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BIODIVERSITY AND CONSERVATION - ORIGINAL ARTICLE

Intraspecific variation in functional traits of *Evodianthus funifer* (Cyclanthaceae) across upland and white-water floodplain forests in the Eastern Amazon

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ABSTRACT

Amazonian rainforests exhibit marked variation in seasonal flooding, water availability, climate, and light conditions, providing an important setting for understanding intraspecific functional adjustments. In this context, *Evodianthus funifer* (Poit.) Lindm., a species widely distributed across Amazonian rainforests, offers an excellent opportunity to investigate the role of intraspecific variation of functional traits in the persistence of species along environmental gradients. We hypothesized that *E. funifer* would exhibit intraspecific variation in leaf and stem traits, reflecting different ecological strategies across light and water gradients. We measured: leaf thickness (LT), stem specific density (SSD), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), petiole length (PL), and plant height (H). Significant intraspecific variation associated with the contrasting forest types was detected in LA, LD, LT, PL, and SLA. Individuals in upland forests exhibited greater LT, a trait associated with enhanced water conservation, increased drought resistance, and reduced transpirational water loss under high irradiance. In turn, higher LA, LD, and PL values were recorded in white-water floodplain forests, reflecting strategies that increase photosynthetic surface area, reduce self-shading, and facilitate leaf positioning above seasonal flood levels. These trait trade-offs illustrate the capacity of *E. funifer* to adjust along environmental gradients. The classic acquisitive–conservative pattern did not apply to intraspecific variation among individuals of the studied species. Knowledge on these adjustments is essential for predicting plant responses to climate change and informing conservation strategies in Amazonian forests.

KEYWORDS: Amazonian vegetation; ecological strategies; functional attributes

Variação intraespecífica em traços funcionais de *Evodianthus funifer* (Cyclanthaceae) entre florestas de terra firme e de várzea na Amazônia Oriental

RESUMO

Florestas amazônicas apresentam diferenças marcantes em relação à inundação sazonal, disponibilidade de água, clima e condições de luminosidade, constituindo um cenário importante para a compreensão de ajustes funcionais intraespecíficos. Nesse contexto, *Evodianthus funifer* (Poit.) Lindm., uma espécie amplamente distribuída pelas florestas da Amazônia, oferece uma excelente oportunidade para investigar o papel da variação intraespecífica de características funcionais na persistência da espécie ao longo de gradientes ambientais. Nós hipotetizamos que *E. funifer* apresenta variações intraespecíficas em características foliares e caulinares, refletindo diferentes estratégias ecológicas entre gradientes de luz e água. Medimos: espessura foliar (EF), densidade específica do caule (DEC), área foliar (AF), área foliar específica (AFE), conteúdo de matéria seca foliar (CMSF), densidade foliar (DF), comprimento do pecíolo (CP) e altura da planta (A). Variações intraespecíficas foram detectadas em AF, AFE, CP, DF e EF. Indivíduos em florestas de terra firme exibiram maior EF, característica associada à maior conservação de água, maior resistência à seca e menor perda de água por transpiração sob alta luminosidade. Valores mais altos de AF, DF e CP foram registrados em florestas de várzea, refletindo estratégias que aumentam a área de superfície fotossintética, reduzem o auto-sombreamento e facilitam o posicionamento das folhas acima dos níveis de inundação sazonal. Essas compensações ilustram a capacidade de *E. funifer* de se adaptar a gradientes ambientais. O padrão clássico das estratégias aquisitiva-conservativa não foi encontrado na variação intraespecífica entre os indivíduos da espécie estudada. O conhecimento sobre essas adaptações é essencial para prever as respostas das plantas às mudanças climáticas e orientar estratégias de conservação em florestas amazônicas.

PALAVRAS-CHAVE: vegetação amazônica; estratégias ecológicas; atributos funcionais

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INTRODUCTION

Functional traits serve as indicators of plant ecological strategies, providing insights into how species adapt or adjust to diverse environmental conditions (Araújo et al. 2023). Despite advances in understanding functional variation in tropical rainforest, most progress has been concentrated on trees (e.g. Baraloto et al. 2010), while other life-forms such as nomadic climbers remain poorly studied from a functional trait perspective (Riordan et al. 2023). Contrasting environments associated with seasonal flooding and variation in water availability, drought, and light conditions provide an important framework for investigating intraspecific functional adjustments in tropical rainforests (Fortunel et al. 2013). Differences among individuals of the same species (intraspecific variation) can expand niche breadth and enhance species persistence under contrasting environmental conditions by promoting functional adjustments in response to environmental filters (Violle et al. 2012). Understanding intraspecific variation in leaf and stem traits is therefore essential for elucidating the main mechanisms that enable species persistence across heterogeneous environments.

For example, leaf thickness (LT) is commonly associated with resistance to abiotic stress and herbivory (Fyllas et al. 2022), whereas specific leaf area (SLA) is closely related with light capture capacity and nutrient cycling (Hietz et al. 2022). Leaf density (LD) reflects adaptation to variation in water and nutrient availability (Poorter et al. 2009), and leaf area (LA) informs light capture (Assunção et al. 2020). Leaf dry matter content (LDMC) is indicative of plant growth rates and carbon assimilation strategies (Botelho et al. 2025). Plant height (H) is associated with reproductive output and competitive ability, often linked to traits like petiole length (PL) and light acquisition efficiency (Assunção et al. 2020). Stem specific density (SSD), in turn, reflects structural support and capacity to endure mechanical stress (Wagner et al. 2021). Collectively, these functional traits provide a comprehensive framework for understanding the diverse ecological strategies that plants employ to cope with complex, dynamic environments and respond to environmental filtering (Fortunel et al. 2013).

The adoption of distinct ecological strategies (driven by ecological trade-offs) is a key mechanism underlying plant species coexistence in ecosystems. Because resources are limited and environmental conditions vary, investment in one trait often constrains investment in another (Costa et al. 2020). In Amazonian ecosystems, some studies have shown that compensatory responses reflect adaptations to environmental heterogeneity. For example, acquisitive strategies are characterized by traits that maximize resource capture and use—such as high LA, SLA, PL, and photosynthetic efficiency (Zuleta et al. 2022; Rebelo et al. 2024). In contrast, conservative strategies prioritize longevity and stress tolerance, typically involving higher LD, LDMC, and LT (Steege et al. 2025). In general, resource-rich environments favor acquisitive strategies, while resource-poor or stressful environments select conservative strategies that maintain function under constraint (Maracahipes et al. 2018).

Upland forests and white-water floodplain forests differ markedly in light availability, humidity, and evapotranspiration rates (Haugaasen & Peres 2006). These environmental contexts can significantly influence the mechanisms underlying variation in plant functional traits (Gama et al. 2005). In the Amazon, upland forests are characterized by high light and temperature regimes intensity (Hawes & Peres 2016). Under these conditions, species are expected to adopt predominantly conservative strategies, exhibiting thicker and denser leaves that enhance temperature regulation and water retention to cope with water stress during prolonged periods of drought (Carvalho et al. 2024). In turn, forests flooded by white-water rivers are subject to seasonal flooding that can last up to 7 months per year (Hawes & Peres 2016). They are inundated by white-water rivers carrying a large amount of suspended matter and nutrients, which are deposited in the moist soils (Parolin et al. 2010). This high seasonal availability of water and nutrients in white-water floodplain forests can favor the development of characteristics associated with acquisitive strategies such as rapid plant growth, larger LA, SLA, and reduced structural investment in tissues (Steege et al. 2025).

Shifts in ecological strategies in response to variation in light, water availability, and soil fertility are expected in nomadic climbers (Lopes and Melo Júnior 2019; Rebelo et al. 2024) — plants that germinate in the soil, establish on a phorophyte, and often lose their connection to the ground, becoming epiphytic (Zotz et al. 2021). Despite their ecological relevance, the functional responses of these species remain largely understudied (Riordan et al. 2023).

In this context, we investigated the functional traits of *Evodianthus funifer* (Poit.) Lindm. (Cyclanthaceae), a conspicuous Neotropical nomadic climber widely distributed across South America and valued for its use in handicrafts (Oliveira et al. 2006; Leal and Forzza 2012), across upland and white-water floodplain forest environments in the Eastern Amazon. Specifically, we aimed to answer the following question: Does *E. funifer* exhibit intraspecific adjustments to these environments, reflecting distinct trade-offs associated with the contrasting environmental conditions of these forest types? We hypothesized that *E. funifer* exhibits significant intra-specific variation in functional traits, and that different combinations of stem and leaf traits correspond to different ecological strategies shaped by the specific environmental conditions of upland versus white-water floodplain forests.

MATERIALS AND METHODS

Study site

The study was conducted in the Parque Estadual do Utinga Camillo Vianna (PEUt; 1°23'58"- 1°26'25" S; 48°25'19" - 48°25'16" W), located in the municipalities of Ananindeua

and Belém, Brazil, in the Eastern Amazon (Figure 1). According to the Köppen classification (1948), the climate is of the Af type (humid equatorial) with an average annual temperature of 26 °C and precipitation of 2.225 to 3.300 mm per year (Vasconcelos et al. 2011). PEUt comprises well-preserved Amazon Forest and is one of the largest remnants of native vegetation in the metropolitan region of Belém, with approximately 1,340 hectares (Costa et al. 2006).

The protected area harbors high plant diversity across multiple habitat types, including *terra-firme* (upland) forests, white-water floodplain forests, back-water floodplain forests, white-sand forests, natural lakes, and artificial reservoirs (Ferreira et al. 2022). Upland and white-water floodplain forests are readily distinguishable: the first exhibit a closed canopy, well-drained, nutrient-poor soils, whereas the later occur in more humid environments influenced by tidal dynamics and river-level fluctuations, with greater deposition of nutrients in the soil (Bredin et al. 2020a; Figure 2).

Sampling design

We selected three sites in each forest type, and randomly selected five phorophytes in each site (Freiberg and Freiberg 2000), maintaining a minimum distance of 100 meters between sites (Gradstein et al. 2003; Pos and Sleegers 2010). A total of 30 individuals of *E. funifer* were sampled (15 in upland forest and 15 in white-water floodplain forest). From each individual, five mature leaves were collected, totaling 150 leaves. Leaves showing damage, disease or herbivory were excluded (Pérez-Harguindeguy et al. 2016) (Figure 3a). Sampling was conducted during the rainy season (December 2023 to March 2024) using a long-reach pruning shear (Costa et al. 2011). One fertile specimen of *E. funifer* (*J.F. Araújo 3* and *J.F. Araújo 5*) was collected in each vegetation type, prepared using standard taxonomic procedures (Peixoto and Maia 2013), and deposited in the MG herbarium (acronym according to Thiers 2026).

For each individual, height (H, m) was measured in the field as the shortest distance between the point of attachment at the soil and the highest photosynthetic tissue (Wagner et al. 2021). Petiole length (PL, cm) was measured with measuring tapes (Martinelli and Rezende 2024). The collected leaves and stems were stored in sealed plastic bags to prevent dehydration (Carvalho et al. 2026). In the laboratory, the adaxial surface of each leaf blade was photographed alongside a scale for reference using a digital camera (Figure 3b). Leaf area (LA, cm^2) was measured using ImageJ software, version 1.41 (Wang

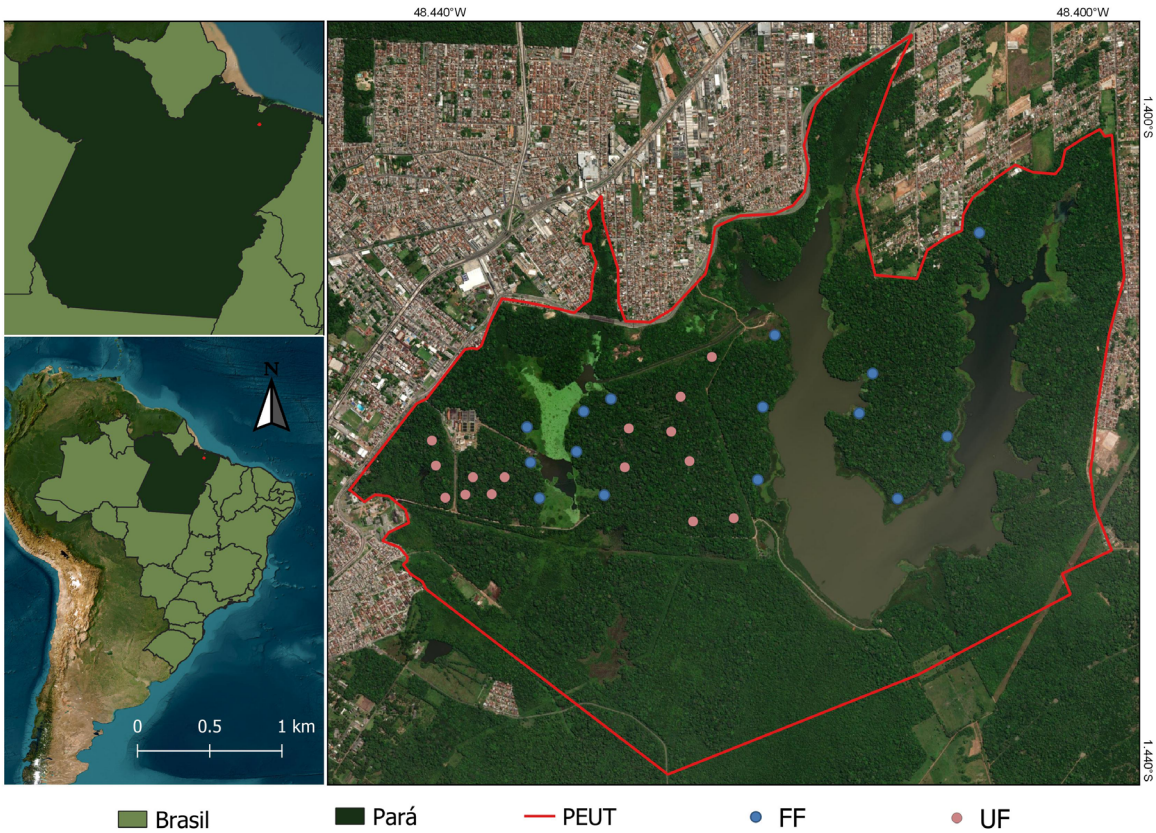


Figure 1. Map showing the Parque Estadual do Utinga Camillo Vianna (PEUt), in the municipalities of Ananindeua and Belém, Pará State, Brazil, Eastern Amazon. The red line delineates the boundary of PEUT. Blue points indicate the phorophytes sampled in white-water floodplain forests (FF) and red points indicate those sampled in upland forests (UF).



Figure 2. Vegetation types in the Parque Estadual do Utinga Camillo Vianna (PEUt), Pará State, Brazil, Eastern Amazon: **A-B**) White-water floodplain Forest; **C-D**) Upland forest.

2016) (Figure 3c). Leaf thickness (LT, mm) was measured at three different points in each leaf blade using a digital caliper (Figure 3d). Fresh mass was determined using a precision digital balance (0.001 g) (Carvalho et al. 2026) (Figure 3e).

Samples were then dried in a forced-air oven at 50 °C until constant weight, and the resulting dry mass was used to calculate leaf dry matter content (LDMC, g), defined as the ratio of dry mass to fresh mass (Pérez-Harguindeguy et al. 2016) (Figure 3f-g). Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated as the ratio of one-sided fresh leaf area to oven-dry mass (Guzmán-Jaco et al. 2022). Leaf density (LD, $g\ m^{-3}$) was determined as the ratio of leaf mass per area to LT (mm).

Stem specific density (SSD, $mg\ mm^{-3}$) was measured from 10 cm stem segments for each individual, calculated as the ratio of stem dry mass to the fresh volume (Wagner et al. 2021). Stem volume was determined using the water displacement method, following Archimedes' principle (Rosado and De Mattos 2010).

Data analysis

Univariate and multivariate analyses were performed from minimum, mean, maximum and standard deviation values of individual's functional traits (Table 1) (Wagner et al. 2021). Data normality was assessed using the Shapiro-Wilk test and homogeneity of variances using Levene's test (Dias-Pereira et al. 2022). Depending on the fulfillment of parametric assumptions, either the Student's t-test or the non-parametric Mann–Whitney U test was used to test for differences in the measured traits between individuals from upland and white-water floodplain forests (Bredin et al. 2020a). This approach was applied to traits with a single measurement per individual (H and SSD). For traits measured multiple times per individual (LA, LD, LDMC, LT, SLA, and PL), we used

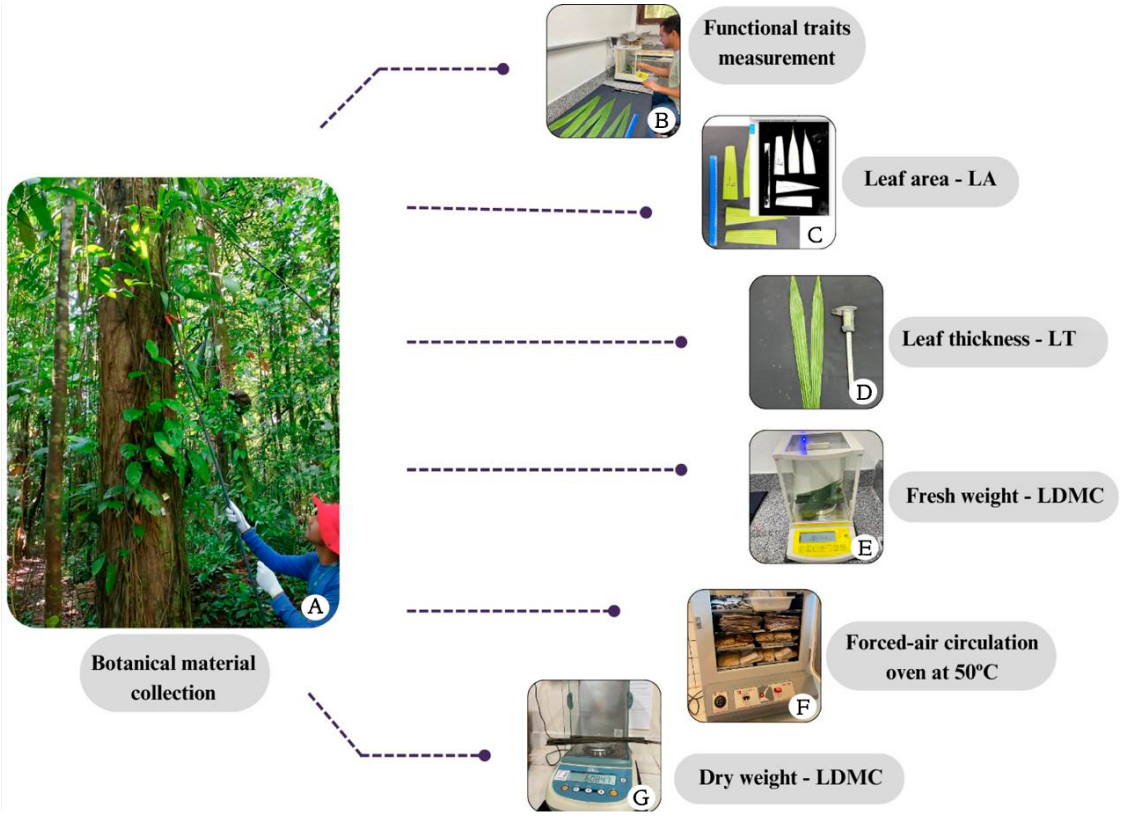


Figure 3. Field collection and laboratory procedures used in this study, to obtain: **A**) Botanical material; **B**) Measurements of LA; **C**) LA processing using ImageJ software; **D**) LT measurements; **E**) Fresh mass measurement for LDMC calculation; **F**) Leaves dried in a forced-air circulation oven at 50 °C for measurement of dry weight and LDMC; **G**) Dry mass measurement for LDMC and SLA calculations.

Table 1. Summary statistics (minimum [Min], mean, standard deviation [SD], and maximum [Max]) for the traits measured for *Evodianthus funifer* in upland and white-water floodplain forests.

Traits	Upland forest			Floodplain forest		
	Min	mean ± SD	Max	Min	mean ± SD	Max
H (m)	0.670	1.934 ± 0.758	3.370	1.000	2.549 ± 0.935	4.880
LA (cm^2)	0.014	0.031 ± 0.007	0.040	0.021	0.042 ± 0.011	0.062
LD ($g\ m^{-3}$)	0.100	0.172 ± 0.051	0.272	0.162	0.373 ± 0.247	1.141
LDMC (g)	0.231	0.275 ± 0.035	0.345	0.233	0.295 ± 0.025	0.336
LT (mm)	0.287	0.593 ± 0.181	0.960	0.247	0.377 ± 0.151	0.713
SLA ($cm^2\ g^{-1}$)	5.711	12.998 ± 6.674	32.726	2.871	9.655 ± 2.950	16.652
SSD ($mg\ mm^{-3}$)	0.278	0.261 ± 0.271	0.680	0.271	0.242 ± 0.257	0.750
PL (cm)	9.800	23.568 ± 5.036	30.020	17.460	31.816 ± 6.897	45.220

Linear Mixed-Effects Models (LMMs), with vegetation type treated as the fixed effect and individuals as a random effect to account for non-independence among leaves from the same individual (Bredin et al. 2020b).

Principal component analysis (PCA) was used to examine the patterns of leaf trait variation across contrasting environments (Batista et al. 2021). Functional traits were standardized prior to the analysis (El-Abeid et al. 2025). Pearson's correlation analysis was used to explore the relationships among the functional leaf traits (Carvalho et al. 2026). All analyses were performed in R software version 4.3.1 (R Core Team 2026). LMMs were fitted using the *lme4*, *lmerTest* (Kuznetsova et al. 2017) and *performance* packages (Lüdecke et al. 2021). PCA and graphical outputs were generated using the *FactoMineR, factoextra, vegan* in PCA and *ggplot2* packages (El-Abeid et al. 2025).

RESULTS

Individuals of *E. funifer* showed intraspecific variation between upland and white-water floodplain forests in several functional traits. Forest type significantly affected LA, LD, LT, PL and SLA, according to the linear mixed models. Variance partitioning indicated a strong contribution of the random effect to trait variation among individuals (Table 2). Individuals in white-water floodplain forests exhibited greater LA (Figure 4a), LD (Figure 4b), PL (Figure 4d) and SLA (Figure 4e), whereas those from upland forests showed greater LT (Figure 4c). These differences indicate significant trait responses to contrasting environmental conditions. However, LDMC (Figure 4f), SSD (Figure 4g) and Height (Figure 4h) did not differ significantly between forest types (Figure 4).

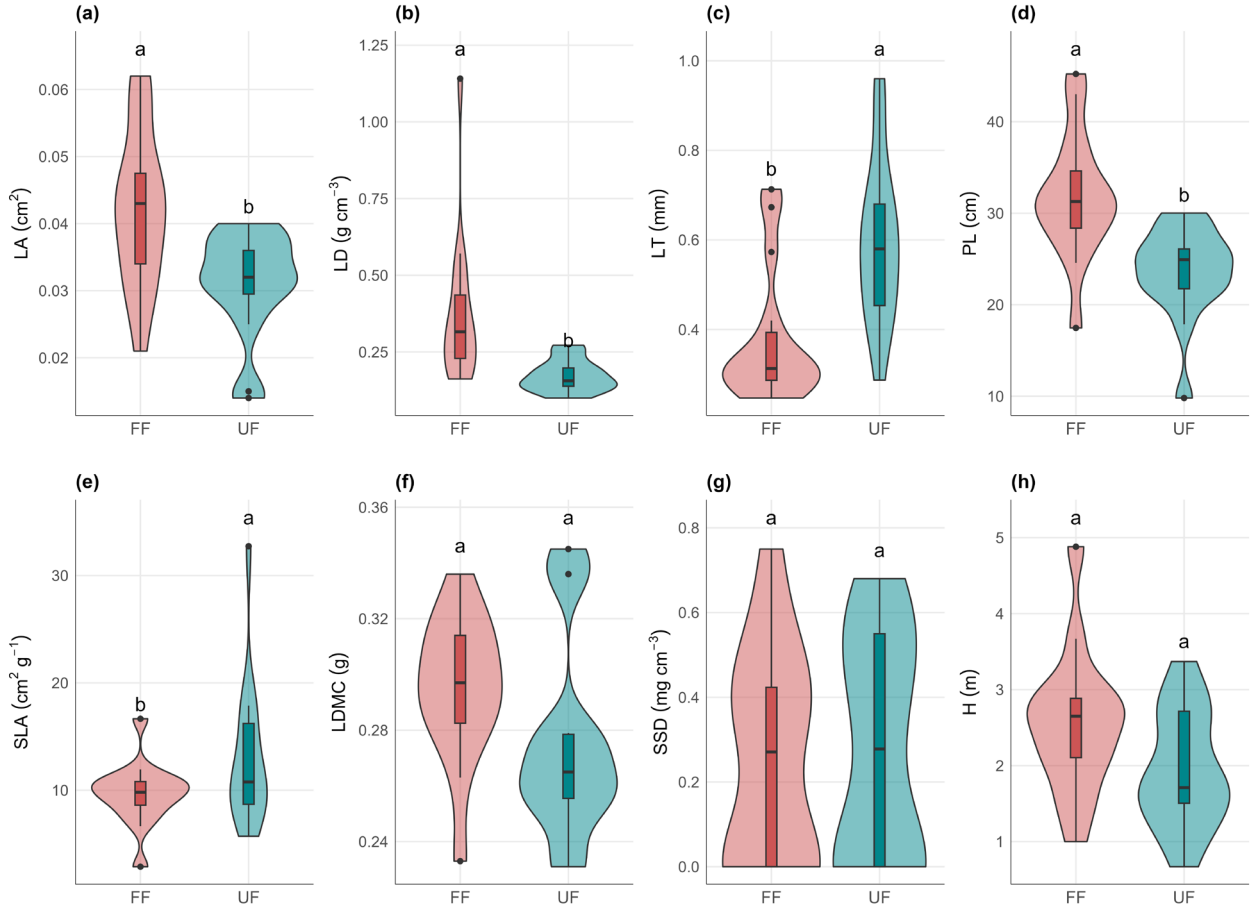


Figure 4. Violin plots showing the comparisons of **A**) leaf area (LA), **B**) leaf density (LD), **C**) leaf thickness (LT), **D**) petiole length (PL), **E**) specific leaf area (SLA) (analyzed with Linear Mixed-Effects Models), **F**) leaf dry matter content (LDMC), **G**) stem specific density (SSD) (analyzed with Wilcoxon test), and **H**) height (H) (analyzed with T-tests) of n (30) *Evodianthus funifer* individuals between white-water floodplain (FF) and upland forests (UF). Different letters indicate significant differences between vegetation types ($p < 0.05$).

The first and the second PCA axes explained 30.373% and 18.136% of total variance, respectively (Table 3). Individuals from upland and white-water floodplain forests were separated along the PC1 axis, which was positively associated with H, LA, LD, LDMC and PL, and negatively associated with LT, SLA and SSD. PC2 was associated with variation in LT

Table 2. Summary statistics of the linear mixed models testing the difference between forest types (upland and floodplain forests). Conditional R^2 is the variance explained by the fixed effect (forest types) plus the random effect (leaves within individuals), and marginal R^2 is the variance explained by the fixed effect (forest types).

Traits	Estimate	t value	p value	Conditional R^2	Marginal R^2
LA (cm^2)	-0.010	-2.669	0.012	0.474	0.112
LD (g m^{-3})	-0.196	-2.948	0.006	0.677	0.167
LDMC (g)	-0.013	-0.894	0.379	0.296	0.011
LT (mm)	0.216	3.526	0.001	0.867	0.263
SLA (cm^2 g^{-1})	-8.248	-3.74	0.001	0.684	0.239
PL (cm)	3.775	2.077	0.047	0.391	0.065

Table 3. Results of the two-axis principal component analysis (PCA) based on eight functional traits measured for *Evodianthus funifer* in upland and floodplain forests of Eastern Amazon. Trait loadings on the first two components, eigenvalues, variance explained (%) and broken-stick criterion are presented.

Traits	PC 1	PC 2
H (m)	0.149	-0.336
LA (cm^2)	0.626	-0.083
LD (g m^{-3})	0.643	-0.188
LDMC (g)	0.610	0.597
LT (mm)	-0.427	0.842
SLA (cm^2 g^{-1})	-0.564	-0.475
SSD (mg mm^{-3})	-0.384	-0.004
PL (cm)	0.764	-0.068
Broken-Stick	0.340	0.215
Eigenvalue	2.429	1.450
% explanation	30.373	18.136

and SLA, and this variation was higher for upland forest individuals. Two distinct leaf trait patterns were observed: higher values of H, LA, LD, LDMC, and PL were strongly associated with white-water floodplain forests individuals, whereas higher values of LT, SLA, and SSD were more closely associated with upland forest individuals (Figure 5).

Significant negative correlations (Figure 6) were observed between LA and LT ($r = -0.376$; $p = 0.040$), LD and LT ($r = -0.433$; $p = 0.017$), LD and SLA ($r = -0.499$; $p = 0.004$), and LDMC and SLA ($r = -0.442$; $p = 0.014$). A significant positive correlation was observed between LA and LDMC ($r = 0.520$; $p = 0.003$). No significant correlations were found between the other analyzed leaf traits ($p > 0.05$).

DISCUSSION

Our findings reveal clear intraspecific variation in the leaf functional traits of *Evodianthus funifer* across contrasting environments. *E. funifer* individuals exhibited distinct combinations of leaf and stem traits that reflect adaptive strategies in response to the contrasting environmental pressures of each forest type, partially supporting our hypothesis. Variance partitioning further showed that a substantial proportion of trait variation was attributable to random effects, highlighting the high degree of intraspecific variation within individuals. Rather than conforming to a classical acquisitive–conservative pattern, functional trait variation in *E. funifer* appears to be primarily driven by abiotic differences in light and water availability, key environmental factors influencing the functional traits of understory plants.

Intraspecific variation in leaf traits enables the species to adopt alternative strategies for resource acquisition and conservation depending on habitat conditions (Mantuano et al. 2021). For example, in white-water floodplain forests, individuals exhibited greater leaf area, more elongated petioles and higher leaf density. Larger leaves imply increased photosynthetic surface, while elongated petioles reduce self-shading (Weijschedé et al. 2006) and facilitate leaf positioning above the seasonal flood (Cox et al. 2004). These traits, acting in combination, likely confer advantages such as water balance (Wright et al. 2007; Guzmán-Jaco et al. 2022), and photosynthetic performance under contrasting understory light conditions (Petter et al. 2016). In turn, higher LD may increase mechanical resistance to abiotic stresses, favoring the plant's persistence in the habitat (Zheng et al. 2025). They may also enhance tolerance to the hydrological variation associated with seasonal flooding, a major abiotic factor in floodplain systems (Mori et al. 2019; Roa-Fuentes et al. 2022).

Ecophysiological adjustments driven by contrasting conditions of light and water availability also affected leaf area and leaf thickness. Smaller and thicker leaves are expected under situations of water limitation—typical in upland environments—because they have extended longevity and lower water loss rates (Wright and Westoby 2002; Hu et al. 2020). Reduced leaf area may minimize transpirational water loss and leaf tissue heating in drier habitats (Lopes and Melo Júnior 2019). Adaptations to limited water availability also include increased leaf thickness, which enhances thermal protection, reduces evaporation, and increases water storage capacity to cope with water scarcity in drier regions of the Amazon (Rebelo et al. 2024). Consistent with these expectations, individuals in upland forests exhibited significantly greater LT than those in white-water floodplain forests. Increased LT in drier environments is a strategy that promotes leaf resistance and resource-use efficiency, serving as an ecological adaptation to reduce water loss, increase

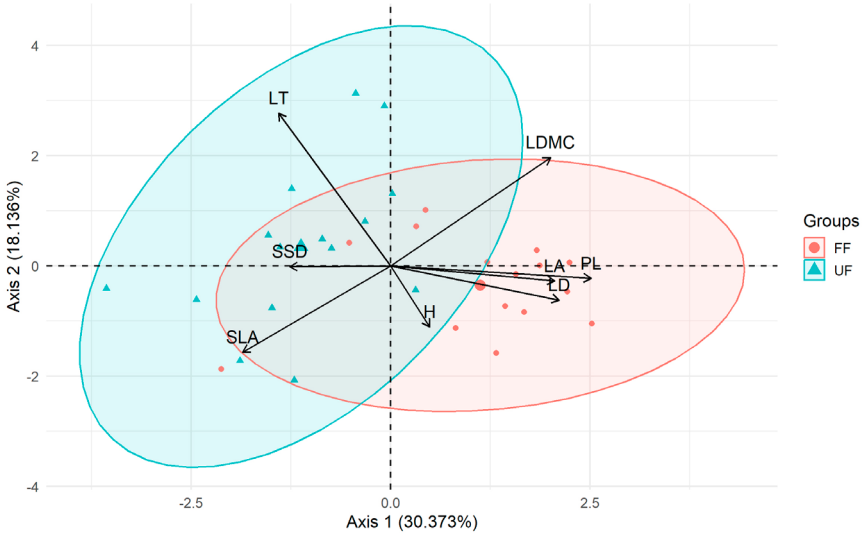


Figure 5. Principal component analysis (PCA) of functional traits of *Evodianthus funifer* in floodplain (FF) and upland forests (UF). Plant height = H, leaf area = LA, leaf density = LD, leaf dry matter content = LDMC, leaf thickness = LT, petiole length = PL, specific leaf area = SLA, stem specific density = SSD.

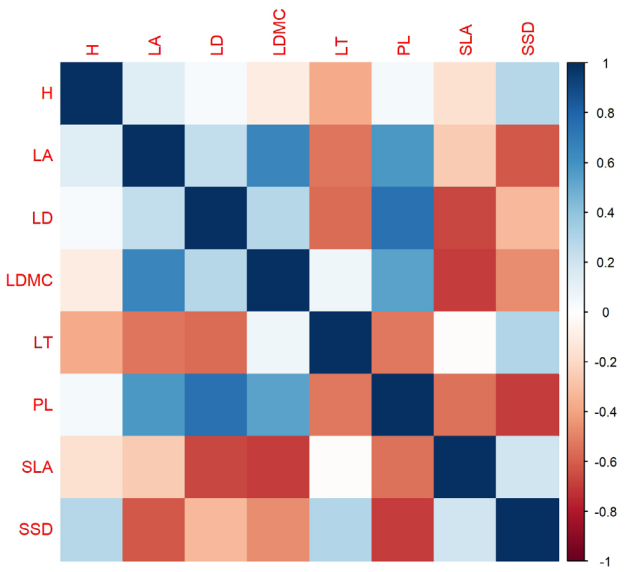


Figure 6. Correlations between leaf functional traits of *Evodianthus funifer* (Poit.) Lindm. (Cyclanthaceae). Significant correlations ($p < 0.05$) are shown in color, whereas non-significant correlations ($p \geq 0.05$) are shown in white. The intensity of the correlation ranges from −1 (strong negative correlation, red) to +1 (strong positive correlation, blue). Plant height = H, leaf area = LA, leaf density = LD, leaf dry matter content = LDMC, leaf thickness = LT, petiole length = PL, specific leaf area = SLA, stem specific density = SSD.

drought tolerance, and reduce evaporative water loss (Simioni et al. 2017; Silva et al. 2019). Thicker leaves also help prevent overheating and water loss through transpiration under dry and sunny conditions (Petter et al. 2016; Simioni et al. 2017). Leaf functional traits that favor water storage are particularly important in drier environmental conditions, enhancing plant tolerance to water scarcity in less humid areas (Costa et al. 2020), such as those of the Amazonian upland forests.

Variation in SLA indicates morphological adjustments of leaves to environments with different light levels (Araújo et al. 2023). The higher SLA values observed in individuals from the floodplain forest may reflect the maximization of photosynthetic area per unit of biomass invested, thereby enhancing light capture in the forest understory and indicating a high degree of plasticity in this functional trait under low-light conditions (Hietz et al. 2022). As a classical plastic response to reduced light availability, increased SLA is often associated with the production of less dense leaves, resulting in lower LD and LDMC values (Charles et al. 2022).

However, low LD was observed in upland individuals, potentially associated with increased intercellular air spaces. This adjustment can enhance internal water transport and support transpiration and photosynthesis (Poorter et al. 2009), which may be advantageous in upland forests characterized by drier environments (Zuleta et al. 2022). Conversely, higher LD observed in floodplain individuals may reflect a greater mesophyll fraction or a higher concentration of lignified tissue, contributing to increased mechanical resistance and potentially enhancing plant survival (Niinemets 1999; Poorter et al. 2009). These traits may help maintain leaf structural integrity in environments subject to seasonal hydrological fluctuations (Matos et al. 2018).

While SLA and LD differed significantly between environments, no significant differences in LDMC were detected between the two environments. However, our results regarding LDMC are consistent with those of Charles et al. (2022), who suggested limited influence of abiotic factors, such as flooding, on this trait. Furthermore, interactions such as herbivory (Bröcher et al. 2023) and symbiotic associations can also affect leaf allocation patterns (Botelho et al. 2025). This decoupling among LT, SLA, and LDMC indicates that the different components of leaf construction respond independently to environmental conditions. These findings stress our conclusion that the observed functional variation does not conform to the classical acquisitive–conservative patterns commonly described for Amazonian vegetation.

No significant differences were observed between vegetation types for SSD and H, suggesting that functional traits related to mechanical support and competitive ability remained relatively conserved between Amazonian environments. Instead, traits that showed significant intraspecific variation (LA, LD, LT, PL, and SLA) were linked to water-use and light strategies, suggesting that water availability and light exert a stronger influence on functional trait leaf variation than functional trait stem between forest types (Baraloto et al. 2010). These findings underscore the significant role of hydric stress and light in shaping species' ecophysiological strategies and suggest adjustments that enhance water supply to leaves under varying environmental conditions (Carvalho et al. 2024).

The observed correlations among leaf traits were partially consistent with our hypothesis. Significant negative relationships were observed between LA and LT, LD and LT, LD and SLA, and LDMC and SLA, indicating functional adaptations of leaves of *E. funifer* to the contrasting environmental conditions. These patterns reflect key trade-offs in *E. funifer* populations in the Eastern Amazon. Specifically, there appears to be a trade-off between investment in thicker, denser and more durable leaves (high LD and LMDC values), which enhances water retention and durability under drier conditions, and investment in larger, thinner leaves (high SLA values), which may increase photosynthetic efficiency but reduce structural robustness and longevity (Mori et al. 2019; Rebelo et al. 2024). Such contrasting strategies likely reflect selective pressures imposed by differences in resource availability and environmental stress in tropical forests (Mantuano et al. 2021).

Previous studies in the Amazon region have focused primarily on trees, revealing ecological strategies that are closely related to variations in soil nutrient availability (e.g.,

Matos et al. 2018; Bredin et al. 2020b; Batista et al. 2021; Carvalho et al. 2024; Chaves et al. 2025; Carvalho et al. 2026). In contrast, the present study adopted a novel perspective by focusing on a nomadic climber—an understudied plant group that may be particularly vulnerable to climate change due to its sensitivity to environmental variation and dependence on both soil conditions and host availability throughout its life cycle (Riordan et al. 2023). Furthermore, rather than emphasizing edaphic factors alone, we highlight functional adaptations across environmental gradients. By investigating *E. funifer*, we highlight the role of phenotypic plasticity in mediating responses to contrasting hydrological and light conditions in upland and white-water floodplain forests.

CONCLUSIONS

Evodianthus funifer exhibited intraspecific adjustments to the contrasting environments in upland and white-water floodplain forests. These adjustments underscore the species' ability to adjust to distinct environmental constraints. The classic acquisitive–conservative pattern did not apply to intraspecific variation among individuals of the studied species. Understanding such functional adaptations provides insight into how nomadic climbers balance survival strategies across contrasting habitats, especially considering the imminent challenges posed by climate change to Amazonian ecosystems. Future research should explore gaps such as genetic variability, biotic interactions, herbivory pressure, and successional dynamics to better understand the functional diversity of *E. funifer*. Our study supports the view that environmental filtering across hydrological gradients can shape functional strategies not only at the community level but also within species.

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