



Functional diversity in an alluvial atlantic forest

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Abstract

Atlantic Forest alluvial ecosystems experience strong environmental filtering driven by seasonal flooding and hydrological variability, shaping their structure and functioning. This study investigated how leaf and demographic traits organize functional groups and structure functional diversity in an 11.5-ha urban fragment in Guarapuava, Paraná, southern Brazil. We surveyed 103 permanent plots (1.03 ha), assessing 34 species based on six traits (specific leaf area – SLA, leaf length – LL, leaf dry matter content – LDMC, leaf thickness – LT, mortality rate (M), and relative growth rate (RGR)). Functional groups were identified using Ward's clustering and PCoA, group comparisons were tested using Generalized Linear Models (GLMs), and functional diversity was assessed with FRic, FEve, FDiv, FDis, and RaoQ indices. The community was dominated by *Gymnanthes klotzschiana*, *Ligustrum lucidum*, and *Matayba elaeagnoides*. Clustering revealed four coherent functional groups along the acquisition–conservation axis. The PCoA explained 64.64% of trait variation, highlighting the coexistence of acquisitive species (high SLA, elevated mortality) and conservative species (thicker leaves, reduced mortality), with partial overlap among groups and complementary niches. Overall, the community maintained moderate to high functional diversity (FRic=4.62; FEve=0.67; FDiv=0.79; FDis=1.33; RaoQ=2.71). We conclude that both functional redundancy and differentiation underpin the resilience of this system under hydrological variability and anthropogenic disturbance. We propose prioritizing acquisitive species in early restoration phases and conservative ones in advanced stages to optimize resource-use efficiency and ensure long-term ecosystem stability.

Keywords Conservation and restoration · Demographic rates · Ecological strategies · Forest structure · Functional groups · Leaf functional traits

Introduction

The Brazilian Atlantic Forest is recognized as one of the most biodiverse biomes worldwide, harboring numerous endemic species and a wide array of unique ecosystems. Listed among the 25 global biodiversity hotspots, this biome combines extraordinary biological richness under intense anthropogenic pressure, mainly resulting from forest fragmentation, agricultural expansion, and urbanization (Londe et al. 2020). Within this ecological mosaic, the Mixed Ombrophilous Forest (MOF) occupies a strategic position due to its role in hydrological regulation, geomorphological stability, and regional biodiversity maintenance. The importance of these functions is particularly evident in the context of global debates on ecosystem services, as shifts in species composition—including the introduction of exotic species—may alter the provision of these services, ultimately affecting processes such as water cycling, soil fertility, and landscape stability (Castro-Díez et al. 2021).

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Among the different formations of the MOF, alluvial forests stand out, occurring in environments periodically saturated by seasonal flooding. These conditions impose intense abiotic filters, restricting the pool of species able to establish and favoring specific adaptive strategies. Moreover, alluvial forests perform critical ecological functions, including water resource protection, erosion control, nutrient flux regulation, and providing habitats for a wide array of plant and animal species (Missio et al. 2020). Despite their ecological relevance, coupled with their vulnerability to climate change and anthropogenic pressures, the functional processes structuring their tree communities remain insufficiently understood. Most studies in the Atlantic Forest have focused on slope and highland forests, whereas the role of functional traits in structuring and maintaining alluvial forests is still underexplored, representing a key knowledge gap (Forgiarini et al. 2015).

In recent years, advances in functional ecology have highlighted how species traits—morphological, physiological, and phenological traits directly linked to species performance—shape community organization and ecosystem resilience (Petisco-Souza et al. 2023; Larsen et al. 2024). Within this framework, functional trait analysis has emerged as a powerful approach to elucidating coexistence mechanisms and species responses to environmental change. In alluvial forests, where resource availability, disturbance frequency, and water saturation vary across temporal and spatial scales, functional traits play a central role in determining species persistence and interaction patterns.

Leaf attributes rank among the most informative traits for such analyses, particularly specific leaf area (SLA) and leaf dry matter content (LDMC), both directly associated with resource-use efficiency and growth strategies (Poorter et al. 2008). Species with high SLA tend to exhibit thin, short-lived leaves that promote high photosynthetic rates, rapid growth, and colonization of gaps or disturbed environments. This acquisitive profile, however, entails greater vulnerability to herbivory, water stress, and higher mortality under adverse conditions (Reich 2014; Wang et al. 2022). In contrast, species with higher LDMC and thicker leaves show slower growth but greater stress resistance and longer leaf lifespan, representing a conservative resource-use strategy (Levine 2016). Beyond leaf traits, demographic traits such as relative growth rate (RGR) and mortality (M) provide complementary insights into species' adaptive strategies. Fast-growing species typically exhibit higher mortality, whereas slow-growing species tend to persist longer, contributing to community stability (Sakschewski et al. 2016; Sun et al. 2022). The interaction among these traits generates a continuous spectrum of strategies, often described as the resource acquisition–conservation axis, which reflects

trade-offs between growth rate and stress tolerance (Reich 2014).

Trait variability is a key mechanism underlying species coexistence, as it promotes niche differentiation and reduces direct competition (Violle et al. 2007). In alluvial forests, such variability may be crucial for enhancing resilience to disturbances such as floods, droughts, and extreme climatic events, thereby ensuring ecological process continuity and community stability. Recent evidence indicates that leaf trait variation occurs both among and within species, reflecting species' differentiated responses to environmental gradients. In a study on dominant shrubs of the Pine Barrens, United States, Goud and Roddy (2022) showed that light and water availability accounted for much of the variation in traits such as SLA, LDMC, and leaf thickness, suggesting that both intra- and interspecific plasticity expand adaptive potential in heterogeneous environments. This principle underscores the importance of functional diversity as a key component of ecological stability in tropical alluvial ecosystems.

In this context, our study fills an important gap by investigating how leaf traits and demographic rates are distributed across tree species in an Atlantic alluvial forest. Specifically, we tested three hypotheses: (i) species form distinct functional groups structured along the acquisition–conservation axis; (ii) variation in leaf traits and demographic rates reflects contrasting adaptive strategies that facilitate species coexistence across ecological niches; and (iii) the community exhibits moderate to high functional diversity, indicating wide occupation of functional space despite strong environmental filters and structural dominance, which contributes to its ecological stability and resilience.

Materials and methods

Study area

Data were collected within an 11.5-ha urban fragment of Alluvial Mixed Ombrophilous Forest (AMOF), located in the municipality of Guarapuava, Paraná, Brazil, between 25°23'00" S, 51°30'00" W and 25°22'47" S, 51°29'43" W. The fragment lies within the Cascavel River Basin (CRB), bordered to the north by the Carro Quebrado stream and to the west by the Cascavelzinho River. Elevation ranges between 1000 and 1020 m, under a humid subtropical mesothermal climate (Cfb, Köppen classification). The predominant soils are Brown Latosols with alluvial influence (Rodrigues et al. 2016; Stocki et al. 2024a, b). The land-use history indicates anthropogenic disturbances, including the deposition of urban waste through surface runoff

(Watzlawick et al. 2021) and selective logging of commercially valuable species.

Vegetation sampling

The tree community was inventoried in 103 permanent 10×10 m plots (100 m² each), totaling 1.03 ha in total. Community structure was characterized using species relative density (DR), relative dominance (DoR), and relative frequency (FR) (Freitas and Magalhães 2012). For functional analyses, we considered the species with the highest importance value (IV), calculated as $IV = (DR + DoR + FR)/3$.

Collection and measurement of functional traits

We evaluated six functional and demographic traits reflecting resource-use efficiency and biomass allocation: specific leaf area (SLA), leaf length (LL), leaf dry matter content (LDMC), leaf thickness (LT), mortality rate (M), and relative growth rate (RGR). Leaf collection followed the standardized protocol described by Pérez-Harguindeguy et al. (2016). For each species, 20 leaves were sampled from 10 adult individuals ($n=200$ leaves/species), stored in airtight plastic bags with added moisture and CO₂, labeled, and refrigerated. Leaf area was determined with an HP Scanjet G4050 scanner (300 dpi) and processed using ImageJ software. For compound leaves, both petiole and rachis were included. Leaves were weighed fresh on an analytical balance, oven-dried at 67 °C for 72 h, and reweighed to obtain dry mass. SLA was calculated as leaf area divided by dry mass, and LDMC as dry mass divided by fresh mass. Leaf length (LL) was measured using ImageJ or a graduated ruler for larger leaves. LT was determined following Vile et al. (2005; Eq. 1). Mortality rate (M) and relative growth rate (RGR) were calculated according to Forgiarini et al. (2015; Eqs. 2 and 3).

$$LT = (SLA \times LDMC)^{-1} \quad (1)$$

$$M = 1 - \left[1 - \frac{N_i - N_f}{N_i} \right]^{\frac{1}{(t_f - t_i)}} \times 100 \quad (2)$$

$$RGR = \frac{\ln \left(\frac{DBH_f}{DBH_i} \right)}{(t_f - t_i) \ln (DBH_i)} \quad (3)$$

Where: SLA is the specific leaf area, LDMC is the leaf dry matter content, N_i is the number of trees recorded in the 2017 inventory, N_f is the number of surviving trees in

the second inventory conducted in 2024 ($t=7$ years), DBH refers to diameter at breast height, and t is the time interval between the initial (2017) and final (2024) measurements.

Functional diversity

Functional diversity was estimated from a matrix of species leaf traits and demographic rates, combined with the species-by-plot abundance matrix. All traits were standardized (mean=0, SD=1) to minimize scale differences among variables. We calculated five indices of functional diversity: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (RaoQ) (Villéger et al. 2008; Laliberté and Legendre 2010).

Statistical analyses

Species were grouped using hierarchical clustering with Ward's method and Euclidean distance, based on six traits: SLA, LL, LDMC, LT, M, and RGR. Clustering quality was assessed with the cophenetic correlation coefficient (CCC). The number of groups was determined based on internal trait coherence within clusters, and results were interpreted within the framework of the resource acquisition–conservation spectrum (Wright et al. 2004; Reich 2014). Normality of group trait means was tested using the Shapiro–Wilk test. For normally distributed data, generalized linear models (GLMs) with an identity link were applied; for non-normal data, a gamma distribution with log link was used. Multiple comparisons were adjusted using the Bonferroni correction ($\alpha=0.05$). Functional variation among groups was further explored through Principal Coordinates Analysis (PCoA), with convex hulls delineating the functional space of each group to assess overlap and differentiation along trait gradients (Larsen et al. 2020).

Functional diversity indices were obtained for each plot to estimate mean values and 95% confidence intervals. To visualize functional structure, traits were projected into a two-dimensional functional space using PCoA based on Gower distance, applying the Cailliez correction for negative eigenvalues. All analyses were performed in R v.4.x (R Core Team 2022) with the packages factextra (Kassambara and Mundt 2020), vegan (Oksanen et al. 2019), and FD (Laliberté et al. 2015).

Results

The community structure revealed a total of 2013 individuals ha^{-1} , with a basal area of $486.4 \text{ m}^2 \text{ ha}^{-1}$, comprising 34 species and 20 families (Supplementary Material 1). The most abundant species was *Gymnanthes klotzschiana*, accounting for 53.57% of relative density (DR) and 41.53% of relative dominance (DoR), with an importance value (IV) of 37.55%. Other highly representative species were *Ligustrum lucidum*, an exotic invasive species (IV=14.45%), and *Matayba elaeagnoides* (IV=9.25%). Together, these three species accounted for more than 60% of the total IV of the fragment, indicating strong structural dominance. The 34 species used in the functional analyses represented more than 85% of the total individual density and 90% of the basal area, ensuring community representativeness in the trait-based analyses.

The analyzed functional traits exhibited high interspecific variability within the community. Specific leaf area (SLA) had a mean of $12.79 \text{ mm}^2 \text{ mg}^{-1}$ (SD=5.01), ranging from $7.32 \text{ mm}^2 \text{ mg}^{-1}$ in *Handroanthus albus* to $29.26 \text{ mm}^2 \text{ mg}^{-1}$ in *Allophylus edulis*. Leaf length (LL) averaged 12.96 cm, with values from 4.34 cm in *Araucaria angustifolia* to 39.11 cm in *Jacaranda micrantha*. Leaf dry matter content (LDMC) showed the lowest variability (mean=0.44 mg g^{-1} ; CV=15.78%), whereas leaf thickness (LT) ranged from 0.10 mm in *A. edulis* to 0.34 mm in *Ilex brevicuspis*. Among demographic rates, mean mortality was 1.99% per year, with extreme values in *Mimosa scabrella* (9.43% per year) and *Zanthoxylum rhoifolium* (8.21% per year). Relative growth rate (RGR) averaged $0.0070 \text{ cm}^{-1} \text{ year}^{-1}$, with higher values in *Luehea divaricata* ($0.0125 \text{ cm}^{-1} \text{ year}^{-1}$) and *Ligustrum lucidum* ($0.0118 \text{ cm}^{-1} \text{ year}^{-1}$) (Table 1).

The Ward's clustering analysis yielded a cophenetic correlation coefficient of 0.70, indicating adequate consistency in group formation (Fig. 1). Using a 60% cutoff of the total distance among species, four groups (G1–G4) were defined based on six traits: SLA, LL, LDMC, LT, M, and RGR. G1 included species such as *Vitex megapotamica*, *Allophylus edulis*, and *Mimosa scabrella*; G2 comprised *Matayba elaeagnoides*, *Handroanthus albus*, and *Jacaranda micrantha*; G3 grouped *Myrcia retorta*, *Ilex brevicuspis*, and *Eugenia involucrata*; whereas G4 included species such as *Araucaria angustifolia*, *Ilex paraguariensis*, and *Luehea divaricata* (Fig. 1).

For leaf and demographic traits (Fig. 2a), G1 showed the highest mean SLA ($20.68 \pm 6.03 \text{ mm}^2 \cdot \text{mg}^{-1}$), significantly higher than the other groups. G2, G3, and G4 did not differ significantly for this trait. LL was highest in G2 ($35.30 \pm 4.33 \text{ cm}$), whereas G1, G3, and G4 showed similar values ($\sim 9 \text{ cm}$). LDMC did not differ significantly among groups, although G2 exhibited greater variability. For LT,

the mean value of G1 ($0.14 \pm 0.04 \text{ mm}$) was lower than in the other groups, which did not differ from each other. Mortality (M) was highest in G1 ($4.94 \pm 3.31\% \text{ year}^{-1}$), significantly higher than in the other groups, which showed similar values. Regarding RGR, G1 ($0.91 \pm 0.13 \text{ cm} \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$) and G3 ($0.86 \pm 0.15 \text{ cm} \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$) exhibited the highest means, not differing from each other but higher than G2 ($0.65 \pm 0.15 \text{ cm} \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$) and G4 ($0.43 \pm 0.15 \text{ cm} \cdot \text{cm}^{-1} \cdot \text{year}^{-1}$), with G4 being significantly lower than G2.

The Principal Coordinates Analysis (PCoA) revealed clear separation among groups (Fig. 2b). The first two axes explained 64.6% of the total variation (PCoA1: 43.1%; PCoA2: 21.6%). PCoA1 was negatively correlated with SLA ($r = -0.8377$) and positively with LT ($r = 0.8203$), representing the acquisition–conservation gradient. PCoA2 was negatively correlated with LDMC ($r = -0.4919$) and positively with RGR ($r = 0.5277$), indicating additional variation related to growth and survival. Convex hulls indicated partial overlap among G2, G3, and G4, reflecting functional similarity, whereas G1 occupied a distinct region, driven by higher SLA and lower LT.

The tree community of the alluvial forest exhibited a mean functional richness (FRic) of 4.62, indicating broad species occupation of functional space (Fig. 3a). Functional evenness (FEve) averaged 0.67, showing moderate distribution of species across trait axes (Fig. 3b). Functional divergence (FDiv) averaged 0.79, indicating that a substantial portion of community abundance was associated with species positioned at the periphery of the functional space (Fig. 3c). Functional dispersion (FDis) averaged 1.33, while Rao's quadratic entropy (RaoQ) averaged 2.71 (Fig. 3d), confirming consistent among-plot variation and substantial trait differentiation within the community.

The graphical representation of indices (Fig. 3) illustrated different aspects of functional structure. FRic emphasized the breadth of functional space occupied by species, whereas FEve revealed a partially even distribution in trait space. FDiv indicated the coexistence of species near the centroid and at the periphery, and the FDis/RaoQ panel indicated the simultaneous presence of common and specialized species, with long lines connecting the centroid to the most extreme ones. Collectively, these results show that the community exhibits moderate to high functional diversity, ensuring the representation of multiple ecological strategies within the analyzed fragment (Fig. 3 – Supplementary Material 2)

Table 1 Taxonomic identity, leaf functional traits, and growth rates of dominant tree species in an alluvial Atlantic forest

Family	Species	SLA (mm ² mg ⁻¹)	LL (cm)	LDMC (mg g ⁻¹)	LT (mm)	M (% year ⁻¹)	RGR (cm ⁻¹ year ⁻¹)
Araucariaceae	<i>Araucaria angustifolia</i> (Bertol.) Kuntze	8.65	4.34	0.39	0.33	0	0.0031
Sapindaceae	<i>Allophylus edulis</i> (A.St.-Hil. et al.) Hieron. ex Niederl.	29.26	9.14	0.36	0.10	1.81	0.0093
Myrtaceae	<i>Campomanesia guazumifolia</i> (Cambess.) O.Berg.	7.7	11.76	0.53	0.26	0	0.0034
Salicaceae	<i>Casearia decandra</i> Jacq.	23.24	8.48	0.37	0.12	2.44	0.0098
Canellaceae	<i>Cinnamodendron dinisii</i> Schwacke	9.74	7.84	0.43	0.30	2.57	0.0078
Clethraceae	<i>Clethra scabra</i> Pers.	11.39	11.02	0.49	0.19	3.53	0.0093
Sapindaceae	<i>Cupania vernalis</i> Cambess.	13	36.21	0.5	0.16	3.14	0.0084
Myrtaceae	<i>Eugenia involucrata</i> DC.	8.41	7.39	0.52	0.23	0	0.0092
Myrtaceae	<i>Eugenia pyriformis</i> Cambess.	12.29	7.05	0.48	0.17	0	0.0058
Myrtaceae	<i>Eugenia uniflora</i> L.	11.6	6.16	0.51	0.18	0	0.0056
Euphorbiaceae	<i>Gymnanthes klotzschiana</i> Müll.Arg.	11.74	6.84	0.51	0.19	1.43	0.0064
Bignoniaceae	<i>Handroanthus albus</i> (Cham.) Mattos	7.32	30.59	0.52	0.27	2.18	0.0052
Aquifoliaceae	<i>Ilex brevicuspis</i> Reissek	7.83	6.93	0.39	0.34	0	0.0088
Aquifoliaceae	<i>Ilex dumosa</i> Reissek	11.87	7.01	0.59	0.20	2.1	0.0031
Aquifoliaceae	<i>Ilex paraguariensis</i> A.St.-Hil.	12.52	12.54	0.36	0.23	0	0.0030
Aquifoliaceae	<i>Ilex theezans</i> Mart. ex Reissek	12.84	7.8	0.36	0.24	1.82	0.0082
Bignoniaceae	<i>Jacaranda micrantha</i> Cham.	12.93	39.11	0.46	0.18	0	0.0079
Oleaceae	<i>Ligustrum lucidum</i> W.T.Aiton	12.18	12.23	0.35	0.25	0.73	0.0118
Anacardiaceae	<i>Lithraea molleoides</i> (Vell.) Engl.	9.06	11.49	0.48	0.24	0	0.0083
Malvaceae	<i>Luehea divaricata</i> Mart.	14.69	13.39	0.46	0.16	1.89	0.0027
Sapindaceae	<i>Matayba elaeagnoides</i> Radlk.	15.36	27.37	0.35	0.20	2.02	0.0062
Fabaceae	<i>Mimosa scabrella</i> Benth.	18.14	8.39	0.55	0.11	9.43	0.0103
Myrtaceae	<i>Myrcia palustris</i> DC.	10.63	7.06	0.45	0.21	2.57	0.0065
Myrtaceae	<i>Myrcia retorta</i> Cambess.	8.05	6	0.45	0.30	0	0.0087
Primulaceae	<i>Myrsine coriacea</i> (Sw.) R.Br. Ex Roem. & Schult.	9.03	7.6	0.38	0.29	0	0.0090
Lauraceae	<i>Ocotea puberula</i> (Rich.) Nees	12.95	15.06	0.42	0.19	5.63	0.0066
Lauraceae	<i>Ocotea pulchella</i> (Nees & Mart.) Mez	11.37	8.39	0.51	0.18	1.89	0.0037
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	10.02	7.71	0.43	0.24	2.79	0.0061
Anacardiaceae	<i>Schinus terebinthifolia</i> Raddi	9.69	16.36	0.45	0.26	4.69	0.0101
Solanaceae	<i>Solanum mauritianum</i> Scop.	15.47	23.25	0.27	0.24	3.14	0.0051
Asteraceae	<i>Vernonanthura discolor</i> (Spreng.) H.Rob.	7.79	13.7	0.45	0.30	0	0.0034
Lamiaceae	<i>Vitex megapotamica</i> (Spreng.) Moldenke	24.42	19.42	0.41	0.12	2.18	0.0093
Salicaceae	<i>Xylosma ciliatifolia</i> (Clos) Eichler	17.57	10	0.45	0.14	1.49	0.0068
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	16.04	12.91	0.4	0.19	8.21	0.0098
Average		12.79	12.96	0.44	0.21	1.99	0.0070
Standard deviation		5.01	8.68	0.07	0.06	2.28	0.0025
Coefficient of Variation (CV%)		39.14	67.02	15.78	29.09	1.14	36.02

Where: SLA: specific leaf area (mm² mg⁻¹); LL: leaf length (cm); LDMC: leaf dry matter content (mg g⁻¹); LT: leaf thickness (mm); M: mortality rate (% year⁻¹); and RGR: relative growth rate (cm⁻¹ year⁻¹).

Discussion

Our results show that the tree community of an alluvial Atlantic Forest is organized into four distinct functional groups, structured by trade-offs between resource acquisition and conservation. Despite the strong dominance of a few species (*Gymnanthes klotzschiana*, *Ligustrum lucidum*, and *Matayba elaeagnoides*), the community exhibited moderate to high functional diversity, as reflected by the wide

occupation of functional trait space (FRic=4.62), a moderate yet uneven distribution of species across functional space (FEve=0.67), and consistent differentiation of adaptive strategies (FDiv=0.79; FDis=1.33; RaoQ=2.71). This combination supports the coexistence of both generalist and specialist species, conferring ecological resilience to the fragment under environmental variation and anthropogenic disturbance.

Fig. 1 Ward's cluster analysis based on leaf functional traits (SLA, LL, LDMC, LT, M, and RGR) and growth rates of dominant tree species in an alluvial Atlantic Forest. The dashed line indicates the 60% cutoff of total distance among species

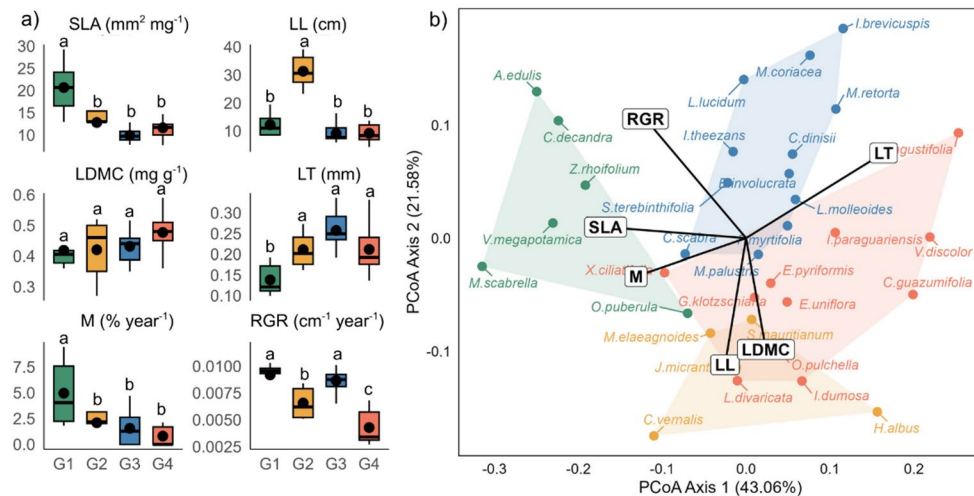
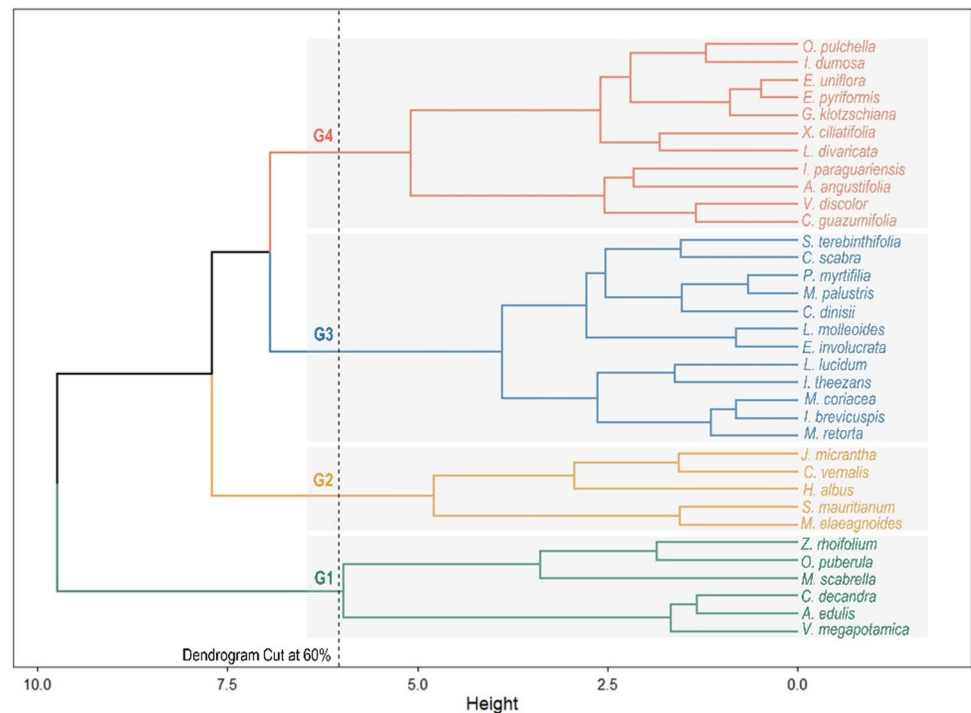


Fig. 2 Functional traits of tree species groups in an alluvial Atlantic Forest. (a) Boxplots showing variation in leaf functional traits and growth rates among groups (SLA, LL, LDMC, LT, M, and RGR). (b) Principal Coordinates Analysis (PCoA) illustrating trait-based differentiation among species groups, with vectors indicating trait contributions. SLA: specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); LL: leaf length (cm); LDMC:

leaf dry matter content (mg g^{-1}); LT: leaf thickness (mm); M: mortality rate ($\% \text{ year}^{-1}$); and RGR: relative growth rate ($\text{cm cm}^{-1} \text{ year}^{-1}$). Significant differences among groups were determined using Bonferroni-corrected pairwise comparisons ($\alpha = 0.05$). Black dots inside boxes indicate mean values, and horizontal lines indicate medians

The coexistence of contrasting strategies—ranging from acquisitive profiles with high SLA and rapid growth to conservative profiles with low SLA, thicker leaves, and slower growth—reflects the acquisition–conservation trade-off described in other subtropical communities (Souza et al. 2014). In our case, the simultaneous presence of these profiles is explained by the heterogeneity of the alluvial environment, driven by flood pulses, sediment deposition,

and light gradients, which promote alternative resource-use strategies and trade-offs. Within the groups, species with thinner leaves, high SLA, and elevated mortality rates favored rapid growth in more open environments. Wang et al. (2022) demonstrated that high-SLA leaves maximize light and nutrient capture but have reduced longevity, which explains their prevalence in dynamic microhabitats such as canopy gaps and disturbed sectors. These traits facilitate

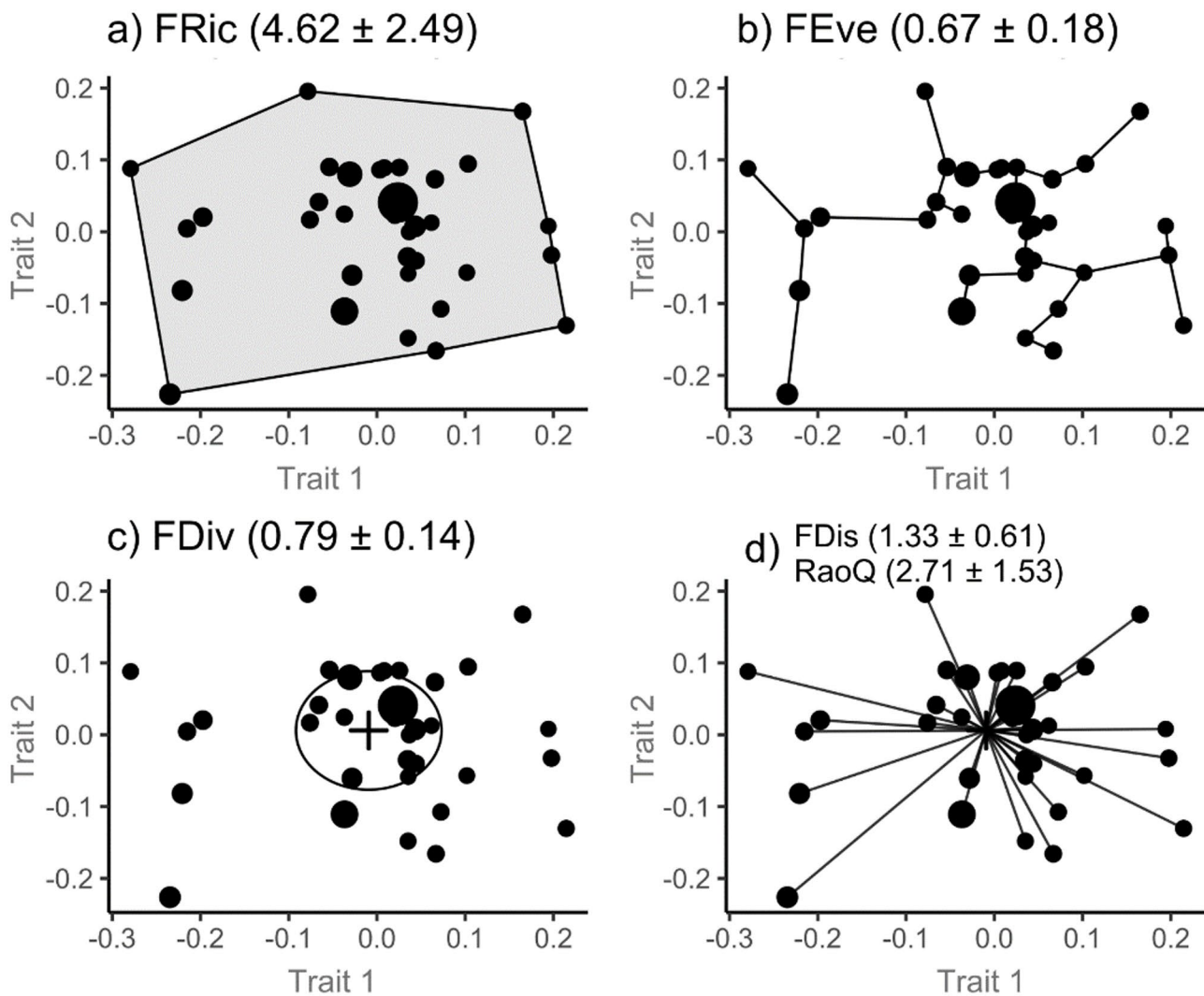


Fig. 3 Functional diversity patterns of tree species in an alluvial Atlantic Forest. **(a)** Functional richness (FRic), represented by the convex hull delimiting species in functional space. **(b)** Functional evenness (FEve), illustrated by the minimum spanning tree (MST) connecting species in trait space. **(c)** Functional divergence (FDiv), showing spe-

cies distribution relative to the community centroid (cross) and the weighted mean radius (circle). **(d)** Functional dispersion, illustrated by lines connecting species to the community centroid. Mean values $\pm$ SD of functional dispersion (FDis) and Rao's quadratic entropy (RaoQ) are shown in the panel. Point size is proportional to species abundance.

rapid structural recovery, albeit with the cost of elevated mortality. In contrast, species with thicker leaves, lower SLA, reduced mortality, and intermediate growth rates contributed to community stability in areas less directly affected by flooding. Onoda et al. (2011) showed at a global scale that mechanically robust leaves exhibit greater longevity and resistance to physical stress, although associated with lower photosynthetic rates, making them particularly advantageous in stable environments such as shaded understories or alluvial zones with lower disturbance frequency.

We also identified species that combine thick leaves with faster growth, a profile that may indicate adaptive flexibility under environmental variability. This intermediate arrangement reduces losses from physical damage without fully compromising growth efficiency, favoring niche occupation

where competition and stress coexist. In this context, Matsuo et al. (2021) demonstrated that successional advancement in tropical secondary forests promotes structural changes that increase light heterogeneity, creating vertical and horizontal gradients that shape regeneration opportunities. These patterns of light availability help explain why different trait combinations may coexist along succession. In contrast, slow-growing species with thick leaves and low SLA represent a conservative strategy typical of later successional stages. Poorter et al. (2021) showed that, in humid forests, succession is driven by shade-tolerance traits, favoring conservative species that prioritize survival in low-light environments, consolidating forest structure in shaded and less disturbed sectors and ensuring long-term stability.

The variability observed in SLA, LL, LT, RGR, and mortality indicates that multiple functional strategies coexist by exploiting different niches, reinforcing the importance of ecological trade-offs in community structuring. As demonstrated by Poorter et al. (2021) and Van Der Sande et al. (2017), greater variation in traits promotes stronger niche complementarity, improving resource-use efficiency and ultimately productivity at the community level. Our results support this perspective by showing that the diversity of strategies broadens the adaptive capacity of the community and supports ecosystem functioning even under external pressures, confirming the central role of functional diversity, as emphasized by Sakschewski et al. (2016), as a pillar of forest resilience.

When considering the environmental filters characteristic of alluvial systems, we observed that flood-tolerant species occupied a wider portion of the gradient, whereas fast-growing species were concentrated in drier or more disturbed sectors. This differentiation aligns with Silva et al. (2022), who highlighted the adaptive advantage of tolerance to extreme hydrological conditions in heterogeneous environments. The observed structure thus reflects a predictable distribution of strategies across microhabitats, reducing competitive overlap and favoring coexistence. This pattern is consistent with mechanisms of biotic and abiotic filtering in tree community organization (Oliveira-Filho et al. 2014; Missio et al. 2016), whereby environmental variation restricts the pool of species able to establish but simultaneously promotes functional diversity through specialization under distinct conditions. As emphasized by Loehle (2000), such functional trade-offs constitute adaptations to different disturbance regimes, enabling species to exploit resources complementarily and reduce direct competition, thereby ensuring the maintenance of diversity in alluvial ecosystems.

Studies in tropical alluvial forests underscore the role of environmental heterogeneity in driving floristic, structural, and functional diversity (Silva et al. 2009). In várzea and igapó forests of the Amazon, Mori et al. (2019) demonstrated that species in nutrient-rich environments (white-water rivers) display acquisitive traits, whereas species in nutrient-poor environments (black-water rivers) show conservative profiles, with greater investment in thicker, longer-lived leaves. Similarly, Bonilla et al. (2020) reported low functional richness but high functional divergence in Orinoco floodplain forests, confirming that even species-poor forest communities can sustain strong functional differentiation.

The tree community of the alluvial forest showed moderate functional richness ($FRic=4.62$), reflecting wide trait-space occupation despite the dominance of a few structurally dominant species. Functional evenness ($FEve=0.67$) and functional divergence ($FDiv=0.79$) indicated a relatively

balanced distribution, although part of the abundance was associated with species at the periphery of functional space. These patterns reveal the coexistence of generalist and specialist species, supporting niche complementarity and resource-use efficiency, as described by Van Der Sande et al. (2017). Values of functional dispersion ($FDis=1.33$) and Rao's quadratic entropy ($RaoQ=2.71$) revealed trait differentiation among plots, indicating multiple adaptive strategies along the alluvial gradient. This moderate to high functional diversity suggests that the forest combines both redundancy and functional differentiation, supporting resilience to environmental variation and anthropogenic disturbance. In line with previous studies (Sakschewski et al. 2016; Poorter et al. 2021; Roa-Fuentes et al. 2022), these results underscore the central role of functional diversity in maintaining ecosystem functioning and provide practical insights for conservation and restoration strategies.

These local patterns align with observations from other alluvial systems. For example, Roa-Fuentes et al. (2022) demonstrated that flooded and non-flooded forests in the Magdalena River valley (Colombia) maintained similar levels of functional diversity ($FRic$, $FEve$, $FDiv$) despite contrasting inundation regimes, even under marked differences in structure and species richness. In this context, the role of functional redundancy and strategy complementarity is central: even with reduced taxonomic richness, the coexistence of acquisitive and conservative species ensures stability in ecosystem processes.

In summary, the coexistence of species with contrasting strategies translates into a system capable of complementarily using resources and maintaining ecosystem functioning under environmental variation. These findings not only elucidate successional mechanisms in alluvial forests (Poorter et al. 2021) but also provide practical implications for conservation and restoration efforts. Prioritizing acquisitive species during early restoration phases and conservative species at later stages may improve resource-use efficiency and enhance ecological resilience. Overall, this functional spectrum suggests that even forest fragments dominated by a few species may sustain resilience, offering valuable guidance for the conservation and restoration of Atlantic Forest alluvial systems. These results reinforce the need for management strategies that integrate local environmental filters, functional dynamics, and the risks associated with invasive species.

In conclusion, our results are consistent with the three proposed hypotheses: (i) tree species in the alluvial forest formed distinct functional groups, structured along the resource acquisition–conservation axis; (ii) variation in leaf traits and demographic rates reflected contrasting adaptive strategies that enable coexistence across ecological niches along the environmental gradient; and (iii) the community

exhibited moderate to high functional diversity, with wide trait-space occupation even under strong environmental filtering and structural dominance, supporting community stability and ecological resilience.

Author contribution ACS wrote, reviewed, and edited the manuscript, and prepared figures and tables. JAM reviewed the manuscript. ACS and JAM performed fieldwork and collected data. LFW supervised the research and performed the formal analysis. All authors approved the final version of the manuscript for publication.

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Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

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Consent to participate All authors have read and agreed to the published version of the manuscript.

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