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Functional patterns of wood traits in Terra Firme and Igapó (tropical moist forests), Colombian Orinoquia

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Abstract: Wood anatomical traits, considered hard traits, are ecologically relevant due to their relationship with the function of aboveground biomass storage in trees. In contrasting soil conditions, these traits can enhance our understanding of the role of species in ecosystem processes. We compared tree vegetation in Terra firme and Igapó within the tropical moist gallery forest of the Colombian Orinoquia, focusing on wood traits. Data were processed from five permanent monitoring plots, three in Terra firme and two in Igapó. We mounted tissue slices from wood cores to measure functional traits. We identified three functional types of trees with two strategies: conservatives and intermediate conservatives (characterized by hydraulic safety and fiber investment), and intermediate acquisitive (characterized by hydraulic efficiency and storage). In Terra fime, we recognized a functional type corresponding to palms (fiber investment and storage). Three trade-offs were observed in both forests: fiber traits vs. parenchymatic traits; fiber investment vs. storage, and hydraulic efficiency vs. hydraulic safety. We found a wide range of trait values within the same wood density range. Terra firme and Igapó forests exhibited similar functional patterns.

Keywords: wood anatomical traits, plant functional types, tree community ecology

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Introduction

Plant functional traits are associated with ecosystem functioning (Díaz & Cabido, 2001). The trait values of species within a plant community are linked to their potential to generate ecosystem services (Tilman, 2001). For this reason, understanding how plants respond to ecological conditions and influence ecosystem processes is essential for recognizing their impact on aboveground biomass stocks and productivity (Shen et al., 2016). Stem traits have been used to explain shifts in aboveground biomass in trees (Baker et al., 2004), with wood density being the most significant trait (Baker et al., 2009). However, wood density is considered a soft trait influenced by hard traits (Marchand, 2022) related to wood anatomical traits. For instance, higher wood density correlates with lower vessel diameter (Preston et al., 2006) and axial parenchyma (Zheng & Martínez-Cabrera, 2013), and greater fiber wall thickness (Fortunel et al., 2014). Additionally, wood density exhibits varying trends depending on soil nutrients availability: higher soil fertility is associated with lower wood density (Castro et al., 2017).

On the other hand, functional balance of a community leads species to form groups that integrate different traits to coexist, clustering into plant functional types – PFT – (Walker, 1992). In this process, some clusters develop certain traits while others do not, a phenomenon known as a trade-off (Roscher et al., 2012). Trade-offs in wood traits show clear patterns under local conditions (Pulido-Rodriguez et al., 2019) but remain ambiguous for global trends (Gleason et al., 2016). Understanding these trends is essential for interpreting acquisitive and conservative strategies (Maynard et al., 2022). This is particularly important in tree vegetation gradients, such as soils under flooding conditions, where contrasting eco-physiological responses to ecosystem processes may occur (Lourenço et al., 2022).

In this context, this research aimed to compare the functional patterns of tree vegetation in tropical moist forests of Terra firme and Igapó in the Colombian Orinoquia, focusing on wood traits. To achieve this, we characterized wood traits and trade-offs, identified clustering patterns and functional strategies, and examined relationships between wood traits and wood density. Our first hypothesis posits that wood traits exhibit the fiber-parenchyma trade-off (Janssen et al., 2020). The second hypothesis suggests the presence of more than two functional types (Kunstler et al., 2016), displaying acquisitive, conservative, and intermediate strategies (Lohbeck et al., 2015). Finally, we hypothesize a directly proportional relationship between wood density and wood traits, mainly fiber traits (Ziemińska et al., 2013, 2015).

Methods

The study area includes five permanent monitoring plots analyzed by González-Abella et al. (2021) in the Tomo Grande Reserve (Vichada Department, Tomo River). Two forest types are present in this area: Terra firme and Igapó. The locations of the plots are shown in Table 1. Terra firme forests are unflooded areas crisscrossed with riparian vegetation (Fig. S1), characterized by kaolinitic clays with lower ionic activity (Pitman et al., 2001), while Igapó forests are floodplain areas (Fig. S3) subject to seasonal flooding by rivers influenced by the presence of leaf litter (Lobo et al., 2019). According to Holdridge's (1967) classification, the life zone corresponds to a tropical moist forest. We selected tree species that accounted for 70% of the aboveground biomass and extracted wood cores from 23 dominant species in Terra firme (Table S1, Table S5, Table S6) and 9 in Igapó (Table S2, Table S7), using Chave's (2006) parameters and a Haglöf increment borer: extraction at 1.3 m, a depth of 10 cm, and a diameter of 5.15 mm. These cores were used to measure wood density (Williamson & Wiemann, 2010) and prepare microscopic slides for wood anatomy analysis. The laboratory phase was conducted at the Timber Lab "Jose Anatolio Lastra Rivera" and the Forest Herbarium "Gilberto Emilio Mahecha Vega" of the District University of Bogotá. We used a "RM2255" rotary microtome, an "AxioStar Plus" trinocular microscope with an "AxioCam ERC5S" camera, and a "Discovery V12" stereoscope with an "AxioCam ICc5" camera.

We prepared the samples from May of 2021 to April of 2022 according to the IAWA Committee methods (Alfonso et al., 1989), cutting them into transverse, tangential, and radial sections for each species. Microtome cuts were made at intervals ranging from twelve to forty micrometers, considering that some species have high wood density (> 0.6 g cm^{-3}), using parts from the sapwood (Pande, 2013). Nevertheless, some samples were thick or contained imperfections due to the angle of the cut. Microscopy mounting was made using Canada balsam. Photographs were taken at 5x magnification to generate images of 1 mm^2. We performed macerations to obtain fiber cells following the method of Jansen et al. (1998). Small wood pieces were cut from the cores along the fiber direction and placed in a 1:1 solution of glacial acetic acid (CH_3CO_2H) and hydrogen peroxide (H_2O_2). The solution was heated in test tubes at 60 °C for 24 hours, and the precipitate was washed with 50% ethanol. We then stained the samples with safranin for 48 hours, to complete the process even for some species with low content of lignin (Bond et al., 2008) and mounted them on microscope slides. For fiber length, we made temporary mountings using glycerol. Images of 2 mm^2 were captured at 70× magnification using the stereoscope to identify morphological structures in palms. We employed Zen Lite software version 2.5 (blue edition) to record photos and generate scales. We measured the wood traits shown in Table 2 using ImageJ software (Rueden et al., 2017) version 1.52r. Although inter-vessel pits were measured, we did not include them as a hydraulic trait because determining this requires the membrane width (Wheeler et al., 2005; Sperry & Hacke, 2004), which could not be obtained due to the lack of an electron microscope in the laboratory. Finally, we transformed the vessel grouping into a qualitative variable using the clustering index for vessels proposed by Scholz et al. (2013). The following categories were determined: null, very low, low, medium low, medium, medium high, high, very high, and dominant. These categories correspond to variations of 12.5% in the index (Table S3).

Table 1. Plots, species, and acronyms

Plot Location	Family	Species	Author	Acronym
Terra Firme, Plot 1. 4.839N, −70.272W	Bignoniaceae	*Jacaranda copaia*	(Aubl.) D. Don	Jc1
	Areceaceae	*Attalea maripa*	(Aubl.) Mart.	Am1
	Goupiaceae	*Goupia glabra*	Aubl.	Gg1
	Burseraceae	*Protium stevensonii*	(Standl.) Daly	Pst1
	Vochysiaceae	*Erisma calcaratum*	(Link) Warm.	Ec1
	Sapotaceae	*Pouteria multiflora*	(A. DC.) Eyma	Pm1
	Apocynaceae	*Aspidosperma excelsum*	Benth.	Ae1
	Leguminosae	*Enterolobium schomburgkii*	(Benth.) Benth.	Es1
	Annonaceae	*Bocageopsis multiflora*	(Mart.) R.E. Fr.	Bm1
	Chrysobalanaceae	*Moquilea subarachnophylla*	(Cuatrec.) Sothers & Prance	Ms1
Terra Firme, Plot 2. 4.835N, −70.275W	Areceaceae	*Attalea maripa*	(Aubl.) Mart.	Am2
	Burseraceae	*Protium stevensonii*	(Standl.) Daly	Pst2
	Apocynaceae	*Couma macrocarpa*	Barb. Rodr.	Cm2
	Goupiaceae	*Goupia glabra*	Aubl.	Gg2
	Bignoniaceae	*Jacaranda copaia*	(Aubl.) D. Don	Jc2
	Areceaceae	*Oenocarpus bataua*	Mart.	Ob2
	Burseraceae	*Trattinnickia lawrancei*	Standl.	Tl2
	Sapotaceae	*Pouteria multiflora*	(A. DC.) Eyma	Pm2
	Chrysobalanaceae	*Moquilea subarachnophylla*	(Cuatrec.) Sothers & Prance	Ms2
	Areceaceae	*Oenocarpus bacaba*	Mart.	Obac2
	Malvaceae	*Pachira speciosa*	Triana & Planch.	Ps2
	Peraceae	*Pera arborea*	Mutis	Pa2
Terra Firme, Plot 3. 4.841N, −70.256W	Areceaceae	*Oenocarpus bataua*	Mart.	Ob3
	Areceaceae	*Attalea maripa*	(Aubl.) Mart.	Am3
	Bignoniaceae	*Jacaranda copaia*	(Aubl.) D. Don	Jc3
	Annonaceae	*Guatteria foliosa*	Benth.	Gf3
	Urticaceae	*Pourouma minor*	Benoist	Pmin3
	Euphorbiaceae	*Alchornea triplinervia*	(Spreng.) Müll. Arg.	At3
	Leguminosae	*Abarema jupunba*	(Willd.) Britton & Killip	Aj3
	Leguminosae	*Stryphnodendron guianense*	(Aubl.) Benth.	Sg3
	Araliaceae	*Didymopanax morototoni*	(Aubl.) Decne. & Planch.	Dmo3
	Annonaceae	*Bocageopsis multiflora*	(Mart.) R.E. Fr.	Bm3
	Apocynaceae	*Himatanthus articulatus*	(Vahl) Woodson	Ha3
Igapó, Plot 4.4.823N, −70.263W	Leguminosae	*Tachigali tinctoria*	(Benth.) Zarucchi & Herend.	Tt4
	Leguminosae	*Tachigali vaupesiana*	van der Werff	Tv4
	Leguminosae	*Copaifera pubiflora*	Benth.	Cp4
	Annonaceae	*Guatteria blepharophylla*	Mart.	Gb4
	Euphorbiaceae	*Mabea trianae*	Pax	Mt4
	Calophyllaceae	*Caraipa llanorum*	Cuatrec.	Cl4
Igapó, Plot 5. 4.830N, −70.250W	Euphorbiaceae	*Mabea trianae*	Pax	Mt5
	Chrysobalanaceae	*Hymenopus heteromorphus*	(Benth.) Sothers & Prance	Hh5
	Leguminosae	*Tachigali tinctoria*	(Benth.) Zarucchi & Herend.	Tt5
	Rubiaceae	*Duroia micrantha*	(Ladbr.) Zarucchi & J.H. Kirkbr.	Dm5
	Lecythidaceae	*Eschweilera parvifolia*	Mart. ex DC.	Ep5
	Calophyllaceae	*Caraipa llanorum*	Cuatrec.	Cl5
	Leguminosae	*Tachigali vaupesiana*	van der Werff	Tv5

Table 2. Functional traits, units and repetitions per species. Acronyms: *, palms

Section	Trait	Unit	Repetitions	References
Transverse	Vessel diameter	μm	100	
	Vessel density	# mm^{-2}	5	Scholz et al. (2013)
	Vessel grouping	Type	50	
	Metaphloem diameter*	μm	3	Thomas & de Franceschi (2013)
	Parenchyma type	Type	–	Alfonso et al. (1989)
	Axial parenchyma area	μm2 mm^{-2}	3	Slupianek et al. (2021)
	Fiber area	μm2 mm^{-2}	3	
	Fiber wall thickness	μm	50	Villareal et al. (2025), Scholz et al. (2013)
	Runkel ratio	Adimensional	50	
Tangential	Ray height	μm	25	
	Ray width	μm	25	
	Ray frequency	# mm^{-1}	10	Alfonso et al. (1989)
	Contents	Type	–	
Macerations	Tracheid presence	Type	–	
	Fiber length	μm	50	Scholz et al. (2013)

We identified plant functional types following a two-step process. First, we conducted a mixed discriminant analysis (Hastie & Tibshirani, 1996) supported by ellipses generated from a normal multivariate distribution at a 99% significance level (Fox & Weisberg, 2011), to recognize functional patterns for palms and trees. Second, we delineated tree functional types using a hierarchical cluster analysis with Ward's method (Ward, 1963) and Euclidean metrics (Elmore & Richman, 2001). We validated the number of groups through repeated results from several clustering indices (Charrad et al., 2014), with Marriot's, Ball's, and Trace's indices indicating an optimum of three clusters. We cut the cladograms at a height of 3.5 for Igapó and 2.2 for Terra firme. A permutational multivariate analysis of variance (Anderson, 2001) and the orthogonal contrast method (Nogueira, 2004), as a post-hoc test, were performed to identify significant differences among the plant functional types. Finally, we associated plant functional types with the functional strategies representative of their species: acquisitive, conservative, and intermediate (Lohbeck et al., 2015). A factor analysis of mixed data was performed to identify trade-off trends (Pagès, 2004), and it was complemented with Spearman coefficients to estimate correlations (Liu et al., 2018). On the other hand, we performed linear regressions on quantitative traits to identify trends in relation to wood density, implementing the least square method. Additionally, we used the Wilcoxon test to evaluate significant differences between Terra firme and Igapó forests (Ruxton, 2006). We used R to process data (Venables et al., 2024). The following libraries were employed: FactoMineR (Husson et al., 2020), NbClust (Charrad et al., 2015), factoextra (Kassambara & Mundt, 2020), mda (Hastie et al., 2020), ggplot2 (Wickham et al., 2025), and PERMANOVA (Vicente-Gonzalez & Vicente-Villardon, 2021).

Results

Wood traits of tree species in Terra firme and Igapó fell within similar ranges. However, significant differences were observed in fiber (length and thickness) and ray (width and frequency) traits (Table 3). We excluded palms from trees as a plant functional type (PFT) in Terra firme through discriminant mixed analysis (Fig. 1), which explained 39.2% of the variance and showed no overlap between ellipses. The

Table 3. Wilcoxon test for wood traits of dominant species in tropical moist forests of Terra firme and Igapó. Values correspond to means and standard deviations. Acronyms: * – $\alpha < 0.1$; ** – $\alpha < 0.05$; *** – $\alpha < 0.01$

Trait	Igapó	Terra Firme	p-value
Fiber length (μm)	629.04 ± 77.95	719.67 ± 104.14	0.007***
Fiber wall thickness (μm)	2.79 ± 1.40	3.24 ± 0.92	0.016**
Ray height (μm)	220.20 ± 90.08	302.39 ± 193.46	0.218
Ray width (μm)	19.59 ± 21.36	26.84 ± 17.74	0.021**
Ray frequency (# mm^{-1})	18.38 ± 8.63	13.67 ± 7.88	0.087*
Vessel density (# mm^{-2})	23.00 ± 13.04	19.85 ± 16.70	0.144
Vessel diameter (μm)	77.01 ± 13.95	92.78 ± 34.28	0.133
Runkel ratio	0.78 ± 0.40	0.77 ± 0.45	0.850
Fiber area (μm2 mm^{-2})	816522.00 ± 77669.28	822486.81 ± 102707.07	0.512
Axial parenchyma area (μm2 mm^{-2})	97817.18 ± 55518.82	75309.77 ± 68837.13	0.107

strategy of palms was focused on storage and tissue investment, as indicated by high values of parenchyma and fiber traits. Tree species exhibited clustering functional patterns that were consistent with plant functional types in both forests, resulting in three PFTs (Fig. 2, Fig. 3) significantly different (Table S4) and three functional strategies. Intermediate acquisitive PFTs displayed aliform parenchyma, longer fibers, larger vessel diameters, and lower values of wood density. Intermediate conservative PFTs were characterized by banded parenchyma, high values of height and width of rays, high values of vessel density, and intermediate values of wood density. Conservative PFTs were defined by low values of fiber length and thickness, high values of ray frequency, diffuse parenchyma, and higher values of wood density; in some species, tracheids were present, though more common in Igapó than in Terra firme. Trade-offs between hydraulic efficiency and safety paralleled the balance between storage in parenchyma and fiber investment (Table 4, Table 5). From intermediate acquisitive to

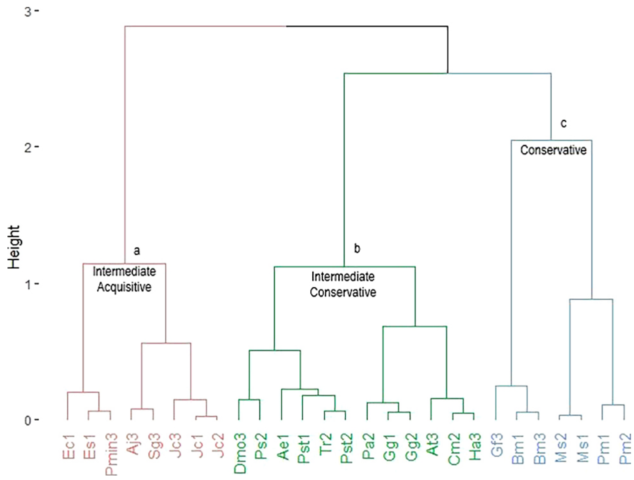

Fig. 2. Cluster dendrogram for PFTs in Terra firme forests. Shifts in letters (a, b, c) indicate significant differences (α < 0.01)

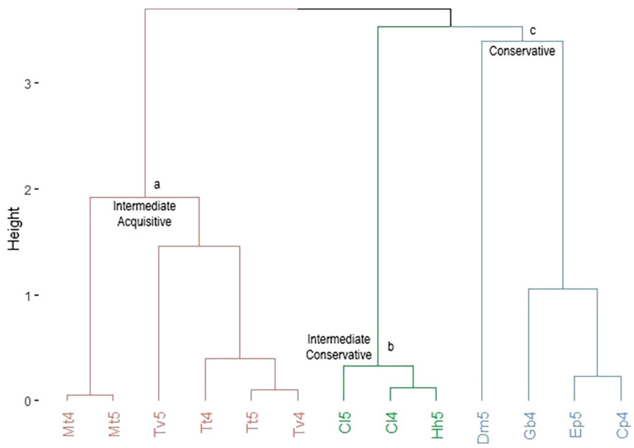

Fig. 3. Cluster dendrogram for PFTs in Igapó forests. Shifts in letters (a, b, c) indicate significant differences (α < 0.05)

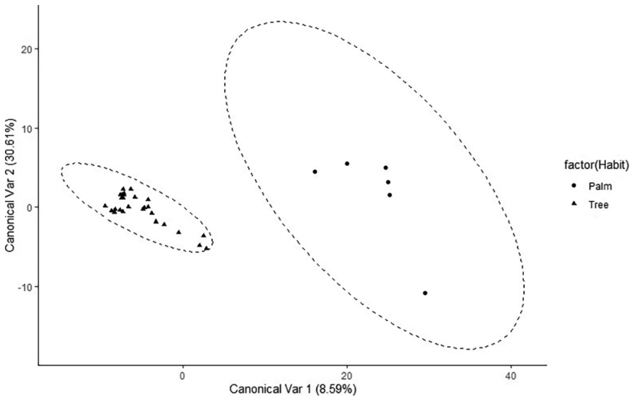

Fig. 1. Mixed discriminant analysis in Terra firme forests

Table 4. Trade-offs correlations for wood traits in Terra Firme. Absolute values for interpreting correlation coefficients: 0–0.2, very low; 0.2–0.4, low; 0.4–0.6, medium; 0.6–0.8, high; 0.8–1, very high. Acronyms: * – α < 0.1; ** – α < 0.05; *** – α < 0.01

	Fiber length	Fiber wall thickness	Ray height	Ray width	Ray frequency	Vessel density	Vessel diameter	Runkel ratio	Fiber area	Parenchyma area	Wood density
Fiber length	1	0.709***	0.515***	−0.190	0.437**	0.031	−0.064	0.312	0.162	−0.125	0.163
Fiber wall thickness		1	0.413**	0.073	0.139	−0.023	0.023	0.485**	0.209	−0.296	−0.043
Ray height			1	0.395**	−0.151	−0.240	0.151	0.095	−0.330*	−0.011	−0.063
Ray width				1	−0.758***	−0.120	0.083	−0.005	−0.400**	−0.157	−0.156
Ray frequency					1	0.040	−0.113	0.139	0.524***	0.001	0.086
Vessel density						1	−0.900***	0.215	0.271	−0.481**	0.436**
Vessel diameter							1	−0.255	−0.264	0.404**	−0.341
Runkel ratio								1	−0.224	0.019	0.423**
Fiber area									1	−0.623***	−0.189
Parenchyma area										1	0.079
Wood density											1

Table 5. Trade-offs correlations for wood traits in Igapó. Absolute values for interpreting correlation coefficients: 0–0.2, very low; 0.2–0.4, low; 0.4–0.6, medium; 0.6–0.8, high; 0.8–1, very high. Acronyms: * – α < 0.1; ** – α < 0.05; *** – α < 0.01

	Fiber length	Fiber wall thickness	Ray height	Ray width	Ray frequency	Vessel density	Vessel diameter	Runkel ratio	Fiber area	Parenchyma area	Wood density
Fiber length	1	0.388	0.615**	0.496*	0.121	−0.179	−0.027	0.070	−0.379	0.220	−0.374
Fiber wall thickness		1	0.482*	0.269	0.369	0.259	−0.235	0.186	0.357	−0.454	−0.078
Ray height			1	0.518	0.256	−0.121	−0.385	−0.118	−0.077	−0.016	−0.456
Ray width				1	−0.334	−0.314	−0.369	−0.018	−0.223	0.320	0.025
Ray frequency					1	0.338	−0.234	0.445	0.569**	−0.704***	−0.146
Vessel density						1	−0.342	−0.034	0.234	−0.441	0.110
Vessel diameter							1	−0.115	−0.181	0.082	−0.269
Runkel ratio								1	0.333	−0.319	0.411
Fiber area									1	−0.852***	−0.071
Parenchyma area										1	0.258
Wood density											1

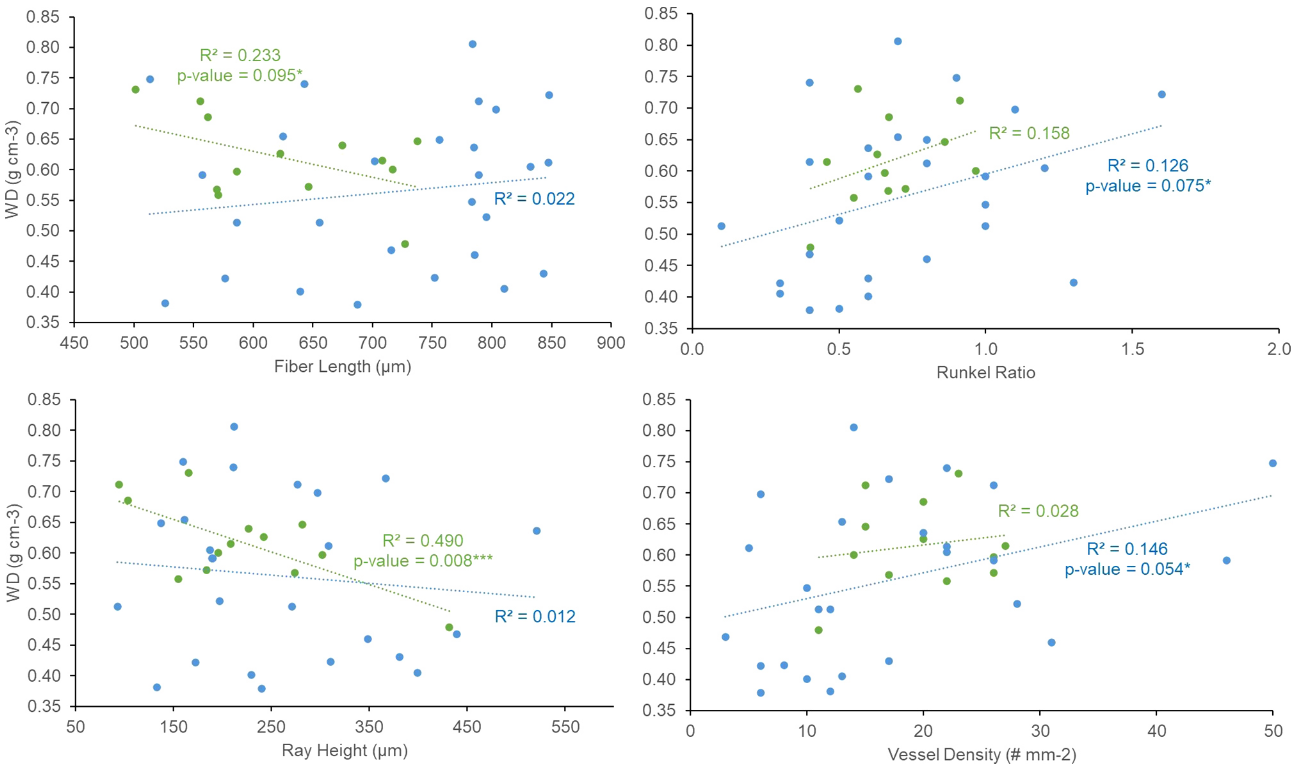

Fig. 4. Relationships between wood density and wood traits. Blue points for Terra firme's species, and green points for Igapó's species. Acronyms: WD, wood density; * – α < 0.1; ** – α < 0.05; *** – α < 0.01

conservative species, trends included increasing axial parenchyma area and decreasing Runkel ratio in fibers (Fig. S2, Fig. S4). Wood-trait trends with respect to wood density were similar in both Terra firme and Igapó forests (Fig. 4). In Igapo, longer fibers and rays were marginally associated with lower wood density (α < 0.1); while in Terra firme, higher values of Runkel ratio and vessel density were marginally associated with higher wood density (α < 0.1). Notably, a wide range of wood-trait values occurred within the same range of wood density.

Discussion

Functional patterns of clustering, strategies and trait trade-offs were similar in Igapó and Terra firme forests in this study, despite significant differences in composition (richness) and structure (trees per hectare) reported by Díaz-C. et al. (2022). Two main ecological statements could explain this behavior. The first is the principle of phylogenetic conservatism (Pyron et al., 2015), which suggests that traits of taxa from the same phylogeny form plant functional types. This principle is supported by our study, as the results for wood traits align with values reported by Macedo et al. (2014) for *Tachigali*, Moutinho et al. (2012) for *Eschweilera*, Koek-Noorman and Westra (2012) for *Guatteria*, Jansen et al. (2002) for *Duroia*, and Thomas and Boura (2015) for the subfamily Arecoideae. However, a few species fell outside the PFTs associated with their taxonomic family. For example, *Copaifera pubiflora* Benth. differed from the *Tachigali* spp. group in ray height, ray width, and axial parenchyma type. Likewise, *Aspidosperma excelsum* Benth. differed from the group of *Couma macrocarpa* Barb. Rodr. and *Himatanthus articulatus* (Vahl) Woodson in vessel diameter and density. The second is the eco-physiological adaptation-to-flooding hypothesis (Parolin et al., 2004), which indicates similarities for species' physiology between Terra firme and flooded forests. This hypothesis is supported by our research, as we found the same quantity and functional strategies for PFTs in Igapó and Terra firme. For instance, intermediate acquisitive strategy includes species similar to those reported by Chazdon et al. (2010) in Costa Rica. The intermediate conservative and conservative strategies include taxa comparable to those reported by Fortunel et al. (2014) in French Guyana. The PFT for palms was an exception in Terra firme, as it was related to investment in height through fiber traits, consistent with findings by Rich (1987) in neotropical palms.

Regarding trade-offs, the shift from hydraulic safety to efficiency (Chen et al., 2025) was parallel to fiber-parenchyma investment (Janssen et al., 2020) in both forests (Méndez-Alonzo et al., 2012). Similarly, the community variance for fiber and hydraulic traits was lower than for parenchyma traits in Terra firme and Igapó, even though parenchyma fractions vary with soil nutrient availability (Morris et al., 2016). These results support our hypothesis of parenchyma-fiber trade-offs (Pratt et al., 2021). On the other hand, wood traits showed similar trends with respect to wood density in Terra firme and Igapó. Nevertheless, our hypothesis that higher fiber traits values correspond to higher wood density was partially supported, as this pattern was observed solely for the Runkel ratio in Terra firme. This result is consistent with the findings reported by Martínez-Cabrera et al. (2012). Furthermore, the fiber wall thickness values obtained in both forests fell within the ranges reported by Alvarado and Terrazas (2023). In contrast, fiber length exhibited a weak inversely proportional trend, with lower values being associated with conservative species (Kiaei & Samariha, 2011). Likewise, vessel density was higher for this PFT, which is characterized by a hydraulic safety strategy (Martínez-Cabrera et al., 2011).

It is important to note that these patterns between wood traits and wood density are valuable for analyzing shifts in aboveground biomass, given the role of wood density in this ecosystem function (Poorter et al., 2017). We think that soft traits, such as fibers, can enhance the understanding of functional tree ecology and the interpretation of plant functional types and their strategies. Additionally, we demonstrated that different values for wood traits can exist within the same range for wood density, indicating a degree of plasticity in a hard trait that has been prioritized as an indicator of functional recovery in tropical forest ecology (Poorter et al., 2021). Therefore, we recommend including wood anatomical traits in future research. This information can be applied to species selection for forest restoration, helping to identify acquisitive and conservative strategies (Zuidema & Lohbeck, 2025). We acknowledge, however, that preparing mountings from increment borer cores is challenging, even with rotary microtomes. Difficulties in controlling the angle of the blade when cutting slices can affect samples and image quality. Nevertheless, this is not a limiting factor for the final measurements, as the flexibility of the software and the experience in trait recognition allow for reliable results. Finally, we highlight that this research addresses a significant knowledge gap concerning palm traits, an ecological component that has not been thoroughly explored in forests and can substantially contribute to the development of functional ecology (Trujillo et al., 2021) in regions where such studies are uncommon.

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