



Relationship Between Growth Trajectories and Functional Traits for Woody Trees in a Secondary Tropical Forest

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Absolute growth rates change with tree size and age, shifting throughout species ontogeny. The study on interspecific variation in plant traits has generated important insights into the life-history strategies and their consequences for ecosystem functioning. However, it remains unknown to what extent – and even if – species' functional traits are related to the variation in their growth trajectories. We set out to model growth trajectories of 45 woody species from the Brazilian Atlantic Forest in a secondary subtropical forest under regeneration, aiming to understand if species can be grouped by their growth patterns throughout ontogeny and if these groups could be classified in distinct ecological strategies based on key plant traits. We used a maximum likelihood estimation approach to predict growth trajectories using three ecologically relevant parameters [maximum growth rate (G_{max}), diameter at maximum growth rate (D_{opt}), and the ontogenetic variability in growth rate (K)] followed by multivariate analyses to detect associations among phylogenetic relationships, plant traits, and growth parameters and classify species into growth pattern groups. Across species, growth trajectory parameters varied widely. The cluster analysis identified three distinct groups based on growth trajectories parameters, which were not functionally or ecologically well defined. Our findings supports the idea that traits describing plant size and tree shape, such as maximum height, canopy volume and height to diameter ratio, were generally the best predictors of species growth parameters throughout ontogeny, even though traits representing resource-use and reproductive strategies also played a significant role. Growth-trait framework can be understood as a continuum of multi-trait combinations where, at one end of the gradient, we find trees with higher growth rate and larger diameters supporting a voluminous canopy combined with lower investment in leaf tissue and smaller diaspore; at the other end, taller trees supporting a smaller

canopy with higher investment in leaf tissue and longer diaspore. Ultimately, we have shown that tree architecture, leaf and reproductive traits significantly influence growth trajectory along tree ontogeny, which may be the reason why objectively grouping species based on growth-trajectories parameters is ineffective, at least in highly diverse secondary subtropical forests undergoing regeneration.

Keywords: leaf traits, wood density, Atlantic forest, absolute growth rate, ontogeny

INTRODUCTION

Plant growth rates drive landscape productivity and carbon sequestration and are determinants of species competitive abilities (Grime, 1977; Westoby et al., 2002). Thus, understanding their drivers is crucial not only to determine the structure, composition and dynamics of forests, but also to uncover how vegetation will respond to human-induced disturbances and climate change (Rees et al., 2001; Beer et al., 2010). However, in addition to a strong variation among species, there is a markedly variability within species throughout ontogeny (Clark and Clark, 1999; Herault et al., 2011), which makes predicting growth rates particularly challenging. Indeed, the main factors underpinning interspecific and intraspecific variation in growth rates remain contested (Bowman et al., 2013; Paine et al., 2015), but should be generally related to plant traits that describe carbon use strategies.

The relationship between plant growth rate and traits have been extensively studied (Chaturvedi et al., 2011; Visser et al., 2016; Wills et al., 2018; Gray et al., 2019). Growth rate is positively associated with maximum tree height (Rüger et al., 2012), maximum diameter (Herault et al., 2011; Visser et al., 2016), and key leaf traits, such as N and P leaf concentration, C:N ratio, and maximum photosynthetic assimilation rates (Wills et al., 2018; Gray et al., 2019). On the other hand, growth rate usually shows negative correlation with wood density (Herault et al., 2011; Rüger et al., 2012; Paine et al., 2015; Visser et al., 2016; Chaturvedi et al., 2021) and seed mass (Adler et al., 2014; Paine et al., 2015; Visser et al., 2016). These relationships reveal important trade-offs between growth rates and the ecological strategies describing resource use, spanning from conservative to acquisitive strategies, which directly relates to tissue construction costs (Wright et al., 2004; Chave et al., 2009).

Consequently, it is expected that the correlation between growth rates and plant traits to be strongly influenced by ontogeny between the newly germinated seedling and the mature individual, since the proportion of different tissues changes throughout the plant life, altering the costs associated with it. In woody species, the contribution of leaf mass to the total biomass of the individual tends to decrease along the ontogeny, while the contribution of stem biomass tends to increase (Falster et al., 2018). Therefore, to fully understand the relationship between growth and plant traits, there is the need to account for intraspecific variation over plant ontogenetic stages (Herault et al., 2011). This ontogenetic perspective on growth rate can provide an understanding of species-specific growth trajectories shape, which can potentially significantly vary among tree species in highly diverse tropical forests and unravel meaningful relationships with species ecological strategies. Determining the

drivers of plant growth rates is particularly relevant in tropical forests, since they account for a significant proportion of global primary productivity (Beer et al., 2010).

One of the first attempts to model growth trajectory curves and group tropical forest species based on an objective characterization of size-growth relationship resulted in 41 species groups, with few of them revealing ecological affinities between the tree species (Vanclay, 1991), which discouraged such approach. However, with a further understanding of the trade-offs involved in functional traits and growth (Poorter et al., 2008; Baraloto et al., 2010; Gibert et al., 2016; Visser et al., 2016) and a significant advance in the development of a trait-based model of growth through ontogeny (Canham et al., 2004; Herault et al., 2011), we may elucidate how traits can help explain growth trajectories of tropical tree species.

While the search for relationships between plant traits and tree growth has advanced in recent years, our ability to use this information to classify species into groups and explain ecological processes is still incipient. For example, during the secondary succession, seminal studies have identified ecological groups unique to each phase of the succession, based on characteristics such as shade tolerance, diaspore characteristics (type, size, and quantity), life cycle and type of growth (Budowski, 1965; Brokaw, 1985; Swaine and Whitmore, 1988). Early succession sites are occupied by pioneer species that grow rapidly, reproduce and die within an interval of less than 30 years (Chazdon, 2008), ensuring rapid colonisation of the newly opened area. In more advanced sites, non-pioneer species (early and late secondary) grow slowly and have a long cycle, ensuring a longer stay in the ecosystem. Despite the recognition that two more contrasting strategies are present at the extremes of the successional gradient, we still cannot fully understand how species characteristics respond and how they are explained in an environmental gradient of light availability and soil physical and chemical attributes. Thus, if the growth trajectory of a species can be associated with plant traits representing a range of individual functions, it would be possible to better predict the ecosystem effects of a given species during ecological succession. This information is potentially useful for understanding the successional process and for planning tropical forest restoration and management.

In our study, we explored the determinants of growth trajectories in a secondary subtropical forest undergoing regeneration, with two major aims. Firstly, we modelled growth trajectories for each of the most abundant species and investigated if they could be aggregated into different growth trajectory groups. Secondly, we assessed whether key leaf, stem and reproductive traits explain variation in growth parameters among species. This approach can potentially classify species into

groups using objective parameters and provide optimisation for tropical forest species growth modelling and yield predictions. In addition, by including ecologically descriptive information exploring the relationship between growth and functional traits, this study can be useful for understanding forest dynamics and its structure more broadly.

Specifically, we sought to answer the following questions:

1. Can we classify species into groups based on growth trajectories patterns? We expect that species will show unique growth trajectories, which will be aggregated into groups with similar growth habits.
2. Will these formed groups describe different ecological strategies at the community level? We expect that species groups resulting from growth patterns will exhibit distinct sets of plant traits.
3. Will species stem economics traits explain growth strategy parameters? Based on previous findings, we expect that maximum absolute diameter growth rate will increase with adult stature and decrease with increasing wood density whereas species with lower wood density should result in greater ability to modulate growth rates and respond to external factors throughout ontogeny.
4. What is the influence of reproductive (seed and diaspore size) and leaf traits on growth? We expect that maximum growth rates will be associated with traits representing a more resource-acquisitive strategy, such as higher specific leaf area and leaf N concentration and lower leaf dry matter content and seed and diaspore length.

MATERIALS AND METHODS

Site Description

Study areas were in two private nature reserves operated by the Society for Wildlife Research and Environmental Education (SPVS, a non-governmental organization) in the Antonina municipality in the state of Paraná, southern Brazil (“Guaricica” Nature Reserve – 25°19’S, 45°42’W, 8600 ha; the “das Águas” Nature Reserve – 25°21’S, 48°46’W, 508 ha). This is a well preserved region and a total 68% of area is occupied by forests in advanced stages of succession (Kauano et al., 2012). Climate is humid subtropical (Cfa in the Köppen system), with annual averages of 3300 mm rainfall and 20°C (Ferretti and De Britez, 2006).

The sample design was established in areas that were once deforested for pasture for cattle grazing in 1980’ years and later abandoned to recover through natural regeneration, and which varied in age since abandonment. The age of each area was established by overlapping aerial photos, vegetation map, and through interviews with residents of the region. From this information, it was possible to place the sample plots into four age classes since abandonment: 7 – 16, 20 – 30, 35 – 55, and >85 years. These permanent plots have been monitored for the last 10 years, since 2010. We considered the areas of >85 years old as old growth forests (*sensu* Chazdon, 2014), since their species

richness is similar to others previous studies in old growth forests in the region (Liebsch et al., 2008; Marques et al., 2014; Martins et al., 2015; Dalmaso et al., 2020). The plots were randomly selected in both Reserves and were distributed over two soils types, Cambisol and Gleysol. Within each age class, we delimited 10 circular (14 m radius) plots (except > 85), totalizing 35 plots occupying 2.2 ha. In old forests (>85 years), we limited the number of plots to five, due to the difficulty of finding regions of the lowland forests in advanced stages of succession. In all plots, we identified and measured (DBH, height) all trees (DBH \geq 5 cm) in 2010 and 2016. All specimens were identified by using specialised literature and comparison with material in herbarium. When vegetal material was reproductive, vouchers were deposited in the herbarium UPCB of the Universidade Federal do Paraná.

Survey and Cleaning Protocol

The first survey resulted in 3,726 individuals of 235 woody species, and the second 3,901 individuals of 238 species [see Cequinel et al. (2018) and Capellesso et al. (2020) for details]. As a long-term study, here we use a part of the dataset that has been accumulated over the last 15 years from one of the longest running projects done in the Brazilian Atlantic Forest. Previous studies have focused on diverse issues associated with succession theory. For example, Cequinel et al. (2018) explored the factors that determine the structuring of communities in succession and Capellesso et al. (2020) explored the factors that determine carbon accumulation in succession communities. Both addressed community and ecosystem-related theories, which differ greatly from the questions posed in this study (organismic theories). We selected only individuals that survived in the second survey for this study. We indistinctly accessed the growth of individuals growing in the four successional phases. This procedure was necessary because (1) of the difficulty in finding a sufficient number of individuals in all stages, and (2) we wanted to capture the maximum growth variation within each species, in the different environmental conditions of each successional stage. Despite relying on only two growth measurement censuses within 5 years interval (2010 and 2016), our diameter cutoff of >5 cm, rather than the commonly used 10 cm diameter cutoff for tropical forests, provides information for the earlier life-history stages (Clark and Clark, 1999).

We selected the number of species and individuals for the study after possible errors in data collection were eliminated. Then, we proceeded with the following cleaning protocol: First, when DBH had decreased by more than 5% before census, it was deemed as an unreasonable measurement, following common practices for growth datasets (Condit et al., 1993). After, all additional unreasonable high measurements were deleted after plotting for being visually an obvious outlier (i.e., exceeding maximum annual growth by 50%). The clean dataset comprised records of 1,728 individuals of 45 species from the different successional stages (**Supplementary Table 1**), with species having at least 10 individuals with at least two individuals sampled in each quartile of the species DBH range. The selected 45 species represented over 80% of the stand basal area.

Trait Data

We selected thirteen traits that are direct or indirectly associated with tree growth and resource use (**Supplementary Table 2**). Data from leaf traits and tree size (height and DBH – crown and stem) were collected during field expeditions in 2016 [more details in Capellesso et al. (2020)] and are available. All measurements followed standardised protocols for functional traits measurements, according to Perez-Harguindeguy et al. (2016). Maximum Height (H_{\max}) and Maximum Diameter (D_{\max}) are the maximum values of height and diameter measured for each species. Canopy Volume (CV) was calculated according to Antin et al. (2013), which considers the crown as half-ellipsoid shape:

$$CV = \frac{1}{2} * \frac{4}{3} * CA * CD$$

Where, CV is canopy volume (m^3), CA is the Canopy Area (m^2) obtained from the projection of two perpendicular measured radius of the crown ($CA = \text{radius}_1 \times \text{radius}_2 \times \Pi$) and CD is Canopy Depth (m) obtained by the difference between total height and crown base height. Tree Height:Diameter Ratio (HDR) was calculated for each species from the maximum height divided by the maximum diameter of that species. Specific Leaf Area (SLA) was calculated as the ratio of leaf fresh area to leaf dry mass, whereas Leaf Dry-Mass Content (LDMC) was calculated as the ratio of leaf dry mass and leaf saturated mass. Leaf Carbon Content (C_{foliar}) and Leaf Nitrogen Content (N_{foliar}) were obtained by combustion with elemental analyser Vario EL III (Elementar Analysensysteme Comp., Hanau, Germany). Leaf Carbon-Nitrogen ratio (C:N) was calculated as the ratio of the carbon to nitrogen leaf concentration and Nitrogen content by area (N_{area}) was calculated as the ratio of N_{area} by SLA. Seed Length (SL), Diaspore Length (DL), and Wood Density (WD) were obtained from literature in published and unpublished databases (Burkart and Reitz, 1979; Lorenzi, 2002; Carvalho, 2003; Wanderley, 2003; Zanne et al., 2009; Zimmermann Oliveira et al., 2019; Kattge et al., 2020).

Our traits dataset presented only 6% of missing information and we used random forest technique for imputation of the missing data. We used the “missForest” package in R (Stekhoven and Bühlmann, 2012) that performs more accurately than other approaches for various trait types (Stekhoven and Bühlmann, 2012; Penone et al., 2014) (**Supplementary Table 3**).

Data Analyses

All analyses were performed using the statistical environment R 4.0.1 (R Core Team, 2019).

To fit species-specific growth trajectories curves, we followed Canham et al. (2004) growth-model equation, an individual-based model where the absolute growth rate (AGR) is assumed to vary with the DBH of the target tree species in a one-dimensional log-normal function. This equation yields to three ecological meaningful parameters: the maximum ontogenetic variation rate (G_{\max}), the DBH where the growth rate achieves its

maximum (D_{opt}) and the kurtosis of the curve (K), representing the ontogenetic variation in growth rate:

$$\log(AGR_{is} + 1) = G_{\max_s} * \exp(-0.5 * \log\left(\frac{DBH_{is}}{D_{\text{opt}_s}}\right))^2$$

We fitted models using maximum likelihood estimation and simulated annealing (Goffe et al., 1994), assuming residuals to be normally distributed. The function “anneal” from the package “likelihood” (Murphy, 2012) was used and resulted in global algorithms converging on the global maximum for all species.

We then performed model-based cluster analyses to identify species groups using the three growth trajectories parameters (G_{\max} , D_{opt} , and K) as input and the R package “mclust” (Scrucca et al., 2016), enabling us to verify if species could be aggregated into distinctive groups based on their growth trajectory shapes (Question 1).

Comparing Traits

Prior to the analyses, we checked for data normality and transformed variables accordingly (specifically, we log10-transformed D_{opt} , G_{\max} , K, Canopy volume, D_{\max} , Seed and Diaspore lengths, SLA, C_{leaf} , and N_{area}). We also checked for data multicollinearity using the function “vif” (variance inflation factor – VIF) from the package “car” (Fox et al., 2012) and removing variables when $VIF \geq 10$ to avoid multicollinearity between variables (Hair et al., 1995). After the VIF analysis, only N_{area} was removed, totalling 12 independent variables.

To investigate specific trait differences between the groups suggested by the cluster analyses (Question 2), we used a multivariate analyses of variance (MANOVA) followed by one-way ANOVA’s for each trait. We used Tukey-Kramer post-hoc tests, appropriate for different sample sizes, to verify differences between the groups when ANOVA P -values were significant (<0.05), using package “agricolae” (de Mendiburu, 2021).

To understand which traits better explained growth parameters obtained from growth-trajectories models (Questions 3 and 4), we built three individual linear regression models for G_{\max} , D_{opt} and K as response variables with all the 12 traits as independent factors. We then used the function dredge from the package “MuMIn” (Barton and Barton, 2015) to select the best model based on corrected Akaike’s information criteria (AICc).

Comparing Species Growth Trajectories and the Phylogenetic Relationship

We accessed the phylogenetic relationship between the studied plant species based on the phylogenetic supertree proposed by Smith and Brown (2018) with dates from Magallón et al. (2015). This super tree was built based on the most recent phylogenetic relationships proposed by Chase et al. (2016). The manipulation of the phylogenetic supertree was done on the “V.PhyloMaker” package (Jin and Qian, 2019).

Based on the phylogenetic relationship of the species used in this study, we calculated the cophenetic distance between species based on the phylogeny (PhyDist). We then checked for relationships between the Phylogenetic Distance and growth by performing Mantel tests between PhyDist and distance matrices

based on the growth trajectories parameters (G_{\max} , D_{opt} , and K) all together and separately. We also checked for phylogenetic signals in growth trajectories parameters of each species by using the lambda (λ) index (Pagel, 1999) and the K-statistic (Blomberg et al., 2003), both checked for significant phylogenetic signal based on 10,000 randomizations (Ives et al., 2007). The cophenetic distance was calculated on the “stats” and the Mantel tests performed in the “ape” packages. The phylogenetic tree figures and the phylogenetic signal analyses were built using “phytools” package (Revell, 2012).

RESULTS

Using only diameter growth measurements over time (mm year^{-1}) as an input, we developed growth trajectories curves with the Canham et al. (2004) model for the 45 Atlantic forest woody species (Figure 1 and Supplementary Figure 1). Individual species growth trajectories from which G_{\max} , D_{opt} , and K were estimated as shown in Supplementary Figure 1 and parameter estimations can be found in Supplementary Table 1. Maximum growth rate (G_{\max}) varied from $0.34 \text{ mm year}^{-1}$ for *Rudgea jasminoides* to $5.66 \text{ mm year}^{-1}$ for *Vochysia bifalcata*, and averaged $1.98 \text{ mm year}^{-1}$ across species. Optimum diameter, where species reach maximum growth rates, ranged from 51.66 to 566.49 mm, averaging 159.70 mm. There was a peak at intermediate stem diameters showing a strong influence of tree size on growth rates (Figure 1A). For the majority of species, maximum growth was reached at less than 50% of their potential size. Only eight out of the 45 species attained maximum growth rate at over 70% of their maximum size. The ontogenetic variation, represented by K estimates, varied from 0.18, implying a strong size-dependency growth peak (such as for *Garcinia gardneriana*), to 2.99, which can be translate to a flat growth curve (such as for *Jacaranda puberula*, *Myrsine coriacea* and *Rudgea jasminoides*), averaging 1.41 for all species (Supplementary Table 1).

Cluster analysis identified three species groups, where Cluster 1 was represented by 15 species, Cluster 2 by 23 species and Cluster 3 by 7 species (Supplementary Figures 2, 3). The mean posterior probability for a species belonging to a cluster was 0.348, 0.497, and 0.155, respectively. There were marked differences in growth trajectories shapes between the three distinct groups (Figures 1B–D). Cluster 1 was characterized by species with higher maximum growth rates (mean \pm sd: 3.09 ± 1.20) and higher D_{opt} (mean \pm sd: 241.12 ± 149.03), whereas Cluster 2 was composed by species with lower G_{\max} and D_{opt} but a marked ontogenetic influence on growth (i.e., low K ; mean \pm sd: 0.83 ± 0.31); Cluster 3 also showed species with lower G_{\max} and D_{opt} but a flat growth curve (i.e., high K ; mean \pm sd: 2.94 ± 0.08).

The first two principal components of the PCA explained 47.44% of the data variation. First component was mostly related to tree structure (H_{\max} , D_{\max} , canopy volume and HDR), while PC2 was more related to leaf and reproductive traits (Figure 2A). However, there was not a clear separation between the three groups formed by the cluster analyses using growth parameters.

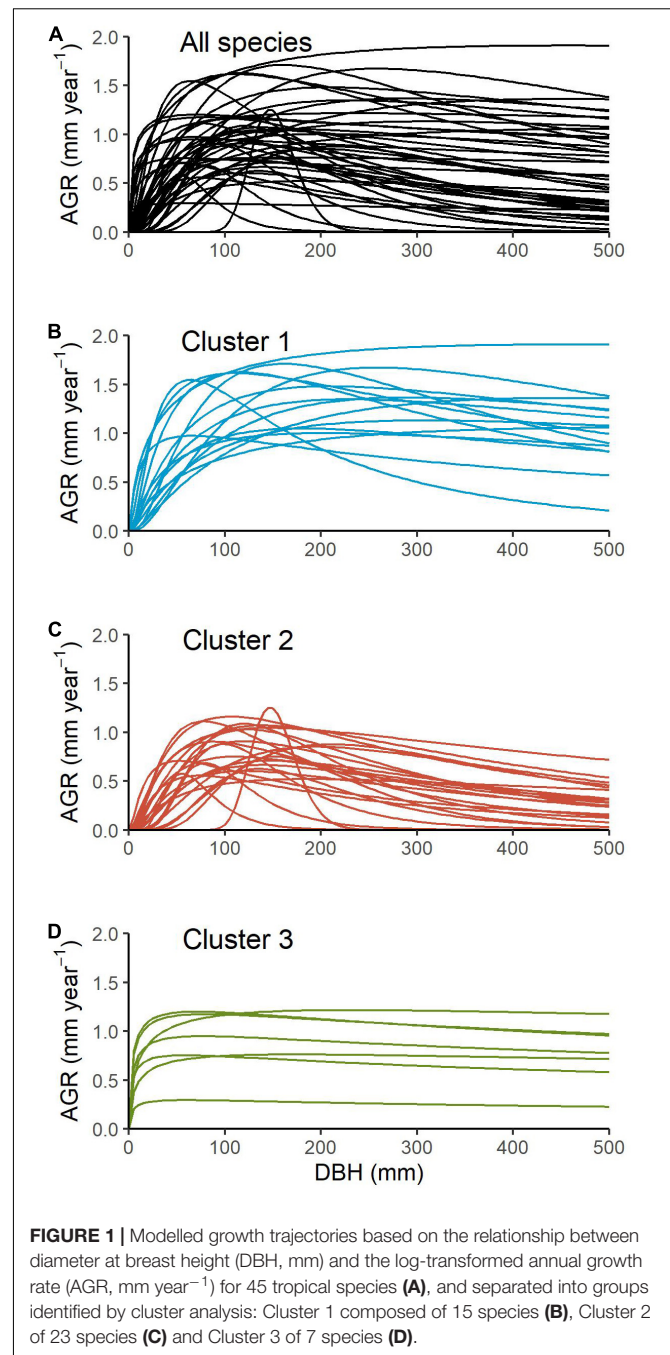
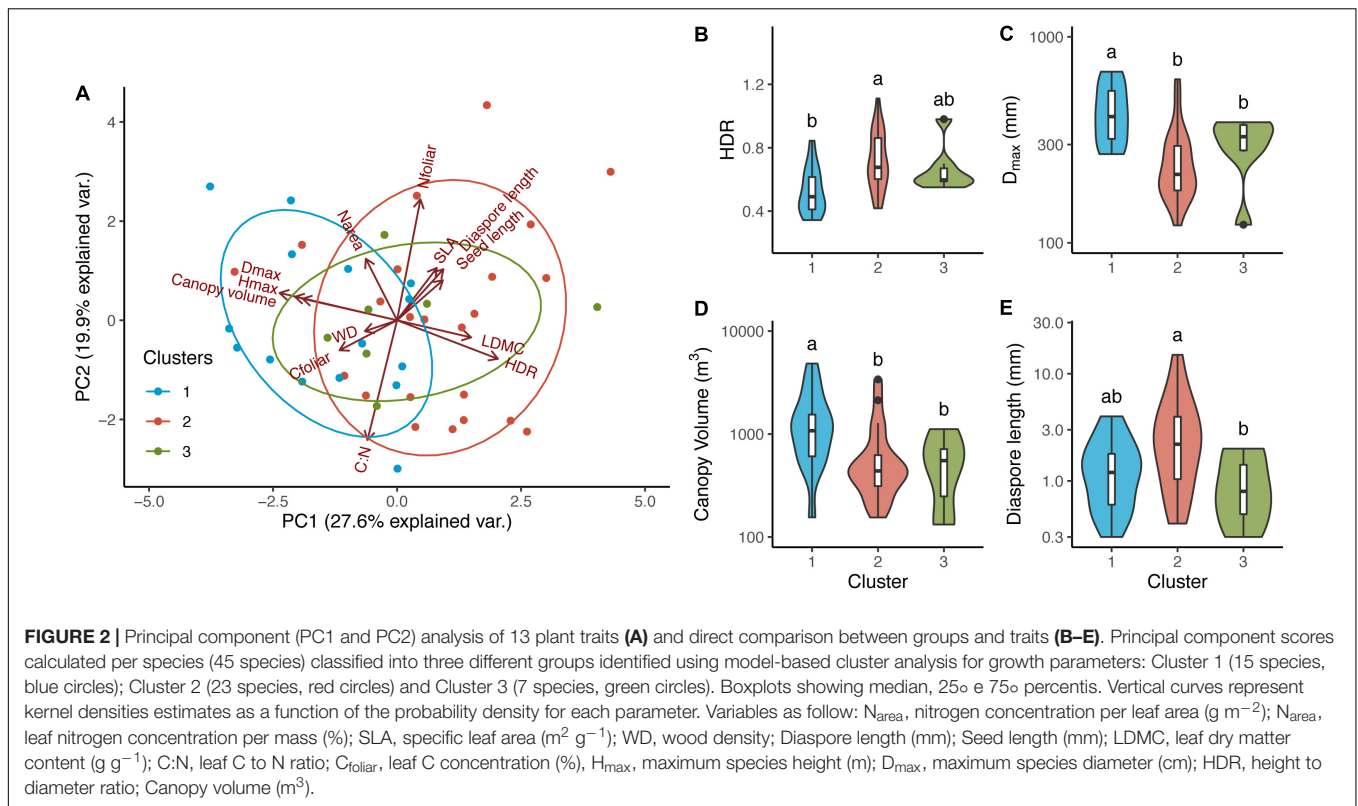


FIGURE 1 | Modelled growth trajectories based on the relationship between diameter at breast height (DBH, mm) and the log-transformed annual growth rate (AGR, mm year^{-1}) for 45 tropical species (A), and separated into groups identified by cluster analysis: Cluster 1 composed of 15 species (B), Cluster 2 of 23 species (C) and Cluster 3 of 7 species (D).

Direct comparison between traits from species groups also did not show differences for the majority of the traits analysed. Most differences occurred between Cluster 1 and 2 regarding HDR, D_{\max} , canopy volume and diaspore length (Figures 2B–E), but we found mixed trait response for species forming Cluster 3. Cluster 1 species showed lower HDR and diaspore sizes, but higher D_{\max} and canopy volume compared to Cluster 2 species. Cluster 3 species showed similar D_{\max} and canopy volume to Cluster 2 (lower than Cluster 1) but smaller diaspore (similar to Cluster 1).



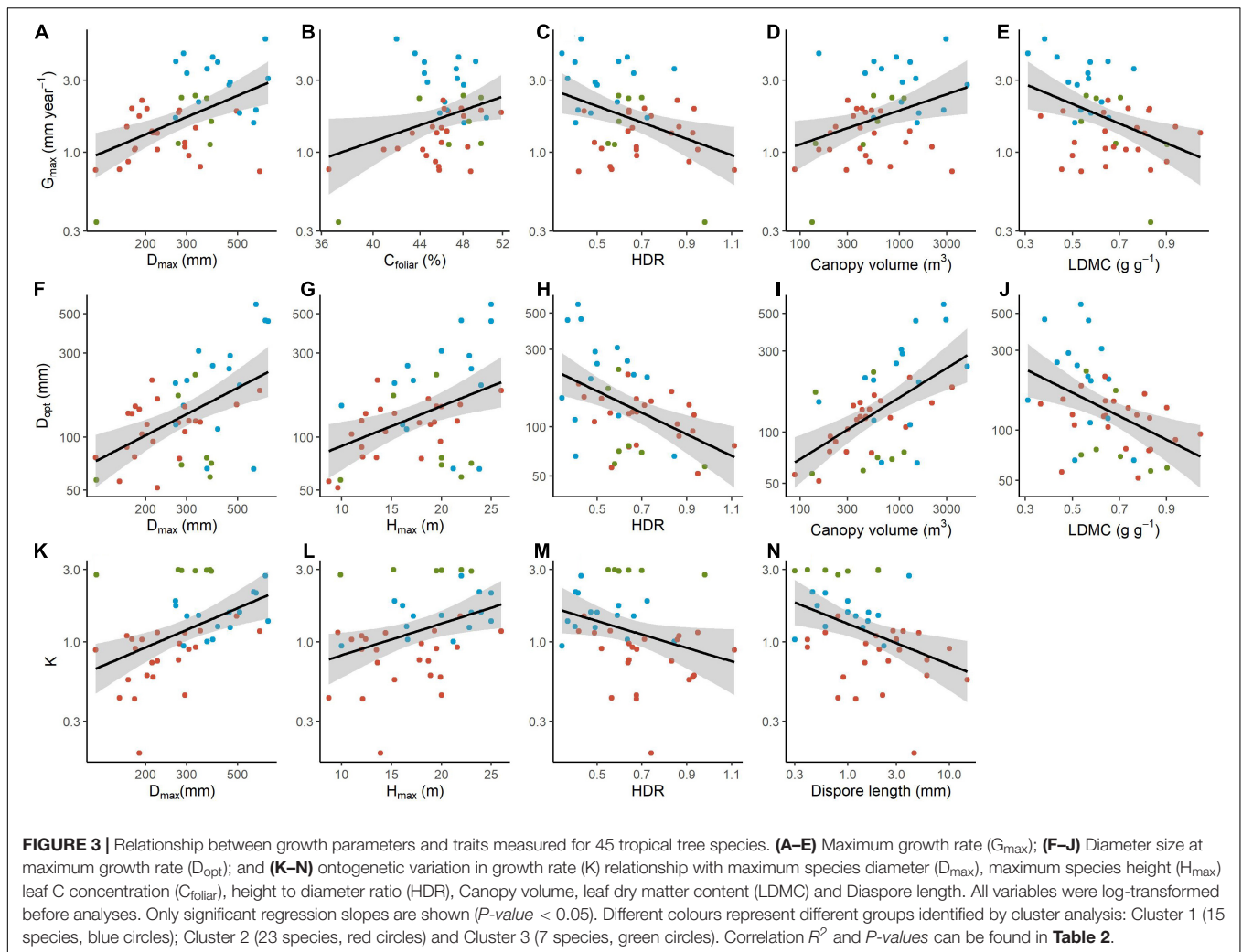
G_{max} was best predicted by a regression model that included H_{max}, D_{max} and leaf C concentration, while D_{opt} was better predicted by LDMC and canopy volume (Table 1). The

TABLE 1 | Estimated coefficients, adjusted intervals and P-values for each of the best model predictors for maximum growth rate (G_{max}), diameter at maximum growth rate (D_{opt}), and the ontogenetic variability in growth rate (K). Full model correlation coefficients (R²) are also shown. All models were significant at P < 0.001. Abbreviations as follow: maximum height (H_{max}), maximum diameter (D_{max}), leaf carbon content (C_{foliar}), leaf dry-mass content (LDMC), wood density (WD), nitrogen content (N_{area}).

Response predictor	Estimates	SE	P-value	R ²
G _{max}				0.28
H _{max}	-0.02	0.01	0.065	
D _{max}	0.96	0.27	<0.001	
C _{foliar}	0.87	0.52	0.101	
Intercept	-5.13	2.01	0.015	
D _{opt}				0.36
LDMC	-0.44	0.20	0.038	
Canopy volume	0.30	0.08	<0.001	
Intercept	1.57	0.30	<0.001	
K				0.42
Diaspore length	-0.34	0.10	0.001	
Seed length	0.20	0.09	0.044	
WD	-0.96	0.28	0.001	
H _{max}	0.04	0.01	<0.001	
N _{area}	-0.15	0.13	0.256	
Intercept	0.45	0.31	0.161	

ontogenetic response to growth, represented by parameter K, was better predicted by the model that included diaspore and seed length, wood density, H_{max} and N_{area} (Table 1). Species that achieved higher maximum growth rates also achieved greater diameters (higher D_{max}) and exhibited higher canopy volume and higher leaf C concentration, but lower LDMC and lower HDR (Figures 3A–E and Table 2). The optimum diameter (D_{opt}) was also positively related to canopy volume, H_{max} and D_{max}, but negatively associated with HDR and LDMC (Figures 3F–J). Species with greater ontogenetic growth variation were also the ones achieving greater sizes (higher D_{max} and H_{max}, reflected in lower HDR; Figures 3K–M), but also associated with lower diaspore length (Figure 3N and Table 2).

Although we found no correlation between phylogenetic distance (PhyDist) and the growth trajectory parameters (together and separately; Mantel tests P > 0.05), we found phylogenetic signals for G_{max} by both methods (λ = 0.5532, P = 0.0054; K = 0.3791, P = 0.0055, Supplementary Figure 4). We also checked the phylogenetic signal for all traits that show relation with G_{max} (H_{max}, D_{max}, C_{foliar}, Canopy volume and LDMC). We found signals on D_{max} (K = 0.3553, P = 0.0232) and C_{foliar} (λ = 0.7221, P = 0.0054; K = 0.4645, P = 0.0049). Thus, to contrast whether the relations between G_{max} and D_{max} and C_{foliar} were mediated by the phylogenetic structure of the relationship among the analysed species, we decompose the phylogeny in orthogonal eigenvectors (Diniz-Filho et al., 1998) and performed linear models using each trait (D_{max} and C_{foliar}) and the three first eigenvectors to predict the G_{max}. When using the phylogenetic structure as cofactor, the relation between G_{max}



and D_{max} is still significant, but not for C_{foliar} (**Supplementary Table 4**), indicating that the relationship between G_{max} and C_{foliar} is mediated by the phylogenetic structure.

DISCUSSION

Growth rate is commonly interpreted as a single parameter, which can be considered an oversimplification, since it changes throughout tree ontogeny. Here, by considering growth as a multi-trait value across a lifetime describing it in three different modelled parameters, we aimed at better understanding the influence of commonly measured plant traits on plant growth. We modelled growth trajectories of 45 woody species from the Brazilian Atlantic Forest in a secondary subtropical forest undergoing regeneration, and investigated the relationship between growth patterns and key functional traits. We found that, while there was not a clear patterning of traits by trajectory clusters, growth parameters were related to tree architecture, leaf and reproductive traits. Our results represent a first investigation into how growth trajectories and plant traits are related in

Atlantic Forest woody species using a regeneration gradient, and here we discuss general outcomes and possible explanations for our findings.

Grouping Species Into Growth-Trajectories Strategies

We have found three distinct groups with different growth trajectory shapes (Question 1): Cluster 1, composed of canopy and sub-canopy species with fast growth rates that respond opportunistically to light; Cluster 2, composed of understory species with slow maximum growth and higher investment in leaf tissue; and Cluster 3 composed of small sub-canopy shade-tolerant trees with constant slow growth rate. The majority of species were classified within cluster 1 (15 species) and 2 (23 species) marked by a size-dependent growth, with only 7 species in cluster 3. Size-dependent growth might be favoured as a strategy probably because growth increasing with tree size would provide better access to light and larger canopy area, representing a larger photosynthetic area (Sterck et al., 2003), a clear advantage for increasing carbon assimilation in closed-canopy environments.

TABLE 2 | Regression statistics for individual linear regressions between growth trajectory parameters (maximum growth rate – G_{max} , diameter at maximum growth rate – D_{opt} , and the ontogenetic variability in growth rate – K) and traits (maximum height – H_{max} , maximum diameter – D_{max} , leaf carbon content – C_{foliar} , nitrogen content – N_{area} , leaf dry-mass content – LDMC, height to diameter ratio – RatioHD, Canopy volume, Diaspore length, seed length, wood density – WD, leaf carbon–nitrogen ratio – C:N, specific leaf area – SLA) for 45 tropical tree species. Tree species list are provided in **Supplementary Table 1**. Parameters in bold represent the best model. Significant P -values and slopes are also highlighted in bold.

Parameters traits	R^2	P -value	Slope (SE)
G_{max}			
~ H_{max}	0.05	0.067	0.65 (0.17)
~ D_{max}	0.23	<0.001	0.64 (0.16)
~ C_{foliar}	0.08	0.036	1.16 (0.54)
~ N_{area}	0.01	0.402	0.12 (0.14)
~ RazaoHD	0.14	0.007	–0.54 (0.19)
~ Canopy volume	0.11	0.016	0.10 (0.04)
~ Diaspore length	0.01	0.237	–0.11 (0.09)
~ Seed length	0.01	0.446	–0.07 (0.09)
~ WD	0.01	0.459	0.22 (0.30)
~ C:N	0.00	0.338	0.01 (0.01)
~ LDMC	0.16	0.004	–0.65 (0.21)
~ SLA	0.04	0.089	–0.34 (0.20)
D_{opt}			
~ H_{max}	0.16	0.004	0.02 (0.01)
~ D_{max}	0.25	<0.001	0.68 (0.17)
~ C_{foliar}	0.02	0.158	1.81 (1.26)
~ N_{area}	0.02	0.588	0.16 (0.30)
~ RazaoHD	0.21	<0.001	–0.66 (0.18)
~ Canopy volume	0.31	<0.001	0.36 (0.08)
~ Diaspore length	0.01	0.4	0.07 (0.09)
~ Seed length	–0.02	0.945	0.01 (0.09)
~ WD	0.02	0.201	0.38 (0.29)
~ C:N	0.01	0.226	0.01 (0.01)
~ LDMC	0.18	0.002	–0.70 (0.21)
~ SLA	0.03	0.124	–0.54 (0.34)
K			
~ H_{max}	0.11	0.014	0.02 (0.01)
~ D_{max}	0.20	0.001	0.65 (0.19)
~ C_{foliar}	–0.01	0.472	0.99 (1.36)
~ N_{area}	0.02	0.763	0.09 (0.32)
~ RazaoHD	0.07	0.044	–0.44 (0.21)
~ Canopy volume	0.05	0.080	0.08 (0.04)
~ Diaspore length	0.14	0.006	–0.27 (0.09)
~ Seed length	0.00	0.376	–0.08 (0.09)
~ WD	0.03	0.114	–0.49 (0.31)
~ C:N	–0.02	0.993	–0.00 (0.00)
~ LDMC	–0.01	0.650	–0.12 (0.25)
~ SLA	–0.02	0.754	–0.05 (0.16)

However, although model-based clustering may be helpful to identify general ecological-evolutionary distinctions among species, we noted a large overlap concerning species traits, and few traits that allowed for a clear distinction among the groups (Figure 2). Moreover, by looking at species within the groups

formed and the traditional succession classification of species into gap-dependent and shade-tolerant species (Lieberman et al., 1985; Clark and Clark, 1992) and across forest strata (i.e., canopy vs. understory), the three groups are composed of mixed species with various distinctive succession strategies. Thus, here we argue that the general relationship between traits and growth parameters may better contribute to elucidate resource use trade-offs than grouping species into mutually exclusive classes.

Grouping species into “functional groups” or guilds may have numerous advantages in ecology, from enabling better predictions of patterns and processes generality to minimising the cost associated with field studies, especially in high species diversity systems (Swaine and Whitmore, 1988). However, contrary to our expectations (Question 2), it was not possible to describe ecologically meaningful groups based on modelled growth parameters, at least not for the 45 species considered in our study. One possible reason is that our data encompasses a regeneration gradient, with species and individuals growing on a range of successional stages and environmental conditions. Even though we did not evaluate specific differences between stages, we should not disregard that there may be different growth strategies among these successional stages. During succession, there is a variation in environmental conditions and resources over time that can directly influence tree growth, such as changes in light availability modulating tree height investment (Chazdon, 2008; Iida et al., 2011). Indeed, the growth–trait relationships vary along environmental gradients (Paine et al., 2015). Biotic interactions (Bongers et al., 2020) or even community composition and diversity (Thomas and Vesk, 2017; Bongers et al., 2020) significantly influences the relationship between traits and growth rates. Nonetheless, these differences in successional stages are common in old-growth tropical forests, where natural disturbances often trigger regeneration and successional processes (Chazdon, 2003) and should play a similar role in forest dynamics and species growth trajectories.

Trait-Growth Relationships

As expected (Question 3), maximum height and maximum diameter measured for the species were positively associated with most of the growth-trajectories parameters (i.e., G_{max} , K , and D_{opt}) meaning that tree size is generally important in describing growth, as also noted by earlier studies (Lieberman et al., 1985; Swaine and Whitmore, 1988; Clark and Clark, 1992). In addition, tree architecture, such as the height-diameter ratio (HDR) and canopy volume (CV) were also important, both explaining differences between the groups (Figure 2) and correlating with growth trajectories parameters (Figure 3). Specifically, the height-diameter ratio seems to be a key variable to describe growth strategies throughout the tree life. Together, our findings corroborate that those traits describing plant size and general tree shape (H_{max} , D_{max} , CV and HDR) were generally the best predictors of species growth parameters throughout ontogeny. In fact, they describe one of the axes of variation regarding the capacity for competitive dominance (Hodgson et al., 1999), which is a major aspect in forest dynamics, structure and composition. In a canopy-closed environment, such as tropical forests, trees that invest in height could have an adaptive advantage compared

to shorter ones, because their leaves would have more access to light (Poorter et al., 2005). Therefore, they can shade competitors and elevate reproductive or dispersal organs to the canopy (Aarssen, 1995). However, to maintain stability with high heights and a large canopy, trees have to invest in higher wood density or in larger diameters (Niklas, 1994; King et al., 2006). Species that can grow larger to a given height and support a larger canopy achieve higher D_{opt} and G_{max} compared to species that invest more on height than on diameter and bear a smaller canopy. Moreover, species with high HDR (more height than diameter) have a more accentuated peak in growth rate at a certain size throughout ontogeny (lower value of K), while species with low HDR (more diameter than height) grow more constantly.

Interestingly, wood density (WD) proved to add little explanatory power to growth parameters, although it contributes to K best model, which also included diaspore and seed length, H_{max} and N_{area} , suggesting that the ontogenetic behaviour of the species growth trajectory (K) is driven by a multi-set of traits. Contrary to our expectations (Question 3) and to previous findings in tropical forests from Australia (Gray et al., 2019), Panama (Rüger et al., 2012) and French Guiana (Herault et al., 2011), the relationship between K and WD was negative, meaning that the greater ontogenetic flexibility concerning growth is not prevented by a higher wood density. Perhaps, in a subtropical rainforest context, wood density is not a decisive factor for survival or competition between species. Indeed, according to Chave et al. (2009), the Subtropical Atlantic Rain Forest is the region where forest communities show the lowest wood density ranges in Brazil, for yet unknown reasons. The negative correlation of K with diaspore size and positive with H_{max} and D_{max} (Figure 3) indicates that the investment in the early stage survival is associated with smaller plants but with greater ontogenetic flexibility in terms of growth, which may favour the use of scarce opportunities to obtain light. Larger seeds increase the probability of successful seedling establishment and plant persistence (Westoby et al., 2002; Moles et al., 2005), although it is associated with low survival and growth in later ontogenetic phase, at least in early successional stages (Coelho et al., 2016).

Although leaf traits have often been uninformative in explaining larger trees growth rates (Wright et al., 2010; Herault et al., 2011; Paine et al., 2015), in our study key leaf traits were also important describing growth trajectories, together with structural traits, as predicted (Question 4). Indeed, SLA did not help explain any of the growth parameters, but leaf dry matter content (LDMC) was an important factor explaining D_{opt} (Table 1) and negatively related to G_{max} and D_{opt} (Table 2 and Figure 3). LDMC is considered a better predictor of aboveground net primary productivity than SLA (Smart et al., 2017) and a better variable to locate the plant species on the resource-use axis of variation (Wilson et al., 1999). While LDMC tends to be negatively related to growth rates (Cornelissen et al., 2003), as found in our study, a positive influence of SLA on growth rate is expected, since SLA indicates the efficiency of biomass investment for a given light interception (Reich et al., 1998). However, possibly because ontogenetic changes in leaf to wood ratio, SLA and growth traits, despite correlated for seedlings, are mostly uncorrelated in larger trees (Poorter

et al., 2008; Rüger et al., 2012; Paine et al., 2015; Gibert et al., 2016; Wright et al., 2019). During early life, when leaves comprise a large part of the plant, increasing SLA has an overwhelmingly positive effect on growth rate (Gibert et al., 2016; Falster et al., 2018). As trees increase in size, light interception and carbon gain depend not only on leaf area, but also are largely determined by the whole tree architecture (Sterck and Bongers, 2001) and the costs and benefits associated with SLA variation (Westoby and Wright, 2003). A second possible reason is that self-shading in the crown decreases light interception (Duursma et al., 2010), dissipating the effect of SLA on resource acquisition. In addition, the C_{foliar} relationship with ontogenetic variation deserves further investigation. At this point, we are not capable to affirm if this relation is indeed causal or an artefact of the phylogeny, since our analyses showed it was mainly mediated by the phylogenetic structure of the relationships among the species.

Finally, it is important to highlight that here we used a secondary forest regenerating after a severe disturbance in a relatively short time as a model to test the relationship between growth and functional traits. As the most threatened tropical forest in the world (Laurance, 2009; Ribeiro et al., 2011), the Brazilian Atlantic Forest has only 10% conserved mature forest in small and isolated patches and therefore, most of the biome is composed by secondary forests undergoing regeneration (Ribeiro et al., 2009). Undoubtedly, there are expected changes in forest structure, species composition and functional diversity along an age gradient in secondary succession (Chazdon, 2008), which could have influenced our findings. However, earlier studies in the area showed that despite the taxonomic diversity being higher in late successional stages, species turnover remained relatively constant along the time gradient (see Cequinel et al., 2018). This could be explained by a rapid recovery during succession facilitated by nearby forested areas (Cheung et al., 2010) through increasing landscape connectivity and seed dispersal processes (Zwiener et al., 2014). Additional studies on the relationship of growth trajectories and functional traits within old-growth and secondary tropical forests are still needed to untangle the mechanisms underlying this system.

CONCLUSION

Our findings showed that aggregating species within well-defined groups based on growth parameters was especially challenging. The lack of discreet grouping highlights the complex set of strategies for tree resource acquisition and survival in this highly diverse tropical system. We propose that there is a continuum regarding tree architecture, leaf and reproductive traits that influence growth parameters. The extremes in this continuum are represented by: (1) Trees that can grow larger than taller, supporting a voluminous canopy, with lower LDMC and smaller diaspore, achieving higher maximum diameter and growth rate, but maintaining a more constant growth through ontogeny; and (2) Trees that grow taller than larger, supporting smaller canopy, with higher LDMC and longer diaspore, achieving maximum growth rate at a given size during ontogeny. Our

study represents a novel approach and a first exploration on the relationship of growth trajectories and traits for tropical forest species under restoration, however, the complexity and variation of megadiverse tropical forests represent a major challenge, as such it would benefit from a longer time interval for growth measurements and the inclusion of more species. Further studies on this particular topic hold significant potential to disentangle the drivers of intraspecific and interspecific growth variation, especially by considering growth as a multi-parameter variable.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: <https://doi.org/10.1016/j.ppees.2018.08.007> and <http://dx.doi.org/10.5380/bdc/34>.

AUTHOR CONTRIBUTIONS

MS and MM conceived the idea, questions and hypotheses, and developed study design and methodology. MM, GC, VM-S, VZ, AB, LM, RA, RS, and WT collected the data. MS, VM-S, AB, and WT analysed the data. MS led the writing of the manuscript. MM obtained the funding. All authors critically contributed to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2022.754656/full#supplementary-material>

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