Received: 21 March 2024 | Revised: 9 July 2024 | Accepted: 15 July 2024

DOI: 10.1111/jvs.13296

Journal of Vegetation Science IAVS

RESEARCH ARTICLE

The effect of neighbor species' phylogenetic and trait difference on tree growth in subtropical forests

Joice Klipel[1,2] | **Rodrigo Scarton Bergamin**[2,3,4] | **Kauane Maiara Bordin**[2] | **Rayana Caroline Picolotto**[2] | **Sandra Cristina Müller**[2] | **Francesco de Bello**[5,6]

[1]Leuphana University of Lüneburg, Institute of Ecology, Lüneburg, Germany

[2]Laboratório de Ecologia Vegetal (LEVEG), Programa de Pós-Graduação Em Ecologia, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[3]School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK

[4]Birmingham Institute of Forest Research (BIFoR), University of Birmingham, Birmingham, UK

[5]Centro de Investigaciones Sobre Desertificación, CSIC-UV, Moncada, Spain

[6]Department of Botany, Faculty of Sciences, University of South Bohemia, České Budějovice, Czech Republic

Correspondence
Joice Klipel, Leuphana University of Lüneburg, Institute of Ecology, Lüneburg, 21335, Germany.
Email: klipeljoice@gmail.com

Funding information
National Institute of Science and Technology (INCT) in Ecology, Evolution, and Conservation of Biodiversity; Conselho Nacional de Desenvolvimento Científico e Tecnológico; Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Programa de Excelência Acadêmica

Co-ordinating Editor: Josep Padullés Cubino

Abstract

Questions: To comprehensively understand ecological dynamics within a forest ecosystem, it is vital to explore how surrounding trees influence the growth of individual trees in a community. This study investigates the importance of biotic interactions on tree growth by examining several metrics of competitive interactions and community structure and considering three classes of intrinsic growth rates among the focal individuals: slower, intermediate, and faster-growing trees. We also separated the focal trees based on their canopy position.

Location: Brazilian subtropical forests.

Methods: We assessed various factors related to the focal trees and their neighbors, including differences in traits, neighborhood crowding, phylogenetic distance, and overall trait composition within the community. We then ran linear mixed-effects models to test how these different metrics influenced the growth rates of the focal trees.

Results: Our results indicate that phylogenetic distance is linked to higher growth. Specific leaf area (SLA), leaf area (LA), and wood density (WD) are significantly related to tree growth. Trees surrounded by neighbors with higher SLA than themselves grow better, particularly smaller trees. Similarly, taller trees with smaller LA than their neighbors grow better. Trees in the intermediary growth class grow better when they have higher WD than their neighbors. Conversely, smaller trees benefit from greater WD difference between the focal trees and their neighbors, while height difference negatively impacts faster-growing trees. Moreover, communities with higher SLA and WD positively impact the growth of faster-growing trees.

Conclusions: We conclude that the interactions between trees are mediated by their ecological differences, but the performance and responses to surrounding competitors vary along with their grow class and position within a community. This study has revealed that the tree's intrinsic growth rate mediates the effect of traits and phylogeny of surrounding trees on individual tree growth.

J Veg Sci. 2024;35:e13296.
https://doi.org/10.1111/jvs.13296

KEYWORDS
absolute trait difference, focal tree, growth rate, hierarchical trait difference, neighborhood

1 | INTRODUCTION

Tree growth involves changes in physical dimensions over time, which are accompanied by distinct physiological and morphological traits that enable the plant to acquire essential resources such as light, water, and nutrients (West & Ratkowsky, 2022). The availability of resources strongly depends on neighboring plants, making tree interactions crucial for individual growth (Coomes & Allen, 2007; Britton et al., 2023). Moreover, these interactions can be scaled up to generate emergent community-level properties (Webb et al., 2002; Uriarte et al., 2010; Hart et al., 2016). For instance, the coverage and size of neighboring plants, trait similarities and phylogenetic relatedness of interacting trees can impact resource availability (Castillo et al., 2010; Kunstler et al., 2012) and consequently, the ability of a tree to compete with its neighbors will determine how well it can grow. Investigating the linkage between individual tree performance and the strength of neighborhood interactions is a promising approach to understand the organization and dynamics of forest communities in response to future climates or other anthropogenic factors.

Understanding the impact of neighborhood interactions is crucial for comprehending the complexities of tree performance. Previous studies have demonstrated that neighborhood interactions can have both positive (Lasky et al., 2014) and negative effects (Ding et al., 2019; Yang et al., 2021) on tree performance in tropical, subtropical, and temperate forests. The neighborhood crowding index (NCI) is a common measure that relates to neighborhood interaction and considers both neighborhood density and the distance between a tree (hereafter, focal tree) and its neighbors within a specified area (Lasky et al., 2014; Uriarte et al., 2016). High tree density in a limited area can result in negative density dependence caused by shading and competition for light, when photosynthesis is negatively affected and ultimately reduce growth rate (Yang et al., 2021). However, the relationship between NCI and tree growth can be context-dependent. Additionally, if resources such as water and soil nutrients are abundant, trees may be able to sustain their growth rates even in crowded conditions (Russo et al., 2008). Thus, overcrowding of trees can stimulate them to grow taller and escape light competition, leading to increasing growth rates and adding a layer of complexity to our understanding of the effects of neighborhood interactions.

Regardless of negative density dependence, biotic interactions may also vary according to the functional and phylogenetic structure of the neighborhood in relation to the focal trees. By examining the dissimilarity of functional traits between focal trees and their neighbors, we can enhance our understanding of how neighborhood interactions mediate the focal tree growth rate (Uriarte et al., 2010; Kraft et al., 2014; Kunstler et al., 2016; Cadotte & Tucker, 2017). With such an approach, similar trait values between focal individuals and neighboring trees may be expected to lead to stronger competition (Macarthur & Levins, 1967), resulting in lower focal growth (hereafter, absolute trait difference). Absolute trait difference follows the limiting similarity principle (Mason et al., 2011), with values closer to zero indicating a greater similarity between the focal individual and its neighbors (i.e., a non-directional trait dissimilarity). However, these trait-based density dependence effects can be asymmetric and species can establish a trait-based competitive hierarchy, where a dominant phenotype emerges (Mayfield & Levine, 2010; Kunstler et al., 2012). In this scenario, as the dissimilarity in traits increases (i.e., more dissimilar from the dominant phenotype), competition intensifies, ultimately forming trait-based competitive hierarchies (hereafter, hierarchical trait difference) (Kunstler et al., 2012). The prevalence of the hierarchical trait difference mechanism indicates the directional trait dissimilarity between the focal tree and its neighbors (Carmona et al., 2019), with positive values indicating higher trait values in the focal tree compared to its neighbors and negative values indicating the opposite. Therefore, it is important to note that both mechanisms of trait differentiation can coexist simultaneously for different functional traits (Carmona et al., 2019; Yin et al., 2021).

In addition, the phylogenetic structure of the neighborhood can elucidate the potential influence of phylogenetic relatedness in facilitating coexistence and reducing competition. It also serves as a valuable surrogate for characterizing species similarity of unmeasured traits, particularly for those displaying phylogenetic conservatism (Swenson et al., 2007; Lebrija-Trejos et al., 2014). Thus, phylogenetic and community-level trait metrics can provide insights into the effects of biotic interactions on tree growth. For instance, higher functional diversity and phylogenetic dissimilarity are expected to increase resource partitioning and reduce susceptibility to attack by natural enemies (Uriarte et al., 2010; Yue et al., 2022), thereby enabling species to coexist and avoid competition (Chen et al., 2016). This approach assumes that focal trees in communities with greater trait diversity and phylogenetic distance will exhibit higher growth rates compared to those surrounded by more similar neighbors. Additionally, the mean trait values of the neighboring community can reflect the overall resource-use and acquisition strategies (HilleRisLambers et al., 2012), which can drive individual tree growth as well. For example, in tropical rain forest a community where the predominant resource-use strategy is conservative can lead to reduced growth rates among neighboring trees, allowing focal trees greater access to resources and thus facilitating their growth (Westbrook et al., 2011). Conversely, in tropical dry forests, communities displaying conservative trait values have been noted to enhance overall productivity (Prado-Junior et al., 2016). Despite advancements in understanding crowding, trait, and phylogenetic-based influences on tree growth, research gaps persist. Exploring the specific conditions under which these mechanisms operate and factors influencing their prevalence can enhance our understanding of biotic interactions in forest ecosystems.

In this study, we simultaneously investigated the influence of functional traits and phylogenetic dissimilarities, NCI, and functional community structure on individual tree growth (Figure 1). We utilized two approaches to explore these factors: quantifying interaction strength by measuring the influence of neighboring individuals on the growth rate of focal trees (Figure 1a) and examining the effect of community structure on individual tree growth (Figure 1b). For this purpose, we selected focal trees growing in mature subtropical Brazilian Atlantic forests. Additionally, we categorized focal trees based on growth rate (fast, intermediate, and slow) and position within the community canopy, as taller focal trees may respond distinctly different than smaller ones in relation to their neighbors' height (West & Ratkowsky, 2022). In these groups of focal trees, we expected overcrowding of trees restricting individual tree growth, and increased functional diversity and phylogenetic distance between focal trees and their neighbors enhancing focal tree growth. Similarly, higher functional diversity should aid resource partitioning, promoting the improvement of focal tree growth. Notably, neighborhood effects on focal tree growth also can depend on their growth class and canopy position.

2 | METHODS

2.1 | Study site

The study was conducted in permanent forest plots located in the Long-term Ecological Research in Subtropical Atlantic Forests (LERSAF) project, in southern Brazil (Appendix S1). Studied plots are located in *Araucaria* forests, at elevations from 900 to 930 m a.s.l. The climate is humid subtropical, with temperate summers—Cfb according to Köppen's climate classification (Alvares et al., 2013). The mean temperature in our study region is 18°C, frost is frequent in the winter, and the mean annual precipitation is 1800 mm, without a dry season.

We used vegetation data of six permanent plots in old-growth forests within protected areas distributed in two sites: Pró-Mata Nature Research and Conservation Center (29°26′27″ S and 50°14′ W) and Aparados da Serra National Park (29°07′–29°15′ S and 50°01′–50°10′ W). Almost all remnants of old-growth forests in the

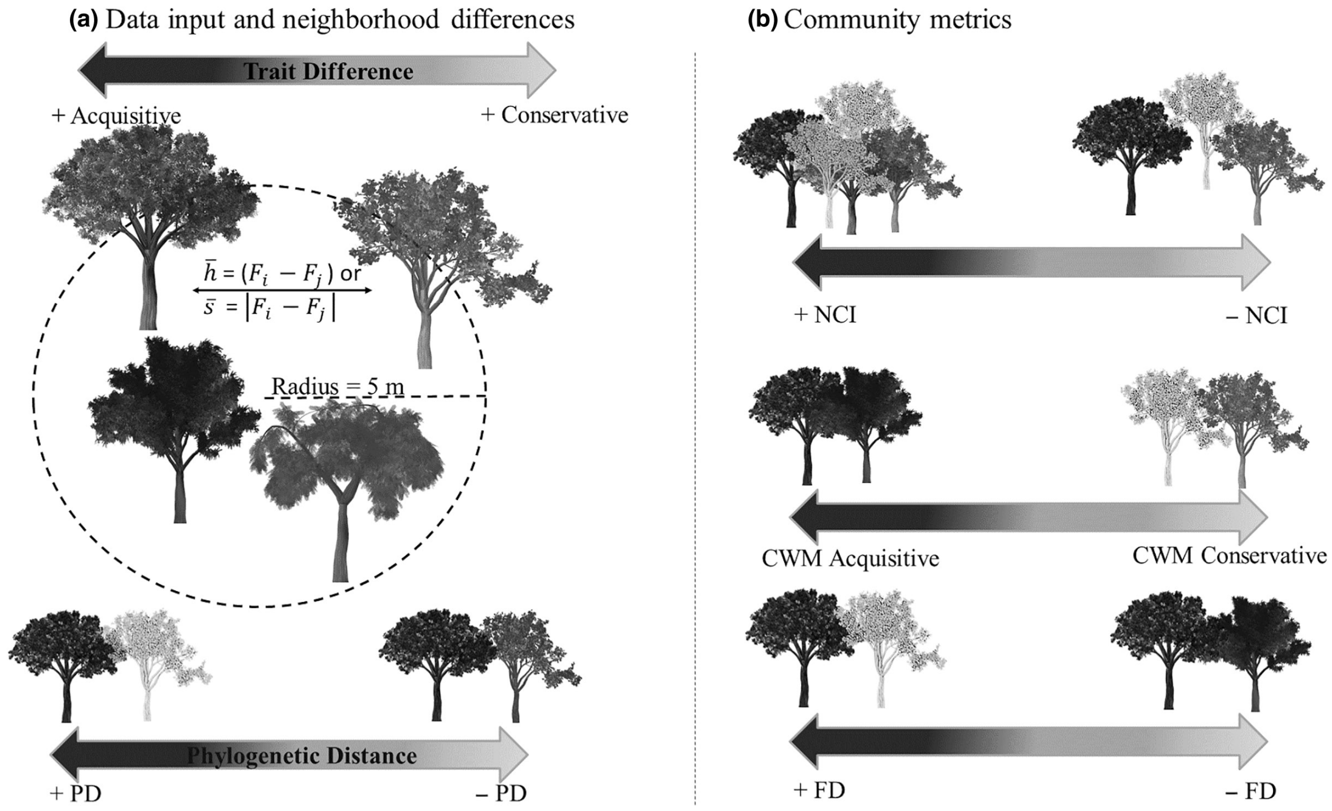

FIGURE 1 Schematic representation of the data collection and biotic interactions metrics potentially affecting individual tree growth in forests. In (a) differences between focal trees and their neighboring individuals are considered, including trait differences ($\bar{h}$ = neighborhood hierarchical mean trait difference and $\bar{s}$ = neighborhood absolute mean trait difference) between focal tree (F_i) and neighbor tree (F_j), as well as the mean phylogenetic distance (PD) between the focal individual and all neighboring trees. In (b), overall community metrics were evaluated, including the neighborhood crowding index (NCI), community-weighted mean (CWM), and functional diversity (FD).

region may have suffered selective logging in the past century, but there was no clear cut in our permanent plots and no selective logging activity has been registered in both sites for at least the past 100 years. The plots were censused in 2014 and 2019 following the RAINFOR protocols (Phillips et al., 2010). In each plot, every individual with a woody stem of at least 5 cm diameter at breast height (DBH measured at 1.3 m above the ground) was tagged with a unique number and identified to the species level, and we measured its height (average ± SD = 9 ± 4.27meters) and stem diamater (average ± SD = 14.2 ± 11.7 centimeters). The number of tree individuals (DBH ≥5 cm) per hectare in the permanent plots ranged from 1056 to 1828, with the five more abundant species being the Myrtaceae *Myrceugenia myrcioides*, *Myrcia retorta*, *Myrceugenia miersiana*, and *Myrceugenia euosma* together with the Brazilian pine *Araucaria angustifolia*.

1.1 *Sampling design*

For this study, we randomly selected a subset of trees from the forest plots. For 826 trees, we firstly computed the annual growth rate (AGR), which was calculated as (basal area$_{t+1}$ − basal area$_{t}$)/years interval, where years is the number of years between the two censuses (2014 and 2019). Secondly, the trees were divided into three growth classes using quartiles: the lower growth rate in the first interval (25th percentile and growth rate between 0.00008 and 0.0006 cm^2 ha^{-1} year^{-1}), the medium growth rate in the second interval (50th percentile and growth rate between 0.0006 and 0.003 cm^2 ha^{-1} year^{-1}), and the higher growth rate in the third interval (75th percentile and growth rate between 0.003 and 0.06 cm^2 ha^{-1} year^{-1}). Thirdly, from each growth class in each site, 20 trees were randomly selected (totaling 120 focal trees, 60 in each site) using the "slice_sample" function, in the *dplyr*package (Wickham et al., 2023). Finally, to measure the neighborhood of each focal tree, we identified all trees of at least 5 cm DBH within a 5-m radius using a laser rangefinder (Figure 1a). We identified the species, and then measured the stem size, height, and distance between the focal tree and each neighboring tree (d_{ij}) while also identifying the species of each tree. All radiuses selected had at least two species (Appendix S2). This information was used to calculate neighborhood variables used in the models.

We utilized plant functional traits, which are indicators of plant functional strategies and are expected to be related to individual tree growth and performance (Wright et al., 2004; Poorter et al., 2008; Chave et al., 2009; Díaz et al., 2015). These traits included height (H, m), leaf area (LA, cm^2), specific leaf area (SLA, cm^2 g^{-1}), leaf dry matter content (LDMC, mg g^{-1}), and wood density (WD, g cm^{-3}). Focal tree leaf traits were collected at the individual level (i.e., 10 leaves per individual), while neighborhood-tree leaf traits were obtained from our Plant Ecology Lab database, available within the Try Plant Trait Database (Kattge et al., 2020), and the average value per species was considered. The species trait value within the database is based on collected leaves from individuals of the same study region. Tree height data were collected at the individual level using a laser rangefinder, while WD information was obtained mostly from regional measurements (Missio et al., 2017; Oliveira et al., 2019), but also from a global database (Chave et al., 2009). Measurements and procedures to obtain information on functional traits from species available in our database followed standardized protocols (Pérez-Harguindeguy et al., 2013).

2.2 | Neighborhood and community metrics

To evaluate the impact of local neighborhood on focal tree growth, we measured neighborhood variables. We calculated a NCI based on the stem size and spatial distance of neighboring trees within a fixed radius of 5 m. The calculation is as follows (Equation 1):

$$\mathrm{NCI}_j = \sum_j \frac{\mathrm{DBH}_j^2}{d_{ij}^2} \tag{1}$$

where d_{ij} is the spatial distance between a focal individual *i* and a neighbor tree *j* and DBH$_j$ is the DBH of neighbor tree *j*.

To enhance our comprehension of the relationship between tree growth and neighborhood competition, we calculated distinct indices for measuring the influence of neighborhood in the growth of focal trees by using the neighborhood hierarchical mean trait difference ($\bar{h}$) and neighborhood absolute mean trait difference ($\bar{s}$) (Figure 1a), following Equations (2) and (3):

$$\bar{h} = \sum \frac{F_i - F_j}{n_j} \tag{2}$$

and

$$\bar{s} = \frac{\sum \left| F_i - F_j \right|}{n_j} \tag{3}$$

The values of the functional trait of interest for the focal individual (*i*) and neighbors (*j*) are represented by F_i and F_j, and n_j is the number of neighbors. The individual focal trait data were obtained from the tree used to measure growth, while the average trait value at the species level was used to represent the neighbors' traits, except for tree height, which was used at an individual level. Specific traits used for Equations (2) and (3) are hereafter identified by the letters '$\bar{h}$' and '$\bar{s}$', respectively, as for example H$\bar{h}$ and H$\bar{s}$ for the trait height (H).

These indices are associated with the trait-mediated ranks of competitive abilities and niche differentiation, respectively (Kunstler et al., 2012; Lasky et al., 2014; Carmona et al., 2019). We also calculated both these indices weighted by neighbor coverage and size (Yang et al., 2021), but as they were strongly correlated with the previous ones, we employ only Equations (2) and (3).

Also, to test if the tree neighbors influence the focal tree's growth, the mean phylogenetic distance of the focal tree to all their neighborhood trees (mean PD), the community FD, and community trait composition (CWM) were calculated. To calculate mean PD, we constructed an ultrametric phylogeny using the *V.PhyloMaker* package for all 73 species in the data set. We used the *PhytoPhylo* megaphylogeny as a backbone and added species absent from the megaphylogeny as basal polytomies within their genera (scenario 1; Qian & Jin, 2016). Our phylogenetic tree contains polytomies, which result in uncertainty about the correct branching order of taxa. To address this, we used the "bifurcatr" function in the *PDcalc* package (Rangel et al., 2015) to randomly resolve polytomies. We ran the algorithm 1000 times to explore the range of plausible phylogenetic trees. Based on each of the 1000 phylogenetic trees, we calculated the mean PD between the focal individual and all neighbor trees within the radius (Castillo et al., 2010) and averaged the 1000 PD values around each focal individual. Thus, this FD and trait composition were community metrics here. To compute FD, we calculated Rao's quadratic entropy weighted by species' relative abundance in each community, that is, all trees within the radius ("mpd" function in the *picante* package) (Kembel et al., 2010; de Bello et al., 2016). We calculated FD using all traits (H, LA, SLA, LDMC, and WD). Finally, we calculated the mean trait values of each community of tree neighbors (CWM) accounting for species' relative abundance in each community (function "functcomp" in the *FD* package) (Laliberté et al., 2015). We excluded the focal trees from the CWM and FD calculations.

2.3 | Statistical analyses

To assess the effects of neighborhood interactions and community structure on tree growth, we performed linear mixed-effect models with AGR as the response variable and non-correlated neighborhood variables as predictor. Species nested in sites were included as a random variable, which allows us to show the conditional and marginal coefficients of determination (R^2_{c} and R^2_{m}, respectively). Before constructing the models, we analyzed Pearson's correlation between predictor variables to improve model estimation and reduce collinearity (Appendix S3). We selected variables for our models among those with correlation below 0.7. The variables selected included NCI, neighborhood hierarchical trait difference ($\overline{h}$), neighborhood absolute trait difference ($\overline{s}$, except for SLA), CWM, FD, and mean PD (Appendix S4).

To better understand how neighborhood variables affect focal tree growth, we constructed three types of models based on the categories of focal trees described above: (a) a model including all focal trees, (b) models separating trees by growth class (i.e., faster, intermediary, or slower growth), and (c) models separating trees by height (i.e., taller or smaller focal trees) by using the height hierarchical difference (H$\overline{h}$, Equation 3). We considered the tree height because the competitive effects of trees may be proportional to their size (West & Ratkowsky, 2022). The H$\overline{h}$ equation postulates that positive values indicate that the focal tree has higher trait values than neighboring trees (or taller focal trees), while negative values indicate that the focal tree has lower trait values than neighboring trees (or smaller focal trees).

In the specific models considered, we fitted global linear mixed-effect models (i.e., AGR ~ NCI + neighborhood hierarchical trait difference ($\overline{h}$) + neighborhood absolute trait difference ($\overline{s}$) + mean PD + FD + CWM, random = ~focal species identity/site) to predict the AGR of focal trees (Appendix S4). Separate models were considered for each type of model. To identify the most parsimonious set of neighborhood variables influencing focal tree growth, we used stepwise backward regression analysis based on the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002; McCullagh & Nelder, 1989). The "stepAIC" function in the *MASS* package was used for this purpose (Venables & Ripley, 2002). To enable a better comparison between predictors at different measurement units, we standardized these variables to zero mean and unit variance (Schielzeth, 2010). We used the "lme" function in the *nlme* R package (Pinheiro & Bates, 2023). We conducted a further analysis to unveil general patterns using quantile regression models (see Appendixes S5, S6 and S7). All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023).

3 | RESULTS

In this study, we selected 120 focal trees from 43 species and measured 1518 neighboring trees from 71 species (Appendix S2). Most frequent focal trees were *Araucaria angustifolia* (16 individuals), *Myrceugenia myrcioides* (10 individuals), and *Ilex microdonta* (nine individuals). The most common neighboring tree species are *Myrceugenia myrcioides* (180 individuals), *Myrcia retorta* (137 individuals), and *Araucaria angustifolia* (131 individuals). Overall, there were 1518 neighboring individuals from 142 species (for more details see Appendix S2). The average number of species in neighborhood communities was seven, with a range from two to 14 species, indicating considerable variability in composition. When considering all focal tree individuals together, the best predictors included SLA hierarchical trait difference (SLA$\overline{h}$) and mean PD of the focal tree and its neighborhood (Table 1 and Figure 2). Lower SLA$\overline{h}$ values and higher mean PD values were linked to higher growth (Figure 2a), which means that trees with lower SLA values than their neighbor species (i.e., negative SLA$\overline{h}$ values, Appendix S4) and surrounded by more distantly related species (i.e., higher mean PD) are growing better. These effects were maintained only partially when separating the focal trees by growth class and size. SLA$\overline{h}$ affected smaller individuals more strongly and PD taller ones. PD also affected faster-growing individuals, whereas SLA$\overline{h}$ was not significant in models splitting the trees into growth class categories. Moreover, when splitting focal individuals by growth classes and size, we found some different predictors. We specifically found faster-growing trees were negatively associated with height absolute trait difference (H$\overline{s}$) (Figure 2b) and positively associated with mean PD, CWM SLA, and CWM WD (Figure 2c). While the increase in CWM SLA could be conceptually linked to SLA$\overline{h}$ (i.e. neighbors having higher SLA values than focal trees), the two values were considerably related to growth. So, trees that are in the faster AGR category grow more when they are more similar in height but distantly related to the neighborhood, and these neighbors reveal higher SLA and WD

TABLE 1 Results of linear mixed-effect models used to assess the impact of neighborhood trait differences, both hierarchical ($\bar{h}$) and absolute ($\bar{s}$), mean phylogenetic distance (PD), and community-weighted mean of traits (CWM) on the annual growth rate (AGR) of focal trees.

Models	Neighborhood difference	Coef.	Community structure	Coef.
All Focal	SLA$\bar{h}$	−0.27*		
	WD$\bar{s}$	0.21		
$R^2_m=0.15$; $R^2_c=0.17$	Mean PD	0.42**		
Faster AGR	H$\bar{s}$	−0.17*	CWM SLA	0.27**
$R^2_m=0.47$; $R^2_c=0.47$	Mean PD	0.30**	CWM WD	0.31**
Intermediary AGR	LDMC$\bar{h}$	−0.10	NCI	−0.10
	WD$\bar{h}$	0.11	CWM LA	−0.09
$R^2_m=0.36$; $R^2_c=0.36$	LA$\bar{s}$	0.10	CWM H	0.07
	WD$\bar{s}$	0.09		
Slower AGR	SLA$\bar{h}$	0.20	CWM LDMC	−0.19
$R^2_m=0.20$; $R^2c=0.20$	H$\bar{h}$	0.17		
Taller	LA$\bar{h}$	−0.36*	NCI	−0.23
$R^2_m=0.27$; $R^2_c=0.39$	Mean PD	0.69**	CWM WD	0.31
Smaller	SLA$\bar{h}$	−0.65*	NCI	−0.40
	LDMC$\bar{h}$	−0.52	CWM LA	−0.37
$R^2_m=0.27$; $R^2_c=0.39$	H$\bar{h}$	−0.34	CWM LDMC	−0.37
	LA$\bar{s}$	−0.41		
	WD$\bar{s}$	0.54*		

Note: The models were analyzed separately for all focal trees and for focal trees categorized by growth classes (slower, intermediary, and faster) and height (smaller and taller). The functional traits include specific leaf area (SLA), individual height (H), leaf area (LA), and wood density (WD). Information on R^2 values, standardized coefficients (Coef.), and significant effects (**, $p<0.005$; *, $p<0.05$) in the models are represented.

mean community values. The growth of trees of the intermediary and slower-growth class was not associated with any variable. Finally, the growth of taller focal trees was negatively associated with LA$\bar{h}$ (i.e., those with smaller leaves than their neighbors grow more, Figure 2a), while smaller trees were negatively associated with SLA$\bar{h}$ (as for all trees) and positively with WD$\bar{s}$ (i.e., more dissimilar trees grow more, Figure 2b) (Table 1). NCI and FD were not relevant in predicting the growth rates of studied trees.

4 | DISCUSSION

In our study, we aimed to investigate the influences of neighboring trees on the growth of focal trees. Our findings revealed that both functional and phylogenetic distances play a role in shaping the growth of focal trees but that their effects are modulated depending partially on the traits examined and the growth class, and on the light capture ability of the focal trees analyzed. We need to highlight that we measure AGRs based on basal area increment, which may not always align with long-term wood productivity. Additionally, other variables influence the seasonal dynamics of tree growth and woody biomass production, including intra-annual climatic variability, which remains largely unexplored (Cherubini, 2024). This demonstrates the complexity of trait interactions with the individual growth capacity in determining tree growth rates of forest communities. We found that the surrounding assembly composed of species from different clades (higher phylogenetic distance) lead focal trees, independently of their growth class, to grow more, indicating limiting similarity. Additionally, we observed that the absolute height and WD differences between a focal tree and its neighbors did impact the growth rate of faster-growing trees and smaller trees, respectively. Among other consistent effects, communities composed of species with acquisitive leaves (higher CWM SLA) but denser steam structures (higher WD) positively affected faster-growing trees. In general, greater SLA than focal trees (SLA$\bar{h}$) decreased the growth of focal trees, although the relationship was weak, which was also observed for smaller trees. For taller trees, greater LA than focal individuals (LA$\bar{h}$) decreased the growth of trees. Thus, different specific predictors depend on focal AGR and size. Overall, our models revealed that differences in trait hierarchies, specifically related to leaf construction cost and structural support, significantly influenced the growth of trees in South Atlantic forests. By examining the relationships between neighboring trees and focal tree growth, our study provides valuable insights into the complex dynamics of tree interactions and their implications for overall forest ecosystem dynamics.

4.1 | Overall strategies that improve tree performance

The AGR considering all focal trees together and the most successful ones, which had faster growth and reached the taller ones, were positively correlated with the mean phylogenetic distance between the focal tree and its neighboring trees. Our results indicate that the evolutionary relationships among co-occurring species in our study area significantly predict individual performance. Specifically, the greater the phylogenetic distance between the focal tree and its neighbors, the greater the individual performance. This finding emphasizes that functional and ecological similarities are influenced by common ancestry patterns (Webb et al., 2008), as distantly related species contribute to coexistence patterns and individual performance. Consequently, more distantly related species may exhibit greater ecological differentiation due to limited similarity (i.e., lower niche overlap) (Webb, 2000), reducing competition and enhancing growth. Additionally, phylogenetic relatedness can impact individual performance indirectly since phylogenetically distant species can promote reduced competition by avoiding host-specific pathogens and pests (Gilbert et al., 2015).

Differences in trait hierarchies were a significant growth driver, considering all focal and taller trees. However, it is important to

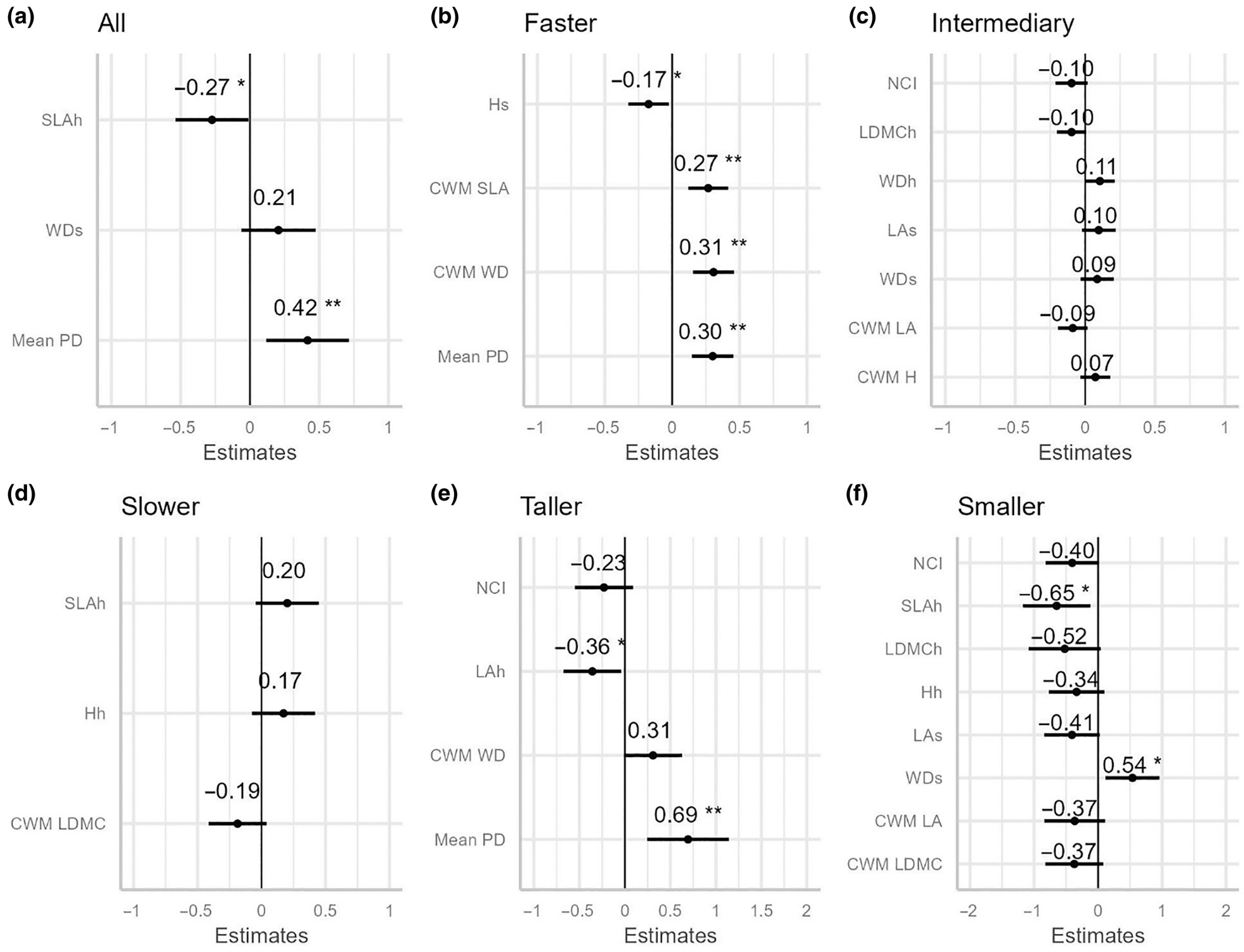

FIGURE 2 Standardized regression coefficients of the best-fitted model for modeling focal tree growth by neighborhood hierarchical ($\bar{h}$) and absolute trait difference ($\bar{s}$), mean phylogenetic distance (mean PD), and community-weighted mean (CWM) of functional traits. The models include (a) all focal trees, model separating trees by (b) faster, (c) medium, and (d) slower growth class, and model separating trees by height, with (e) taller and (f) smaller focal trees. The functional traits considered were SLA, LA, WD, and individual H. Each point is a standardized regression coefficient, and each line segment is a 95% percentile confidence interval respectively. Confidence intervals that do not cross the zero baseline indicate statistically significant effects (**, $p < 0.005$; *, $p < 0.05$).

highlight that the relationships between traits and specific types of focal trees exhibited variation. Notably, traits related to nutrient conservation (lower SLA values) showed a negative association with growth for all focal trees and smaller trees, although the relationship was weak (Figure 2a). In addition, traits associated with light capture (LA) exhibited a similar negative association with growth, but specifically for taller trees. These patterns follow a hierarchical structure, reflecting competitive dynamics. For instance, trees with relatively lower SLA and LA values than their neighbors demonstrated improved individual performance.

The observation that focal trees with better performance and greater competitive ability have tougher and smaller leaves compared to their neighbors suggests that local conditions, including low nutrient availability and temperatures, favor conservative leaf strategies associated with lower SLA and LA values to optimize resource uptake in an environmental context of low temperatures (Kraft et al., 2014; Bennett et al., 2016; Klipel et al., 2023). Additionally, it is important to note that taller trees are likely to receive an adequate amount of light for photosynthesis, but they are also exposed to varying temperatures, ranging from low to high temperatures in the forest canopy. Therefore, having smaller leaves becomes a successful strategy for thriving in the community in such subtropical Atlantic forests. The weak relationship between SLA$\bar{h}$ and SLA of all focal trees may be due to the different sizes of focal trees and, therefore, the different spaces these trees occupy in the forest canopy.

We observed that the absolute height difference (H$\bar{s}$) between a focal tree and its neighbors did affect the growth rate of faster-growing trees. Tree height is a good predictor of crown exposure and light competition. It is widely observed that taller trees tend to have a competitive advantage over smaller ones, leading to variations in tree heights (Kraft et al., 2014). However, contrary to findings in other studies (Goldberg et al., 2017; Carmona et al., 2019;

Yue et al., 2022), our study revealed that individuals surrounded by neighbors of more similar heights exhibited greater growth. The mechanisms explaining this effect still need to be fully understood but could result from complementary crown architectures where species coexist and compete relatively equally (Hubbell, 2006; Sapijanskas et al., 2014). In this scenario, the improvement in tree performance due to strong height similarity may indicate a symmetrical competition. The height growth of one tree encourages another tree's growth, leading to higher stem growth rates in a community with similar heights.

Furthermore, the local neighborhood trait composition was significantly associated with the performance of faster-growing trees. For instance, faster-growing trees tend to be surrounded by a trait environment characterized by high WD and SLA values. The WD represents the plant's investment in biomass per unit of wood volume, indicating that tree communities with denser wood are often associated with slow-growing species (Chave et al., 2009), and can also be an indicator of a late-successional or old-growth forest. Typically, species with low WD prioritize height growth for better light conditions in the canopy, while species with high WD focus on expanding their crowns horizontally for enhanced light interception in the shaded forest understorey (Iida et al., 2012). Then, the similar heights of faster-growing trees and their neighbors, with the predominance of high WD in the community, can again be an indication of the presence of interacting complementary crown architectures and an old-growth neighborhood structure.

Additionally, tree communities with thinner and lighter leaves, represented by high SLA values, generally exhibit high photosynthetic assimilation, respiration rates, and shorter leaf lifespan (Wright et al., 2004). High SLA enables rapid resource acquisition (acquisitive strategy) and generally predominates in communities under less stressful conditions, whereas species with more conservative leaf strategies predominate under more stressful conditions (e.g., lower temperature and soil fertility). Concerning the local environmental conditions in subtropical Brazilian Atlantic forests, in a community where neighboring trees generally possess softer leaves and denser wood, focal individuals may experience facilitation rather than competition from their neighbors. The coexistence of trees differing in architecture and light capture strategy can result in faster growth for the focal trees. This scenario reflects how the coexistence of different tree species or individuals within the forest can be context-dependent and structurally complex.

4.2 | Additional strategies for performance enhancement—the case of smaller trees

Smaller trees improve performance when they possess lower SLA values than their neighbors ($\mathrm{SLA}\bar{h}$), reflecting competitive dynamics within the smaller trees. This finding aligns with the pattern identified in the overall focal trees model. The local conditions (i.e., low nutrient availability and temperatures) favor conservative leaf strategies associated with lower SLA to optimize resource uptake, mainly for smaller individuals where competition for resources can be more intense. Furthermore, these smaller trees exhibit increased growth when surrounded by trees that exhibit high dissimilarity in $\mathrm{WD}\bar{s}$. WD is associated with the hydraulic properties of the xylem and the acquisition of soil nutrients (Chave et al., 2009), with higher dissimilarity in WD indicating a greater level of niche differentiation among individual trees, facilitating resource partitioning. The presence of trees with diverse WD patterns may contribute to greater FD within the community. In challenging environments, this diversity can offer broader adaptive responses to specific conditions, thereby favoring the performance of smaller focal trees. These differences in $\mathrm{WD}\bar{s}$ and $\mathrm{SLA}\bar{h}$ contribute to smaller trees' growth dynamics within their specific environmental context such as the understorey and shade conditions.

5 | CONCLUSION

Overall, our results indicate that multiple factors influence the relative growth and competitive outcome among subtropical trees. These factors include differences in leaf construction cost, hydraulic conductance, and tree size, as well as the PD between the focal tree and its neighboring trees. In general, trees with more conservative leaves relative to their neighborhood performed better than the opposite, which seems to be a better strategy considering the local environmental conditions of the studied forests (cold and low fertility). Similar heights but more distinct WD relative to the neighbors also affected the growth rate of focal trees, revealing the influence of whole-plant structure on tree growth patterns inside mature forests. Finally, being phylogenetically distant from species present in the neighborhood positively impacts the individual performance of studied tree species. We emphasize that to accurately assess the effects and predict the consequences of climate change, including tree mortality and migration, it is crucial to obtain tree dynamic data from long-term forest plot monitoring. Field-based data enable us to gain a deeper understanding of how competition and functional characteristics influence tree performance, growth, and forest productivity. This knowledge constitutes a baseline for implementing effective ecological restoration and conservation strategies to mitigate the impact of global change on biodiversity and ecosystem services.

AUTHOR CONTRIBUTIONS

Joice Klipel—conceptualization, formal analysis, software, writing: original draft, data curation, investigation, methodology. Rodrigo Scarton Bergamin—supervision, writing: review and editing. Kauane Maiara Bordin—writing: review and editing. Rayana Caroline Picolotto—writing: review and editing. Sandra Cristina Müller—supervision, writing: review and editing. Francesco de Bello—supervision, writing: review and editing.

ACKNOWLEDGEMENTS

We would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)—Finance Code 001 for the scholarship of Joice Klipel and Rayana Caroline Picolotto, the Programa de Excelência Acadêmica (PROEX) and the Portal de Periódicos; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number 309874/2015-7 to Sandra Cristina Müller); and the Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS; process number 2218—2551/12-2 and 19/2551-0001698-0). Kauane Maiara Bordin and Sandra Cristina Müller are members of the National Institute of Science and Technology (INCT) in Ecology, Evolution, and Conservation of Biodiversity, supported by MCTIC/CNPq and FAPEG.

FUNDING INFORMATION

We would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)—Finance Code 001 for the scholarship of Joice Klipel and Rayana Caroline Picolotto, the Programa de Excelência Acadêmica (PROEX) and the Portal de Periódicos; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number 309874/2015-7 to Sandra Cristina Müller); and the Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS; process number 2218—2551/12-2 and 19/2551-0001698-0). Kauane Maiara Bordin and Sandra Cristina Müller are members of the National Institute of Science and Technology (INCT) in Ecology, Evolution, and Conservation of Biodiversity, supported by MCTIC/CNPq and FAPEG.

CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article.

ORCID

Joice Klipel https://orcid.org/0000-0003-3936-9692
Rodrigo Scarton Bergamin https://orcid.org/0000-0002-2405-9977
Kauane Maiara Bordin https://orcid.org/0000-0003-3871-6293

REFERENCES

Alvares, C.A., Stape, J.L., Sentelhas, P.C. & de Moraes Gonçalves, J.L. (2013) Modeling monthly mean air temperature for Brazil. *Theoretical and Applied Climatology*, 113, 407–427. Available from: https://doi.org/10.1007/s00704-012-0796-6

Bennett, J.A., Riibak, K., Tamme, R., Lewis, R.J. & Pärtel, M. (2016) The reciprocal relationship between competition and intraspecific trait variation. *Journal of Ecology*, 104, 1410–1420. Available from: https://doi.org/10.1111/1365-2745.12614

Britton, T.G., Richards, S.A. & Hovenden, M.J. (2023) Quantifying neighbour effects on tree growth: are common 'competition' indices biased? *Journal of Ecology*, 1365-2745, 14095. Available from: https://doi.org/10.1111/1365-2745.14095

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.

Cadotte, M.W. & Tucker, C.M. (2017) Should environmental filtering be abandoned? *Trends in Ecology & Evolution*, 32, 429–437. Available from: https://doi.org/10.1016/j.tree.2017.03.004

Carmona, C.P., de Bello, F., Azcárate, F.M., Mason, N.W.H. & Peco, B. (2019) Trait hierarchies and intraspecific variability drive competitive interactions in Mediterranean annual plants. *Journal of Ecology*, 107, 2078–2089. Available from: https://doi.org/10.1111/1365-2745.13248

Castillo, J.P., Verdú, M. & Valiente-Banuet, A. (2010) Neighborhood phylodiversity affects plant performance. *Ecology*, 91, 3656–3663. Available from: https://doi.org/10.1890/10-0720.1

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366. Available from: https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chen, Y., Wright, S.J., Muller-Landau, H.C., Hubbell, S.P., Wang, Y. & Yu, S. (2016) Positive effects of neighborhood complementarity on tree growth in a Neotropical forest. *Ecology*, 97, 776–785. Available from: https://doi.org/10.1890/15-0625.1

Cherubini, P. (2024) Dendrochronology: large datasets help explain when and how trees grow but not why. *Current Biology*, 34, 237–239. Available from: https://doi.org/10.1016/j.cub.2024.01.051

Coomes, D.A. & Allen, R.B. (2007) Effects of size, competition and altitude on tree growth. *Journal of Ecology*, 95, 1084–1097. Available from: https://doi.org/10.1111/j.1365-2745.2007.01280.x

de Bello, F., Carmona, C.P., Lepš, J., Szava-Kovats, R. & Pärtel, M. (2016) Functional diversity through the mean trait dissimilarity: resolving shortcomings with existing paradigms and algorithms. *Oecologia*, 180, 933–940. Available from: https://doi.org/10.1007/s00442-016-3546-0

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. et al. (2015) The global spectrum of plant form and function. *Nature*, 529, 167–171. Available from: https://doi.org/10.1038/nature16489

Ding, Y., Zang, R., Huang, J., Xu, Y., Lu, X., Guo, Z. et al. (2019) Intraspecific trait variation and neighborhood competition drive community dynamics in an old-growth spruce forest in northwest China. *Science of the Total Environment*, 678, 525–532. Available from: https://doi.org/10.1016/j.scitotenv.2019.05.014

Gilbert, G.S., Briggs, H.M. & Magarey, R. (2015) The impact of plant enemies shows a phylogenetic signal. *PLoS One*, 10, e0123758. Available from: https://doi.org/10.1371/journal.pone.0123758

Goldberg, D.E., Martina, J.P., Elgersma, K.J. & Currie, W.S. (2017) Plant size and competitive dynamics along nutrient gradients. *The American Naturalist*, 190, 229–243. Available from: https://doi.org/10.1086/692438

Hart, S.P., Schreiber, S.J. & Levine, J.M. (2016) How variation between individuals affects species coexistence. *Ecology Letters*, 19, 825–838. Available from: https://doi.org/10.1111/ele.12618

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248. Available from: https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hubbell, S.P. (2006) Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398. Available from: https://doi.org/10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Wirth, C. et al. (2020) TRY plant trait database—enhanced coverage and open access. *Global Change Biology*, 26, 119–188. Available from: https://doi.org/10.1111/gcb.14904

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. Available from: https://doi.org/10.1093/bioinformatics/btq166

Klipel, J., Müller, S.C., Gliesch, M., Duarte, L., Carlucci, M.B. & Bergamin, R.S. (2023) Variability in leaf traits reveals contrasting strategies between forest and grassland woody communities across southern Brazil. *Flora*, 305, 152340. Available from: https://doi.org/10.1016/j.flora.2023.152340

Kraft, N.J.B., Crutsinger, G.M., Forrestel, E.J. & Emery, N.C. (2014) Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos*, 123, 1391–1399. Available from: https://doi.org/10.1111/oik.01311

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C. et al. (2016) Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207. Available from: https://doi.org/10.1038/nature16476

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E. et al. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, 15, 831–840. Available from: https://doi.org/10.1111/j.1461-0248.2012.01803.x

Laliberté, E., Legendre, P. & Shipley, B. (2015) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package: Version 1.0-12.

Lasky, J.R., Uriarte, M., Boukili, V.K. & Chazdon, R.L. (2014) Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5616–5621. Available from: https://doi.org/10.1073/pnas.131934211

Lebrija-Trejos, E., Wright, S.J., Hernández, A. & Reich, P.B. (2014) Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. *Ecology*, 95, 940–951. Available from: https://doi.org/10.1890/13-0623.1

Iida, Y., Poorter, L., Sterck, F.J., Kassim, A.R., Kubo, T., Potts, M.D. & Kohyama, T.S. (2012) Wood density explains architectural differentiation across 145 co-occurring tropical tree species. *Functional Ecology*, 26, 274–282. Available from: https://doi.org/10.1111/j.1365-2435.2011.01921.x

Macarthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377–385. http://www.jstor.org/stable/2459090

Mason, N.W.H., de Bello, F., Doležal, J. & Lepš, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, 99, 788–796. Available from: https://doi.org/10.1111/j.1365-2745.2011.01801.x

Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093. Available from: https://doi.org/10.1111/j.1461-0248.2010.01509.x

McCullagh, P. & Nelder, J.A. (1983) *Generalized linear models*. New York: Chapman and Hall.

Missio, F.D.F., Da Silva, A.C., Higuchi, P., Longhi, S.J., Brand, M.A., Rios, P.D. et al. (2017) Functional traits of tree species in a fragment of araucaria forest in Lages, Santa Catarina state. *Ciência Florestal*, 27, 215–224. Available from: https://doi.org/10.5902/1980509826460

Oliveira, L.Z., Uller, H.F., Klitzke, A.R., Eleotério, J.R. & Vibrans, A.C. (2019) Towards the fulfillment of a knowledge gap: wood densities for species of the subtropical atlantic forest. *Data Descriptor*, 4, 1–10. Available from: https://doi.org/10.3390/data4030104

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. Available from: https://doi.org/10.1071/BT12225_CO

Phillips, O., Baker, T., Feldpausch, T. & Brienen, R. (2010) RAINFOR field manual for plot establishment and Remeasurement.

Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. New York: Springer. Available from: https://doi.org/10.1007/b98882

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. et al. (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, 89, 1908–1920. Available from: https://doi.org/10.1890/07-0207.1

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M. et al. (2016) Conservative species drive biomass productivity in tropical dry forests. *Journal of Ecology*, 104, 817–827. Available from: https://doi.org/10.1111/1365-2745.12543

Qian, H. & Jin, Y. (2016) An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, 9, 233–239. Available from: https://doi.org/10.1111/1365-2745.12543

R Core Team. (2023) *R: a language and environment for statistical Computing_*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Rangel, T.F., Colwell, R.K., Graves, G.R., Fučíková, K., Rahbek, C. & Diniz-Filho, J.A.F. (2015) Phylogenetic uncertainty revisited: implications for ecological analyses. *Evolution*, 69, 1301–1312. Available from: https://doi.org/10.1111/evo.12644

Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008) Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, 96, 192–203. Available from: https://doi.org/10.1111/j.1365-2745.2007.01330.x

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. (2014) Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, 95, 2479–2492. Available from: https://doi.org/10.1890/13-1366.1

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113. Available from: https://doi.org/10.1111/j.2041-210X.2010.00012.x

Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical Forest communities. *Ecology*, 88, 1770–1780. Available from: https://doi.org/10.1890/06-1499.1

Uriarte, M., Lasky, J.R., Boukili, V.K. & Chazdon, R.L. (2016) A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. *Functional Ecology*, 30, 157–167. Available from: https://doi.org/10.1111/1365-2435.12576

Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., John Kress, W., Erickson, D. et al. (2010) Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters*, 13, 1503–1514. Available from: https://doi.org/10.1111/j.1461-0248.2010.01541.x

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edition. New York: Springer.

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain Forest trees. *The American Naturalist*, 156, 145–155. Available from: https://doi.org/10.1086/303378

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. Available from: https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Webb, C.O., Cannon, C. & Davies, S. (2008) *Ecological organization, biogeography, and the phylogenetic structure of tropical forest tree communities*. Oxford: Tropical Forest Community Ecology, pp. 79–97.

West, P.W. & Ratkowsky, D.A. (2022) Problems with models assessing influences of tree size and inter-tree competitive processes on individual tree growth: a cautionary tale. *Journal of Forestry Research*, 33, 565–577. Available from: https://doi.org/10.1007/s11676-021-01395-9

Westbrook, J.W., Kitajima, K., Burleigh, J.G., Kress, W.J., Erickson, D.L. & Wright, S.J. (2011) What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant Woody species in a Neotropical Forest. *The American Naturalist*, 177, 800–811. Available from: https://doi.org/10.1086/659963

Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023) Dplyr: a grammar of data Manipulation_. R Package Version 1.1.3.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, 428, 821–827. Available from: https://doi.org/10.1038/nature02403

Yang, J., Song, X., Zambrano, J., Chen, Y., Cao, M., Deng, X. et al. (2021) Intraspecific variation in tree growth responses to neighbourhood composition and seasonal drought in a tropical forest. *Journal of Ecology*, 109, 26–37. Available from: https://doi.org/10.1111/1365-2745.13439

Yin, D., Liu, Y., Ye, Q., Cadotte, M.W. & He, F. (2021) Trait hierarchies are stronger than trait dissimilarities in structuring spatial co-occurrence patterns of common tree species in a subtropical forest. *Ecology and Evolution*, 11, 7366–7377. Available from: https://doi.org/10.1002/ece3.7567

Yue, Q., Geng, Y., Von Gadow, K., Fan, C., Zhang, C. & Zhao, X. (2022) Effects of neighborhood interaction on tree growth in a temperate forest following selection harvesting. *Ecological Indicators*, 136, 108663. Available from: https://doi.org/10.1016/j.ecolind.2022.108663

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Location of the six permanent plots in the subtropical Brazilian Atlantic Forest showing the distribution patterns of altitude (elevation, m) in the background.

Appendix S2. List of focal trees with their neighboring species and the number of individuals for each neighboring species.

Appendix S3. Correlations of variables examined, including neighborhood crowding index, absolute and hierarchical trait differences, community-weighted mean, functional diversity, and mean phylogenetic distance.

Appendix S4. List of focal trees selected for this study, including their growth class and annual growth rate data. The table also displays data for the community surrounding the focal tree.

Appendix S5. Details of quantile regression models.

Appendix S6. Results of quantile regression models.

How to cite this article: Klipel, J., Bergamin, R.S., Bordin, K.M., Picolotto, R.C., Müller, S.C. & de Bello, F. (2024) The effect of neighbor species' phylogenetic and trait difference on tree growth in subtropical forests. *Journal of Vegetation Science*, 35, e13296. Available from: https://doi.org/10.1111/jvs.13296