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Structural variation of secondary xylem and acclimation responses of two Atlantic Forest tree species in heterogeneous environments

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Abstract

Biodiversity loss exacerbated by climate change compromises habitat conservation and restoration strategies. Analyzing the functional traits of secondary xylem is a valuable tool for understanding how species respond to environmental conditions. This study aimed to characterize the anatomical structures of the secondary xylem in *Miconia prasina* (Sw.) DC. (Melastomataceae) and *Nectandra membranacea* (Sw.) Griseb. (Lauraceae) and investigate how wood anatomical variations contribute to understanding intraspecific variation in these species across the ombrophilous forest and *restinga* areas. To achieve this, we collected branches from five individuals of each species in both study areas, totaling 20 samples. The secondary xylem samples were subjected to plant anatomy techniques, including transverse, tangential, radial sectioning, staining, and microscopic analysis. We observed low intraspecific variability in the anatomical traits of the secondary xylem of *M. prasina* and *N. membranacea* across different phytophysiognomies. In *M. prasina*, the tangential vessel diameter, wall thickness, and vessel element length were greater in the ombrophilous forest than in the *restinga*. In contrast, *N. membranacea* exhibited functional stability, with conservative traits such as sparse axial parenchyma in both phytophysiognomies, reflecting a strategy focused on safety and water storage. Understanding these variations is essential for predicting species acclimation in heterogeneous environments and contributing to conservation strategies in the face of anthropogenic impacts and extreme climatic events.

Keywords: acclimation strategies; conservation and restoration; ecological anatomy; wood anatomy.

Introduction

The Atlantic Forest is one of the most vulnerable biomes to climate change, with projections indicating increased temperatures and more intense dry periods (Bellard et al., 2014; IPCC, 2022). This biodiversity hotspot features diverse phytophysiognomies, challenging species in fragmented environments (Ribeiro et al., 2009). Ilha Grande, in Rio de Janeiro, exemplifies the ecological complexity of the region, being an environmental protection area with four protected areas (INEA, 2024) and native forests at different successional stages, such as climax ombrophilous forests (Oliveira, 2002; Callado et al., 2009). However, some areas suffer human impacts, such as secondary formations in regeneration and the destruction of restinga areas, without adequate knowledge (Thomazi et al., 2013; Cruz & Nunes-Freitas, 2019). Biodiversity loss, exacerbated by climate change, affects habitat conservation and restoration strategies. Tropical plants are already facing thermal conditions close to their physiological germination limits (Sentinella et al., 2020), and temperatures above 32 °C result in biomass and productivity losses (Sullivan et al., 2020). These climatic stressors may induce structural and functional changes in wood anatomy, affecting xylem tissues and modulating hydraulic performance through environmentally driven adjustments in embolism resistance along precipitation gradients (Schuldt et al., 2016). Understanding these impacts is essential for developing effective conservation and restoration strategies.

Ombrophilous forests and *restinga* ecosystems exhibit contrasting environmental conditions that act as ecological filters influencing plant structure and function, particularly the anatomy of secondary xylem. Ombrophilous forests are characterized by dense canopy cover, reduced solar radiation at ground level, and soils with higher moisture retention, organic matter content, and nutrient availability, resulting in more stable water conditions (Callado & Manão, 2022; Castelar *et al*., 2023; Salomão *et al*., 2020). In contrast, *restinga* ecosystems are coastal environments with sandy, shallow, and nutrient-poor soils, high salinity, intense solar radiation, and low water-holding capacity, leading to frequent drought stress (Scarano, 2002; Matallana *et al*., 2005; Salgado & Vasquez, 2009). These differences in light exposure, water availability, and edaphic properties can influence secondary xylem structure and function. In drier and nutrient-poor environments, plants often develop denser wood, thicker vessel walls, and narrower lumens to increase hydraulic safety and reduce the risk of cavitation (Hacke & Sperry, 2001a; Hacke *et al*., 2001b; Jacobsen *et al*., 2005; Lens *et al*., 2011), while in more favorable conditions, wider vessels and thinner walls may enhance hydraulic efficiency (Loepfe *et al*., 2007; Gleason *et al*., 2016; Li *et al*., 2016). Soil fertility

also affects wood development by modulating growth rates, carbon allocation, and cell wall structure (van Maarschalkerweerd & Husted, 2015; De Bang *et al*., 2021). Therefore, investigating how these environmental parameters affect xylem traits is key to understanding intraspecific functional responses and species acclimation in heterogeneous ecosystems.

Vegetal communities at different successional stages face restrictive environmental conditions that act as environmental filters, limiting survival strategies and influencing species functional traits (Violle *et al*., 2007; Boukili & Chazdon, 2017). In areas with greater solar exposure, high transpiration rates reduce water potential and increase the risk of xylem embolism, leading plants to develop anatomical and hydraulic strategies to optimize water conduction (Tyree & Zimmermann, 2002; Martin-StPaul *et al*., 2017; Simioni *et al*., 2023). In this context, wood density shaped by the organization of secondary xylem cellular elements can serve as a good predictor of plant drought tolerance. Denser woods, with a higher proportion of fibers surrounding the vessels, provide greater resistance to negative xylem pressures and lower susceptibility to embolism (Hacke *et al*., 2001b; Bertolli *et al*., 2015; Oliveira *et al*., 2015; Fu *et al*., 2019). Other xylem vessel traits, such as diameter and wall thickness, vary to optimize both hydraulic efficiency and safety (Loepfe *et al*., 2007; Zanne *et al*., 2010; Lens *et al*., 2011; Gleason *et al*., 2016; Li *et al*., 2016). Furthermore, the thickness of intervessel pit membranes and vessel lumen area contributes to reducing the risk of implosion under negative pressure (Hacke *et al*., 2001b; Jacobsen *et al*., 2005). Investigating the variation of these traits in species growing under contrasting environmental conditions can provide valuable insights into their functional responses and acclimation strategies.

As soil conditions are also a crucial factor for the acclimation of species, insufficient levels of nutrients to fulfill their metabolic functions lead to a deficiency state, triggering physiological responses specific to each element (van Maarschalkerweerd & Husted, 2015; De Bang *et al*., 2021). On Ilha Grande, different phytophysiognomies result in distinct edaphic characteristics that directly influence the species established in the region. According to Salomão *et al*. (2020), soil quality is closely related to its capacity to support essential functions, being mainly influenced by organic matter content and nutrient availability. Organic matter plays a fundamental role in improving soil structure, promoting aggregate formation, water retention, and nutrient cycling. The proper maintenance of these factors ensures natural soil fertility, which is essential for ecosystem sustainability and the continuity of ecological processes.

Ombrophilous forests and *restinga* environments differ markedly in soil properties, water availability, and atmospheric exposure (Salomão *et al.*, 2020), imposing contrasting environmental constraints on plant species occurring in both phytophysiognomies (Castelar *et*

al., 2023). In this context, this study aimed to characterize the anatomical structures of the secondary xylem in *Miconia prasina* (Sw.) DC. and *Nectandra membranacea* (Sw.) Griseb., two tree species that occur in both ombrophilous forest and *restinga* environments on Ilha Grande, Rio de Janeiro, Brazil. We hypothesize that these species exhibit intraspecific variation in wood anatomical traits associated with hydraulic adjustments to each environment, *e.g.*, smaller, shorter, and more frequent vessels, increased vessel grouping, thicker fiber walls, and higher wood density in *restinga* environments, favoring hydraulic safety, in contrast to larger and longer vessels diameters, lower wood density, and higher conductive efficiency in ombrophilous forests (Carlquist, 2001; Hacke & Sperry, 2001a; Hacke *et al*., 2001b; Tyree & Zimmermann, 2002; Swenson & Enquist, 2007; Gleason *et al.*, 2016; Li et al., 2016). Such variation may reflect adaptive strategies to cope with differences in water availability, nutrient content, and light exposure, influencing plant performance and survival in heterogeneous landscapes (Apgaua *et al.*, 2022). Therefore, investigating wood anatomical variability based on hydraulic architecture may provide important insights into the mechanisms underlying the functional adaptation of plant species to distinct environmental constraints.

Materials and Methods

Study Area

This study was conducted on Ilha Grande, on the southern coast of the state, in Ilha Grande Bay, in Angra dos Reis – Rio de Janeiro (23°04'31" – 23°13'36" S; 44°05'27" – 44°22'43" W). Its geographical orientation features a northern face facing the mainland, while the southern face extends toward the ocean. These faces are separated by a prominent mountain range, including the Pedra d'Água and Papagaio Peaks, with altitudes of 1,035 and 982 meters, respectively (Gama *et al*., 2009). Rainfall distribution in the region is uneven, ranging from 1,245 mm to 4,531 mm in hillside areas. The average temperature varies between 20 °C and 26 °C, with extremes reaching 39 °C in summer and 15 °C in winter (Salgado & Vasquez, 2009).

The collections were made in two areas of the Vila Dois Rios region, characterized by distinct phytophysiognomies: ombrophilous forest and *restinga*. The ombrophilous forest is associated with the presence of bodies of water, such as rivers and waterfalls, as well as high humidity conditions, shaded areas, abundant litter, and good water retention in the soil (Callado & Manão, 2022; Castelar *et al*., 2023). The study area in the ombrophilous forest is

located at an altitude of approximately 200 meters and features nutrient-rich soils, clay, silt, and iron (Fe), in addition to a higher sum of exchangeable bases (SB) and potential acidity (Tab. 1; Fig. 1).

The restinga is a coastal ecosystem characterized by harsh environmental conditions, including high light intensity and sodium saturation index (ISNa) but lower cation exchange capacity at pH 7.0, lower organic matter content, and reduced availability of essential nutrients like potassium (K), calcium (Ca), and magnesium (Mg). Regarding microclimatic parameters, the *restinga* shows higher average temperatures and lower relative humidity than the ombrophilous forest (Tab. 1; Fig. 1).

Selection of species

The species were selected based on the floristic survey conducted by Castilhori *et al*. (2025, in press), which identified the most frequent native species in both study areas (ombrophilous forest and *restinga*). Thus, five individuals of each of the following species were selected (Tab. 2): ***M. prasina*** (Melastomataceae) (**HUENFw 1061**) - Commonly known as *pixirico*, this species has a wide geographical distribution across Brazil, occurring in the North (Acre, Amazonas, Amapá, Pará, Rondônia, Roraima, Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Sergipe), Central-West (Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), and South (Paraná) regions. It is found in various environments, including anthropogenic areas, riparian and/or gallery forests, upland forests, seasonal semideciduous forests, ombrophilous (tropical) forests, coastal forests (*restinga*), and rocky outcrop vegetation. Its broad distribution and ecological versatility highlight its importance in distinct Brazilian biomes (Reflora, 2024). ***Nectandra membranacea*** (Lauraceae) (**HUENFw 1060**) - This species, known as *canela branca*, occurs in the North (Acre, Amazonas, Amapá, Pará, Rondônia, Roraima, Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Pernambuco), Central-West (Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo), and South (Paraná, Rio Grande do Sul, Santa Catarina) regions. It inhabits different vegetation formations, including *Caatinga* (strict sense), *Cerrado* (broad sense), riparian and/or gallery forests, upland forests, and seasonal semideciduous forests. Its broad adaptability and presence in various ecosystems emphasize its importance for Brazilian biodiversity (Reflora, 2024).

Analysis of soil conditions

After selecting the study sites, miniature weather stations (Perseptec DHT1400 data loggers) equipped with temperature and relative humidity sensors were installed in each sampling area. These devices recorded data at 2-hour intervals over the course of one year. From the collected data, the absolute mean of each microclimatic parameter was calculated. To assess edaphic variables, a WET-150 sensor (Delta-T Devices Ltd., UK) was used to measure soil electrical conductivity (μS/cm) and temperature (°C). Measurements were taken near each selected individual, and the absolute mean was calculated per species. Soil samples were collected at a depth of 30 cm near the selected individuals using a Dutch auger, following the protocol established by the Brazilian Agricultural Research Corporation (EMBRAPA, 2017). Samples were analyzed by the Fundação Norte Fluminense de Desenvolvimento Regional (FUNDENOR) for porosity, pH, particle size distribution, soil saturation index, moisture content, and concentrations of exchangeable bases.

Wood anatomy

Branch samples were collected from third-order branches with diameters ranging from 2 to 3 cm, from five individuals per species (*M. prasina* and *N. membranacea*) per area (ombrophilous forest and *restinga*), totaling 20 samples. The samples were oriented and sectioned using a sliding microtome (SM2010R, LEICA, Germany) to obtain histological sections in three anatomical planes: transverse, radial and tangential, with thicknesses between 15 and 20 μm (Muñiz & Coradin, 1992). The sections were then clarified in a 50% sodium hypochlorite solution, washed in acidulated water (0.1%), and stained with Astra blue and hydroalcoholic safranin (Safrablau). The material was then dehydrated in an increasing series of ethanol (50% to 100%), immersed in butyl acetate, and mounted on permanent slides with synthetic resin Entellan® (Merck) (Johansen, 1940). This methodology allowed us to assess the following attributes: vessel lumen diameter (VLD), vessel wall thickness (VWT), vessel density (VD), vessel grouping index (VGI), axial parenchyma percentage (APP), radial parenchyma percentage (RPP), fiber percentage (FP), vessel percentage (VP), and total parenchyma percentage (TPP).

We used a maceration methodology to assess wood cellular traits. Fragments of approximately 1 cm were placed in vials containing a 1:1 solution of glacial acetic acid and hydrogen peroxide and incubated at 60 °C for 48 hours or until complete cellular dissociation (Sass, 1951). The material was then rinsed with distilled water, stained with 1% aqueous safranin, and mounted in 50% glycerin to prepare semi-permanent slides. From these

macerated samples, we analyzed cellular traits such as vessel element length (VEL), fiber diameter (FD), fiber lumen diameter (FLD), fiber length (FL), and fiber wall thickness (FWT). For each individual and trait, 25 or 10 microscopic images were acquired using 5×, 10×, or 40× objective lenses.

Tissue percentage

The fractions of cell types in the secondary xylem were quantified by selecting 10 images per individual in the transverse plane (10x objective), totaling 50 images per species. Each image was measured using the Grid Mask tool in Image-Pro Plus software (Media Cybernetics, USA), whereby four cell type categories were considered: axial parenchyma, radial parenchyma, vessels, and fibers. A total of 100 random points were placed on each image, and the number of times each cell type appeared under a point was counted. The percentage of each tissue type was calculated for each image based on the number of points.

Wood density

To determine wood density, we selected two branches from each individual. Fresh volume was measured using the water displacement method (Williamson & Wiemann, 2010) by immersing the samples in a beaker filled with water on a digital scale. The volume was calculated based on the weight of the displaced water (e.g., 1 g = 1 cm^3). The dry mass of the samples was determined after oven-drying at 105 °C for 72 hours. Finally, wood density was calculated using the formula: D = P/V, where D = basic density (g/cm^3), P = dry weight of the wood after reaching a constant value (g), and V = volume of the water-saturated wood until reaching a constant weight (cm^3).

Microscopic analysis

Histological analyses were conducted using 10 slides per individual for both species across different phytophysiognomies. Observations were performed with a bright-field optical microscope (Axioplan, ZEISS, USA) with an attached camera (Moticam Pro 282B, Hong Kong). Cell element measurements and counts were done using Image-Pro Plus software, version 4.0 for Windows (Media Cybernetics, USA). Wood anatomical description and measurement of secondary xylem traits followed the recommendations of the IAWA Committee (1989). The measured traits derived from secondary xylem processing included: vessel density (mm^2), vessel lumen diameter (μm), vessel element length (μm), vessel wall thickness (μm), fiber diameter (μm), fiber lumen diameter (μm), fiber wall thickness (μm),

fiber length (µm), axial parenchyma percentage (%), radial parenchyma percentage (%), fiber percentage (%), vessel percentage (%), total parenchyma percentage (%), and vessel grouping index (VGI), following Carlquist (2001), calculated as: VGI = total number of vessels / total number of groups or solitary vessels. Each solitary vessel counts as 1, and each vessel group in contact counts as 1, regardless of the number of vessels it contains.

Statistical analysis

The anatomical traits of the wood were compared separately for each species between phytophysiognomies (ombrophilous forest vs. *restinga*) using the permutation t-test with the *RVAideMemoire* package (Hervé, 2021). Subsequently, a principal component analysis (PCA of correlation) was performed to examine how the anatomical traits were distributed between phytophysiognomies, utilizing the *vegan* (Oksanen *et al*., 2020) and *psych* (Revelle & Revelle, 2020) packages. To better understand the factors explaining the variation in each anatomical trait, a variance partitioning approach was applied using generalized linear mixed models, following the methodology of Zuur *et al*. (2009). The models were fitted individually for each wood anatomical trait (Rosas *et al*., 2019). Based on this approach, phytophysiognomy type and intra- and interspecific variations were included as nested random factors, while wood anatomical traits were used as response variables in each model.

Result

Anatomical description of wood

Miconia prasina (Sw.) DC. (Melastomataceae)

The results indicate that *M. prasina* exhibits the following anatomical characteristics in the ombrophilous forest and *restinga*, respectively (Fig. 2; Table S1): wood density of 0.59 g/cm³ and 0.53 g/cm³; distinct growth rings marked by thick-walled and radially flattened fibers (Fig. 2A); diffuse porosity with an average vessel frequency of 89/mm² and 123/mm²; solitary and radial multiple vessels with an average length of 416.4 µm and 376.6 µm, tangential diameter of 44 µm and 34.7 µm (Fig. 2A-B); vessel wall thickness of 2.6 µm and 1.8 µm; simple perforation plates (Fig. 2H); Intervascular pits are alternate and polygonal, distinctly bordered (areolate), with included apertures; vessel–parenchyma and ray–vessel pits are opposite and distinctly bordered (areolate), resembling the intervessel pits in size and shape (Fig. 2E); septate fibers with an average length of 580.7 µm and 555.2 µm (Fig. 2G); average fiber diameter of 15.3 µm and 15.5 µm, and lumen diameter of 8.9 µm and 9.1 µm

(Fig. 2H); axial parenchyma mainly scanty paratracheal, occasionally aliform, and uniseriate rays (Fig. 2A–D); rays composed of upright and square marginal cells (Fig. 2F; Fig. S1).

Nectandra membranacea (Sw.) Griseb. (Lauraceae)

Nectandra membranacea exhibits the following anatomical characteristics in the ombrophilous forest and *restinga*, respectively (Fig. 3; Table S1): wood density of 0.45 g/cm³ and 0.39 g/cm³; distinct growth rings marked by thick-walled and radially flattened fibers (Fig. 3A); diffuse-porous non-uniform arrangement with an average vessel frequency of 56/mm² and 53/mm²; solitary and radial multiple vessels with an average length of 526.8 µm and 474.5 µm; tangential diameter of 51.8 µm and 49.2 µm (Fig. 3A-B); vessel wall thickness of 1.6 µm and 1.3 µm; simple and scalariform perforation plates (Fig. 3H); alternate and polygonal intervessel pits (Fig. 3E); fiber-tracheid fibers (>3 µm) septate, with an average length of 772.5 µm and 704.3 µm; average diameter of 16.6 µm and 17.8 µm and lumen of 10.6 µm and 12.6 µm (Fig. 3G); scanty axial parenchyma and uniseriate to biseriate rays (Fig. 3A, C-D); heterogeneous rays (Fig. 3F, Fig. S2).

Variation of wood anatomical traits between phytophysiognomies

For both species, the anatomical traits with significant differences exhibited higher values in the ombrophilous forest compared to the *restinga* (Table 3). *Miconia prasina* exhibited significant differences in the tangential diameter of the vessel, vessel wall thickness, and vessel element length compared to those in the *restinga* (Table 3; Fig. 4D–F), and *N. membranacea* in vessel wall thickness (Table 3; Fig. 4E). No significant differences were found in the other traits between the phytophysiognomies (*M. prasina*: Table 3; Fig. 4A–C, G–O; *N. membranacea*: Table 3; Fig. 4A, D, F–O)

Principal component analysis (PCA)

PCA explained 71.4% of the total variance across the first two axes (Fig. 5; Tab. S2) and revealed the clustering of individuals within the same species. The first axis (explaining 57.3% of the variance) was positively associated with hydraulic safety and water transport efficiency traits, including wood density, vessel frequency, grouping index, vessel wall thickness, fiber wall thickness, radial and total parenchyma percentage, and vessel percentage. The second axis (explaining 14.1%) was positively correlated with vessel tangential diameter and vessel length and negatively associated with mechanical resistance traits such as fiber diameter and lumen.

Variance partitioning

To separate the effects of physiognomy about species on the characteristics of secondary xylem, we performed a variance partitioning analysis, where the proportion of global variance explained by the physiognomy, interspecific, and intraspecific factors varied according to the wood anatomical traits assessed (Tab. 2). Physiognomy accounted for a high percentage (14–82%) of the variation in most of the analyzed traits, such as wood density (WD), tangential vessel diameter (TVD), vessel length (VL), vessel wall thickness (VWT), fiber diameter (FD), fiber lumen (FL), fiber wall thickness (FWT), axial parenchyma percentage (APP), and radial parenchyma percentage (RPP). The interspecific factor also proved significant, explaining (17–85%) of the variation in traits such as vessel frequency (VF), grouping index (GI), fiber length (FL), fiber percentage (FP), vessel percentage (VP), and total parenchyma percentage (TPP). In contrast, the intraspecific factor did not explain any variation in the analyzed wood anatomical traits (Fig. 6).

Soil and microclimatic condition analysis

Microclimatic variables did not show statistically significant differences between the *restinga* and forest areas (Table 1). In contrast, some edaphic conditions varied significantly between these areas. The forest soil exhibited higher clay and silt content, which confers greater water retention capacity and electrical potential compared to the *restinga* soil. Additionally, this area showed higher mean values of organic matter, sum of exchangeable bases, and cation exchange capacity (CEC), indicating greater availability of ions, especially K^{+}, Ca^{2+}, Mg^{2+}, and Fe^{2+}. Conversely, the *restinga* soil presented lower acidity (higher pH) and higher Na^{+} concentration.

Discussion

This study revealed low intraspecific variability in the secondary xylem anatomical traits of *Miconia prasina* and *Nectandra membranacea* across contrasting phytophysiognomies (ombrophilous forest and *restinga*). In *M. prasina*, individuals from the ombrophilous forest exhibited slightly higher tangential vessel diameters, cell wall thickness, and vessel element length compared to those from the *restinga*, indicating moderate anatomical adjustments mainly associated with hydraulic efficiency. Conversely, *N. membranacea* showed strong conservatism in taxonomic features, such as scanty axial parenchyma in both environments, suggesting a stable functional strategy centered on water security and storage (Borchert &

Pockman, 2005). The overall low intraspecific variation observed for both species suggests a limited influence of environmental heterogeneity on secondary xylem structure. However, this apparent anatomical stability does not necessarily indicate the absence of acclimative responses. These species may adjust their functional mechanisms through other anatomical or physiological attributes not assessed in this study, such as leaf structural or physiological traits, supporting acclimation to contrasting edaphic and microclimatic conditions, as proposed by Wyka et al. (2022).

The results of this study align with previous works (Wheeler *et al.*, 2007; Dória *et al*., 2016; Simioni *et al*., 2023; Castelar *et al*., 2023), which highlight similar resource utilization strategies by plant species in contrasting habitats. These strategies reflect the plant's ability to maintain relatively stable functional mechanisms despite distinct environmental conditions, supporting the idea proposed by Abrams *et al*. (1994) that specific adaptations enable species to optimize resource use, ensuring their survival and performance in ecologically diverse environments.

Miconia prasina and *N. membranacea* displayed distinct anatomical differences in the secondary xylem, including vessel organization, fiber types, wall composition, and growth ring definition, aligning with previous descriptions (Welle & Koek-Noorman, 1981; Heerdt & de Melo Jr., 2016). *Miconia prasina* shows distinct growth rings, solitary and radial vessels, simple perforation plates, and linear aliform axial parenchyma. *Nectandra membranacea* shows distinct growth rings, diffuse-porous vessels, and uniseriate or biseriate rays. Growth ring analysis helps investigate environmental changes and reconstruct the historical dynamics of ombrophilous and *restinga* regions (Blagitz *et al*., 2019; Marcelo-Peña *et al*., 2020). These anatomical features are essential for taxonomic, phylogenetic, and ecological studies, aiding species classification and understanding evolutionary relationships (Baas, 1982; Dickison, 2000; Carlquist, 2001). Furthermore, the rapid pace of climate change raises concerns, suggesting significant alterations may occur before functional responses are observed (Melo *et al*., 2015; Aguiar *et al*., 2017). Integrating anatomical analysis with existing literature enhances our understanding of the interactions between taxonomic, climatic, and ecological factors in plant communities.

Our results showed low variation in the anatomical traits of the wood in *M. prasina* and *N. membranacea* across the different phytophysiognomies of the Atlantic Forest. *Miconia prasina* individuals in the ombrophilous forest exhibited increased cell types (e.g., vessel tangential diameter, vessel element length, and vessel wall thickness) compared to individuals in the *restinga*. This increase in cellular growth may reflect the higher water availability in

the ombrophilous forest, allowing individuals to develop structures for greater water conduction efficiency. The individuals from the *restinga*, an environment characterized by high temperatures and scarce water resources, exhibit structures adapted for hydraulic safety. These findings suggest that these variations may be linked to strategies plants adopt to prevent embolism, an essential selective pressure (Loepfe *et al*., 2007; Zanne *et al*., 2010; Lens *et al*., 2011; Gleason *et al*., 2016; Li *et al*., 2016). Anatomical and hydraulic strategies, such as reducing vessel diameter, increasing vascular element frequency, and decreasing vessel element length, aim to minimize embolism while improving water conduction safety. These mechanisms are essential for maintaining the functional integrity of plants in contrasting environments (Hacke & Sperry, 2001a; Baas *et al*., 2004).

Soils may also explain this anatomical variation, as the ombrophilous forest showed significantly higher levels of clay, silt, organic matter, carbon, cation exchange capacity (CEC), and base saturation, as well as elevated concentrations of Ca, Mg, and K compared to the *restinga*. As highlighted by Costa *et al.* (2020), "the organic fraction contributed from 32% to 84% of the CEC, depending on the soil studied, whereas the mineral fraction contributed from 24% to 67%," further emphasizing that "this contribution is extremely important for nutrient retention and supply to plants." Thus, soils richer in clay and organic matter, such as those in the ombrophilous forest, tend to retain and make available water over prolonged periods, increasing water availability, as well as essential cations such as Ca^{2+}, Mg^{2+}, and K^{+}. These edaphic conditions may partly explain the anatomical patterns observed in *M. prasina*, which exhibits larger vessel diameters, longer vascular elements, and thicker walls, reflecting strategies that favor hydraulic efficiency in environments with greater water and nutrient availability.

The variation in vessel wall thickness in *N. membranacea* among phytophysiognomies shows greater thickness in individuals from the ombrophilous forest compared to those from the *restinga*. Vessel wall thickness contributes to the structural resistance of plants, reinforcing narrower vessels against hydraulic tensions (Hacke & Sperry, 2001a; Hacke *et al*., 2001b; Cochard *et al*., 2004; Jacobsen *et al*., 2007). Our results suggest that the high proportion of fibers associated with vessels may enhance resistance to water stress, preventing their implosion (Jacobsen *et al.*, 2005; 2007). Although the literature associates thinner vessel walls with environments of low water availability, we suggest that this pattern is related to vessel diameter. Da-Silva & Melo Júnior (2017) observed that wood anatomical traits remained consistent among populations, whereas leaves exhibited greater variation.

The collection area in the *restinga* resulted from a restoration process, where intraspecific plant variability depends on resource availability, environmental predictability, and species' response time to changes (Alpert & Simms, 2002; Vázquez *et al*., 2017). Studies on functional traits typically focus on spatial variations between environments, often overlooking changes throughout an individual's life cycle (Fonti *et al.*, 2010). In this context, secondary xylem anatomical traits tend to be more stable than leaf traits due to their higher heritability, although they still exhibit plasticity in response to edaphic and environmental factors (De Kroon *et al.*, 2005). As a future perspective, we propose jointly evaluating wood and leaf traits to better understand species acclimation mechanisms and investigate the *trade-off* between these tissues, identifying the most relevant traits for plant resistance and hydraulic efficiency.

The present study characterized the anatomical structures of the secondary xylem of *Miconia prasina* and *Nectandra membranacea*, revealing that intraspecific variation of these species in tropical rainforests and *restinga* is limited. This pattern suggests greater functional stability of the wood under contrasting environmental conditions. Understanding this variability is essential for assessing species acclimation to heterogeneous environments, providing insights for conservation strategies in the face of anthropogenic impacts and extreme climatic events. Additionally, the results reinforce the relevance of xylem anatomical traits for ecological studies, highlighting their role in understanding species' adaptive strategies. These findings highlight the importance of integrating multiple anatomical features to advance understanding of species' acclimatization strategies.

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Authors' Contributions

Amanda S. Victorino - Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review and editing; Priscila F. Simioni - Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review and editing; Supervision; Laís A. Bezerra - Formal analysis, Investigation, Methodology, Writing – original draft; Igor Araújo - Formal analysis,

Investigation, Methodology, Writing – original draft; Nicolly Bautz - Formal analysis, Investigation, Methodology; Maura Da Cunha - Conceptualization, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review and editing; Supervision, Funding acquisition, Project administration

Conflict of Interest

The authors declare that they have no conflicts of interest.

Data Availability Statement

Datasets related to this article will be available upon request to the corresponding author.

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Supplementary Material

The following online material is available for this article:

Table S1 - Mean values of quantitative wood anatomical traits of Miconia prasina and Nectandra membranacea in ombrophilous forest and restinga areas of the Atlantic Forest.

Table S2 - Eigenvalues of the functional traits of wood from tree species in phytophysiognomies (restinga and ombrophilous forest areas of the Atlantic Forest).

Figure S1 - Comparative histology of the secondary xylem of Miconia prasina in restinga and ombrophilous forest areas of the Atlantic Forest.

Figure S2 - Comparative histology of the secondary xylem of Nectandra membranacea in restinga and ombrophilous forest areas of the Atlantic Forest.

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Table and Figure Captions

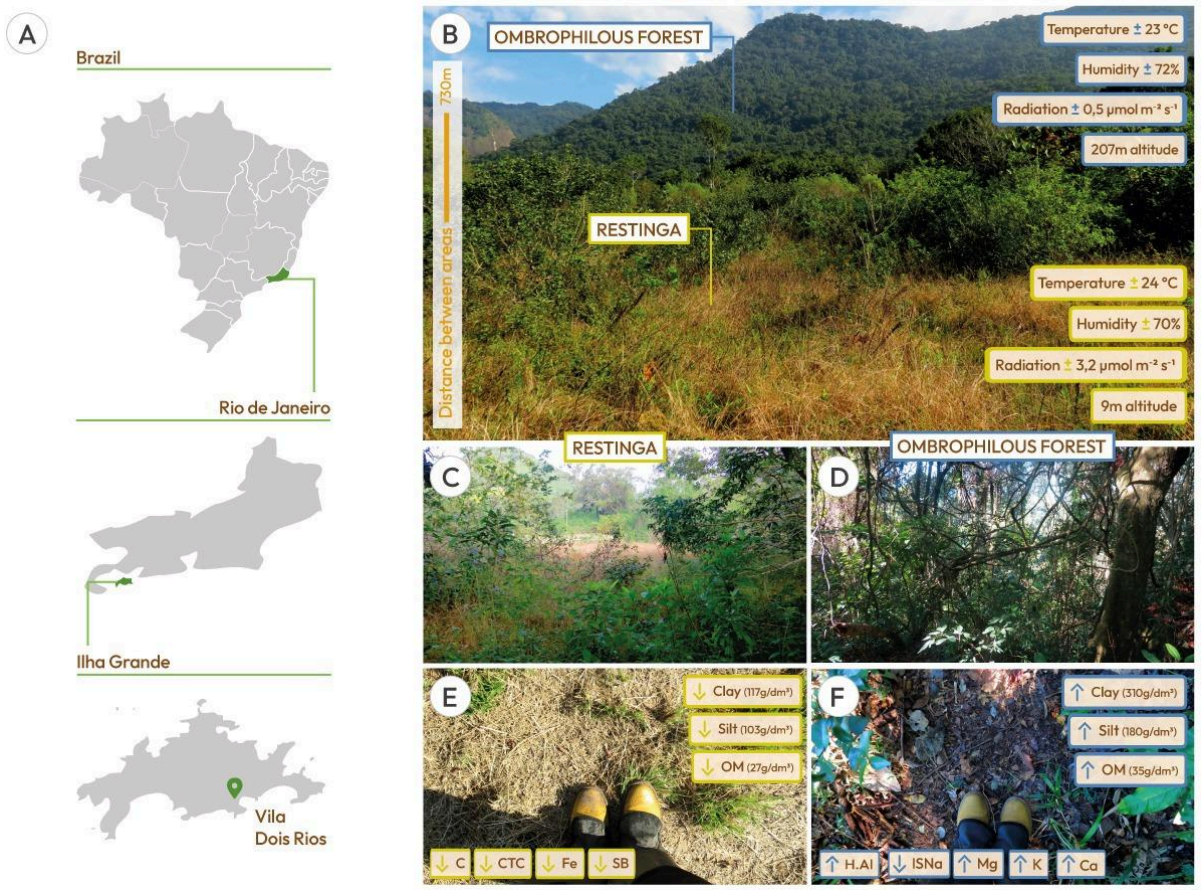

Figure 1 - Map highlighting Vila Dois Rios, the location of the study areas on Ilha Grande, Angra dos Reis, RJ (A). Microclimatic parameters of the study areas (B). *Restinga* vegetation (C) and ombrophilous forest vegetation (D). Edaphoclimatic parameters of the *restinga* (E): Clay (%), Silt (%), OM (organic matter, g/kg), CEC (cation exchange capacity at pH 7.0, $cmol_a/kg$), and SB (sum of exchangeable bases, $cmol_a/kg$). Edaphoclimatic parameters of the ombrophilous forest (F): Clay (%), Silt (%), OM (organic matter, g/kg), V (base saturation index, %), m (aluminum saturation index, %), ISNa (sodium saturation index, %), and SB (sum of exchangeable bases, $cmol_a/kg$).

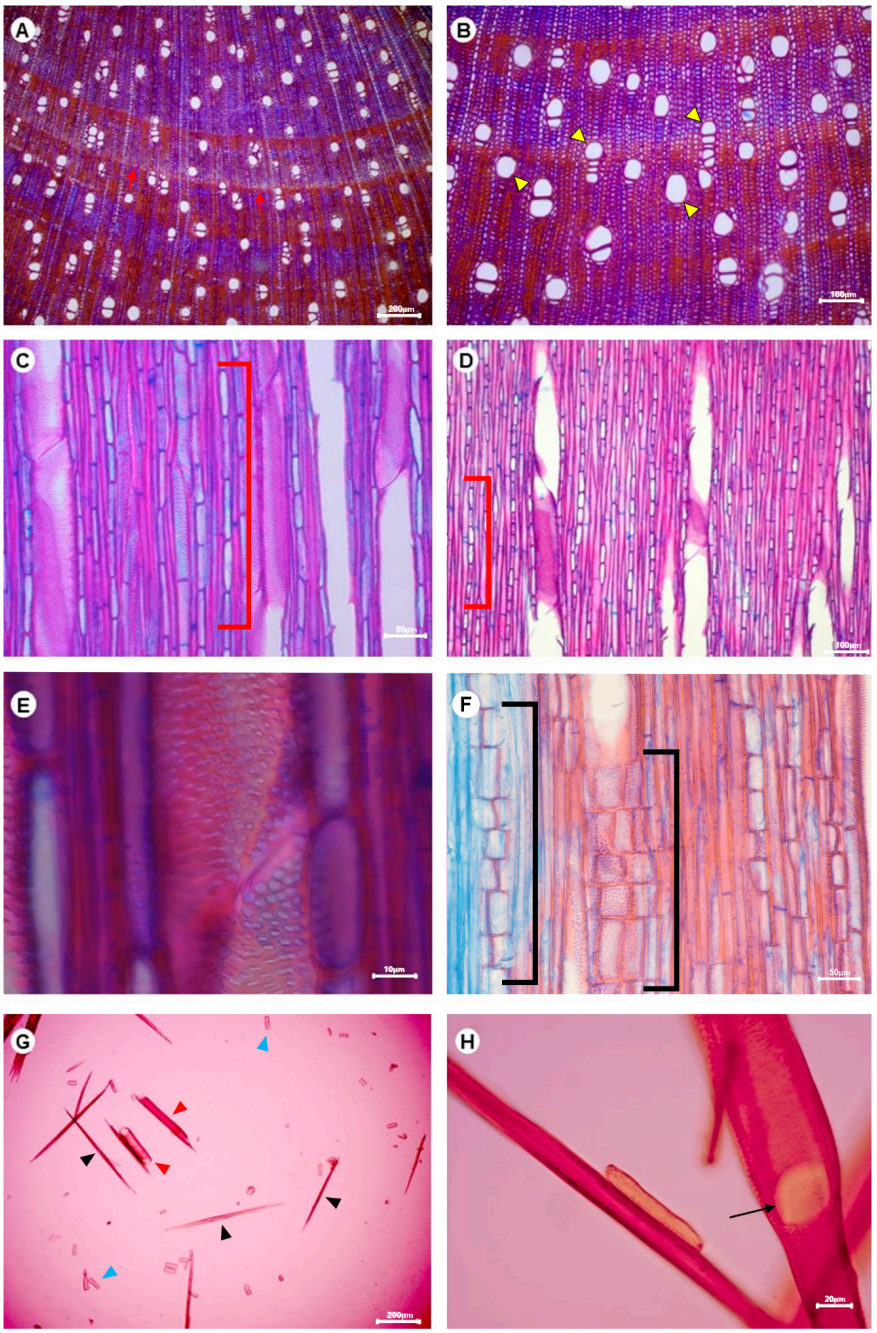

Figure 2 – Histological sections of secondary xylem of *Miconia prasina*. A-H: Light microscopy. A e B: Cross sections, showing the distribution and variations in the shape of the vessels (A: Red arrow) (B: Yellow arrowheads) and axial parenchyma. C e D: Tangential longitudinal section showing the uniseriate ray parenchyma (Red parentheses). E: Tangential longitudinal section showing vestured intervessel pits. F: Radial longitudinal section showing the rays (Black parentheses). G e H: Macerations showing vessel elements and simple perforation plates. (Black arrow), fiber (Black arrowheads) and parenchyma (Blue arrowhead).

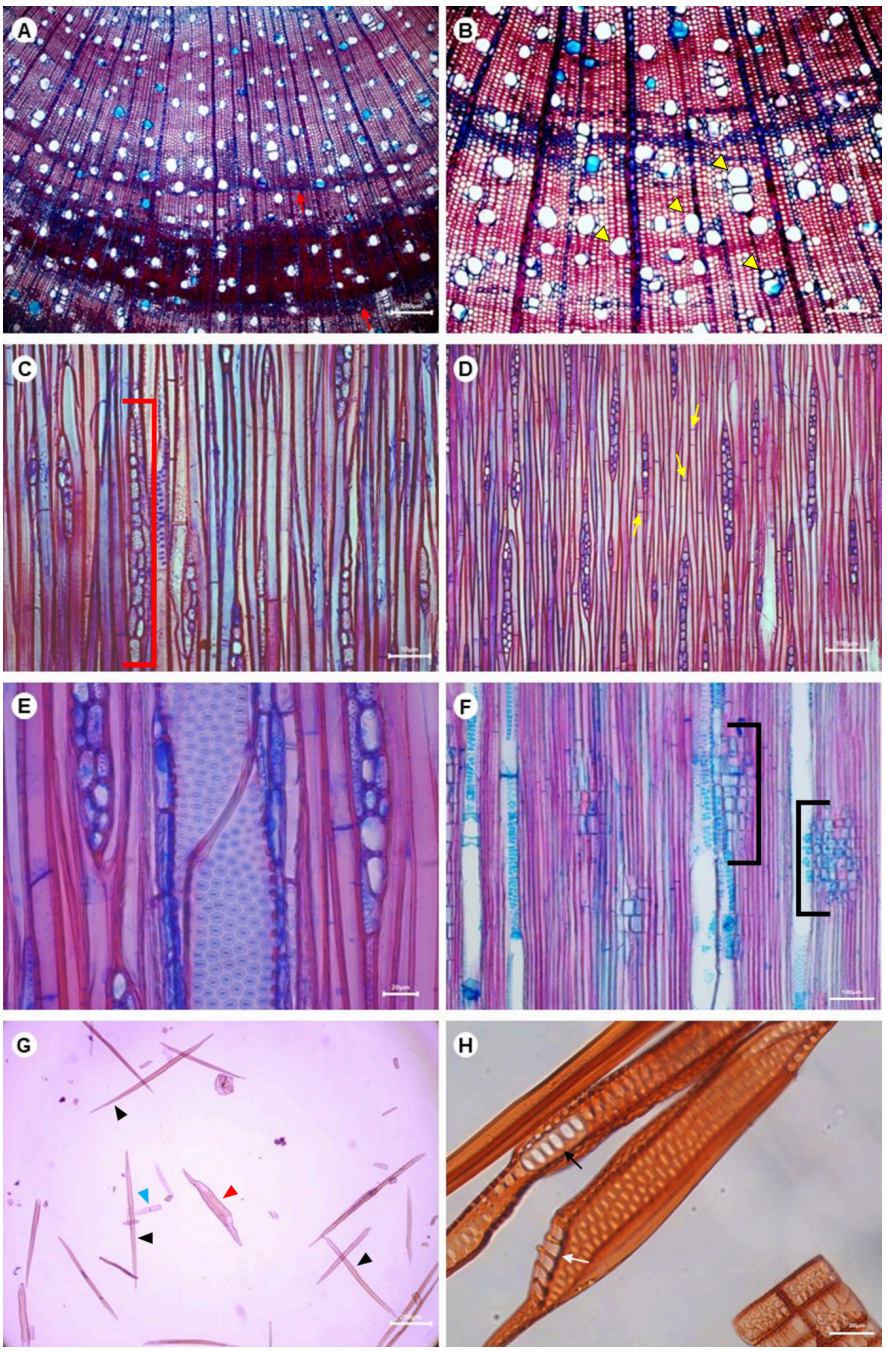

Figure 3 – Histological sections of secondary xylem of *Nectandra membranacea.* A-H: Light microscopy. A e B: Cross sections, showing the distribution and variations in the shape of the vessels (A: Red arrow) (B: Yellow arrowheads) and axial parenchyma. C: Tangential longitudinal section showing the uniseriate and biseriate ray parenchyma (Red parentheses). D showing septate fiber (Yellow arrow). E: Tangential longitudinal section showing vestured intervessel pits. F: Radial longitudinal section showing the rays (Black parentheses). G e H: Macerations showing vessel elements and simple (Black arrow) and scalariform (White arrow) drilling plates, fiber (Black arrowheads) and parenchyma (Blue arrowhead).

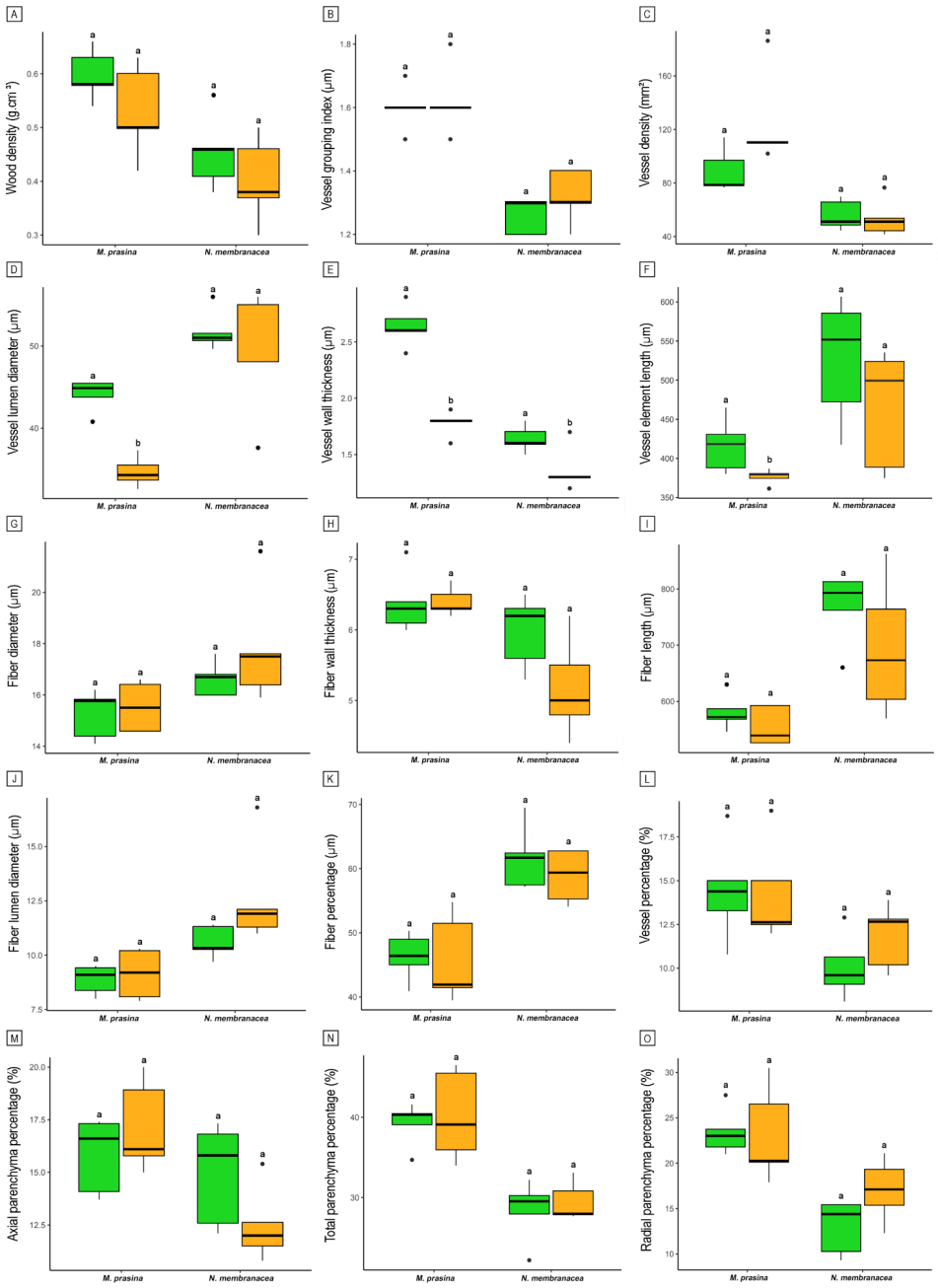

Figure 4 - Box plots representing the variation in the anatomical traits of wood from woody species between the Atlantic Forest phytophysiognomies. The boxplot shows the medians and the upper and lower quartiles; different lowercase letters indicate significant differences (permutation T-test). Green boxes represent the ombrophile forest and beige boxes represent the *restinga*.

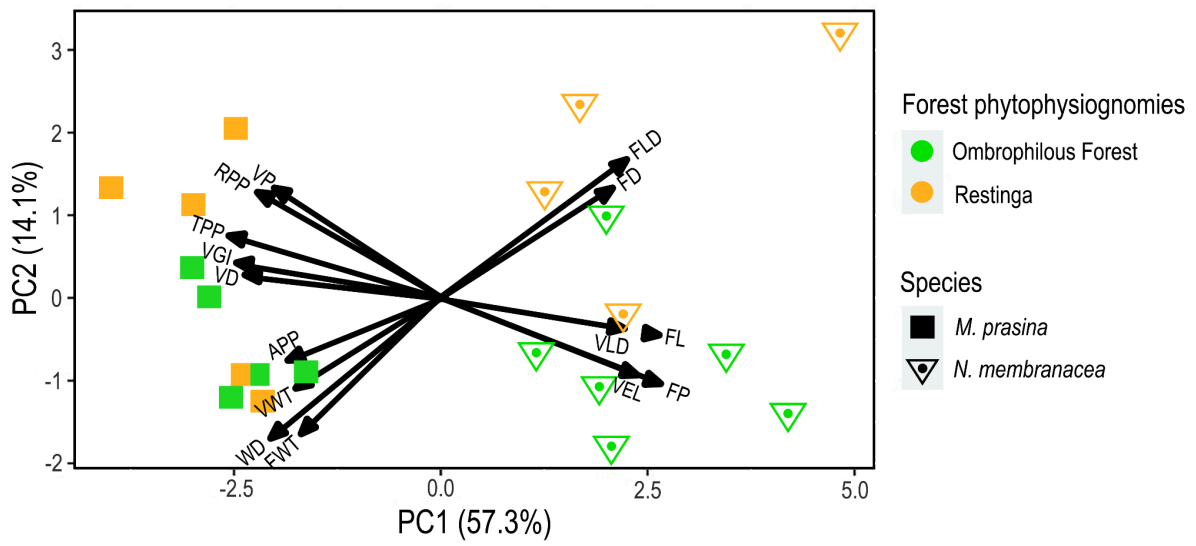

Figure 5 – Principal component analysis based on the distribution of the anatomical traits of wood from woody species across the Atlantic Forest phytophysiognomies. Legend: Wood density (WD), Vessel density (VD), Vessel grouping index (VGI), Vessel lumen diameter (VLD), Vessel element length (VEL), Vessel wall thickness (VWT), Fiber diameter (FD), Fiber lumen diameter (FLD), Fiber length (FL) Fiber wall thickness (FWT), Axial parenchyma percentage (APP), Radial parenchyma percentage (RPP), Fiber percentage (FP), Vessel percentage (VP), Total parenchyma percentage (TPP).

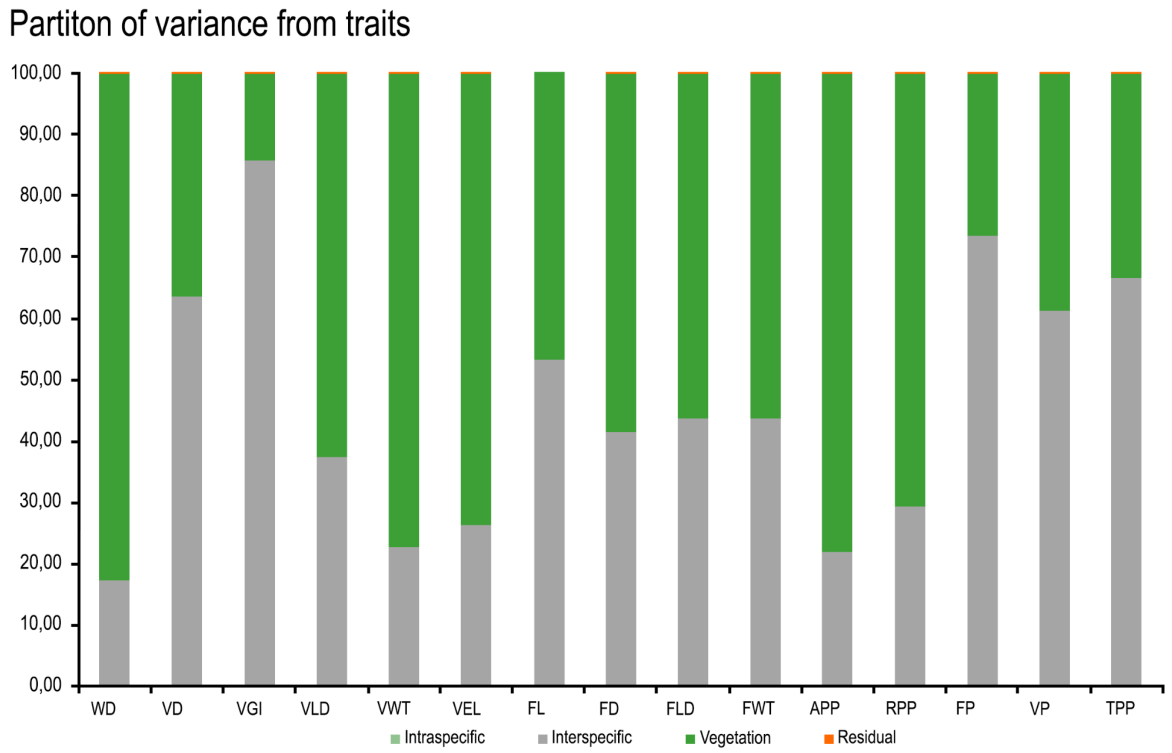

Figure 6 – Partition of variance for secondary xylem characteristics of co-occurring woody species in Atlantic Forest phytophysiognomies. Legend: Decomposition of the variance of the anatomical traits of secondary xylem at different ecological scales in vegetation levels (dark green bars), interspecific (gray bars), intraspecific (light green bars), and residual error (orange bars) for: Wood density (WD), Vessel density (VD), Vessel grouping index (VGI), Vessel lumen diameter (VLD), Vessel element length (VEL), Vessel wall thickness (VWT), Fiber diameter (FD), Fiber lumen diameter (FLD), Fiber length (FL), Fiber wall thickness (FWT) Axial parenchyma percentage (APP), Radial parenchyma percentage (RPP), Fiber percentage (FP), Vessel percentage (VP), Total parenchyma percentage (TPP).

Table 1: Physical-chemical properties of the soil in the study areas. Mean values followed by the standard deviation. *Represents a significant difference with a 95% confidence interval (p); OM: Organic matter; CEC: Cation exchange capacity at pH 7.0; SB: Sum of exchangeable bases; V: Base saturation index; m: Aluminum saturation index; ISNa: Sodium saturation index.

Edaphoclimatic Parameters	Areas		
	Restinga	Ombrophilous Forest	P-value
Temperature	24.29±1.61	23.34±0.50	0.259
Humidity	70.61±2.15	72.64±1.14	0.09732
Soil temperature	25.28±1.43	23.44±1.56	0.08248
Radiation	3.26±5.06	0.56±0.82	0.02966 *
Electrical conductivity	1761.52±595.67	1368.20±463.20	0.09633
Clay (g/dm^3)	117.62±70.64	310.86±72.9	0.001166 *
Silt (g/dm^3)	103.30±70.53	180.89±29.27	0.01107 *
pH	4.88±0.10	4.78±0.19	0.1079
S.SO^4 (mg/dm^3)	2.86±1.57	6.74±4.09	0.05502
P (mg/dm^3)	14.75±17.50	3.25±1.21	0.401
K (mmolc/dm^3)	0.57±0.06	1.23±0.07	0.002141 *
Ca (mmolc/dm^3)	4.85±1.37	12.04±7.24	0.002331 *
Mg (mmolc/dm^3)	1.99±0.48	6.81±2.48	0.0005828 *
Al (mmolc/dm^3)	5.82±1.61	7.15±2.38	0.2086
H.Al (mmolc/dm^3)	37.16±6.68	59.68±5.76	0.0005828 *
Na (mmolc/dm^3)	0.58±0.05	0.55±0.24	0.561
C (g/dm^3)	15.75±1.62	20.26±2.53	0.004079 *
MO (g/dm^3)	27.15±2.80	34.93±4.37	0.004079 *
CTC (mg/dm^3)	45.43±6.77	80.33±9.48	0.0005828 *
SB (mg/dm^3)	8.014±1.64	20.64±9.66	0.002141 *
V (%)	18.39±5.04	24.85±8.62	0.09732
m (%)	42.58±9.50	29.27±12.48	0.05303
ISNa (%)	1.32±0.31	0.77±0.28	0.01393 *
Fe (mg/dm^3)	72.74±29.38	118.54±24.31	0.01107 *
Cu (mg/dm^3)	1.12±1.12	0.41±0.32	0.1282
Zn (mg/dm^3)	4.82±4.28	2.54±1.25	0.9015
Mn (mg/dm^3)	8.37±3.40	11.93±3.95	0.1282
B (mg/dm^3)	0.21±0.03	0.24±0.05	0.4057

Table 2: Morphological and ecological characteristics of *Miconia prasina* and *Nectandra membranacea* in restinga and ombrophilous forest areas of the Atlantic Forest.

Species	*Miconia prasina*		*Nectandra membranacea*	
Area	Restinga	Forest	Restinga	Forest
Coordinates	52318365° W044.19066°	523.18144° W04419466°	52318365° W044.19066°	523.18144° W04419466°
Species height	1.8 - 3	3.5 - 6	2.0 - 6	4.5 - 9
Growth habit	Shrub - Small tree	Tree	Small tree	Tree
Diameter at Breast Height	NA	8.5 - 25.3	3 - 18	15 - 107
Predation	Low - High	Low - Medium	Low	Low

Table 3: Mean values (min–max) of quantitative wood anatomical traits of *M. prasina* and *N. membranacea* co-occurring in restinga and ombrophilous forest environments in the Atlantic Forest. Different letters indicate significant differences between phytophysiognomies within each species; p-values indicate differences based on a permutation t-test.

Traits/species	*Miconia prasina*			*Nectandra membranacea*		
	Restinga	**Ombrophilous Forest**	***p-value***	**Restinga**	**Ombrophilous Forest**	***p-value***
Wood density ($g \cdot cm^{-3}$)	0.53[a] (0.42-0.63)	0.59[a] (0.54–0.66)	0.20	0.40[a] (0.30–0.50)	0.45[a] (0.38–0.56)	0.39
Vessel grouping index (µm)	1.62[a] (1.50–1.80)	1.60[a] (1.50–1.70)	1	1.32[a] (1.20–1.40)	1.26[a] (1.20–1.30)	0.37
Vessel density (mm^2)	123.9[a] (102.0–186.3)	88.9[a] (76.76–114.08)	0.07	53.5[a] (41.7–76.6)	56.0 (44.5–69.9)	0.84
Vessel lumen diameter (µm)	34.7[a] (32.6–37.3)	44.0[b] (40.8–45.4)	0.02	49.2[a] (37.6–56.0)	51.8[a] (49.7–56.0)	0.58
Vessel wall thickness (µm)	1.80[a] (1.60–1.90)	2.64[b] (2.4–2.9)	0.008	1.35[a] (1.2–1.7)	1.63[b] (1.50–1.80)	0.03
Vessel element length (µm)	376.6[a] (361.5–386.9)	416.4[b] (380.2–464.8)	0.016	474.5[a] (374.8–585.6)	526.8[a] (417.7–606.8)	0.32
Fiber diameter (µm)	15.53[a] (14.6–16.6)	15.27[a] (14.1–16.2)	0.49	17.79[a] (15.9–21.6)	16.62[a] (16.0–17.6)	0.38
Fiber wall thickness (µm)	6.41[a] (6.2–6.7)	6.39[a] (6.0–7.1)	1	5.19[a] (4.40–6.20)	6.01[a] (5.3–6.5)	0.09
Fiber length (µm)	555,22[a] (525,6–592,5)	580,74[a] (546,2–629,9)	0.17	704,33[a] (569,6–862,3)	772,46[a] (660,3–833,8)	0.33
Fiber lumen diameter (µm)	9,13[a] (7,9–10,3)	8,89[a] (8,0–9,5)	0.55	12,63[a] (11,0–16,8)	10,61[a] (9,7–11,4)	0.06
Fiber percentage (µm)	45,82[a] (39,5–54,8)	46,32[a] (40,9–50,3)	0.65	58,68[a] (54,1–62,4)	61,66[a] (57,2–69,5)	0.36
Vessel percentage (%)	14,22[a] (12,0–19,0)	14,44[a] (10,8–18,7)	0.67	11,84[a] (9,6–13,9)	10,06[a] (8,1–12,9)	0.21
Axial parenchyma percentage (%)	17,16[a] (15,0–20,0)	15,82[a] (13,7–17,4)	0.25	12,46[a] (10,8–15,4)	15,30[a] (12,1–19,2)	0.09
Total parenchyma percentage (%)	40,22[a] (34,0–46,5)	39,22[a] (34,7–41,6)	0.72	29,50[a] (27,7–33,1)	28,42[a] (22,2–32,2)	0.64
Radial parenchyma percentage (%)	23,06[a] (17,9–30,5)	23,40[a] (21,0–27,5)	0.82	17,04[a] (12,3–21,1)	12,96[a] (9,3–15,4)	0.11

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