Coexistence of understory tree species via architecture differentiation in the Atlantic Forest of southern Brazil

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Abstract – Resource allocation, plant architecture, and ontogenetic differences are important axes of niche differentiation that promote plant species coexistence in tropical forests, contributing to the high diversity observed in these ecosystems. To test the predictions of species coexistence, differences in tree architecture were compared in a seasonal, semi-deciduous forest throughout the developmental stages. Four 3000 m^2 stands with canopy cover higher than 90% were established in a protected area in southern Brazil. All individuals from three understory species were identified, and their diameter, height, and crown were measured, and comparisons in the architecture of species were made with height-class specific allometric relationships. *Inga marginata* invested primarily in vertical growth, with pronounced development of crown area and plasticity in crown morphology only in the last height class, while *Sorocea bonplandii* invested more in lateral growth to ensure mechanical stability, reducing the likelihood of trunk breakage. The same was observed in juveniles of *Actinostemon concolor*, which maximized investment in crown development after reaching a certain height. Although only three understorey species were studied, understanding how these species coexist is important for providing valuable insights into the mechanism of species coexistence in tropical ecosystems. Despite their location in the understorey stratum, these species play critical roles in structuring and maintaining species diversity in the forest. Focused studies on a smaller number of species can help to understand the underlying mechanisms that regulate coexistence and provide important information for the management and conservation of biodiversity in tropical ecosystems.

Keywords: *Actinostemon*. Atlantic Forest. *Inga*. Niche. Stratum. *Sorocea*.

1 Introduction

The resource allocation pattern and the architecture of plants are important niche axis differentiation promoting coexistence in a forest [1,2]. According to niche theory, species that share similar resource needs tend to compete intensely within the same environmental area, often leading to the exclusion of the less competitive species under specific resource and condition combinations. Consequently, coexistence in diverse communities becomes feasible when species utilize the same resources in distinct ways or inhabit separate environmental niches, demonstrating niche differentiation [3–5]. Individuals of a particular tree species can have different architectures during their development and these differences are important to explain the richness pattern of tree species in tropical forests [1,6,7]. Tropical forests exhibit vertical stratification of vegetation due to different strategies adopted by trees to maximize light absorption. The vertical stratification creates a gradient with different luminosity levels. The light intensity ranges from 1% to 4% on the forest floor to 100% above the canopy (emergent layer) [8]. So, the understory species need to have adaptations in architecture, which permits their establishment in a forest stratum where luminosity is extremely limiting [9]. For instance, shade-intolerant species have high growth and mortality rates, presence correlated to gaps, and tend to decline in populational abundance when the forest regenerates. On the other hand, shade-tolerant species exhibit slow growth and low mortality, which allow survival and growth in the shaded forest understory [10,11].

Tree architecture refers to the overall shape of the tree and the spatial position of its components [8,12,13]. It is a result of a trade-off between vertical (Height) and lateral growth (Crown) [14,15] determining its position in the forest canopy and hence its access to light. Finally, the tree architecture reflects the current conditions under the individual is growing, associated with genetic and environmental factors that operate from the initial

stages until maturity [16,17]. Differences in architecture can be quantified through allometric relationships between diameter, height, and crown [16,18].

One important factor that determines the success of a tree species in terms of light interception is crown architecture. However, it should also be noted that the height of the tree plays a crucial role in determining its position along the vertical light gradient and therefore, in determining the amount of light intercepted [8,13,19]. In rain forests understories, the light is an extremely limiting resource [1,8]. For instance, in a Tropical Forest located in southeast Liberia, the researchers found just 13% of 53 species living in darker light environments than expected [11]. On the other hand the same 13% of 53 species ocurred in brighter environments than expected and the majority (~75%) showed a random distribution related to luminosity, suggesting that the species are partitioning the light gradient, and niche differentiation may occur.

Understory and juveniles of canopy/emergent species were hypothesized to have architectural changes to adapt in a light-limited environment [1,18,20]. But understory species are adapted to live their entire life cycle in the understory environment, characterized by limited light availability. As a result, they tend to have wider crowns and smaller investment in height, maximizing investments in crown development. In addition, these species allocate carbon to an increase in diameter, which provides a greater safety margin against breakage. This allocation strategy is related to their expansion in horizontal branches, as understory species are always shorter than canopy species and tend to have wider crowns [18,20].

The present study aimed to compare tree architecture of three understory species in a seasonal semi-deciduous forest. We predicted that individuals exhibit differences in allometric relationships throughout development stages and these differences may be contributing to species coexistence in the tree community. We predict that although the

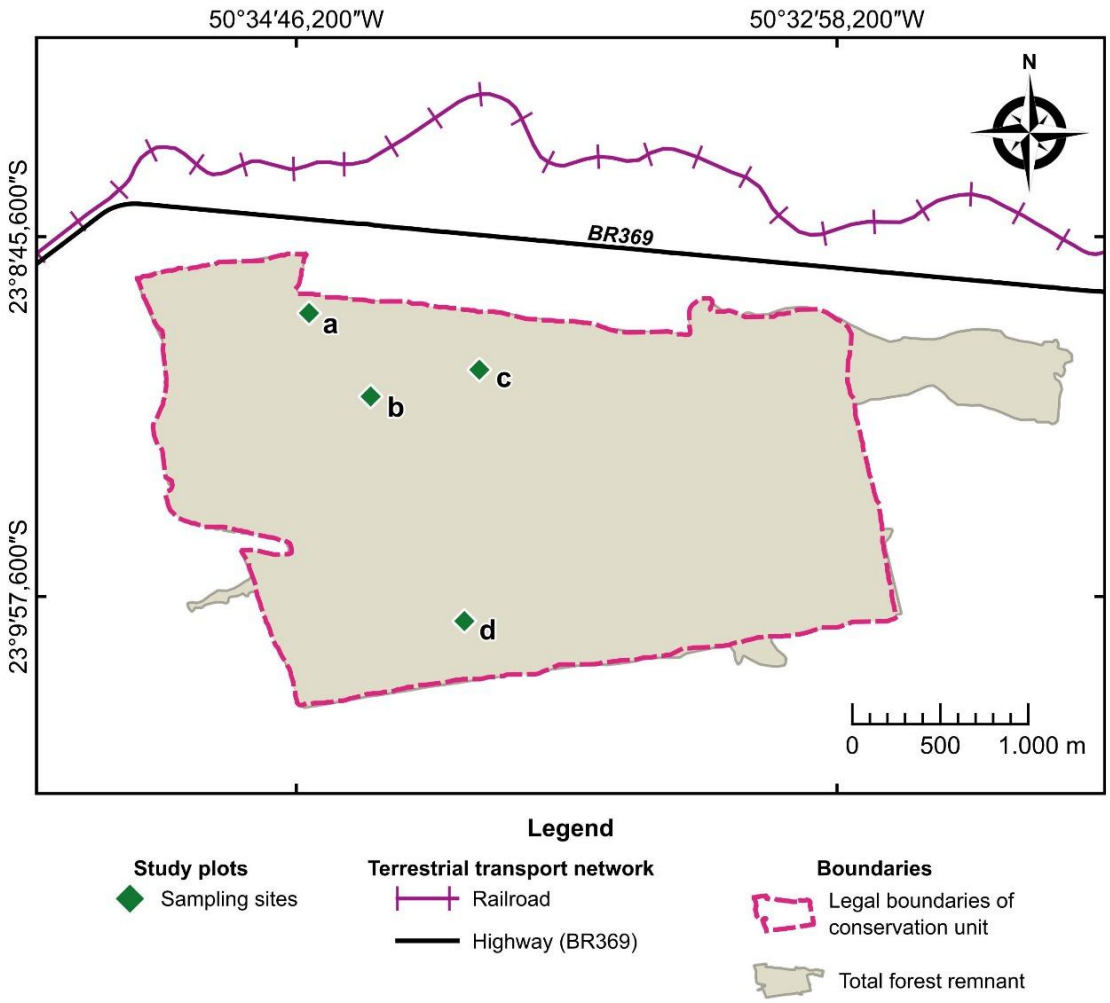
three species belong to the same stratum (understory) and exhibit more similar allometric relationships, they may show differences in their architecture, enabling the coexistence of multiple species in a single stratum. We also predict that the architecture of species will show differences in allometric relationships in the upper height classes, allowing coexistence in the understory.

2 Methods

2.1 Site description

The study was conducted in a seasonal semi-deciduous forest Conservation Unit remnant classified as a phytophysiognomy of Atlantic Forest Biome in northern Paraná state, southern Brazil [21]. The Mata São Francisco State Park (SSFSP) (23º09'55"S, 50º33'51"W; center of the fragment) has ~833 hectares and for many years, the selective logging of commercial tree species (wood or food) in the fragment was the main anthropogenic activity (Fig. 1). These anthropogenic interferences ended in 1994 when it became a protected area. As a result of selective logging, wide gaps, excessive lianas and bamboos are present [22,23], but the disturbance occurred in the past was not homogeneous throughout the fragment, resulting in a mosaic of preserved areas with highly impacted areas and intermediate areas of conservation [22–26].

The region's climate, according to Köppen classification, is characterized as Cfa – humid subtropical mesothermal, with average rainfall between 1200–1400 mm, distributed unevenly throughout the year [27]. The predominant soils are Eutroferric Red Latosols and Eutroferric Red Nitosols, with inclusions of Chernosols and Gleysols, considered as high fertility soils [28].



117

118 **Fig. 1.** Location of São Francisco Forest State Park (SFFSP) Conservation Unit, in northern
119 Paraná, Brazil. Four plots were selected for our study (letters a, b, c and d, green points). Created
120 by Nascimento, J. G. F.

121 **2.2 Selection of study species**

122 Three understory species were selected by the importance value index (IVI) in
123 phytosociological surveys of region [29–31]: *Actinostemon concolor* (Spreng.) Müll. Arg.
124 (Euphorbiaceae) (Eighth in Godoy Forest State Park (GFSP); absent in São Francisco
125 Forest State Park (SFFSP)), *Inga marginata* Willd. (Fabaceae) (Tenth in GFSP;
126 seventeenth in SFFSP) and *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & De Boer
127 (Moraceae) (twenty-first in GFSP; ninth in SFFSP). The Importance Value Index (IVI) is

data numerically expressing the importance of a particular species among trees in a forest community. The IVI species in a community is determined by the sum of its density, frequency and dominance values expressed in percentages.

2.3 Stand investigation

Four plots were allocated in SSFSP with 3000 m^2 (50 m × 60 m) each. Data was collected in four plots within the continuous forest of the park, all plots with a vegetation cover index above 90% (selection criterion for plot), ensuring the same phytophysiognomy for all four plots. Furthermore, selective logging indicators easily observed in the field were selected as criteria for selection of areas based on presence of adult individuals of *A. polyneuron* and absence of dominance by bamboo grass *Merostachys paranaensis* Araujo & Bianchini [32]. *Aspidosperma polyneuron* it was the main species selectively logging exploited due to the high commercial value and quality of wood [33]. The distance between areas is at least 500 meters.

Individuals with a height of ≥ 0.50 m of three species were sampled during 2013 and 2014. All individuals were measured (Table S1, S2 and S3) the diameter at ground height (DGH, in cm), the total height (H, forest floor to top of crown, in m), the height of the lowest branch (forest floor to the first living branch, in m) and the two cross-sectional crown diameters (DI and DII, in m). The individuals that had some breakings were excluded from analysis. The measurements in the field were realized with a caliper and tape measure for the diameters and the smaller individual heights and a laser measuring tool for larger individuals (above 10 m).

For larger individuals, the circumferences at ground height were measured (C, in m) and subsequently transformed into DGH, using the formula: $DGH = C/\pi$. Crown depth (CD, in m) was calculated by subtracting the height of the first living branch from the

total height (H). Horizontal crown area (HCA, in m^2) [34] and vertical crown area (VCA, in m^2) [35] was estimated as an ellipse following the equations, respectively:

$$\mathrm{HCA} = 0.25 \times \pi \times \mathrm{DI} \times \mathrm{DII},$$

$$\mathrm{VCA} = 0.25 \times \pi \times \left(\frac{\mathrm{DI} + \mathrm{DII}}{2}\right) \times \mathrm{CD}.$$

The Crown volume (CV, in m^3) was estimated assuming a half-ellipsoid shape [36] as:

$$\mathrm{CV} = \frac{1}{2} \times \frac{4}{3} \times \mathrm{HCA} \times \mathrm{CD}$$

Trunk slenderness (TS) was estimated by formula: TS = H/DGH [37]. The allometric relationships measured were: DGH×H, CD×H, CV×H.

2.4 Data analysis

To compare tree architecture between species, individuals were divided into four height classes: ≥0.50 m and ≤1.50 m (Class 1), >1.50 m and ≤3.0 m (Class 2), >3.0 m and ≤6.0 m (Class 3), >6.0 m (Class 4). The separation of height classes it is very important because allows comparisons among individuals of similar height and under similar environmental conditions [8,13,18]. Comparisons of allometric relationships among species by height classes were made by Standardized Major Axis (SMA). The SMA analysis is more indicated for this analysis because it assumes that the errors are independent of each other (the variables are dependent on each other) [38]. To express these relationships, the following equation was used:

$$y = \alpha + \beta \mathrm{x}.$$

The differences in allometric comparisons can occur in β (slope regression) or in α (*y* intercept). If β differs among populations, the population with highest β will have the greatest investment in *y* per increment of *x*. If there is no difference in β, but there is

175 difference in α, those with a higher α will possess a greater *y* at any value of *x* [39,40].
176 The comparisons of β and α were considered significant at the 5% level [38].

177 Multiple comparison tests ($p<0.05$) were performed to verify which relations
178 differed. We used ANOVA and Tukey's test ($p<0.05$) to evaluate if had differences in
179 architectural variables between species within each height class. All tests were performed
180 in Rstudio version 2025.05.1 Build 513 [41], using the SMATR library for allometric
181 comparisons [38,42,43] and STATS library for ANOVA and Tukey's test.

182 **3 Results**

183 We sampled 6915 individuals in the four areas (*A. concolor*: 3380; 48.9%); *I.*
184 *marginata:* 785; 11.4%); *S. bonplandii*: 2750; 39.8%). As informed in Methods,
185 individuals with some trunk breakpoints were removed from the analysis, as follows: 479
186 individuals of *A. concolor* (14.17%), 276 individuals of *I. marginata* (35.16%) and 581
187 individuals of *S. bonplandii* (21.13%) were excluded.

188 In all height classes, *I. marginata* showed an architecture that invested more in
189 height than diameter, resulting in the highest slenderness when compared to *A. concolor*
190 and *S. bonplandii* (Table 1, Figure S1-S4).

191 In the first height class, *A. concolor* allocated more resources towards crown
192 architecture, exhibiting the greatest values for HCA, VCA, and CV for the same value of
193 H or DGH, while *I. marginata* had a wider vertical crown and allocated fewer resources
194 towards the crown (Table 1, Figure S1). *Actinostemon concolor* also had the smallest
195 morphological inversion point for crown formation when compared to *I. marginata* and
196 *S. bonplandii* (Table 1).

197 In the second height class, *A. concolor* continued to exhibit an architecture that
198 invested in crown area expansion, with greater values for HCA, VCA, and CV for any
199 value of H, while *I. marginata* allocated more resources towards height growth (Table 1,

Figure S2). In the third height class, *I. marginata* started investing more in crown volume, exhibiting greater values for HCA and CV for the same value of DGH, while *A. concolor* continued to allocate resources towards crown area expansion and diameter growth (Table 1, Figure S3).

In the fourth height class, *A. concolor* continued to invest in crown architecture, with greater values for CD, VCA, and CV for the same value of H or DGH, while *I. marginata* had the lowest investment in crown volume (Table 1, Figure S4).

In summary, *I. marginata* consistently showed an architecture that invested more in height than diameter, resulting in the highest slenderness when compared to *A. concolor* and *S. bonplandii*. *A. concolor* consistently allocated more resources towards crown area expansion, while *S. bonplandii* showed a greater investment in diameter growth (Table 2).

Table 1 Estimation of linear regression (SMA) of the three understorey species (*Actinostemon concolor* - AC, *Inga marginata* - IM, *Sorocea bonplandii* - SB) sampled in Mata São Francisco State Park, southern Brazil. The species were divided into height classes (H). H1 = 0.5 ≥ H ≤ 1.5 m; H2 = 1.5 > H ≤ 3.0 m), H3 = 3.0 > H ≤ 6.0 m; H4 = H > 6.0 m). DGH = diameter at ground height (cm); H = height (m); CD = crown depth (m); CV = crown volume (m^3); n = number of individuals; α = y intercept; β = slope; r^2 = correlation coefficient. The different superscript letters in the same column for each allometric relationship indicate values that are significantly different (multi-comparison test, $p<0.05$); ns, not significant ($p>0.05$); ns = represents the values of allometric relationships (β or r^2 values) that were not significant.

Class	Species	α	β	r^2	α	β	r^2	α	β	r^2	n
H1			DGH×H			CD×H			CV×H		
	AC	0.07	0.92^{a}	0.64^{***}	-0.25	0.76^{a}	0.48^{***}	-0.13	0.22^{a}	0.49^{***}	1529
	IM	0.06	0.81^{b}	0.59^{***}	-0.15	0.67^{b}	0.43^{***}	-0.04	0.05^{c}	0.25^{***}	331
	SB	0.06	0.93^{a}	0.58^{***}	-0.19	0.70^{b}	0.48^{***}	-0.13	0.18^{b}	0.34^{***}	1335
H2			DGH×H			CD×H			CV×H		
	AC	-0.65	1.30^{a}	0.53^{***}	-0.75^{a}		0.41^{***}	-1.60	1.10^{a}	0.49^{***}	753
	IM	-0.24	0.85^{b}	0.48^{***}	-0.94^{c}	0.89^{ns}	0.24^{***}	-0.80	0.50^{c}	0.30^{***}	120

	SB	-0.67	1.20[a]	0.48[***]	-0.79[ab]		0.34[***]	-1.30	0.82[b]	0.35[***]	576
Class	Species	α	β	r^2	α	β	r^2	α	β	r^2	n
H3		DGH×H			CD×H			CV×H			
	AC	-1.90[a]		0.56[***]	-1.11[a]		0.40[***]	-16.00	5.30[a]	0.34[***]	462
	IM	-3.10[c]	1.50[ns]	0.34[***]	-1.70[c]	0.83[ns]	0.00[ns]	-6.00	1.90[c]	0.19[**]	42
	SB	-2.20[b]		0.53[***]	-1.30[ab]		0.37[***]	-14.00	4.40[ab]	0.35[***]	199
H4		DGH×H			CD×H			CV×H			
	AC	-7.90[a]		0.26[***]	-6.40	1.50[a]	0.18[***]	-127.0[a]		0.31[***]	157
	IM	-9.20[a]	2.20[ns]	0.36[**]	-4.80	0.96[b]	0.36[**]	-145.0[c]	22.00[ns]	0.41[**]	16
	SB	-7.80[a]		0.58[***]	-3.60	1.02[ab]	0.33[***]	-131.0[ab]		0.40[***]	59

Table 2 Architectural variables of three understorey species (*Actinostemon concolor* - AC, *Inga marginata* - IM, *Sorocea bonplandii* - SB) sampled in Mata São Francisco State Park, southern Brazil. The species were divided into height classes. H1 = 0.5 ≥ H ≤ 1.5 m; H2 = 1.5 > H ≤ 3.0 m; H3 = 3.0> H ≤ 6.0 m; H4 = H > 6.0 m. DGH = diameter at ground height (cm); CD = crown depth (m); CV = crown volume (m^3); TS = trunk slenderness. Different superscript letters in the same column indicate values that are significantly different (ANOVA and Tukey, $p<0.05$). Means comparisons were made only within height classes.

Class	Species	DGH	CD	CV	TS
	AC	0.94[b]	0.45[b]	0.08[a]	1.02[b]
H1	IM	0.78[c]	0.43[b]	0.02[c]	1.14[a]
	SB	0.98[a]	0.50[a]	0.06[b]	1.02[b]
	AC	2.00[a]	1.09[a]	0.68[a]	1.08[c]
H2	IM	1.57[c]	0.93[c]	0.28[c]	1.38[a]
	SB	1.83[b]	1.03[b]	0.46[b]	1.16[b]
	AC	4.53[a]	2.40[a]	7.58[a]	0.99[c]
H3	IM	2.85[c]	1.54[c]	1.71[c]	1.44[a]
	SB	4.07[b]	2.21[b]	5.12[b]	1.09[b]
	AC	7.86[b]	4.13[a]	30.83[a]	0.94[a]
H4	IM	9.46[a]	3.35[a]	42.95[a]	0.99[a]
	SB	8.98[a]	3.95[a]	37.06[a]	0.89[a]

4 Discussion

In the early stages of plant development (class H1 and H2), *A. concolor* exhibited an architecture based on crown area expansion while *I. marginata* and *S. bonplandii* invested primarily in crown depth. Firstly, by expanding the crown area the juveniles of *A. concolor* species increase light interception, which is crucial in low light environments

233 [18,20,44]. In addition, a larger crown area can also help plants to compete for light with
234 neighboring plants. In the understory, where light is limited and competition for light is
235 high, having a larger crown area can give a plant a competitive advantage over other
236 plants, allowing it to grow taller and access more enlightened stratum [8,37].

237 On the other hand, the crown depth investment exhibited by *I. marginata* and *S.*
238 *bonplandii* can help to increase the amount of diffuse light that reaches the lower leaves.
239 Diffuse light is light that has been scattered by the leaves of other plants or by the
240 atmosphere and is less intense than direct sunlight. In the understory, diffuse light is often
241 the main source of light for plants increasing vertical light interception [8,13,36,45].

242 *Inga marginata* species in the early stages of development (class H1 and H2)
243 exhibited a greater trunk slenderness than *S. bonplandii* and *A. concolor*. This strategy
244 based on a smaller investment in diameter allows a greater investment in height [18,20].
245 This pattern allows individuals to reach strata with greater luminosity faster than other
246 species, consequently allocating more resources for crown development [46,47]. These
247 results are consistent with Batista et al. (2014) [20] which also showed that architecture
248 of *I. marginata* in the initial early stages was similar to that of canopy and emergent
249 species. Differences in allometric relationships suggested different survival strategies
250 among juveniles of these species, related to phenotypic plasticity, essential for
251 coexistence in forests in the tree community [18,20].

252 In the third class, *I. marginata* showed variation in crown shape (low r^2 values for
253 significant for some correlations of crown variables). Plasticity in crown morphology can
254 increase tree survival, adaptive advantage in interspecific competition and the ability to
255 occupy different niches, allowing coexistence in a highly competitive stratum [18,48]. In
256 Addition, *I. marginata* exhibited a smaller investment in diameter and greater investment
257 in volume and crown area in comparison to *A. concolor* and *S. bonplandii*. This strategy

based on reduction of margin safety allows them to reach a higher-light environment although it may represent a risk against breakage [49–51].

Actinostemon concolor and *S. bonplandii* species exhibited a greater investment in stem diameter relative to height in comparison to *I. marginata*, providing greater resistance against breakage [18,51]. Bovolenta (2016) [26] conducted a study in the same plots of study and demonstrated that *I. marginata* exhibits demographic behavior that is opposite to that of *A. concolor*. *Inga marginata* shows a combination of low survival (~70%), high decreasing of height rate, and low growth of individuals, which suggests species shows a risky strategy for height growth with a lower safety margin against mechanical failure.

The tree species that gives up the safety margin against breakage, primarily investing in height in comparison to stem diameter, allow them quickly to reach a higher-light environment at the highest place in the understory (~10m). The high breakage rate of the *I. marginata* species may be related to the properties of the wood, which is highly elastic but with a higher breakage [52]. Wood elasticity may also be related to the high mortality rate of individuals. However, the species compensates for this mortality by presenting a high recruitment rate [26,53].

In the last height class (class H4), the three species began to invest in diameter and crown area in comparison to height, allow better crown support [54,55] promoting mechanical stability against breakage [13,35,51]. Since light is a limited resource in tropical forests, understorey species exhibited a greater investment in expansion of the crown, thereby maximizing light capture [39,46]. It was observed that *A. concolor* and *S. bonplandii* species allocated more resources in crown formation, maximizing light capture, similar to the most understorey species, which is advantageous for the survival in an environment with limited light [1,18]. *Inga marginata* species exhibited a smaller

283 investment in diameter and crown area which also observed by Batista et al. (2014) [20].
284 This architectural pattern enables it to occupy different niches, contributing to coexistence
285 within the community studied [20].

286 *Inga marginata* species primarily investing in vertical growth, crown area
287 development starting only in the last height class and plasticity in crown morphology,
288 while *S. bonplandii* exhibited a greater safety margin against breakage in vertical growth
289 in comparison to *I. marginata* and *A. concolor* maximizing investments in crown
290 development since juveniles with a greater safety margin against breakage.

291 These results confirm the hypothesis that understory species may exhibit
292 differences in their architecture which contributes to the niche partition [36,56–58],
293 allowing the coexistence of different allometric relations throughout the growth to the
294 maturity stage with the crown at the apex of the understory stratum [18,20]. The different
295 growth strategies observed in the different height classes for understory species showed
296 the changes in the resource allocation pattern throughout tree development in response to
297 environmental conditions and genotypes, generating changes in the architecture of the
298 species (Figure S5).

299 This manuscript reports on a plant architecture study from a semi-deciduous
300 seasonal forest in Brazil, demonstrating tree coexistence promoted by ontogenetic
301 differences in morphological traits as height and crown, contributing with valuable
302 information to understanding of community dynamics and the allometric relationships
303 developed be of interest to the modeling tree community.

304 **5 Conclusion**

305 The results of this study demonstrate that the ontogenetic variation in architectural
306 traits, such as differential investment in stem diameter, vertical and horizontal crown
307 development, and trunk slenderness, among coexisting understory tree species is not

random, but rather represents distinct growth strategies finely tuned to maximize light acquisition and mechanical stability under the constraints of the forest understory. These divergent strategies, operating across successive developmental stages, highlight the importance of phenotypic plasticity and niche partitioning as fundamental mechanisms promoting species coexistence and sustaining the structural and functional diversity characteristic of tropical forest communities.

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Ethics Declarations

Declaration of Competing Interest

The authors have no competing interests to declare that are relevant to the content of this article.

Data availability

The datasets generated during and/or analyzed are available from the corresponding author on reasonable request.

Consent to Publish

Not applicable.

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