96)	-5.29 (\pm 2.01)	-0.59 (\pm 0.51)	-3.23 (\pm 0.24)	0.63 (\pm 0.43)
Rainforest	24.44 (\pm 23.46)	-2.39 (\pm 1.30)	-3.49 (\pm 1.94)	-0.09 (\pm 0.08)	-1.75 (\pm 1.10)	0.82 (\pm 0.70)
Seasonal forest	23.69 (\pm 18.11)	-3.24 (\pm 1.31)	-5.05 (\pm 1.99)	-1.42 (\pm 1.50)	-3.06 (\pm 1.11)	0.43 (\pm 0.44)

Numbers after species names indicate species vulnerability curves as numbered in Supplementary Fig. S2.

Table 2. Model selection results for each response variable: predawn water potential (P_{predawn}), minimum seasonal water potential (P_{min}), xylem pressure at which 50% of the maximum gas amount was discharged (P50), hydraulic safety margin (HSM), and theoretical specific hydraulic conductivity (Ks) of lianas for two forest types and five genera. Bold lines are the selected models for each response variable. Gaussian probability distribution was used in all mixed models, including none, one or two fixed factors - forest (categorical) and genus (categorical) - and a random term describing the nested sampling design. Degrees of freedom (df), Second-order Akaike's information criterion (AICc), and ΔAICc (AICc_{model}-AICc_{minimum}) are also shown.

Model	Response variable	Fixed factors	Random term	df	AICc	ΔAICc	Figure
1	Log(P_{predawn})	Forest	1 Genus/Species	5	121.5	0	1A
2		Forest x Genus	1 Genus/Species	13	124.0	2.4	
3		1	1 Genus/Species	4	124.4	2.8	
4		Forest + Genus	1 Genus/Species	9	124.5	3.0	
5		Genus	1 Genus/Species	8	126.1	4.6	
6	P_{min}	Forest x Genus	1 Genus/Species	13	99.2	0	1B
7		Forest + Genus	1 Genus/Species	9	100.8	1.6	
8		Forest	1 Genus/Species	5	102.3	3.1	
9		Genus	1 Genus/Species	8	102.6	3.3	
10		1	1 Genus/Species	4	104.6	5.4	
11	P50	Forest x Genus	1 Genus/Species	13	191.4	0	1C

12		Forest + Genus	1 Genus/Species	9	196.8	5.3	
13		Genus	1 Genus/Species	8	196.8	5.4	
14		Forest	1 Genus/Species	5	199.4	8.0	
15		1	1 Genus/Species	4	199.8	8.3	
16	Safety Margin	1	1 Genus/Species	4	102.5	0	1D
17		Forest	1 Genus/Species	5	103.7	1.2	
18		Genus	1 Genus/Species	8	110.3	7.8	
19		Forest + Genus	1 Genus/Species	9	112.1	9.6	
20		Forest x Genus	1 Genus/Species	13	116.8	14.3	
21	Log(Ks)	1	1 Genus/Species	4	161.7	0.0	1F
22		Forest	1 Genus/Species	5	165.1	3.4	
23		Genus	1 Genus/Species	8	168.3	6.7	
24		Forest + Genus	1 Genus/Species	9	172.1	10.4	
25		Forest x Genus	1 Genus/Species	32	177.4	15.7	
26	Log(Ks)	1	1 Genus/Species	4	159.4	0.3	2
27		P50	1 Genus/Species	5	159.1	0	
28		P50 + Forest	1 Genus/Species	6	160.4	1.3	
29		Forest	1 Genus/Species	5	161.5	2.4	
30		P50 x Forest	1 Genus/Species	7	163.	3.8	

Figure legends

Fig. 1 Comparison of hydraulic features in five pairs of congeneric liana species between two contrasting forest types (Amazon rainforest and Atlantic seasonal forest): (A) we only detected the effect of forest type on the predawn water potential – P_{predawn} (model 1 in Table 2) – the black solid line shows exclusively the average effect of forest type; (B) we detected the interaction effect between forest type and genus on the minimum seasonal water potential - P_{min} (model 6 in Table 2) – solid and dotted colored lines show significant and non-significant changes between forest types for each genus based on multiple t-tests with Bonferroni correction ($p < 0.01$; Supplementary data Table S3); (C) we detected the interaction effect between forest type and genus on the hydraulic safety measured as the xylem pressure at which 50% of the maximum amount of gas was discharged - P_{50} (model 11 in Table 2) – solid and dotted colored lines show significant and non-significant changes between forest types for each genus based on multiple t-tests with Bonferroni correction ($p < 0.01$; Supplementary data Table S3); (D) we detected a neutral effect of forest type and genus on the hydraulic safety margin – HSM (model 16 in Table 2); and (E) we detected a neutral effect of forest type and genus on theoretical specific hydraulic conductivity – K_s (model 21 in Table 2). Colors indicate the five genera analyzed (red: *Adenocalymma*; blue: *Anemopaegma*; green: *Bignonia*; purple: *Fridericia*; orange: *Tynanthus*), and open circles represent the raw hydraulic trait values per individual liana.

Fig. 2 Relationship between theoretical specific hydraulic conductivity (K_s ; on a log scale) and hydraulic safety (P_{50}) across Bignoniaceae liana individuals in the rainforest (blue) and seasonal forest (red). In this analysis, we included 30 liana individuals of each forest type.

Fig. 3 Boxplot of P50 (MPa; i.e., xylem pressure inducing 50% loss of hydraulic conductivity or at which 50% of maximum gas amount discharged) for angiosperm species, trees and shrubs, and lianas (Bignoniaceae lianas in orange) across tropical rainforest (blue) and seasonal tropical forest (red). Open circles were the average of P50 values per species for all angiosperm trees, shrubs, succulents, herbs, and lianas available in the broader meta-data (dataset from: Zhu and Cao, 2009; Choat *et al.*, 2012; Carvalho *et al.*, 2016; Chen *et al.*, 2017, 2021; Oliveira *et al.*, 2019; Tan *et al.*, 2020; De Guzman *et al.*, 2021; Medina-Vega *et al.*, 2021; Smith-Martin *et al.*, 2022). Orange dots were average values of P50 of the five congeneric lianas species from the Amazon rainforest at Ducke Reserve (Amazonas, Brazil) and the seasonal forest at Santa Genebra Reserve (São Paulo, Brazil).

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Figure 1

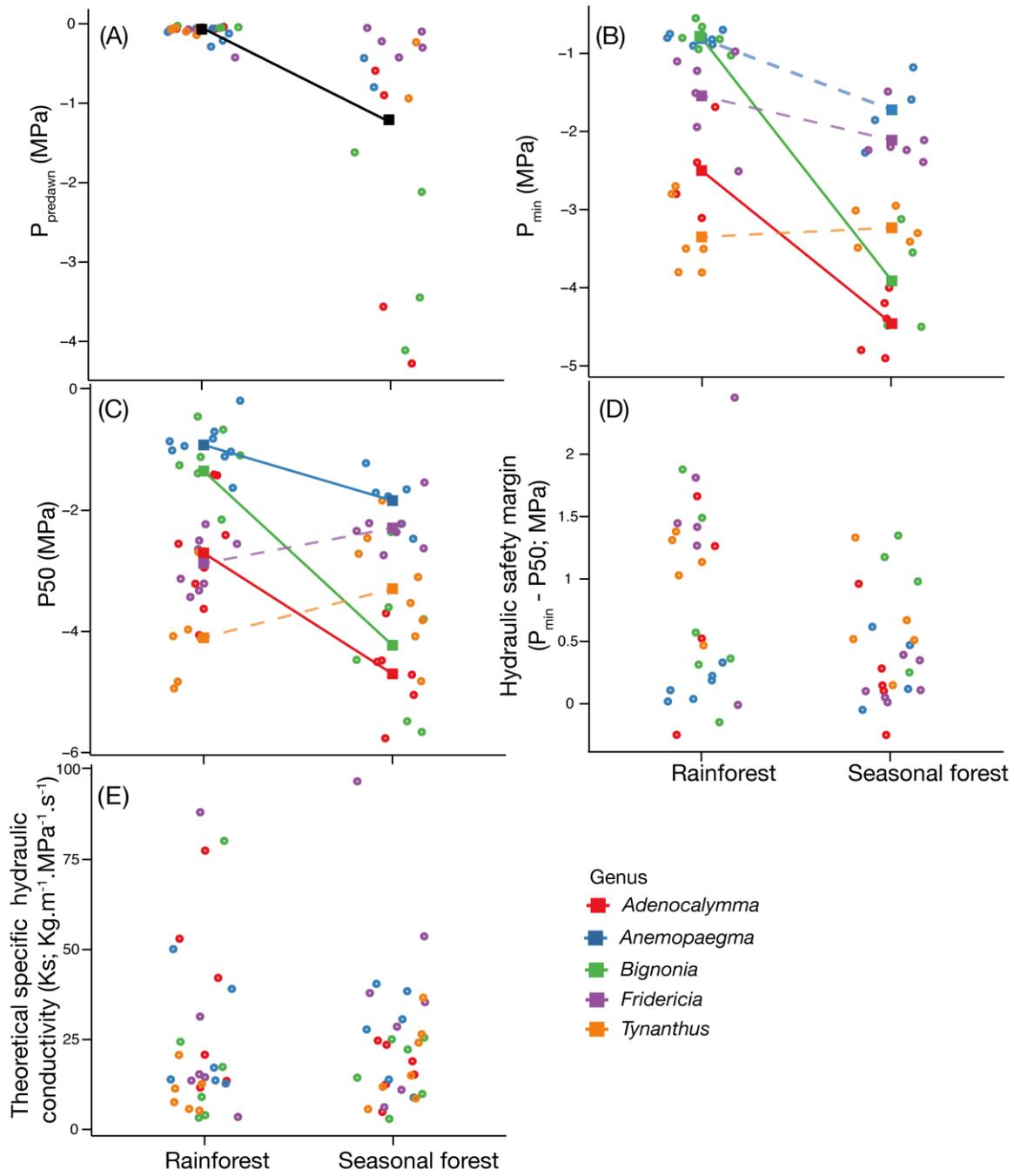
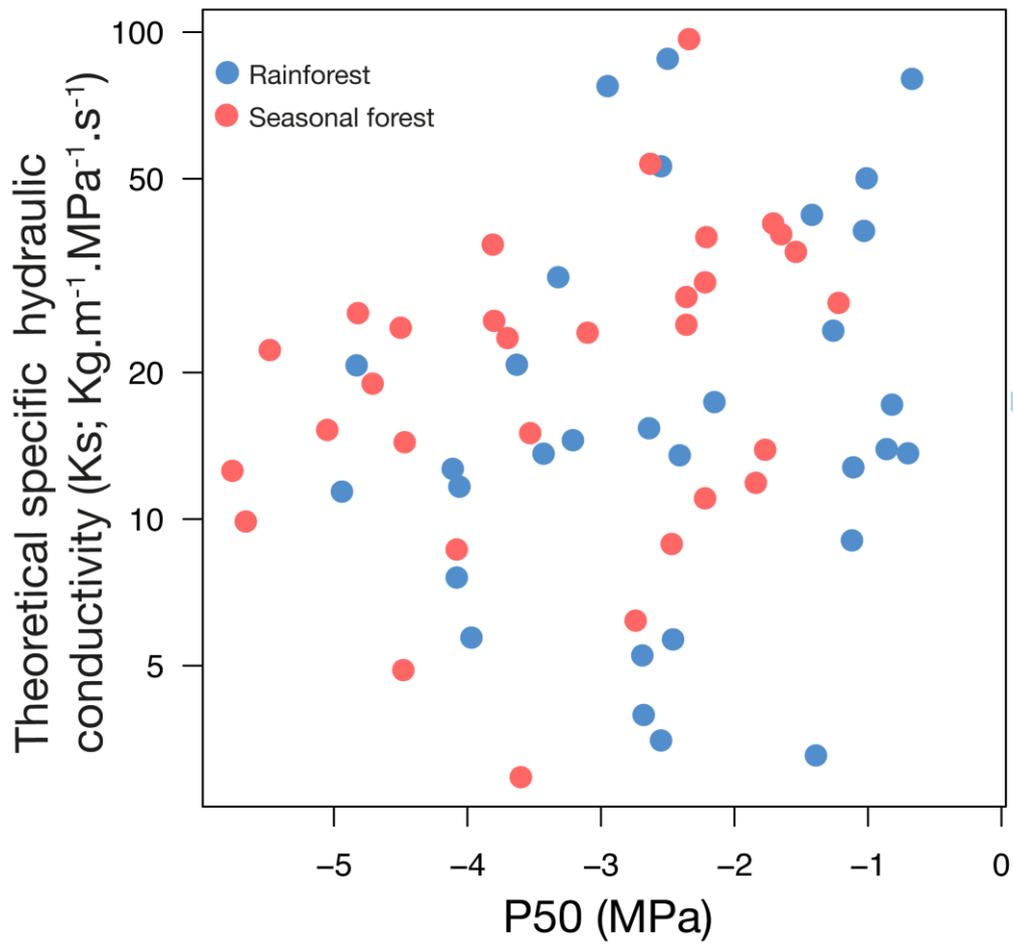
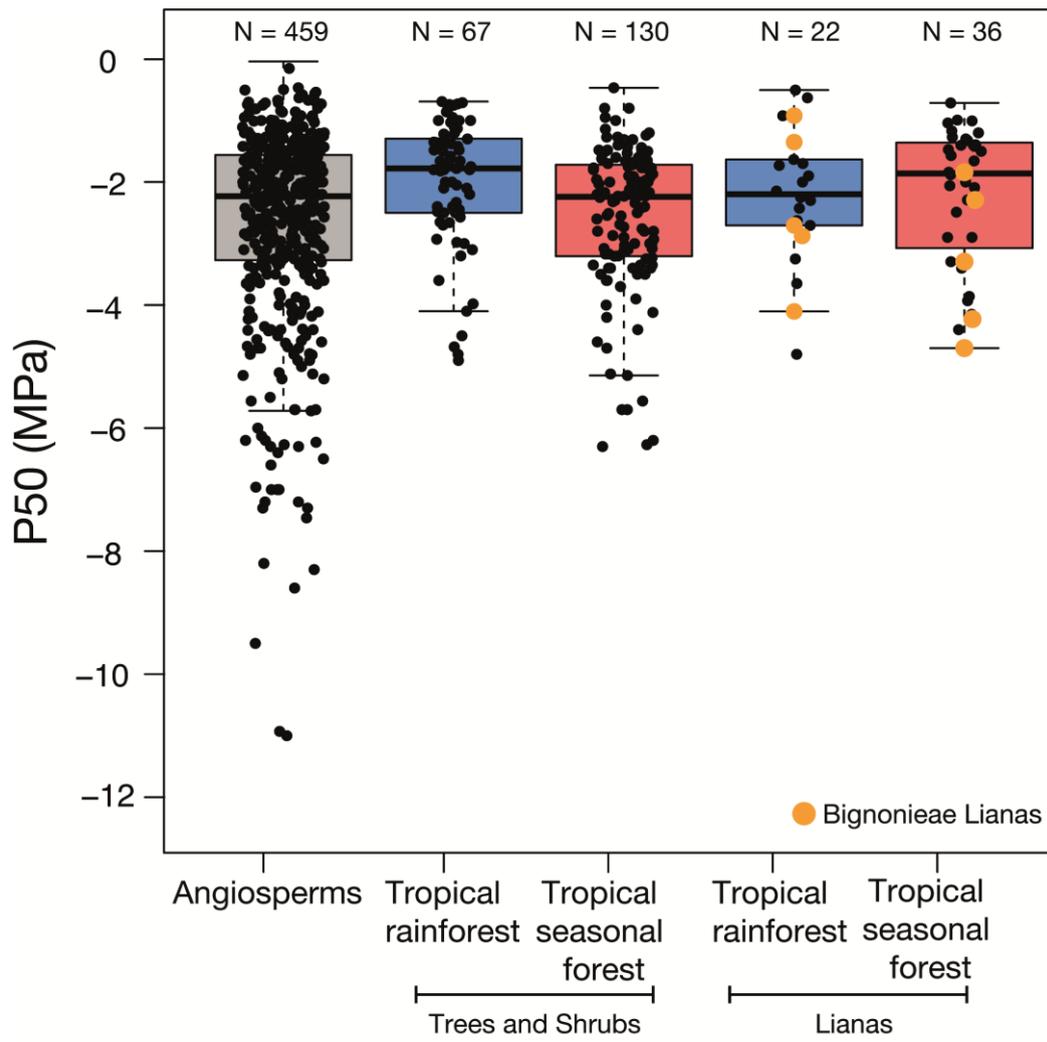


Figure 2



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Figure 3



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