ORIGINAL ARTICLE

Wood anatomical spectrum of co-occurring species in early and late-successional tropical dry forest communities

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Abstract

Key message **Analysis of wood anatomical traits revealed that drought tolerance predominates in early-successional communities, and vessel variability is relevant for species' ecological success in seasonally dry tropical environments.**

Abstract Successional tropical dry forests harbor a diverse array of species subjected to a strong seasonal precipitation regime. Considering that wood encompasses diverse functional properties related to stem hydraulics and mechanical support, in this study, we asked which quantitative anatomical traits are exhibited by co-occurring species in early (EC)- and late (LC)-successional communities. We used generalized linear mixed-effects models to estimate and compare means and standard deviations of wood traits (vessel area, vessel density, vessel grouping, and fiber dimensions) between eight EC and between 13 LC co-occurring species. Wood traits were highly heterogeneous. High vessel redundancy, a property associated with water safety involved in the prevention of hydraulic failure, prevails among species coexisting in EC but is maintained through succession by the same species in LC. Highly variable fiber dimensions indicate that species coexisting in LC possess different characteristics associated with mechanical resistance. Low wood density species typical of LC, which are absent from EC, displayed wood anatomical features associated with drought-evasion mechanisms. This result implies that deforestation not only reduces taxonomic but also functional diversity. Future research should adopt a standard deviation analysis approach, as this will allow confirming the high variability in vessel diameter, even in diffuse porous species, as a key feature for the ecological success of plants facing succession-driven changes in seasonally dry environments.

Keywords Drought-resistance mechanisms · Fiber lumen diameter · Functional anatomy · Potential xylem hydraulic adjustment · Vessel area · Vessel grouping

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Introduction

Analyzing wood anatomical features associated with water transport in species coexisting in recovering vegetation derived from disturbed tropical dry forest (TDF) is essential to understand community-level adaptations to drought. Deforestation for food production is a major threat to TDF persistence, and at present secondary vegetation derived from this forest type covers large areas in the tropics (Jakovac et al. 2022). Woody species coexisting in recovering early and late communities (here referred to collectively as successional species) are subjected to a marked precipitation seasonality, as well as to microenvironmental changes in conditions and resources through succession, the process of natural vegetation recovery over time (Pickett 1976). Thus, successional species are interesting from the point of view of drought-avoidance and drought-tolerance mechanisms. In drought-avoidance mechanisms, the plant has barriers

to desiccation; thus, it is unlikely to suffer general hydraulic failure, while in the drought tolerance mechanisms, the hydraulic system can continue to operate under low water availability without suffering damage, or alternatively, damage repairing takes place (Levitt 1980; McDowell et al. 2008).

Plants interact with the seasonally dry environment and the changing microenvironment mainly through their stems. The secondary xylem (hereafter referred to as wood) that builds up stems represents multiple possibilities of functional traits (*i.e.*, having impact on their fitness components; Violle et al. 2007) related to drought-resistance mechanisms. Certain wood anatomical features (*e.g.*, vessel and fiber dimensions, and vessel spatial arrangement) impact water transport efficiency and safety, ultimately affecting plant survival, growth, and reproduction (Carlquist 1977, 2009; Apgaua et al. 2015, 2017; Baas et al. 2016).

The relationship between wood structure and the maintenance of the water column under drought conditions is complex and remains unclear. Larger vessel diameters are mainly associated with high water transport efficiency, but also with a higher risk of interruptions of the water column under negative pressures (cavitation) and embolisms (air-filled vessels; Aloni and Zimmermann 1983; Hacke et al. 2001; Tyree and Zimmermann 2003). However, this efficiency-safety trade-off is neither universal nor consistent since the intensity of the damage in the hydraulic system and its whole-plant effects vary depending on other anatomical components of the wood (Lopez et al. 2005; Lens et al. 2013; Trifilò et al. 2014). It has been suggested that a high vessel frequency, in combination with the prevalence of vessel grouping, may prevent water transport from being seriously affected when a vessel is blocked by embolism, since water can continue moving through another vessel (an adjacent one in case of grouped vessels). These anatomical features provide high hydraulic pathway redundancy in the xylem (Tyree and Sperry 1988; Tyree et al. 1994; Cruiziat et al. 2002; Tyree and Zimmermann 2003; Ewers et al. 2007). In dry environments, von Arx et al. (2013) found more clustered vessels and a higher number of vessels, supporting hydraulic redundancy as a drought resistance mechanism. By contrast, the finding of less clustered vessels after induced drought stress in rain forest species suggests that grouped vessels may increase in them the risk of embolism spreading through adjacent vessels (Tng et al. 2018).

Variability in vessel diameter between and within individuals of the same species may contribute to drought adaptations in populations growing under changing environments (Ghalambor et al. 2007; von Arx et al. 2013; Hacke et al. 2017; Tng et al. 2018; Rodríguez-Ramírez et al. 2020; Romero et al. 2020b). However, it is noteworthy that statistical analyses in studies addressing vessel diameter are usually based on the mean of this variable and not on the standard deviation (*e.g.,*Hargrave et al. 1994; Lo Gullo et al. 1995; Apgaua et al. 2015, 2017; Pineda-García et al. 2015; Jupa et al. 2016). Analyzing mean vessel diameter may make it difficult to detect whether diffuse porous species show adjustments in vessel diameter depending on seasonal and other intra-annual changes in precipitation, such as heatwave events.

In studies addressing drought resistance mechanisms, the examination of fiber characteristics is very informative. Fibers are not only associated with mechanical support but they can also contribute to hydraulic safety, depending on their characteristics, and can store water while alive (Jacobsen et al. 2005; Jupa et al. 2016). Also, comparative studies have suggested that thicker fiber walls may prevent the risk of implosion under high pressures associated with water stress (Hacke et al. 2001). For example, Aguilar-Rodríguez et al. (2001) found that thick-walled fiber species are more common in dry environments compared to more humid ones; in turn, water can be depleted from fibers during drought (Tyree et al. 1990; Jupa et al. 2016), especially from fibers with thin walls (Hölttä et al. 2009). Thus, fiber lumen diameter may be indicative of free space for water storage capacity.

When scaling from individuals to communities, in situ studies provide insight into the evolutionary outcomes regarding drought resistance mechanisms. However, no in situ study has shown what wood stem anatomical features are actually exhibited by individuals of the different species coexisting in early and in late TDF successional communities. Conducting physiological studies directly in the field is very difficult, and for the planning of those studies, it is desirable to have previous information about the ecology of the selected species and their wood anatomical structure. Therefore, analyzing stem wood anatomical features of species growing in a particular vegetation type can shed light on the responses of the anatomical structure to ecological stimuli. What is known about drought resistance mechanisms in TDF successional species has been revealed through greenhouse experiments (Pineda-García et al. 2013, 2015), in individuals growing along the road (Markesteijn et al. 2011), in saplings from late-successional forests (Wolfe and Kursar 2015), or through meta-analysis for mature TDFs (Xu et al. 2016).

Recovering TDF harbors a diverse assemblage of species that face water scarcity every year during the marked dry season and display different phenological responses (Méndez-Alonzo et al. 2013; Luna-Nieves et al. 2022) and capacities to survive and store biomass along the successional gradient (Lebrija-Trejos et al. 2010). Therefore, assessing and comparing their stem wood anatomical features associated with water transport efficiency and security may allow us to gain insights into their water stress coping mechanisms.

In this study, we asked what set of anatomical traits are exhibited by frequent species occurring in early (EC) and late (LC) successional TDF communities (referred to collectively as successional species). To answer this question, we estimated and compared vessel and fiber dimensions, vessel frequency, and vessel grouping for 13 structurally important species growing in EC and LC. We put forward two hypotheses. The first one states that the physical environment in early-successional TDF acts as a selective force that promotes a drought tolerance strategy, given the relatively water-stressful conditions prevailing in them, particularly in the period of high photosynthesis activity (Lebrija-Trejos et al. 2011), compared to the less stressful conditions prevailing in LC; thus, we expected species in EC to exhibit xylem traits adapted to water stress, such as small vessel diameters and high vessel density. The second hypothesis states that plasticity in vessel attributes contributes to the ecological success of species over TDF succession, as it enables adjustments in the wood hydraulic features to microenvironmental changes over this process. Thus, we expected features associated with safety in water conduction to be homogeneous in EC, such as high vessel redundancy; in turn, because LC are characterized by higher taxonomic diversity, structural complexity, and environmental heterogeneity than EC (Kennard 2002; Lebrija-Trejos et al. 2008; Poorter et al. 2021), we anticipated more diverse ways of dealing with environmental filters in LC, as previously suggested (Prach and Pyšek 1999; Hasselquist et al. 2010; Pineda-García et al. 2015; Pivovaroff et al. 2016). In the study site, three dominant successional species have been recorded. Two of them (*Mimosa eurycarpa* and *Lysiloma divaricatum*) exhibit ring porosity, which could be key to their ecological success as it seems to confer low vulnerability to embolism in the dry season and high-water transport efficiency in the rainy season (Romero et al. 2020b); by contrast, the third dominant species (*Mimosa tenuiflora*) is diffuse porous, a feature shared with other 10 frequent successional TDF species (Romero et al. 2022). Therefore, we also analyzed intraspecific vessel feature variability by estimating and comparing their standard deviations. This approach allowed us to indirectly examine whether successional species, both ring and diffuse porous, exhibit hydraulic adjustments that could be related to the seasonality in precipitation and its intra-annual fluctuations.

Methods

Study area

Fieldwork was conducted near the village of Nizanda, Oaxaca state, southern Mexico (16° 39′ 30″ N, 95° 00′ 40″ W). Mean annual temperature ($\pm$ SD) is 27.7 ± 1 °C (CV = 3.6%)

and mean ($\pm$ SD) total annual rainfall is 902.6 ± 355.4 mm (CV = 39.4%), which concentrates from late May to mid-October (CICESE 2022). TDF is the main vegetation type in the region (Pérez-García et al. 2010), but patches of secondary vegetation derived from traditional agriculture and cattle raising are abundant (Gallardo-Cruz et al. 2012). In the regional mature TDF, some 100 woody species have been recorded (Pérez-García et al. 2010), among which at least 50 species occur also in secondary vegetation (Lebrija-Trejos et al. 2010). Only seven species occur exclusively in secondary vegetation (*i.e.*, have not been recorded in mature TDF; Pérez-García et al. 2010).

Noteworthy, this is one of the few studies that includes successional sites with ages (time since abandonment) ranging from *ca.* 50 to 70 years, as well as young sites (*ca.* 2 years after abandonment). Including older successional sites is important as it takes more than 70 years for the community structure to become similar to that of the mature forest, and even longer for the species richness and composition to recover (Lebrija-Trejos et al. 2008, 2010).

Species selection and their ecological performance

In early successional stages, environmental conditions are particularly unfavorable for vegetation recovery, even during the rainy season (Lebrija-Trejos et al. 2011). In this harsh environment, some species can establish and quickly accumulate a large biomass; interestingly, some of them persist until late-successional stages. These species are rare in sites with more than 50 years of abandonment and are absent in the mature forest, that is, they are exclusive to secondary vegetation (Lebrija-Trejos et al. 2010). In recently abandoned sites, stumps and other remains of individuals that survived the removal of their aerial biomass and are capable of regrowth are common. Consequently, more than half of the species occurring in TDF recovering vegetation (successional species) are also present in the mature forest (Pérez-García et al. 2010). These typical mature forest species capable of establishing in early succession become frequent as succession unfolds, and some attain dominance in terms of relative basal area. The group of successional species included in this study encompasses both these typical mature forest species as well as those that exclusively occur in secondary vegetation.

Based on previous studies (Pérez-García et al. 2010; Lebrija-Trejos et al. 2010) and field observations, we selected 13 species frequent in successional TDF that differ in their presence/absence and biomass accumulation along the successional gradient. We studied eight species that coexist in the early communities (EC; three sites with *ca.* 2 years of abandonment), and 13 species that coexist in the late communities (LC; seven sites with more than 50 years of abandonment). These 13 species occurring in LC include

all eight species coexisting in EC (*Vachellia campechiana* (Mill.) Seigler & Ebinger, *Bonellia macrocarpa* (Cav.) B.Ståhl & Källersjö, *Coccoloba liebmannii* Lindau, *Lonchocarpus lanceolatus* Benth., *Lysiloma divaricatum* (Jacq.) J.F. Macbr., *Mimosa eurycarpa* (Robinson) Poir., *Mimosa tenuiflora* (Willd.) Poir., *Phyllostylon rhamnoides* (J. Poiss.) Taub.), plus five species that are absent in EC (*Bursera ovalifolia* (Schltdl.) Engl., *Cnidoscolus megacanthus* Breckon ex Fern. Casas, *Jacaratia mexicana* A.DC., *Pachycereus pecten-aboriginum* (Engelm. ex S. Watson) Britton & Rose, and *Pilosocereus collinsii* (Britton & Rose) Byles & G.D. Rowley).

Three of the 13 study species are exclusive of secondary vegetation (*Mimosa eurycarpa*, *M. tenuiflora* and *Vachellia campechiana*), whereas the remaining 10 species occur both in secondary vegetation and mature TDF. There are only three dominant successional species (*i.e.*, species that accumulate higher relative basal area values): *Mimosa eurycarpa* and *M. tenuiflora* are dominant in EC, while *Lysiloma divaricatum* is the only dominant species in the studied LC (Lebrija-Trejos et al. 2010).

Wood sample collection and processing

We collected wood samples from 3 to 6 individuals per species, both in EC and LC (Table S1 in Supplementary Information and Materials and Methods in Romero et al. 2020b). For each individual sampled in EC, we cut a cylinder 1 cm long with a saw near the base of its tallest stem. For individuals in LC, we cut with the same saw, a slide of the main stem 5–6 cm wide at 30 cm above the ground. We selected this distance above the ground to avoid longitudinal variation along the axis of the different individuals and because a greater proportion of wood accumulates there in the cacti. Wood samples were fixed in a formaldehyde, alcohol, and acetic acid solution (FAA; Ruzin 1999) for anatomical analyses.

We made wood transverse sections (20–25 μm thick) with a sliding microtome (Leica 2000R, Wetzlar, Germany), stained sections with safranin-fast green and mounted them with synthetic resin (Ruzin 1999). We examined wood sections with an optical microscope (Olympus BX51) and took photographs using a digital camera (Evolution LC Color) adapted to the optical microscope.

We quantified anatomical variables with an Image Analyzer Pro v. 7.1 (ImagePro Plus 7.1, Media Cybernetics, Silver Spring, MD, USA) adapted to a compound microscope Olympus BX51 (Tokyo, Japan). In transverse sections, we measured vessel internal diameters, both tangential and radial (vessel diameters), and fiber diameter and fiber lumen in the area covering the most recently produced wood tissue (approximately inside one or two growth rings, depending on the characteristics of each particular wood sample). For

diffuse porous species, we measured 50 vessels per individual; for ring-porous species, we selected individuals with clear growth rings and measured 50 earlywood vessels and 50 latewood vessels. We measured 50 fibers per individual. In 9 to 12 optical fields of 0.1 mm^2, we counted the number of vessels per group and the number of vessels per 0.1 mm^2 (vessel frequency).

For each vessel element, we calculated vessel lumen area using the ellipse formula as follows:

$$\pi \times (\text{vessel tangential inside diameter})/2$$
$$\times (\text{vessel radial inside diameter})/2$$

For each fiber cell, we calculated fiber wall thickness as:

$$(\text{fiber diameter} - \text{fiber lumen})/2$$

Statistical analysis

First, to synthesize and visualize the variation of anatomical variables, we conducted a Principal Component Analysis (PCA) in R (R Core Team software 2022). The PCA included mean and standard deviation of the number of vessels per group, mean fiber wall thickness, mean wood density (taken from Romero et al. 2020a), mean vessel frequency, mean fiber lumen, mean and standard deviation vessel area, mean tangential vessel diameter, and maximum vessel diameter.

Next, we constructed generalized linear mixed-effects models (GLMMs) to estimate and compare the means and standard deviations of anatomical variables among species. We included the individual tree as a random intercept given the high number of pseudo-replicates (number of measurements done in a single individual) and the few replicates (3 to 6 individuals per species; Table S1). For every response variable (vessel tangential diameter, vessel radial diameter, vessel frequency, number of vessels per group, fiber diameter, fiber lumen, vessel lumen area, and fiber wall thickness), we constructed four GLMMs: (1) a GLMM assuming no between-species differences in their means and standard deviations (i.e., estimating a single mean and a single standard deviation for all species); (2) a GLMM assuming differences in the means between species but equal deviations; (3) a GLMM assuming equal means but different deviations; and (4) a GLMM assuming between-species differences both in their means and standard deviations (i.e., estimating a different mean and a different standard deviation for each species). We explored two appropriate probability distributions for each anatomical response variable: for positive continuous variables (*i.e.*, vessel tangential and radial diameter, fiber diameter and fiber lumen diameter, vessel lumen area, and fiber wall thickness), we used the log-normal and gamma distributions. For vessel frequency, models assumed either a Poisson or a negative
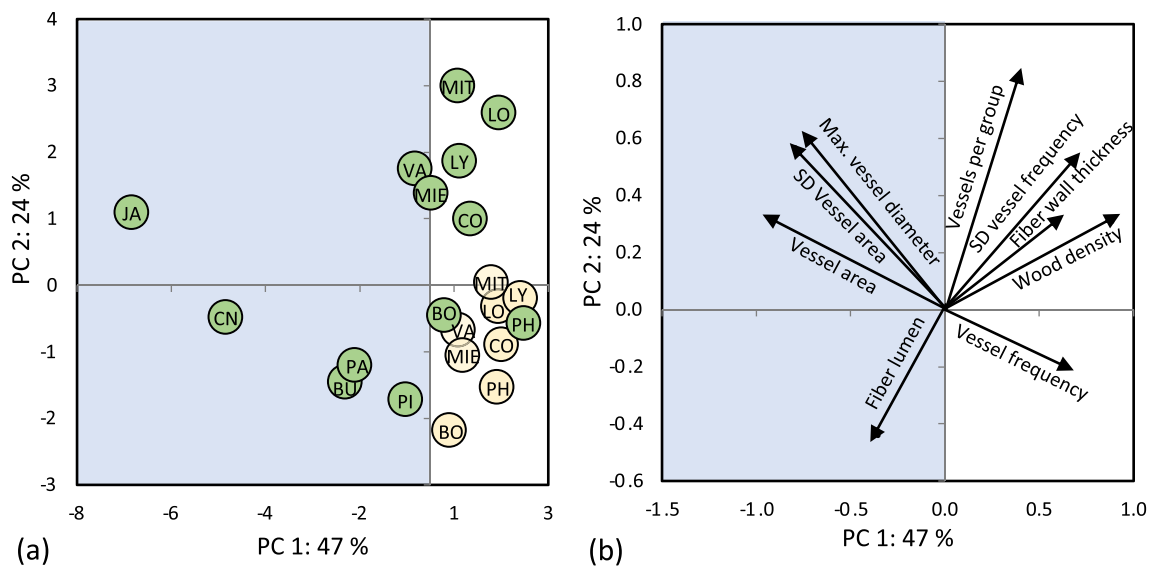
Fig. 1 Principal component analysis of wood features of species coexisting in successional tropical dry forest communities. Shown are PC1 and PC2 of PCA. Species in the shaded area show wood features related to a drought-evasion mechanism, whereas species in the white area show wood features associated with a drought-tolerant mechanism. **a** PCA scores; green circles with capital letters represent species occurring in late-successional communities (> 50 years of abandonment; LC), light yellow circles represent species occurring in young successional communities (2 years of abandonment; EC). Species acronyms: BO, *Bonellia macrocarpa*; BU, *Bursera ovalifolia*; CO, *Coccoloba liebmannii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*; VA, *Vachellia campechiana*. **b** Wood features vectors in the PC1 and PC2 dimensions

binomial distribution; and for the number of vessels per group, the distribution was either a one-inflated Poisson or a one-inflated negative binomial. One-inflated distributions were used because of the large number of solitary vessels (which were taken as groups containing one vessel element only). For each species, we estimated the whole-wood mean, and where it was possible to distinguish earlywood from latewood, we also estimated the earlywood and latewood means. Model selection for each response anatomical variable was based on the Generalized Akaike Information Criterion (GAIC; Akaike 1983). Models were considered to have similar empirical support if ΔGAIC was < 2. Model fitting was performed in R (R Core Team 2022), using the *gamlss* package (Rigby and Stasinopoulos, 2005). Probability distributions of anatomical variables and their best models are shown in Table S2.

Using the estimated mean values from the GLMMs described above, we calculated for each species the relative hydraulic conductivity (RHC) following Reyes-Santamaría et al. (2002), as follows:

$$RHC = (vessel\ radius)^4 \times (vessel\ frequency)$$

To calculate vessel radius, we first calculated D_h, the hydraulically weighted vessel diameter, as follows (Tyree and Zimmermann 2002):

$$D_h = \left(\Sigma D^4 / N\right)^{1/4}$$

where N is the number of vessels in cross section and D are their diameters. Finally, we calculated vessel radius as:

$$vessel\ radius = D_h/2$$

Results

Principal component analysis

The distribution of successional species coexisting both in EC and LC on the PCA ordination space based on their anatomical characteristics is shown in Fig. 1. PC1 explained almost half (47%) of total anatomical trait variation, with the main traits associated with this axis being vessel area (loading = 0.91), maximum vessel diameter (0.73), and standard deviation of vessel area (0.79; Fig. 1b).

The eight successional species coexisting in EC were tightly concentrated in the lower right sector of the ordination space (yellow circles; positive scores on PC1 and negative scores on PC2), unlike successional species coexisting in LC (green circles), which were more widely spread across the ordination space, with presence in all four sectors

(Fig. 1a). According to the loadings of anatomical traits on PC1 and PC2 (Fig. 1b), species coexisting in EC were mainly characterized by high vessel frequency but low values of vessel area (both mean and standard deviation) and vessel diameter, and to a lower extent, by high wood density. Notably, two species coexisting in LC shared this anatomical profile with EC species (*Phyllostylon rhamnoides* and *Bonellia macrocarpa*; PH, BO; Fig. 1a). The remaining species coexisting in LC formed three groups well segregated on the ordination space—the first one was characterized mainly by high vessel grouping and low fiber lumen (CO, LO, LY, MIE, MIT, VA; Fig. 1a). Notably, only in this sector of the ordination, typical EC species that persist over succession until LC were present (MIE, MIT, VA). Distant from this group was located another one formed by BU, PA, and PI (Fig. 1a), two of them being cacti (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*) and the third one being pachycaulous (*Bursera ovalifolia*). This group was mainly characterized by high fiber lumen values. Finally, two species (*Cnidoscolus multilobus* and *Jacaratia mexicana*) formed a loose group at the left far end of the ordination (CN, JA; Fig. 1a); these species were mainly characterized by high vessel area but low wood density and vessel frequency, two attributes that make them clearly distinct from the remaining species coexisting in LC.

The PCA ordination also showed a clear dichotomy for species coexisting in both EC and LC (CO, BO, LO, LY, MIE, MIT, PH, VA; Fig. 1a). Two of these species (*Phyllostylon rhamnoides* and *Bonellia macrocarpa*) retained basically the same anatomy over succession, as their respective positions almost overlapped in the same ordination sector both as EC and LC species; in strong contrast, the remaining species of this group showed a conspicuous displacement toward positive values of PC2, with individuals from LC having higher vessel grouping and larger fiber lumen values than their EC counterparts (Fig. 1b).

Wood anatomical features in early communities

Vessel features in EC can be visualized in Fig. 2a. *Mimosa eurycarpa* had the highest mean vessel area in its earlywood (e-MIE; Fig. 2b) and one of the lowest in its latewood (l-MIE; Fig. 2b), whereas *Lysiloma divaricatum* latewood had the lowest value for this variable. We distinguished three groups of species with different mean vessel area (Fig. 2b). Vessel frequency (Fig. 2c) was high in EC except for *Vachellia campechiana* (VA; Fig. 2c). Vessels are commonly grouped in most EC species (Fig. 2d). In EC, *Phyllostylon rhamnoides* (PH) had the smallest number of vessels per group (Fig. 2d) but the highest vessel frequency (Fig. 2c).

The highest RHC value was displayed by *Phyllostylon rhamnoides* (PH), followed by *Mimosa eurycarpa* (MIE),

Vachellia campechiana (VA), and *M. tenuiflora* (MIT); this group of four species did not differ in their high RHC values (Fig. 3a).

Fiber features in EC can be visualized in Fig. 4a. In this community, fiber lumen (Fig. 4b), fiber diameter (Fig. 4c), and fiber cell wall thickness (Fig. 4d) between species vary in a continuum. *Bonellia macrocarpa* (BO) had the lowest fiber wall thickness of the EC, whereas it ranked high regarding fiber lumen and fiber diameter. The largest values of mean fiber lumen corresponded to the two species in EC with septate fibers (*Coccoloba liebmannii*, followed by *Bonellia macrocarpa*).

Wood anatomical features in late communities

A general view of vessel features of species coexisting in LC is presented in Fig. 5a. Mean vessel area of species in LC varies in a continuum (Fig. 5b), with the lowest value in *Mimosa eurycarpa* latewood (l-MIE), and the highest value in *Jacaratia mexicana* (JA). Mean vessel area in the earlywood of *Mimosa eurycarpa* and *Lysiloma divaricatum* did not differ from each other (e-MIE and e-LY; Fig. 5b), and neither did it between *Mimosa eurycarpa* earlywood and *Cnidoscolus megacanthus* (e-MIE and CN; Fig. 5b). Vessel area of *Mimosa eurycarpa* (wholewood; MIE) and of *Mimosa tenuiflora* (MIT) did not differ from *Bursera ovalifolia* (BU) and *Lysiloma divaricatum* (LY; Fig. 5b). *Pachycereus pecten-aboriginum* (PA) and *Vachellia campechiana* (VA) did not significantly differ in their vessel areas (Fig. 5b). Most species had highly grouped vessels (Fig. 5c), except for a group of five species that also had the lowest vessel frequency in LC (shaded species in Fig. 5d).

Jacaratia mexicana showed the highest mean RHC value (Fig. 3b), followed distantly by a group of five species with mean RHC that did not differ significantly among them (*Bursera ovalifolia*, *Cnidoscolus megacanthus*, *Mimosa eurycarpa*, *M. tenuiflora*, and *Lysiloma divaricatum*).

Figure 6a provides a general view of fiber features in LC. Among LC species, fiber lumen (Fig. 6b), fiber diameter (Fig. 6c), and fiber wall thickness (Fig. 6d) were highly variable. Six species had wide fiber lumen (Fig. 6b), while the majority of the remaining species which had narrower lumina were all legumes, except for *Phyllostylon rhamnoides* (PH). A group of four species (three legumes and a cactus) exhibited the thickest fiber walls of LC (Fig. 6d): *Vachellia campechiana* (VA), *Lonchocarpus lanceolatus* (LO), *Pachycereus pecten-aboriginum* (PA), and *Mimosa tenuiflora* (MIT).

Fig. 2 Wood vessel features of species coexisting in early-successional tropical dry forest communities (~2 years of abandonment; EC). **a** Wood transverse sections of the eight species in this group; scale bar = 100 μm. **b-d** Estimated means of vessel features per species. **b** Vessel area (μm²). **c** Number of vessels per 0.1 mm². **d** Number of vessels per group. Brown horizontal bars indicate lack of significant differences between means; vertical lines represent 95% estimated confidence intervals. Species acronyms: BO, *Bonellia macrocarpa*; CO, *Coccoloba liebmannii*; LO, *Lonchocarpus lanceolatus*; MIT, *Mimosa tenuiflora*; PH, *Phyllostylon rhamnoides*; VA, *Vachellia campechiana*. In ring-porous species: LY, *Lysiloma divaricatum* whole wood; MIE, *Mimosa eurycarpa* whole wood; l-latewood, e-earlywood
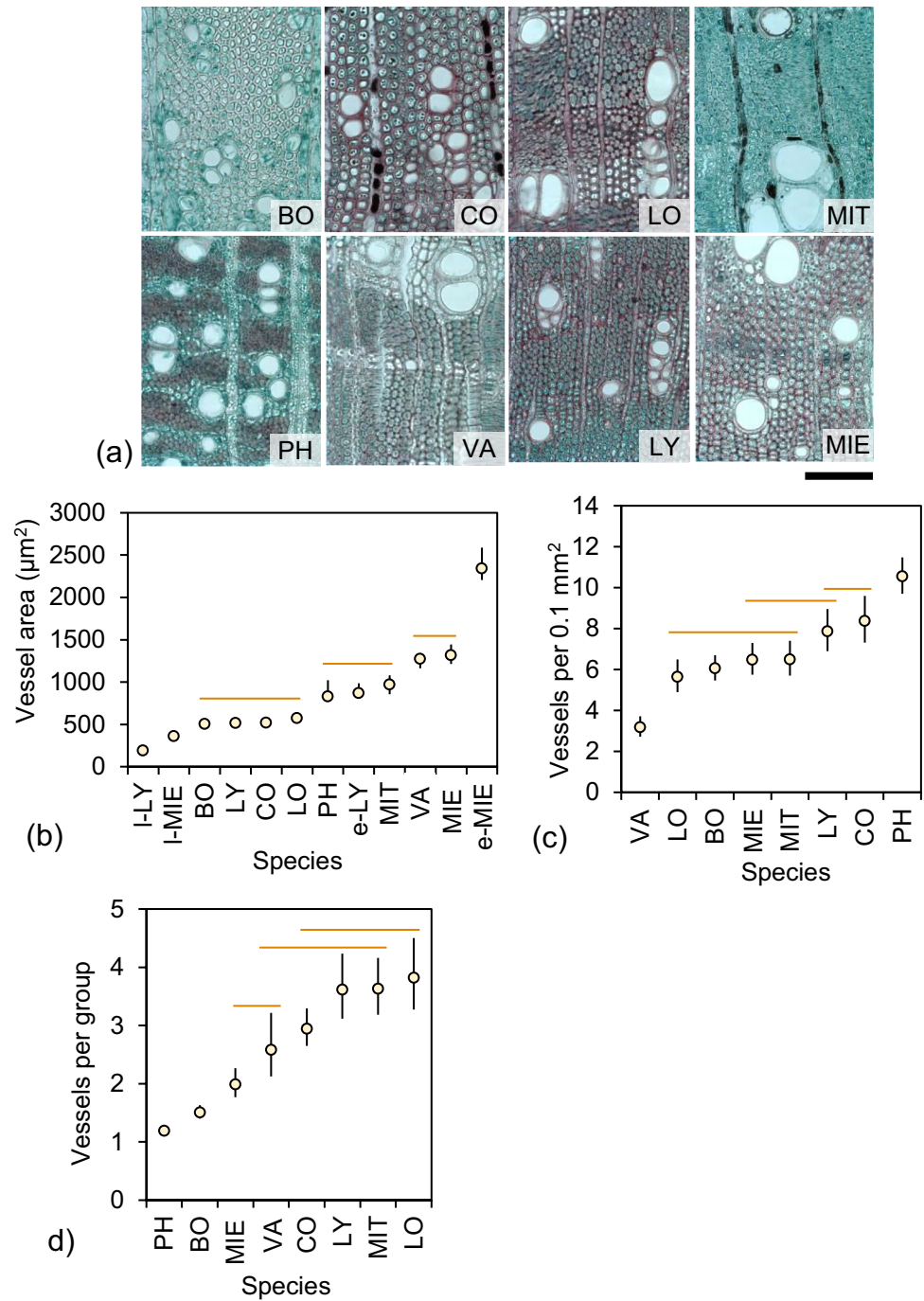
Standard deviation analysis for successional communities

Overall, vessel and fiber traits were highly variable between LC species, as well as vessel area at the intraspecific level. In EC, *Lysiloma divaricatum* latewood (l-LY) and *Bonellia macrocarpa* (BO) showed the lowest variation (Fig. 7a). In LC, latewood of *Lysiloma divaricatum* and *Mimosa eurycarpa* (l-LY and l-MIE) displayed the lowest standard deviations for vessel area (Fig. 7b). Similarly, species coexisting in EC (Fig. 7c) and in LC (Fig. 7d) had wide ranges of vessel tangential diameter values.

Discussion

In this in situ study, we were able to identify those stem anatomical features associated with water transport efficiency and safety exhibited by tree species coexisting in recovering TDF vegetation. In this way, we gained insights into the
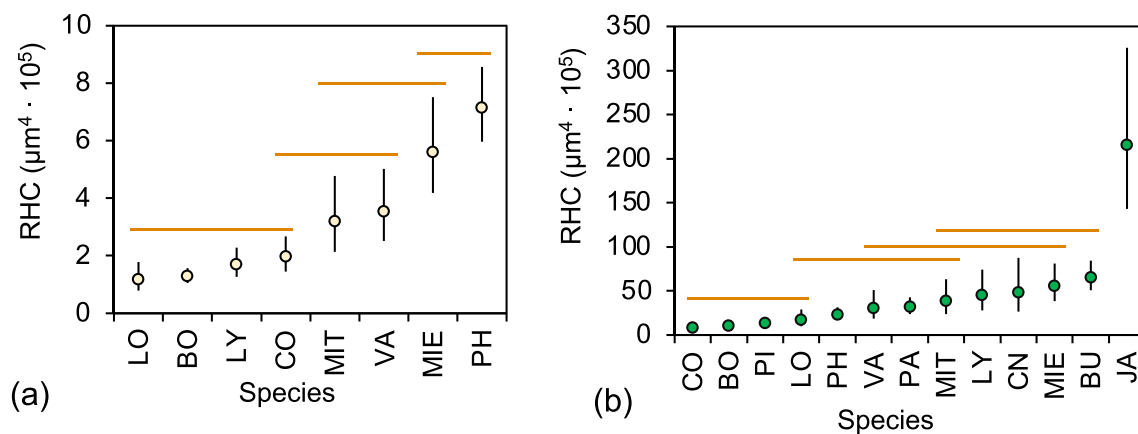
Fig. 3 Estimated means of the relative hydraulic conductivities (RHC) for species coexisting in successional tropical dry forest communities. **a** Early successional communities (yellow circles; 2 years of abandonment). **b** Late successional communities (green circles; >50 years of abandonment). Brown horizontal bars indicate lack of significant differences between means. Vertical lines represent estimated 95% confidence intervals. Species acronyms: BO, *Bonel-* *lia macrocarpa*; BU, *Bursera ovalifolia*; CN, *Cnidoscolus megacan-* *thus*; CO, *Coccoloba liebmannii*; JA, *Jacaratia mexicana*; LO, *Lon-* *chocarpus lanceolatus*; LY, *Lysiloma divaricatum* whole-wood; MIE, *Mimosa eurycarpa* whole-wood; MIT, *Mimosa tenuiflora*; PA, *Pachy-* *cereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Piloso-* *cereus collinsii*; VA, *Vachellia campechiana*

responses of the anatomical structures of these species to ecological stimuli, such as periodical water stress alternated with higher water availability, together with microenvironmental changes taking place during successional vegetation development.

In the study species occurring in EC and LC of successional TDF, some trends in vessel and fiber dimensions, vessel density, their arrangement, and variability became apparent that can be associated with water transport, and with biomass build-up. It is interesting that in general, we failed to recognize discrete groups. In both communities, anatomical trait variation was rather continuous, as previously reported for other functional traits in other TDFs, although species occurring in EC were more homogeneous than those coexisting in LC (Chaturvedi et al. 2021).

Our results both for EC and LC are consistent with the tendency of vessels to be more grouped in dry environments (Barajas-Morales 1985; Carlquist and Hoekman 1985; Lindorf 1994). Particularly, for species coexisting in EC, our results suggest that high vessel frequency provides xylem safety through alternative pathways for water transport in the case of an embolized vessel (Ewers et al. 2007). Seven out of the eight study species coexisting in EC exhibited high vessel frequency and high degree of grouping, both of which are features associated with the redundancy property and the drought tolerance mechanism. Later in succession, the eight species that coexisted in EC still coexist in LC and continue to exhibit the anatomical features associated with the tolerance mechanism. However, in LC, the drought-evading mechanism gains importance, as six of the 13 species coexisting in this

community exhibited anatomical features related to this strategy, as opposed to just one as in EC.

Noteworthy, we also detected a feature that seems important in TDF successional species: high vessel area variability both in EC and LC. This result implies a high degree of xylem hydraulic adjustment in both ring and diffuse porous species coexisting in EC and LC. This property could be key to the ecological success of these species as it potentially confers on them low vulnerability to embolism in the dry season and high-water transport efficiency in the rainy season.

Coincidence of experimentally inferred drought resistance mechanisms with those observed in situ

Our results agree with Pineda-García et al. (2013), who concluded that EC and LC species in TDF vary widely in their drought resistance capacities, and that species with large sapwood water storage are uncommon in EC. Our results contribute to fill the gap identified by these authors, as we have provided evidence supporting the notion that an avoidance strategy involving water storage probably is selected against in EC. Similarly, fiber patterns were generally consistent with Aguilar-Rodríguez et al. (2001), who found a prevalence of thick-walled fibers and high wood density in dry environments such as in EC, whereas species with medium to low specific gravity and thin-walled fibers dominate in more humid habitats like LC. Notwithstanding these consistencies, a sounder (*i.e.*, experimental) test of our hypotheses on the drought resistance mechanisms in the studied successional species is required. The
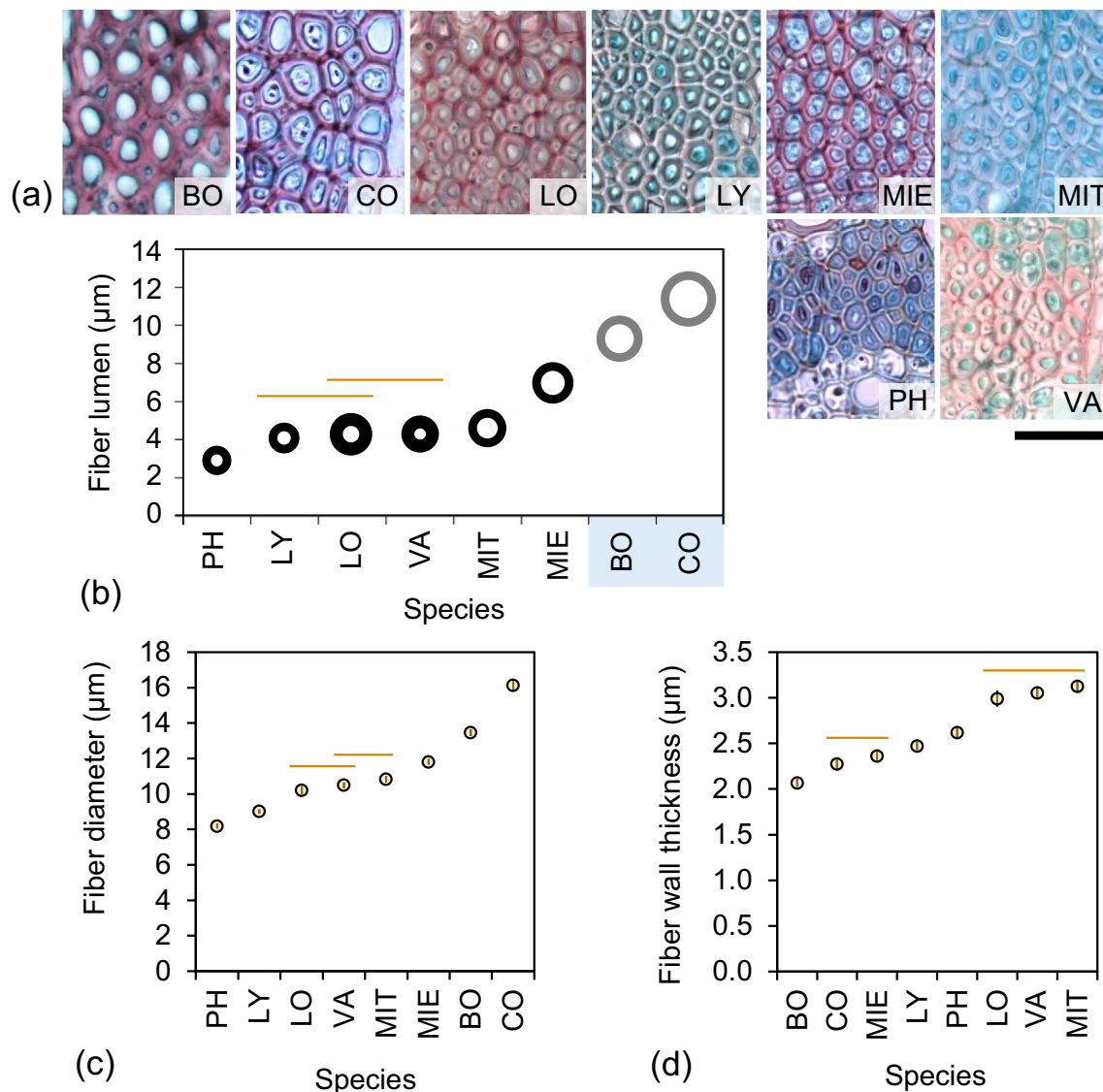
Fig. 4 Wood fiber features of species co-existing in early-successional tropical dry forest communities (~2 years of abandonment; EC). **a** Wood transverse sections of the eight species in this group; scale bar = 40 μm. **b-d** Estimated means of vessel features per species. **b** Mean fiber lumen (μm); species in the shaded area show wood features related to drought-evasion mechanism; circles represent fiber diameter and fiber lumen diameter as well as fiber thickness; gray circles are septate fibers and black circles non-septate fibers. **c** Mean fiber diameter (μm). **d** Mean fiber wall thickness (μm). Brown horizontal bars indicate lack of significant differences between means; vertical lines represent 95% estimated confidence intervals. Species acronyms: BO, *Bonellia macrocarpa*; CO, *Coccoloba liebmannii*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PH, *Phyllostylon rhamnoides*; VA, *Vachellia campechiana*

present study provides information that may be very useful for the experimental design of future research.

Wood anatomical features in early-successional communities

EC are characterized by a harsh environment; hence, we hypothesized that the dry season in TDF has acted as a selective force promoting specific adaptive survival strategies in these communities. As expected, in this community, we observed rather homogeneous wood features, for example high vessel redundancy, which ensures water transport continuity in the event of a cavitated vessel (Ewers et al. 2007). Such high vessel redundancy in all study species coexisting in EC is given by highly clustered vessels and high vessel frequencies (with the exception of *Vachellia campechiana*, which does have highly grouped vessels but few vessels per area).
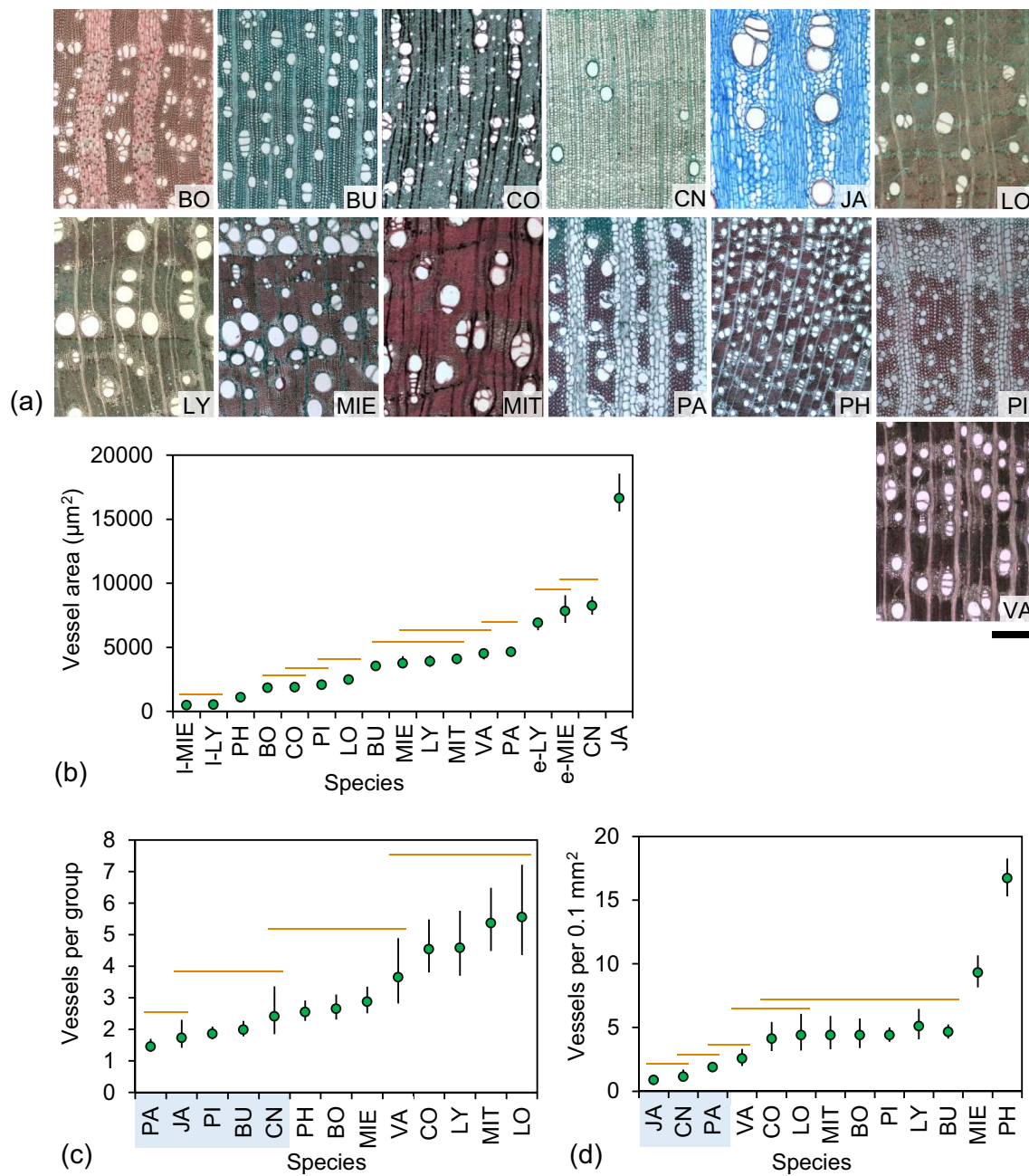
Fig. 5 Wood vessel features of species co-existing in late-successional tropical dry forest communities (>50 years of abandonment; LC). **a** Wood transverse sections of 13 species in this group; scale bar=300 μm. **b-d** Vessel features' estimated means per species. **b** Mean vessel area (μm²). **c** Mean number of vessels per 0.1 mm². **d** Mean number of vessels per group. Species in the gray area exhibit wood features related to drought-evasion mechanism. Brown horizontal bars indicate lack of significant differences between means; vertical lines represent 95% estimated confidence intervals. Species acronyms: BO, *Bonellia macrocarpa*; BU, *Bursera ovalifolia*; CO, *Coccoloba liebmannii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum* (l-latewood; e-earlywood); MIE, *Mimosa eurycarpa* (l-latewood; e-earlywood); MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*; VA, *Vachellia campechiana*
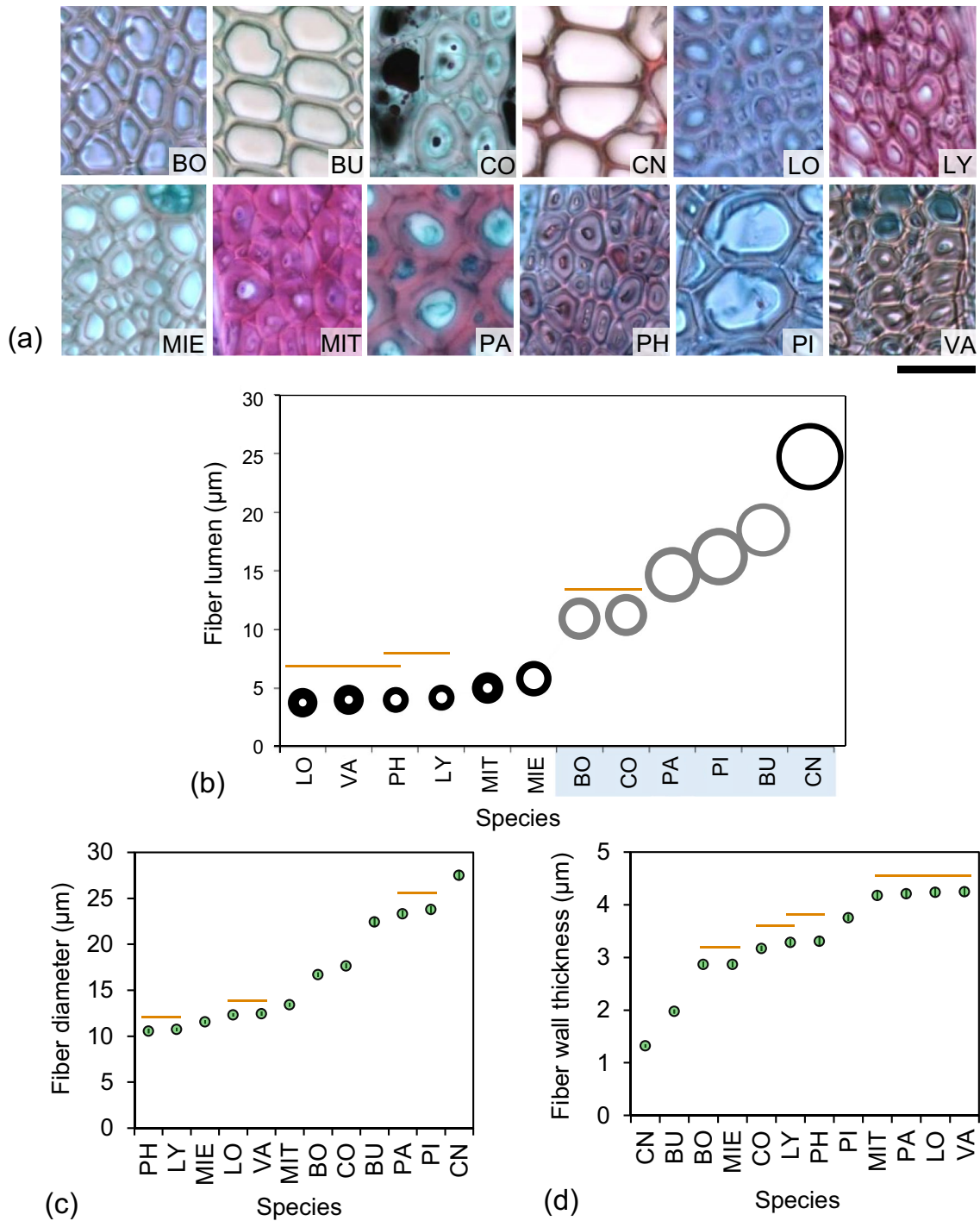
Fig. 6 Wood fiber features of species co-existing in late-successional tropical dry forest communities (> 50 years of abandonment; LC). **a** Wood transverse sections of 12 species in this group; scale bar = 40 μm. **b-d** Estimated means for vessel features per species. **b** Mean fiber lumen (μm); species in the shaded area show wood features related to drought-evasion mechanism; circles represent fiber diameter and fiber lumen diameter as well as fiber thickness; gray circles are septate fibers and black circles non-septate fibers. **c** Fiber diameter (μm). **d** Mean fiber wall thickness (μm). Brown horizontal bars indicate no significant differences between means; vertical lines represent 95% estimated confidence intervals. Species acronyms: BO, *Bonellia macrocarpa*; BU, *Bursera ovalifolia*; CO, *Coccoloba liebmannii*; CN, *Cnidoscolus megacanthus*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum*; MIE, *Mimosa eurycarpa*; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*; VA, *Vachellia campechiana*
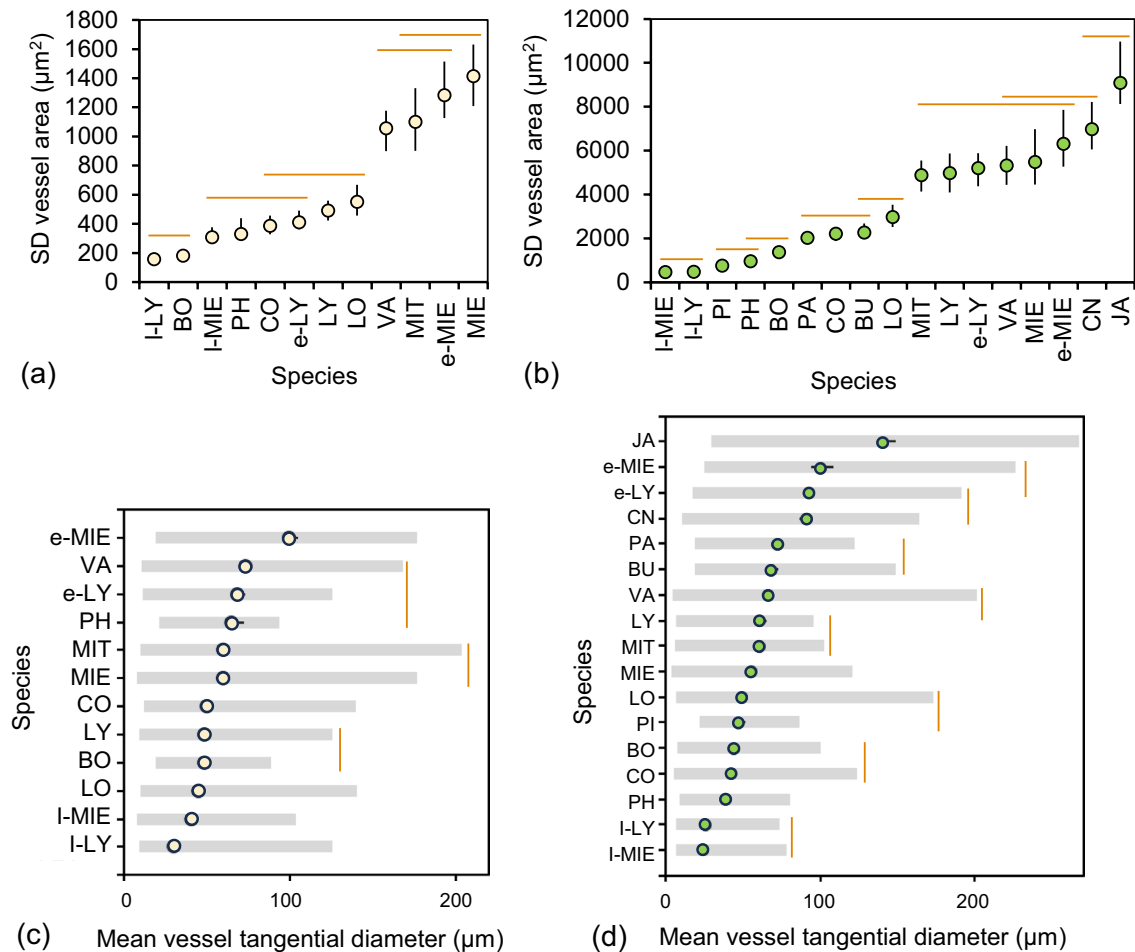
Fig. 7 Estimated means of vessel features variation in the wood of species coexisting in tropical dry forest successional communities. **a**-**c** early-successional communities (~2 years of abandonment; EC). **b**-**d** late-successional communities (>50 years of abandonment; LC). **a** and **b**, mean standard deviation; vertical lines represent 95% estimated confidence interval. Mean vessel tangential diameter of species in EC **c** and in LC **d**; gray bars indicate the range between the minimum and the maximum vessel diameter observed for each species; brown vertical bars indicate lack of significant differences between means. Species acronyms: BO, *Bonellia macrocarpa*; BU, *Bursera ovalifolia*; CO, *Coccoloba liebmannii*; CN, *Cnidoscolus megacanthus*; JA, *Jacaratia mexicana*; LO, *Lonchocarpus lanceolatus*; LY, *Lysiloma divaricatum* (l-latewood; e-earlywood); MIE, *Mimosa eurycarpa* wholewood, l-latewood, e-earlywood; MIT, *Mimosa tenuiflora*; PA, *Pachycereus pecten-aboriginum*; PH, *Phyllostylon rhamnoides*; PI, *Pilosocereus collinsii*; VA, *Vachellia campechiana*

The combination of high RHC with high variation in vessel traits may be advantageous in TDF successional species: during the rainy (growing) season, these features allow an efficient water exploitation while maintaining the capacity to resist water stress periods and take advantage of water pulses. The three species that are exclusive of secondary vegetation (*Mimosa eurycarpa*, *M. tenuiflora*, and *Vachellia campechiana*) are ecologically successful in EC (*i.e.*, they display high frequency, basal area, and relative growth rates (Lebrija-Trejos et al. 2010; Romero 2014); interestingly, they also have high mean vessel area values with the highest variation (mean standard deviation), and the highest RHC of EC (except for *Phyllostylon rhamnoides*, which is a structurally important species in mature forest). These

wood anatomical features in the three species restricted to secondary vegetation suggest an efficient water conduction capacity during the rainy season. *Phyllostylon rhamnoides* has the highest RHC of EC, a feature that is given by the highest vessel frequency recorded in this successional community; however, this species does not exhibit the apparently efficient high vessel area observed for the important species in EC (*Mimosa eurycarpa*, *M. tenuiflora* and *Vachellia campechiana*).

Even during the rainy seasons, soil drought can be notorious in EC (Lebrija-Trejos et al. 2011), and our results strongly suggest that drought tolerance is the main water stress resistance mechanism in EC. Apparently, drought tolerance in EC species is given by high vessel redundancy,

a feature associated with resistance to cavitation (Ewers et al. 2007). In this study, we found a high degree of vessel clustering in six out of the eight early-successional species; all these species but one (*Coccoloba liebmannii*) are legumes with very thick-walled fibers and high wood density (Romero et al. 2020a). The redundancy property in *Phyllostylon rhamnoides* is likely given by a different feature, as it seems to reveal a tradeoff: it is one of the two species with the fewest vessels per group in EC, but it has the highest vessel frequency of all. The other species with few vessels per group, *Bonellia macrocarpa*, is distinctly different from the rest of the species occurring in EC, as it is the only species with inverted phenology (*i.e.*, shedding the leaves in the rainy season and bearing foliage in the dry season), it has the highest wood water content (Romero et al. 2020a), very wide rays (Romero et al. 2022), one of the widest mean fiber lumen diameters, and the lowest variation in vessel area. Therefore, this species appears to be the only one in EC displaying a drought-evasion mechanism, which may additionally rely on large rooting depth, as suggested by field observations.

Mimosa eurycarpa is the uncontested dominant species in early succession (Lebrija-Trejos et al. 2010). This species has an outstanding mean vessel area in earlywood, suggesting that it possesses the most efficient water transport system, compared to all other study species, during the rainy season. Additionally, apparently it has one of the least hydraulically vulnerable wood during the dry season, as its mean latewood-vessel area is one of the smallest in EC.

In line with Prach and Pyšek (1999), we identified a set of wood anatomical features that may contribute to the probability of a species becoming dominant. In addition to its strong dominance in secondary vegetation in the study region (Lebrija-Trejos et al. 2008), *Mimosa eurycarpa* has the highest values of earlywood vessel area and the highest vessel area variation, compared to the rest of the species coexisting in EC; additionally, it has the second lowest EC values of area per vessel in its latewood. In LC, *Lysiloma divaricatum* is the dominant species, and together with *Mimosa eurycarpa* latewood, it has the lowest LC vessel area in its latewood. Narrow vessel diameters are related to low vulnerability to water-stress-induced embolism (Hargrave et al. 1994; Lo Gullo et al. 1995). Additionally, *Lysiloma divaricatum* in LC has highly grouped vessels, which may contribute to greater redundancy, and high and highly variable vessel area. *Lysiloma divaricatum* does not accumulate high amounts of water as drought-evading species, but it attains the same high RHC as three of them: *Bursera ovalifolia*, *Cnidoscolus megacanthus*, and the cactus *Pachycereus pecten-aboriginum*.

Wood anatomical features in late-successional communities

As species coexisting in LC also face seasonal drought, we also expected them to exhibit features associated with drought tolerance mechanisms. In theory, if the number of vessels is high, disabling a given number of vessels by air embolisms formed under water stress will not significantly affect conduction in a plant (Carlquist 1977). *Phyllostylon rhamnoides* and *Mimosa eurycarpa* showed the highest vessel frequency among species occurring in LC, likely rendering them more hydraulically efficient and probably safer than the remaining species in this community.

Fiber lumen clearly divides species from LC in one group having wood features associated with a tolerance mechanism (narrower fiber lumina) and another one displaying drought-evading wood features (wider fiber lumina, almost exclusively septate fibers). This latter group comprises five LC species that exhibit high wood water content (Romero et al. 2020a), and high and wide rays (Romero et al. 2022). Having few vessels per group surrounded by parenchyma cells (Romero et al. 2022) immersed in fibers with wide lumen diameters, these species show low hydraulic redundancy. In addition, they also have the widest vessels among all EC species, as well as septate fibers with wide lumina (with the exception of *Cnidoscolus megacanthus*; Romero et al. 2022). This group includes the two cacti (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsi*), along with *Jacaratia mexicana*, *Bursera ovalifolia* and *Cnidoscolus megacanthus*, all of which are exclusive of LC and mature forest (Pérez-García et al. 2010). Their wide vessels probably contribute to a greater release of water from wood during transpiration (capacitance; but see Ziemińska et al. [2019], who posit that capacitance is an emergent property of the whole wood), likely resting relevance to the redundancy property. In these species, vessels represent compartments capable of releasing water under drought stress, as reported by Jupa et al. (2016). In very dry environments, water released by cavitation events might be important to the short-term survival of trees (Tyree and Yang 1990). In EC and LC of successional TDF, water released from vessels and even from fiber lumina during the dry season (Tyree and Zimmermann 2003) may contribute to species persistence in successional communities.

Jacaratia mexicana had the widest vessels of all species coexisting in LC, and it was followed distantly by *Cnidoscolus megacanthus*, *Mimosa eurycarpa* earlywood, and *Lysiloma divaricatum* earlywood. Although these four species exhibit wide vessel diameters, it is interesting that they seem to have different strategies in their water economy. For one, the two legumes differ between them, as *Mimosa eurycarpa* has intermediate values of wood water content, whereas *Lysiloma divaricatum* has one of the highest values

for this trait in LC (Romero et al. 2020a). Moreover, both legumes differ from *Jacaratia mexicana* and *Cnidoscolus megacanthus* in that the latter two species have few, predominantly solitary vessels along with the highest wood water content among species coexisting in LC (Romero et al. 2020a). *Jacaratia mexicana* and *Cnidoscolus megacanthus* probably move water passively only during the rainy season as both shed their foliage in the dry season; however, it is likely that these two species actively continue transporting water and nutrients during the dry season within their stems (*Jacaratia mexicana* through the living parenchyma, and *Cnidoscolus megacanthus* through the thin-walled fibers; Romero et al. 2022).

Overall, we failed to distinguish discrete groups related to RHC. This result suggests that during the rainy season most LC species can conduct similar amounts of water through their stems. Apparently, the three dominant successional species (*Mimosa eurycarpa*, *M. tenuiflora* in EC, and *Lysiloma divaricatum* in LC), all of which show features related to drought tolerance mechanisms, are as efficient in conducting water as LC species (*Bursera ovalifolia*, *Cnidoscolus megacanthus*, which have features associated with drought-evading mechanisms).

The three legume species that are exclusive of secondary vegetation and structurally important in EC (*Mimosa eurycarpa*, *M. tenuiflora*, and *Vachellia campechiana*) exhibit drought-tolerant wood features, but they also share wood features with drought-evading species that clearly store water in their stems (Romero et al. 2020a). For example, RHCs of *Mimosa eurycarpa* and *Mimosa tenuiflora* did not differ significantly from values recorded for *Cnidoscolus megacanthus* and *Bursera ovalifolia*, the two species from the group of five drought-evading species coexisting in LC and mature TDF. RHCs of *Mimosa tenuiflora* and *Vachellia campechiana* did not differ either from that recorded in the drought-evading cactus *Pachycereus pecten-aboriginum*.

The two study cacti (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*) exhibit very thick fiber walls, a wood feature associated with a drought tolerance mechanism, and they also accumulate high wood water contents in their stems, probably in their wide vessel and fiber lumina. Both cacti belong in the group of species having the thickest fibers in LC; this group includes three high wood density legumes that exhibit drought tolerance wood features (Romero et al. 2020a), unexpectedly along with the two cacti. Interestingly, both cacti bear a strong resemblance in their wood features to the tree *Bursera ovalifolia*. Thicker cell walls imply higher carbon accumulation; therefore, we urge including canopy cacti species in TDF biomass studies. Intriguingly, most such studies systematically exclude cacti from biomass calculations but at the same time they rarely exclude tree species with higher water contents like *Jacaratia mexicana*,

Bursera ovalifolia and *Cnidoscolus megacanthus* (Romero et al. 2020a).

Anatomical features across successional communities

As expected, we found that LC are characterized by a higher functional diversity than EC. In agreement with the results of Chaturvedi et al. (2021) for a mature TDF, both drought avoidance and drought tolerance mechanisms are relevant in the TDF species assemblage. A group of five species having wood features associated with the drought-evading mechanism enter lately in the successional community. Anderegg et al. (2018) concluded that diversity in the hydraulic traits of trees is important for forest drought resilience, which may be the case of LC and mature TDF.

It is worth mentioning that we expected the two cactus species (*Pachycereus pecten-aboriginum* and *Pilosocereus collinsii*) to largely differ from the rest of the successional species; yet, our results show that it was not the cacti but two other woody species (*Jacaratia mexicana* and *Cnidoscolus megacanthus*) which were segregated from the other successional species based on their wood features.

Contrary to Pineda-García et al. (2015), we found evidence supporting a functional differentiation between early and late-successional species. For example, *Mimosa eurycarpa*, the main dominant species in EC, has low wood density compared to *Lysiloma divaricatum* (Romero et al. 2020a), which is not only the dominant species in LC and one of the most prominent species in mature forest but is also present in early stages of the successional process (Lebrija-Trejos et al. 2010; Muñoz-Avilés 2015). *Lysiloma divaricatum* has wider vessel diameters in earlywood (as wide as those in *Mimosa eurycarpa*), although fiber features of *L. divaricatum* indicate a greater mechanical resistance than in *Mimosa eurycarpa*. Apparently, individuals of *Mimosa eurycarpa* reach a point at which their main stem breaks, causing its death (field observations).

Variation of wood anatomical features in successional species

As expected, both ring and diffuse porous successional species coexisting in EC and LC exhibited a high degree of xylem hydraulic adjustments that might be related to the seasonality in precipitation and its intra-annual fluctuations. Large vessel area variability may be key to adaptations to drought in successional TDF species. Intraspecific phenotypic variation is important for adaptations to occur (Abrams 1994; Rosell et al. 2017) and it may contribute to maximizing species' responses to changing environments for locally adapted populations; for example, it has

been suggested that variation in vessel diameter minimizes drought-induced cavitation (Schreiber et al. 2015).

The most variable species regarding vessel area are those that are exclusive of secondary vegetation (*Mimosa eurycarpa*, *M. tenuiflora*, and *Vachellia campechiana*). These three species, especially those in the *Mimosa* genus, are dominant at least during the first 20 years of succession (Lebrija-Trejos et al. 2010). The high adjustment capacity in their hydraulic system probably allows them to persist in mid and late-successional communities, although with low basal areas. These species have the advantage of producing narrow conduits that are potentially more resistant to embolism, and may provide alternate pathways when large vessels become embolized (Hacke et al. 2017). Also, they exhibit vessels with larger diameters, which may be more efficient in water transport when this resource is available.

Mimosa tenuiflora and *Vachellia campechiana* have diffuse porosity and have the same high variability as the whole wood of *Mimosa eurycarpa*, a ring-porous species. *Mimosa eurycarpa* produces very small latewood vessels, and at the same time, it has the widest vessels among all species occurring in EC, which are earlywood vessels. Therefore, we suggest that the ecological success of *Mimosa tenuiflora*, the second dominant species, is associated with the high variation in its xylem, despite having diffuse porosity.

Modification of xylem responses to water availability, given by the high vessel area variation, appears to be advantageous in the species coexisting in LC, even in those species showing wood features associated with a drought-evasion mechanism. Species coexisting in LC grow taller and attain larger basal areas, which implies that they have a higher water demand during the rainy season, and probably also during dry season, as some retain their foliage for longer periods when water availability decreases (Luna-Nieves et al. 2022). The entire set of species coexisting in LC showed coefficients of variation of their vessel area ranging from 34 to 146%, whereas the mean coefficient of variation in the group of species with wood features associated with a drought-evasion mechanism was 54%.

In the particular case of *Mimosa eurycarpa*, the large variation in the vessel area of its wood may be key to explain its outstanding ecological success along the successional gradient. Over the course of succession, this species faces drastic changes in environmental conditions and resource availability (Lebrija-Trejos et al. 2011). This species is not only the main dominant early-successional species but also can persist in more advanced successional stages, albeit with reduced structural importance, for as long as 70 years of succession, a longer persistence time than that of its congeneric species *Mimosa tenuiflora* (field observations; Lebrija-Trejos et al. 2010).

Mean vessel area and mean tangential values conceal valuable information regarding the capacity of wood to adjust to variations in water availability, especially in species growing in seasonally dry forests, and also in species that are capable of surviving successional microenvironmental changes over time. Therefore, we make the call for future studies of xylem features related to drought resistance strategies of species typical of these environments to include the formal analysis of the standard deviations of tangential diameters, as well as to report their ranges (minimum and maximum values).

Conclusions

Our results provide support to the hydraulic redundancy property as an important drought resistance mechanism, which predominates in TDF early succession and is maintained over time, by the same species, in late-successional communities. Several low-wood density species that become established in late-successional communities exhibited wood anatomical features associated with a drought-evasion mechanism. This finding implies that deforestation not only reduces taxonomic diversity, but also the functional diversity associated with drought resistance mechanisms. Finally, we highlight the need to adopt a standard deviation analysis approach. In future, this will allow confirming the high variability in vessel diameter, even in diffuse porous species, as a key feature for the ecological success of plants facing succession-driven changes in seasonally dry environments.

Declarations

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