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Research article

Tall stature and small leaves: ecological strategies that enhance tree growth across the subtropical Brazilian Atlantic Forest



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Oikos

2025: e11235

doi: [10.1002/oik.11235](https://doi.org/10.1002/oik.11235)

Subject Editor: Carolina Bello

Editor-in-Chief: Pedro Peres-Neto

Accepted 26 March 2025

Ecological strategies reflect the mechanisms used for species to sustain a population. Predicting plant growth in ecological communities is crucial, especially with climate change impacting ecosystem functioning. By employing a large dataset for the subtropical Brazilian Atlantic Forest (BAF), we evaluated whether species' relative growth rates (RGR) are explained by their ecological strategies. Principal component analyses summarised the relationships among functional traits (leaf, wood and stature traits) to inform about ecological strategies of 121 tree species. We tested three principal components as predictors of RGR for all species collectively, and canopy and understory species separately. Species exhibiting larger stature with small and structured leaves have faster growth. Tall canopy trees, with small leaves and softer wood grew faster,



Synthesis

Evaluating coordinated ecological strategies is key to understanding the determinants of tree species performance. Using data from 121 tree species in the subtropical Brazilian Atlantic Forest, we examined whether their relative growth rates (RGR) are explained by ecological strategies. A principal component analysis of leaf, wood, and stature traits identified three major strategy axes. Species with greater height and smaller, structured leaves exhibited faster growth. Canopy species with softer wood grew faster, while understory species grew faster with denser wood and nutrient-rich leaves. Coordinated trait strategies, especially greater height and smaller leaf area, determine species RGR and influence ecosystem functioning in this region.



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whereas understory species with taller stature, denser wood, and more structured and nutrient-rich leaves had higher RGR. Therefore, strategies that combine higher stature and smaller leaf area are key determinants of the higher relative growth rates of tree species from subtropical BAF, conferring a greater advantage in converting local resources into stem growth. These findings highlight the importance of understanding the coordination between trait-based ecological strategies and tree growth, which is essential for ecosystem functioning in changing environments.

Keywords: climate change, demographic trade-offs, fast-slow continuum, functional traits, maximum height, species performance

Introduction

Ecological strategies represent mechanisms used by species to sustain a population over time (Westoby et al. 2002), which may be assessed through species functional traits (Wright et al. 2007, Adler et al. 2014). Plant functional traits are morpho–physio–phenological features that impact fitness (Violle et al. 2007), affecting species performance in terms of growth, survival and reproduction (Laughlin et al. 2010, Visser et al. 2016, Siefert and Laughlin 2023). Thus, plant ecological strategies represent phenotypes that resulted from natural selection and enable a species to persist in a given environment (Laughlin 2023). However, the understanding of the relationship between plant species performance and their ecological strategies is not straightforward, varying across ontogenetic stages (Lasky et al. 2014, Klipel et al. 2021) and environmental conditions (Poorter and Bongers 2006, Laughlin et al. 2018, Bialic-Murphy et al. 2024). Therefore, in the context of current global climatic changes, it is crucial to expand our understanding of the link between plant performance and ecological strategies. This should shed light on the species role in the forest dynamics and overall ecosystem functioning (Díaz et al. 2004, Wu et al. 2023).

The effect of traits on performance can be evaluated at the species level, where consistent tradeoffs in the resource economics spectrum, including leaf, wood and stature traits, have been found globally (Wright et al. 2004, Chave et al. 2009, Díaz et al. 2016). The fast-acquisitive and slow-conservative tradeoffs in the plant economic spectrum may reveal species strategies across different environments (Adler et al. 2014, Reich 2014). For instance, in tropical moist forests, the acquisitive leaf and wood trait spectra are often related to light-demanding species that present fast tissue turnover and high resource capture, while the conservative side of the spectrum is related to shade-tolerant species that invest more in resource conservation (Reich et al. 2003, Poorter et al. 2008). In addition, acquisitive species tend to have higher growth but also higher mortality rates, while conservative species usually have higher longevity but lower growth rates (Sterck et al. 2006, Kunstler et al. 2016, Brienen et al. 2020). On the other hand, a second major dimension of ecological strategies is related to the tradeoff between recruitment and stature (i.e. stature–recruitment tradeoff), which ultimately influences the abilities of species for shade tolerance and growth potential (Rüger et al. 2018, 2020, Kambach et al. 2022). Therefore, species that present ecological strategies that confer poor demographic performance (i.e. slow growth,

low survival, and low reproduction) may be selected against and go extinct, as this rare combination might be unsuccessful in sustaining the population over time (Salguero-Gómez 2017, Russo et al. 2021).

The effort to comprehend the relationship between ecological strategies and species fitness (i.e. growth, survival and reproduction) has been extensively explored (Yang et al. 2018, Laughlin et al. 2020, Siefert and Laughlin 2023). However, as trees are long-lived organisms, assessing their survival and reproduction outcomes over time is challenging (Rüger et al. 2018). As a result, tree growth is the most studied fitness component across forest ecosystems (Poorter et al. 2008, Martínez-Vilalta et al. 2010, Bauman et al. 2022, Scalon et al. 2022). Overall, resource acquisition is expected to be a critical strategy for promoting plant growth during early life stages, such as saplings and juveniles (Poorter and Bongers 2006, Wright et al. 2010). Conversely, resource conservation becomes essential for enhancing tree survival in adulthood (Poorter et al. 2008), enabling trees to achieve larger stature (Rüger et al. 2020). However, previous assessments have shown variable relationships between ecological strategies and tree growth, being positive, negative, or absent, which may be linked to ontogenetic stage, taxonomic level, regional species composition, as well as the selected traits (Poorter et al. 2008, 2018, Wright et al. 2010, Paine et al. 2015, Forgiarini et al. 2015, Visser et al. 2016, Yang et al. 2018, Scalon et al. 2022). In addition, the shade tolerance that shapes the forest vertical gradient in light availability (through canopy and understory species, see Rüger et al. 2020) may also be an important factor influencing the relationships among resource-use strategies and tree growth (Rüger et al. 2012, Wills et al. 2018, Modolo et al. 2021). For instance, canopy species may benefit from the access to sunlight, while understory species remain shaded throughout their life cycle (Poorter and Bongers 2006). As a result, similar trait strategies can have distinct effects on tree growth trajectories. Consequently, understanding how ecological strategies are related to species growth in both compartments, forest canopy and understory, is still an open debate.

The effect of traits on fitness depends on the environmental context (Shipley et al. 2016, Laughlin et al. 2018). For instance, in tropical moist forests, structural traits such as larger leaf area (LA) can enhance photosynthetic assimilation by providing a greater surface for light capture (Díaz et al. 2016). However, this also increases exposure to environmental stressors, such as higher evaporative demands and susceptibility to temperature fluctuations. Traits associated with the leaf economic spectrum,

such as specific leaf area (SLA), leaf nitrogen content (LNC), and leaf phosphorus content (LPC), are frequently linked to faster growth rates (Wright et al. 2004, Poorter et al. 2008). In the absence of water limitation or temperature constraints, these traits are typically associated with high resource acquisition, increasing photosynthetic assimilation and enhancing tree growth, but at the cost of reduced tissue longevity and resistance to stressors. Conversely, investments in leaf dry-matter content (LDMC) and small leaves favours the resource allocation in a conservative form to deal with harsh environmental conditions (Fortunel et al. 2009). Similarly, wood density (WD) is typically associated with slower growth over time (Poorter et al. 2008, Kunstler et al. 2016), but it contributes to increased survival rates (Lida et al. 2014a). Whether these strategies still contribute to tree growth and species' performance under constrained environments requires broader empirical studies (Laughlin 2023). Meanwhile, tree height is often positively associated with growth, as taller trees can outcompete shorter individuals for light, conferring greater competitive advantage for resource acquisition in forests (Westoby 1998, Lida et al. 2014a). Assessing these traits and their coordination can help elucidate how tree species optimise their ecological strategies to enhance growth rates under distinct environments.

Highly diverse forests exposed to varying climatic conditions throughout the year may exhibit high dimensionality in ecological strategies (Rodrigues et al. 2021). For instance, the subtropical Brazilian Atlantic Forest (BAF) is characterised by having a great thermal amplitude throughout the year (temperature annual range varying between 16.3 and 23.2°C), with occasional frost and snow, and no dry season (Giehl and Jarenkow 2012, Alvares et al. 2013). This climatic constraint influences community assembly by shaping species composition and trait distributions in this region, favouring conservative traits (Klipel et al. 2023, 2024). Ultimately, the occasional adverse environmental conditions caused by temperature variability create harsh conditions that may shape trait coordination and species ecological strategies, thereby influencing overall ecosystem functioning across subtropical BAF (Forgiarini et al. 2015, Bordin et al. 2021, Klipel et al. 2023).

By using a large network of monitored plots in the Brazilian Atlantic Forest, we assessed whether tree species' relative growth rates (RGR) can be explained by their ecological strategies, in both canopy and understory forest strata. We selected seven functional traits related to species performance, including leaf, wood, and stature traits to obtain the species ecological strategies, and then, related them to the species RGR. We expect to observe a relationship between the ecological strategies and RGR, as well as differences in the ecological strategies of canopy and understory species. We predict that overall species employing more conservative strategies will exhibit higher RGR across the subtropical BAF, given their capacity to withstand adverse environmental conditions throughout the year in this region. However, for canopy species, we predict that those taller species with more acquisitive strategies will show higher RGR, as they typically have better access to sunlight and can allocate resources to growth efficiently. Finally, for understory species, we expect

that those with more conservative strategies will grow faster than their counterparts with acquisitive strategies, as under shaded conditions they may allocate more resources towards survival and stem growth over time.

Material and methods

Study sites and vegetation sampling

The Brazilian Atlantic Forest (BAF), characterised by a high level of biodiversity but also a high level of fragmentation (Ribeiro et al. 2009), covers a broad latitudinal range (from latitude 05°–30°S) with a notable environmental heterogeneity (Oliveira-Filho and Fontes 2000, Marques and Grelle 2021). The subtropical region begins at latitude 23° and acts as a significant abiotic filter for species occurrence, as it is characterised by a high thermal amplitude throughout the year, without seasonal variation in precipitation (Alvares et al. 2013, Forgiarini et al. 2015, Klipel et al. 2023). In addition, the high temperature during the summer usually leads to higher evapotranspiration, generating some atmospheric water deficit, while the winter season may be excessively cloudy in some regions, reducing light availability and consequently, photosynthesis (Cristiano et al. 2014, Díaz Villa et al. 2022). There are three major forest types within the subtropical BAF: Araucaria Forest, Seasonal Forest, and Atlantic Forest sensu stricto (s.s.) (Oliveira-Filho et al. 2015). Some tree species are more associated with a particular forest type, subject to specific climatic conditions. For instance, Araucaria Forest is characterised by the presence of two conifer species (*Araucaria angustifolia* and *Podocarpus lambertii*), as well as other temperate species (e.g. *Weinmannia paulliniifolia*) (Rambo 1951). On the other hand, Seasonal and Atlantic Forest s.s. are mainly characterised by tropical families, such as Lauraceae, Fabaceae and Myrtaceae species (Waechter 2002, Bordin et al. 2019).

We are using data from 60 permanent plots that were established and sampled twice to obtain forest dynamics information. The time census intervals are approximately five years on average, and individual growth may be derived from different time intervals. In addition, see the Supporting information for census intervals, plot size, spatial location, species richness, total number of stems, and average tree height per plot. Most forest inventories followed the RAINFOR protocol (Phillips et al. 2001, ForestPlots.net et al. 2021) (80% of the plots, Supporting information). In most plots, the diameter at breast height (dbh, in mm) was measured for all stems ≥ 50 mm, except for one plot where the dbh cutoff was ≥ 95 mm (FNC-01). For this plot, only the species present in other plots were selected, to avoid size-based bias. Each tree was identified at the species level and had the tree height (m) measured using telemetric or laser tapes. The stem measurements were taken at 1.3 m above the ground or 30 cm above buttresses/trunk irregularities using a diameter tape. This protocol was implemented during the first census (t0) and repeated during the second census (t1) when all surviving stems were re-measured to account for tree growth.

Species relative growth rates

We calculated the relative growth rate of each stem employing the formula from Eq. 1:

$$\text{RGR} = \frac{\text{dbh}_1 / \text{dbh}_0}{t} \quad (1)$$

where dbh_1 and dbh_0 are the final and initial dbh of each individual stem, respectively, and t is the time census interval in years (Kamimura et al. 2023, Rodríguez-Alarcón et al. 2024). To ensure reasonable precision of species-specific growth rate estimates and their functional traits, we selected species that had at least 10 stems within the dataset (Poorter et al. 2008), totalling 121 species and 11 264 stems (Supporting information). We calculated the mean RGR for each species based on the stem growth per species across all plots, resulting in a single value for each species derived from the summarisation of data from all plots. By using this equation, we minimise year-to-year variation in individual measurements, obtaining a robust estimate of the species' relative growth rates.

Functional traits

We selected species-level traits related to the leaf economic spectrum (Wright et al. 2004): specific leaf area (SLA), leaf nitrogen and phosphorous content (LNC and LPC); leaf dry-matter content (LDMC) and leaf area (LA); wood density (WD), a trait related to the wood economic spectrum (Chave et al. 2009); and maximum tree height amongst the tree individuals sampled (Height), which is a trait related to tree stature (Westoby 1998). All traits were measured in individual trees in different sites within the subtropical BAF, and the values used here correspond to the mean species value across this region. The trait sampling followed standardised protocols (Pérez-Harguindeguy et al. 2013) and species values are available elsewhere (Missio et al. 2017, Oliveira et al. 2019, Kattge et al. 2020, Klipel et al. 2021, Müller et al. 2021). For leaf traits, we collected at least ten leaves per individual and at least three individuals per species. Leaf area was calculated from scanned fresh leaves, and all simple leaves were measured including petioles, whereas for compound leaves the leaflet area was considered, without rachis. The functional traits selected to represent species' ecological strategies, their rationale, mean values across the sample, standard deviation and minimum and maximum values can be found in the Supporting information.

Canopy and understory species categorisation

The vertical structure of South American tropical and subtropical forests typically consists of multiple vegetation layers, including understory and canopy strata (Borma et al. 2022). Our analysis focuses specifically on adult trees ($\text{dbh} \geq 50$ mm), excluding other layers primarily composed of saplings, seedlings, shrubs, herbs and tree ferns. According to Borma et al. (2022), understory species in Brazilian moist and rain forests

typically occupy a vegetation layer up to 10 m in height. To ensure that species from the subtropical BAF align with this classification, we conducted a quantitative assessment based on species height measured in our dataset. We first determined the median height of each species within our dataset (see the Supporting information for all species median height) and then divided the data into two quantiles – 70 and 30% – reflecting the higher proportion of individuals in the understory compared to the canopy. Using median values helped minimise potential biases from extreme individual heights, which could skew the results. In our sample, the 70th percentile of median height corresponded to a threshold of 10 m. Thus, species with a median height < 10 m were categorised as understory species, while the remaining 30% (≥ 10 m median height) were classified as canopy species (Supporting information). This classification aligns with the framework proposed by Borma et al. (2022). Although we acknowledge that this classification may not perfectly reflect ecological functional groups – since some canopy species may occupy gaps or receive light without reaching the median height defined here – we are confident that understory species primarily represent shade-tolerant species, while canopy species correspond to shade-intolerant species within the context of subtropical BAF.

Data analysis

First, to evaluate the coordination of traits and assess the species ecological strategies, we performed a principal component analysis (PCA) using the `prcomp` function ('stats' R-package, www.r-project.org). Three principal components, summarising more than 65% of the explained variance, were used as ecological strategies, i.e. potential predictors of species RGR (Supporting information). We acknowledge that species information is present in both predictors and response variables, which may introduce phylogenetic structure. To account for this, we constructed an ultrametric phylogeny for tree species using a complete, time-calibrated phylogeny developed by Smith and Brown (2018) as a backbone, by using the 'V.PhyloMaker' package (Jin and Qian 2019). We then fitted generalised least square models accounting for the phylogenetic correlation among species (i.e. pGLS models) using the `gls` function ('nlme' R-package, Pinheiro et al. 2020). Upon comparing the AIC values between pGLS and ordinary least square models, the latter showed the lowest AIC values (Supporting information), indicating that the ecological strategies summarised in the PC axes are not phylogenetically structured. Therefore, we did not include phylogenetic correlation in the final models. We used AICc (Burnham and Anderson 2002) and followed a parsimony principle (i.e. selecting models with fewer predictors that provide the same explanatory power) to identify the best-fit model explaining species RGR ($\Delta\text{AIC} \leq 2$, Supporting information). The PCA analysis and the modeling procedure were conducted for all species collectively, as well as separately for canopy and understory species. The species RGR and LA were log-scaled to improve the normality and homoscedasticity in the model residuals (Supporting information). All the model coefficients and confidence intervals were

obtained from bootstrap by using the function `Boot` from the 'car' R-package, using 9999 permutations (Fox et al. 2023). All analyses were conducted in R ver. 4.2.2 (www.r-project.org). All the processed data and R codes used to conduct these analyses are available in <https://zenodo.org/records/14911032>.

Results

We analysed the effect of ecological strategies on the relative growth rate of 121 species distributed across the subtropical Brazilian Atlantic Forest (Supporting information). The mean RGR among species was $0.26 \pm 0.09 \text{ mm mm}^{-1} \text{ year}^{-1}$. In addition, there is large variation in growth and median height among canopy and understory species (Supporting information).

The ecological strategies were summarised by principal components of species functional traits, considering all species together and separately for canopy and understory species (Fig. 1a–f, Supporting information). The ecological strategies revealed for all species (Fig. 1a, d), as well as canopy (Fig. 1b, e), and understory species (Fig. 1c, f) segregated the

species along the first axis (PC1) into a strategy associated with the leaf economic spectrum (Supporting information). In the left part of the first axis (negatively associated) for all species, as well as canopy and understory species, there are species with higher values of SLA, LNC and LPC, contrasting with species in the right part that exhibit higher values of LDMC (positively associated). The second axis (PC2) of the ordination for all species was primarily associated with plant structure, revealing a spectrum related to light capture strategies. This axis showed a positive association with larger leaves (LA) and a negative association with greater height and more structured leaves (higher LDMC). A similar pattern emerged for understory species, where PC2 was negatively correlated with LDMC, height, LPC and WD, and positively associated with LA (Fig. 1c, Supporting information). For the canopy species, the second axis captures a spectrum ranging from species with larger leaves (high LA, positively related with PC2) to those with more structured leaves (higher LDMC values) without a clear relationship with height (Fig. 1b). Finally, the third axis (PC3) reflects species investments in stem structures and traits that promote photosynthetic assimilation.

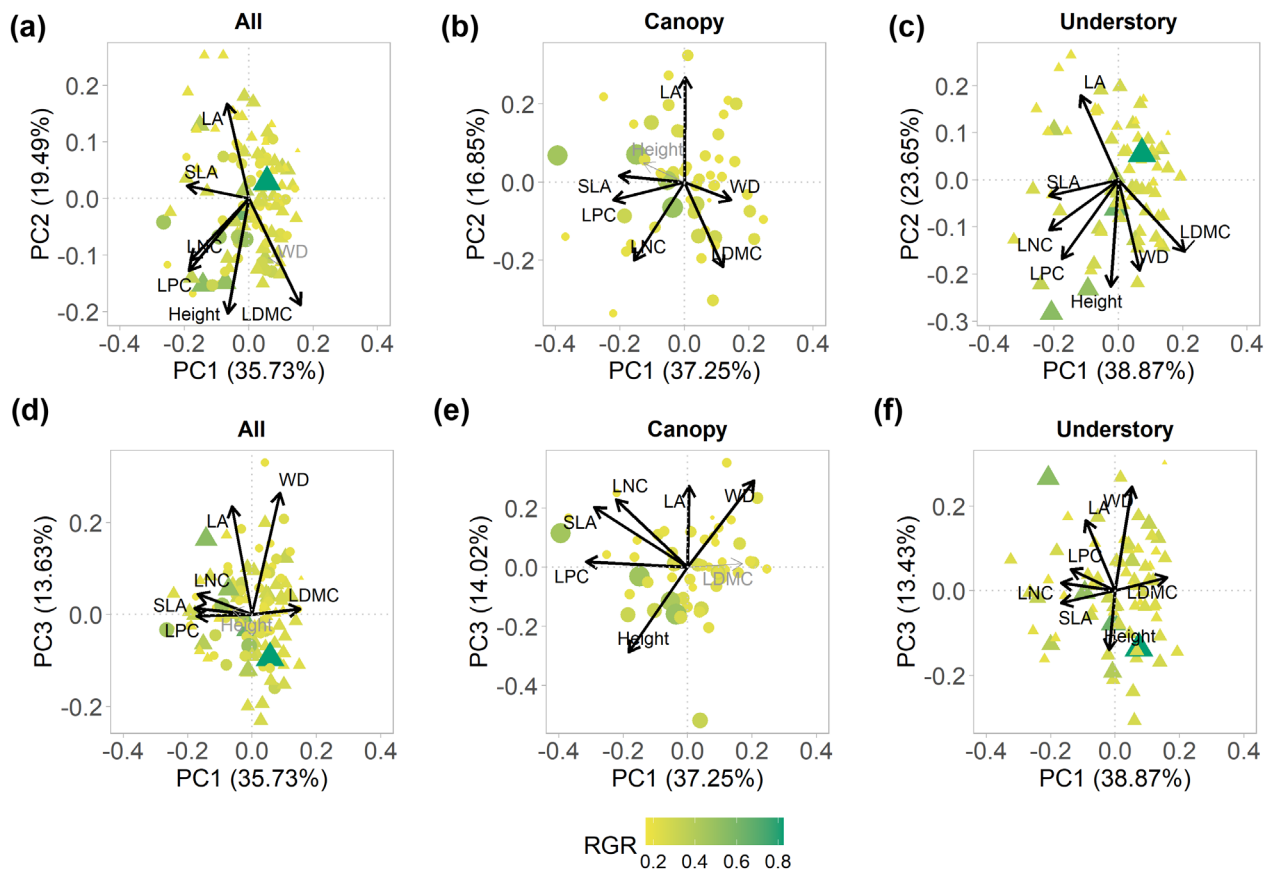


Figure 1. Ordination diagrams of principal component analysis (PCA) depict species traits across the subtropical Brazilian Atlantic Forest. Principal components 1 and 2 for all species (a), canopy species (b), and understory species (c); principal components 1 and 3 for all species (d), canopy species (e), and understory species (f). SLA: specific leaf area, LA: leaf area, LNC: leaf nitrogen content, LPC: leaf phosphorus content, LDMC: leaf dry-matter content, WD: wood density, RGR: relative growth rates. Thicker arrows indicate variables with higher association with the axis (principal components with correlation ≥ 0.35). Dots represent canopy species, and triangles represent understory species. The size and colours of the shapes indicate species RGR; therefore, the largest and greenest shapes represent the species with the RGR. Variables that present a low correlation with the axis are shown in grey colour.

For all species, canopy species, and understory species, PC3 shows a positive correlation with WD and LA (Fig. 1d, f). In addition, for both canopy and understory species, there is also a negative relationship of PC3 with height (Fig. 1d, f).

Our analyses revealed consistent relationships between ecological strategies and species RGR, although these relationships differed when considering all species together *versus* canopy and understory species separately. We summarised the observed effects of ecological strategies on tree species growth in Fig. 2–3. For all species, PC2 negatively predicts RGR, meaning that species strategies combining greater potential stature and higher LDMC with lower LA exhibit faster growth (Fig. 1a). For canopy species, the strategy represented by PC3 (taller species with lower LA and WD) favours higher RGR (Fig. 1e), while PC1 (Fig. 1b, e) suggests a potential correlation between higher SLA and LPC with faster growth rates, but this relationship is weak (Fig. 2). For understory species, PC2 is characterised by higher values of height, LPC, LDMC and WD, contrasting with lower LA (Fig. 1c), and had a positive effect on tree growth (Fig. 2–3). The details of the models selected, model results, and the bivariate relationships between RGR and functional traits are provided in the Supporting information.

Discussion

This is the first assessment of the relationship of plant ecological strategies and species performance across the subtropical Brazilian Atlantic Forest. This study provides a description of the relative growth rates of a large number of tree species, along with a set of functional traits and ecological strategies and their relationship with tree growth in this region. We show here that tree species exhibit two primary ecological strategies: one combining leaf traits along the conservative-acquisitive spectrum and another associated with tree structure, combining plant height, wood density and leaf size. Overall, tree species strategies primarily linked to the leaf

economic spectrum did not strongly predict their RGR. In contrast, species with taller stature and smaller leaf area consistently demonstrated higher RGR, even when categorising all species into canopy and understory species, summarising the importance of this ecological strategy as a driver of tree growth across this broad spatial scale.

The subtropical Brazilian Atlantic Forest' species relative growth rates

The relative growth rates of tree species in the subtropical BAF varies widely. Additionally, canopy and understory species present large variation of RGR and heights, which in turn shape the ecological strategies and structure of these forests. Overall, the species composition across the subtropical BAF presents a few dominant species, with high turnover rates (Bergamin et al. 2017). These differences in species composition highlight that even across similar forest types, a broad range of species performances in terms of growth may be observed, as well as their traits, which will ultimately influence the overall forest dynamics across this region (Forgiarini et al. 2015, R uger et al. 2020).

Species with tall statures and small robust leaves grow faster

Ecological strategies determine species performance, and this effect was found when considering all species together, and more consistently when evaluating canopy and understory species separately. For all species, one ecological strategy summarised in the multivariate space indicates that taller species with high LDMC and small LA – representing the 'plant structure strategy' – have faster growth. Trees that present larger investments in stature, such as greater heights, potentially have a greater advantage to access resources (Westoby 1998) such as light in forest environments (Wang et al. 2022). Additionally, this attribute (tall trees) was combined with

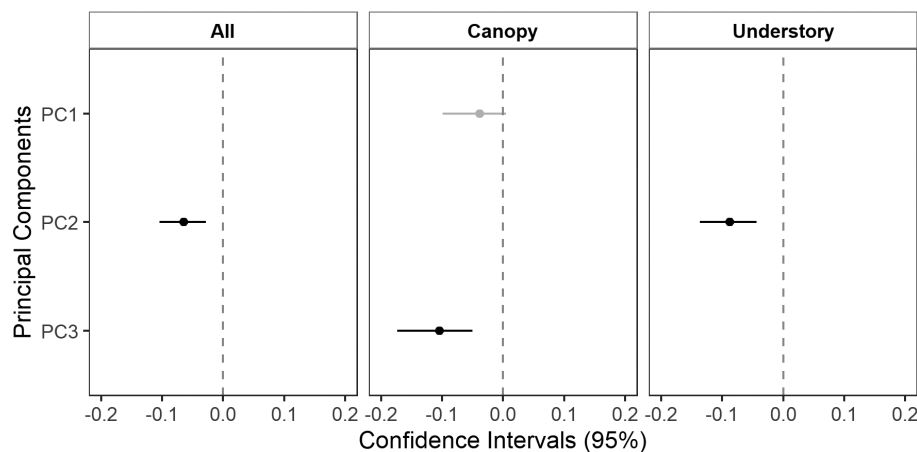


Figure 2. Confidence intervals (95%) of the relationship between relative growth rates and plant ecological strategies summarised in principal components (PC1, PC2 and PC3) for all species, canopy species, and understory species. This information corresponds to the results from the selected models (Supporting information), thus, PCs non included in the selected models are not shown. Significant effects are expressed in black colour when the confidence intervals do not overlap with zero. Weak relationships are shown in grey colour.

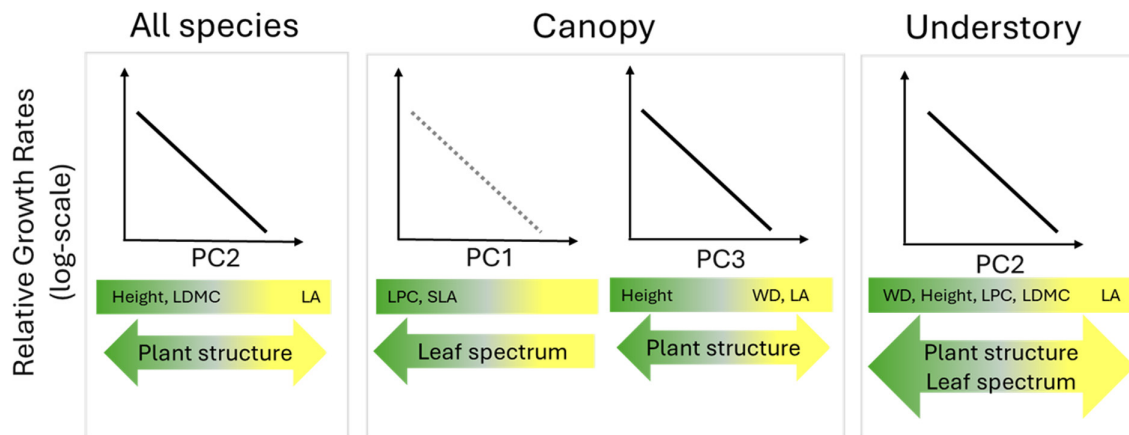


Figure 3. Summarisation of the relationship between relative growth rates and plant ecological strategies according to the principal components (PC1, PC2 and PC3) and their correlated traits for all species, canopy species and understory species. This information corresponds to the results from the selected models (Supporting information). Strong effects are expressed in black straight lines and weak relationships are shown in grey dashed lines. The colour gradient is related to the effect of the trait on tree growth; therefore, the green colour represents the attributes of species with higher relative growth rates, while the yellow colour represents the attributes of species with lower relative growth rates. SLA: specific leaf area, LA: leaf area, LNC: leaf nitrogen content, LPC: leaf phosphorus content, LDMC: leaf dry-matter content, WD: wood density.

robust small leaves (high LDMC and low LA values), which suggests an investment that enables species to cope with occasional adverse environmental conditions such as higher evapotranspiration (in case of Atlantic Forest s.s. and Seasonal Forest), as well as frost and colder temperatures (in case of the Araucaria Forest) (Frangipani et al. 2021, Rodrigues et al. 2021, Klipel et al. 2024). Therefore, species with small structured leaves but that can reach tall statures demonstrate a good strategy for fighting in the competition process and ultimately, be an advantage in terms of radial stem growth across these subtropical forests (Klipel et al. 2024).

When evaluating all species together, we did not find evidence that species with acquisitive strategies exhibit faster growth, or conservative species have slower growth (Salguero-Gómez 2017, Laughlin et al. 2020). We found almost the opposite, as species with higher LDMC and lower LA have faster growth. The alignment of species to the acquisitive-conservative strategies is a general expectation for tropical tree species from moist forests (Poorter et al. 2008, Rüger et al. 2012, Visser et al. 2016), where species should align to a fast-slow continuum (Reich 2014, Salguero-Gómez 2017). In the subtropical BAF region, species with small leaves and higher LDMC values, which indicate a more conservative leaf strategy, exhibited faster growth (see also Augusto et al. 2025). In addition to these leaf attributes, the ecological strategy also incorporates the maximum species height, shaping the overall plant structure strategy of all species. Since this result is based on the performance of adult trees, the association between species growth and the resource acquisition may become more evident at the seedling and sapling stages (Poorter 2001, Spasojevic et al. 2014, Visser et al. 2016). In addition, it overall indicates that the subtropical BAF possesses a remarkable difference in forest structure and dynamics from other tropical forests, which is shaped by the local environmental conditions (Bordin et al. 2021, Klipel et al. 2023) and

leads to distinct tree ecological strategies that influence stem growth rates.

These differences in ecological strategies are reflected in the stratification of subtropical BAF, where species often reach lower maximum heights compared to other tropical forests (de Lima et al. 2023). The structure of subtropical BAF is shaped by a constrained range of trait values, influenced by the limiting environmental conditions in this region (Klipel et al. 2021). Furthermore, the absence of a relationship between all species growth and traits such as SLA or WD potentially indicates that these traits are more prone to be important in different stages of species' life history (Klipel et al. 2021) or even result in contrasting effects depending on the forest stratum evaluated. For instance, it is widely known that SLA has a positive effect on maximising seedling growth in tropical forests (Gibert et al. 2016, Visser et al. 2016), but this relationship frequently does not hold in adult tree species (Poorter et al. 2008, Gray et al. 2019). In the case of WD, this trait might be important for increasing species longevity and reducing mortality rates (Iida et al. 2014b). Additionally, it is essential to note that many studies often examine the impact of individual traits rather than coordinated relationships among traits on species growth, which can lead to varied responses and outcomes in terms of performance (Klipel et al. 2021). Thus, this coordination among different traits into distinct ecological strategies shown here underscores the challenge of understanding the role of each specific trait throughout the life-history of tree species.

Canopy and understory species growth are explained by distinct ecological strategies

Separating species by considering their ability to achieve the forest canopy or to tolerate shaded environments (i.e. canopy and understory species) increased our understanding of how ecological strategies shape tree growth across the subtropical

BAF. The ecological strategies influencing the growth of canopy species integrate a combination of taller stature, low WD, and small LA (Westoby 1998, Chave et al. 2009, Rüger et al. 2018). Given the variation in tree heights among canopy species, which contributes to the structural complexity of these subtropical forests, attaining greater stature represents an efficient strategy for maximising light acquisition, as previously reported (Rüger et al. 2012, Scalon et al. 2022, Klipel et al. 2024). In addition, the negative effect of WD on tree growth was expected, as this trait is related to the resource allocation to enhance survival (Iida et al. 2014b). On the other hand, we could expected a positive relationship between LA and growth, as this trait is related to larger area for the photosynthetic process (Díaz et al. 2016), but we observed the opposite pattern. This might be related to the fact that larger leaves may be more prone to be negatively affected by climatic adversities (such as higher evapotranspiration during the summer or frost events during the winter). Thus, such environmental restriction can favour trees that allocate resources to construct smaller leaves. Moreover, the relationship between RGR and the acquisitive strategy associated with the leaf economic spectrum for canopy species was not strong. This suggests that while some canopy species with acquisitive leaf traits might exhibit faster growth rates, this pattern is not consistent across the studied species.

The ecological strategies that emerged for understory species show a combination between conservative traits (i.e. high WD and LDMC) with greater stature, and small LA, which positively influence their growth in this region. In addition, LPC, an acquisitive trait related to the leaf economic spectrum, also emerged as an important trait in enhancing the growth of understory species. In general, smaller and more structured leaves may reduce self-shading, which can increase the assimilation rates across the plant, even in a light-limited environment (Grady et al. 2024). Additionally, taller trees in the understory layer also show faster growth rates, highlighting the importance of this attribute in maximising the advantage in acquiring resources and enhancing tree growth (Poorter et al. 2008, Scalon et al. 2022, Klipel et al. 2024). On the other hand, while denser wood is often associated with lower growth rates and increased survival in tropical trees (Poorter et al. 2008, Iida et al. 2014a, Kunstler et al. 2016, Kambach et al. 2022), here, higher WD among understory species is also correlated with faster growth rates. Furthermore, the integration of structural conservative traits in the ecological strategy that enhances RGR underscores their dual role in enabling adaptation to constrained environmental conditions while simultaneously promoting tree growth. This strategy also incorporates smaller and nutrient-rich leaves, which might enhance photosynthetic efficiency even in shaded environments (Wright et al. 2004, Easdale and Healey 2009). Therefore, we may conclude that species ecological strategies and their growth performance across the subtropical BAF are acting as a result of a complex set of trait coordination and tradeoffs, primarily related to plant structure (combining tall stature and small leaves), which ultimately shape the overall demographic dynamics across these forests.

Concluding remarks: the challenge in predicting tree species fitness

Understanding the underlying mechanisms that determine species fitness is a major challenge. In this study, we assessed the relationship between plant ecological strategies and their relative growth rates, which is one of the fitness components (Siefert and Laughlin 2023). We found that ecological strategies predict tree growth rates, but they varied when evaluating all species *versus* when assessing canopy and understory species separately. Overall, the analyses indicate a prevailing trend of conservative species with higher stature growing faster. The results presented here are fundamental in the context of ongoing global changes, as the species demography is related to forest dynamics and might be affected by the changes in climate, which will in turn impact species performance over time (Menezes-Silva et al. 2019). Furthermore, this information can be employed in restoration projects, which require refined information to determine the set of species to be used (Coutinho et al. 2023). Species with faster growth rates might be particularly valuable for inclusion in these projects, as they will efficiently remove carbon from the atmosphere, potentially enhancing ecological processes such as carbon storage and carbon sink (Bordin et al. 2021, 2023). Therefore, future studies should focus on other aspects of the demographic dynamics of species, as well as the underlying mechanisms that promote high growth and survival. Understanding these complexities is essential to predict and mitigate the effects of climate change in forest ecosystems.

Funding – This study was developed in the context of the National Institute for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPEG. MVC, SCM, ACS, PH, MCMM, and LSD are supported by CNPq (310296/2023-4, 314309/2023-3, 305916/2017-3, 304902/2019-5, 310315/2023-9 and 306951/2022-3).

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Data availability statement

The raw tree data that support these findings are available at ForestPlots.net under specific request (plot codes are described in the Supporting information). The processed data and R codes that support the findings are openly available in a public repository, please see zenodo.org/records/14911032.

Data are available from the Zenodo: <https://zenodo.org/records/14911032> (Bordin et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S. and Ray-Mukherjee, J. 2014. Functional traits explain variation in plant life history strategies. – *Proc. Natl Acad. Sci. USA* 111: 740–745.
- Alvares, C. A., Stape, J. L., Sentelhas, P. C., Gonçalves, J. L. de M. and Sparovek, G. 2013. Köppen's climate classification map for Brazil. – *Meteorol. Z.* 22: 711–728.
- Augusto, L. et al. 2025. Widespread slow growth of acquisitive tree species. – *Nature* (2025) <https://doi.org/10.1038/s41586-025-08692-x>
- Bauman, D., Fortunel, C., Cernusak, L. A., Bentley, L. P., McMahon, S. M., Rifai, S. W., Aguirre-Gutiérrez, J., Oliveras, I., Bradford, M., Laurance, S. G. W., Delhaye, G., Hutchinson, M. F., Dempsey, R., McNellis, B. E., Santos-Andrade, P. E., Ninantay-Rivera, H. R., Chambi Paucar, J. R., Phillips, O. L. and Malhi, Y. 2022. Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits. – *Global Change Biol.* 28: 1414–1432.
- Bergamin, R. S., Bastazini, V. A. G., Vélez-Martin, E., Debastiani, V., Zanini, K. J., Loyola, R. and Müller, S. C. 2017. Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Rainforest. – *Biodivers. Conserv.* 26: 1557–1568.
- Bialic-Murphy, L., et al. 2024. The pace of life for forest trees. – *Science* 386: 92–98.
- Bordin, K. M., Esquivel-Muelbert, A., Bergamin, R. S., Klipel, J., Piccolotto, R. C., Frangipani, M. A., Zanini, K. J., Cianciaruso, M. V., Jarenkow, J. A., Jurinitz, C. F., Molz, M., Higuchi, P., da Silva, A. C. and Müller, S. C. 2021. Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests. – *For. Ecol. Manage.* 490: 119126.
- Bordin, K. M., Esquivel-Muelbert, A., Klipel, J., Piccolotto, R. C., Bergamin, R. S., da Silva, A. C., Higuchi, P., Capellesso, E. S., Marques, M. C. M., Souza, A. F. and Müller, S. C. 2023. No relationship between biodiversity and forest carbon sink across the subtropical Brazilian Atlantic Forest. – *Perspect. Ecol. Conserv.* 21: 112–120.
- Bordin, K. M., Ferreira, L., Rosina, A., Malacarne, M., Zanotelli, P., Adami, S. F. and Vendruscolo, G. S. 2019. Community structure and tree diversity in a subtropical forest in southern Brazil. – *Biota Neotrop.* 19: e20180606.
- Bordin, K. M., Cianciaruso, M. V., da Silva Duarte, L., Bergamin, R. S., Klipel, J., Piccolotto, R. C., da Cunha Morales, D., Higuchi, P., da Silva, A. C., Capellesso, E. S., Marques, M. C. M. and Müller, S. C. 2025. Data from: Tall stature and small leaves: ecological strategies that enhance tree growth across the subtropical Brazilian Atlantic Forest. – Zenodo, <https://zenodo.org/records/14911032>.
- Borma, L. S., Costa, M. H., da Rocha, H. R., Arieira, J., Nascimento, N. C. C., Jaramillo-Giraldo, C., Ambrosio, G., Carneiro, R. G., Venzon, M., Neto, A. F., van der Hoff, R., Oliveira, B. F. A., Rajão, R. and Nobre, C. A. 2022. Beyond carbon: the contributions of South American tropical humid and subhumid forests to ecosystem services. – *Rev. Geophys.* 60: e2021.
- Brienen, R. J. W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Filippo, A., Helama, S., Locosselli, G. M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. and Gloor, E. 2020. Forest carbon sink neutralized by pervasive growth–lifespan tradeoffs. – *Nat. Commun.* 11: 4241.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. 2009. Towards a worldwide wood economics spectrum. – *Ecol. Lett.* 12: 351–366.
- Coutinho, A. G., Carlucci, M. B. and Cianciaruso, M. V. 2023. A framework to apply trait-based ecological restoration at large scales. – *J. Appl. Ecol.* 60: 1562–1571.
- Cristiano, P. M., Madanes, N., Campanello, P. I., Di Francescantonio, D., Rodríguez, S. A., Zhang, Y.-J., Carrasco, L. O. and Goldstein, G. 2014. High NDVI and potential canopy photosynthesis of South American subtropical forests despite seasonal changes in leaf area index and air temperature. – *Forests* 5: 287–308.
- de Lima, R. B. et al. 2023. Giants of the Amazon: how does environmental variation drive the diversity patterns of large trees? – *Global Change Biol.* 29: 4861–4879.
- Díaz Villa, M. V. E., Bruzzone, O. A., Goldstein, G. and Cristiano, P. M. 2022. Climatic determinants of photosynthetic activity in humid subtropical forests under different forestry activities. – *Remote Sens. Appl. Soc. Environ.* 26: 100735.
- Díaz, S. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. – *J. Veg. Sci.* 15: 295–304.
- Díaz, S. et al. 2016. The global spectrum of plant form and function. – *Nature* 529: 167–171.
- Easdale, T. A. and Healey, J. R. 2009. Resource-use-related traits correlate with population turnover rates, but not stem diameter growth rates, in 29 subtropical montane tree species. – *Perspect. Plant Ecol. Evol. Syst.* 11: 203–218.
- ForestPlots.net. et al. 2021. Taking the pulse of Earth's tropical forests using networks of highly distributed plots. – *Biol. Conserv.* 260: 108849.
- Forgiarini, C., Souza, A. F., Longhi, S. J. and Oliveira, J. M. 2015. In the lack of extreme pioneers: trait relationships and ecological strategies of 66 subtropical tree species. – *J. Plant Ecol.* 8: 359–367.
- Fortunel, C. et al. 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. – *Ecology* 90: 598–611.

- Fox, J. et al. 2023. car: companion to applied regression. <https://cran.r-project.org/web/packages/car/index.html>.
- Frangipani, M. A., Müller, S. C. and Anand, M. 2021. Frost hinders the establishment of trees in highland grasslands in the Atlantic Forest ecotone region of southern Brazil. – *J. Veg. Sci.* 32: e13053.
- Gibert, A., Gray, E. F., Westoby, M., Wright, I. J. and Falster, D. S. 2016. On the link between functional traits and growth rate: meta-analysis shows effects change with plant size, as predicted. – *J. Ecol.* 104: 1488–1503.
- Giehl, E. L. H. and Jarenkow, J. A. 2012. Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. – *Ecography* 35: 933–943.
- Grady, J. M., Read, Q. D., Record, S., Rüger, N., Zarnetske, P. L., Dell, A. I., Hubbell, S. P., Michaletz, S. T. and Enquist, B. J. 2024. Life history scaling in a tropical forest. – *J. Ecol.* 112: 487–500.
- Gray, E. F., Wright, I. J., Falster, D. S., Eller, A. S. D., Lehmann, C. E. R., Bradford, M. G. and Cernusak, L. A. 2019. Leaf:wood allometry and functional traits together explain substantial growth rate variation in rainforest trees. – *AoB Plants*. 11: plz024.
- Iida, Y., Poorter, L., Sterck, F., Kassim, A. R., Potts, M. D., Kubo, T. and Kohyama, T. S. 2014a. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. – *Ecology* 95: 353–363.
- Iida, Y., Kohyama, T. S., Swenson, N. G., Su, S.-H., Chen, C.-T., Chiang, J.-M. and Sun, I.-F. 2014b. Linking functional traits and demographic rates in a subtropical tree community: the importance of size dependency. – *J. Ecol.* 102: 641–650.
- Jin, Y. and Qian, H. 2019. VPhyloMaker: an R package that can generate very large phylogenies for vascular plants. – *Ecography* 42: 1353–1359.
- Kambach, S. et al. 2022. Consistency of demographic tradeoffs across 13 (sub)tropical forests. – *J. Ecol.* 110: 1485–1496.
- Kamimura, V. de A., Loiola, P. de P., Carmona, C. P., Assis, M. A., Joly, C. A., Santos, F. A. M., Vieira, S. A., Alves, L. F., Martins, V. F., Ramos, E., Ramos, R. F. and de Bello, F. 2023. Trait interactions effects on tropical tree demography depend on the environmental context. – *Perspect. Plant Ecol. Evol. Syst.* 59: 125732.
- Kattge, J. et al. 2020. TRY plant trait database – enhanced coverage and open access. – *Global Change Biol.* 26: 119–188.
- Klipel, J., Bergamin, R. S., Seger, G. D. S., Carlucci, M. B. and Müller, S. C. 2021. Plant functional traits explain species abundance patterns and strategies shifts among saplings and adult trees in Araucaria forests. – *Austral Ecol.* 46: 1084–1096.
- Klipel, J., Bergamin, R. S., Cianciaruso, M. V., da Silva, A. C., Jurinitz, C. F., Jarenkow, J. A., Bordin, K. M., Molz, M., Higuchi, P., Picolotto, R. C., Debastiani, V. J. and Müller, S. C. 2023. How do distinct facets of tree diversity and community assembly respond to environmental variables in the subtropical Atlantic Forest? – *Ecol. Evol.* 13: e10321.
- Klipel, J., Bergamin, R. S., Bordin, K. M., Picolotto, R. C., Müller, S. C. and de Bello, F. 2024. The effect of neighbor species' phylogenetic and trait difference on tree growth in subtropical forests. – *J. Veg. Sci.* 35: e13296.
- Kunstler, G. et al. 2016. Plant functional traits have globally consistent effects on competition. – *Nature* 529: 204–207.
- Lasky, J. R., Uriarte, M., Boukili, V. K. and Chazdon, R. L. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. – *Proc. Natl Acad. Sci. USA* 111: 5616–5621.
- Laughlin, D. 2023. Plant strategies: the demographic consequences of functional traits in changing environments. – Oxford Univ. Press.
- Laughlin, D., Leppert, J. J., Moore, M. M. and Sieg, C. H. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. – *Funct. Ecol.* 24: 493–501.
- Laughlin, D. C., Strahan, R. T., Adler, P. B. and Moore, M. M. 2018. Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. – *Ecol. Lett.* 21: 411–421.
- Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M. and Moore, M. M. 2020. The net effect of functional traits on fitness. – *Trends Ecol. Evol.* 35: 1037–1047.
- Marques, M. C. M. and Grelle, C. E. V. 2021. – In: Marques, M. C. M. and Grelle, C. (eds), *The Atlantic Forest: history, biodiversity, threats and opportunities of the mega-diverse forest*. Springer International Publishing.
- Martínez-Vilalta, J., Mencuccini, M., Vayreda, J. and Retana, J. 2010. Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. – *J. Ecol.* 98: 1462–1475.
- Menezes-Silva, P. E., Loram-Lourenço, L., Alves, R. D. F. B., Sousa, L. F., Almeida, S. E. da S. and Farnese, F. S. 2019. Different ways to die in a changing world: consequences of climate change for tree species performance and survival through an ecophysiological perspective. – *Ecol. Evol.* 9: 11979–11999.
- Missio, F. D. F., Da Silva, A. C., Higuchi, P., Longhi, S. J., Brand, M. A., Rios, P. D., Rosa, A. D., Buzzi Junior, F., Bento, M. A., Gonçalves, D. A., Loebens, R. and Pscheidt, F. 2017. Functional traits of tree species in a fragment of Araucaria forest in Lages, Santa Catarina state. – *Cienc. Florestal* 27: 215–224.
- Modolo, G. S., dos Santos, V. A. H. F. and Ferreira, M. J. 2021. Testing for functional significance of traits: effect of the light environment in tropical tree saplings. – *Ecol. Evol.* 11: 6480–6492.
- Müller, S. C., Bergamin, R. S., Bordin, K. M., Klipel, J. and Rosenfield, M. F. 2021. Canopy leaf traits, basal area, and age predict functional patterns of regenerating communities in secondary subtropical forests. – *Front. For. Global Change* 4: 572864.
- Oliveira, L. Z., Uller, H. F., Klitzke, A. R., Eleotério, J. R. and Vibrans, A. C. 2019. Towards the fulfillment of a knowledge gap: wood densities for species of the subtropical Atlantic forest. – *Data* 4: 1–10.
- Oliveira-Filho, A. T. and Fontes, M. A. L. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. – *Biotropica* 32: 793–810.
- Oliveira-Filho, A. T., Budke, J. C., Jarenkow, J. A., Eisenlohr, P. V. and Neves, D. R. M. 2015. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. – *J. Plant Ecol.* 8: 242–260.
- Paine, C. E. T. et al. 2015. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. – *J. Ecol.* 103: 978–989.
- Pérez-Harguindeguy, N. et al. 2013. New handbook for standardized measurement of plant functional traits worldwide. – *Aust. J. Bot.* 61: 167–234.
- Phillips, O. L., Baker, T. R., Feldpausch, T. R. and Brienens, R. J. W. 2001. RAINFOR field manual for plot establishment and remeasurement. https://forestplots.net/upload/manualsenglish/rainfor_field_manual_en.pdf.

- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S. and Van Willigen, B. 2020. Package nlme: linear and nonlinear mixed effects models. – R package, pp. 1–336. <https://cran.r-project.org/web/packages/nlme/nlme.pdf>.
- Poorter, L. 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. – *Funct. Ecol.* 15: 113–123.
- Poorter, L. and Bongers, F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. – *Ecology* 87: 1733–1743.
- Poorter, L., Wright, S. J., Paz, H., Ackerly, D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros, M., Webb, C. O. and Wright, I. J. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. – *Ecology* 89: 1908–1920.
- Poorter, L., Castilho, C. V., Schiatti, J., Oliveira, R. S. and Costa, F. R. C. 2018. Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. – *New Phytol.* 219: 109–121.
- Rambo, B. 1951. O Elemento Andino no Pinhal Riograndense. – *Anais Botânicos do Herbário Barbosa Rodrigues*.
- Reich, P. B. 2014. The world-wide ‘fast – slow’ plant economics spectrum: a traits manifesto. – *J. Ecol.* 102: 275–301.
- Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., Walters, M. B., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M. and Walters, M. B. 2003. The evolution of plant functional variation: traits, spectra, and strategies. – *Int. J. Plant Sci.* 164: S143–S164.
- Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J. and Hirota, M. M. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. – *Biol. Conserv.* 142: 1141–1153.
- Rodrigues, A. V., Pastório, F. F., Bones, F. L. V., Esquivel-Muelbert, A., Vibrans, A. C. and de Gasper, A. L. 2021. A test of the fast–slow plant economy hypothesis in a subtropical rain forest. – *Plant Ecol. Divers.* 14: 267–277.
- Rodríguez-Alarcón, S., González, M. R., Carmona, C. P. and Tordoni, E. 2024. Trait–growth relationships in Colombian tropical dry forests: incorporating intraspecific variation and trait interactions. – *J. Veg. Sci.* 35: e13233.
- Rüger, N., Wirth, C., Wright, S. J. and Condit, R. S. 2012. Functional traits explain plasticity of growth rates in tropical tree species. – *Ecology* 93: 2626–2636.
- Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Wright, S. J. and Wirth, C. 2018. Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. – *Ecol. Lett.* 21: 1075–1084.
- Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., Lopez, O. R., Wirth, C. and Farrior, C. E. 2020. Demographic tradeoffs predict tropical forest dynamics. – *Science* 368: 165–168.
- Russo, S. E. et al. 2021. The interspecific growth–mortality tradeoff is not a general framework for tropical forest community structure. – *Nat. Ecol. Evol.* 5: 174–183.
- Salguero-Gómez, R. 2017. Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. – *New Phytol.* 213: 1618–1624.
- Scalon, M. C., Bohn, A., Coelho, G. C., Meister, L., Alves, R. de F., Secco, R. T., Zwiener, V. P., Marcilio-Silva, V., Trindade, W. C. F. and Marques, M. C. M. 2022. Relationship between growth trajectories and functional traits for woody trees in a secondary tropical forest. – *Front. For. Global Change* 5: 754656.
- Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C. and Reich, P. B. 2016. Reinforcing loose foundation stones in trait-based plant ecology. – *Oecologia* 180: 923–931.
- Siefert, A. and Laughlin, D. C. 2023. Estimating the net effect of functional traits on fitness across species and environments. – *Methods Ecol. Evol.* 14: 1035–1048.
- Smith, S. A. and Brown, J. W. 2018. Constructing a broadly inclusive seed plant phylogeny. – *Am. J. Bot.* 105: 302–314.
- Spasojevic, M. J., Yablon, E. A., Oberle, B. and Myers, J. A. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. – *Ecosphere* 5: art129.
- Sterck, F. J., Poorter, L., Schieving, F. and Sterck, F. J. 2006. Leaf traits determine the growth – survival tradeoff across rain forest tree species. – *Am. Nat.* 167: 758–765.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Visser, M. D., Buijning, M., Wright, S. J., Muller-Landau, H. C., Jongejans, E., Comita, L. S. and de Kroon, H. 2016. Functional traits as predictors of vital rates across the life cycle of tropical trees. – *Funct. Ecol.* 30: 168–180.
- Wächter, J. 2002. Padrões geográficos na flora atual do Rio Grande do Sul. – *Ciência & Ambiente*, pp. 93–108.
- Wang, J., Wang, X., Ji, Y. and Gao, J. 2022. Climate factors determine the utilization strategy of forest plant resources at large scales. – *Front. Plant Sci.* 13: 990441.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. – *Plant Soil* 199: 213–227.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. and Wright, I. J. 2002. Plant ecological strategies: some leading dimensions of variation between species. – *Annu. Rev. Ecol. Syst.* 33: 125–159.
- Wills, J., Herbohn, J., Hu, J., Sohel, S., Baynes, J. and Firn, J. 2018. Tree leaf trade-offs are stronger for sub-canopy trees: leaf traits reveal little about growth rates in canopy trees. – *Ecol. Appl.* 28: 1116–1125.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.
- Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manríquez, G., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M. and Wright, S. J. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. – *Ann. Bot.* 99: 1003–1015.
- Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M. and Zanne, A. E. 2010. Functional traits and the growth–mortality tradeoff in tropical trees. – *Ecology* 91: 3664–3674.
- Wu, A., Xiong, X., González-M, R., Li, R., Li, A., Liu, J., Tang, X. and Zhang, Q. 2023. Climate change reshapes plant trait spectrum to explain biomass dynamics in an old-growth subtropical forest. – *Front. Plant Sci.* 14: 1260707.
- Yang, J., Cao, M. and Swenson, N. G. 2018. Why functional traits do not predict tree demographic rates. – *Trends Ecol. Evol.* 33: 326–336.