Introduction

The main application of models that describe height–diameter (HD) relationships in trees is to improve forest stock predictions (Sullivan et al. 2018). However, tree height and stem diameter are related to fundamental processes involved in individual species performance and whole-ecosystem function (Hulshof et al. 2015). For example, the scaling-exponent or slope-of-power model can be used to measure variations in tree allometry, as well as to assess whether trees optimise their growth strategies according to environment (Zhao et al. 2021; Sun et al. 2020; Banin et al. 2012), based on metabolic scaling theory (MST) (Brown et al. 2004). Such an exponent can represent the steady-state biological growth rate of tree size (Huxley 1932). Therefore, differences between observed parameters and those predicted by MST can elucidate the drivers of variations in tree allometry (Hulshof et al. 2015). Asymptotic height or maximum tree height can be used as a comparative measure of species size and allometric characteristics (Poorter et al. 2005; Thomas 1996) obtained from fitting three-parameter exponential models. Asymptotic height can also be considered an indicator of site capacity, since it is influenced by environmental factors which drive or restrict tree growth and size (Gorgens et al. 2021).

On a broad scale, the scaling exponent and asymptote indicate variations in tree height, for example, between continents, functional groups, gymnosperms and angiosperms, and secondary and primary forests, with significant effects from climate, forest type, stand structure and phylogenetic factors (Duncanson et al. 2015; Hulshof et al. 2015; Banin et al. 2012; Feldpausch et al. 2011; Wang et al. 2006). Although the environmental effects have been investigated, few studies have assessed variations in allometric relationships along stand chronosequences, successional stages and species life history. However, MST predictions are based on simplifying assumptions as forests are assumed to be in a steady state. Such predictions are expected to be consistent only in late successional forests, as opposed to early successional and disturbed forests, where steady-state conditions are violated (Sun et al. 2017; Duncanson et al. 2015). Consequently, regular changes in tree allometric relationships along forest successions can produce a general pattern (Sun et al. 2020). In addition, other sources of local variations may affect tree-height allometry, such as species diversity and neighbouring competition (del Rio et al. 2019; Forrester et al. 2017). Likewise, tree life history and specific size can influence allometric relationships because they regulate light availability and capture (Zhao et al. 2021; Poorter et al. 2005).

Assessing variations in tree allometry is useful for understanding height growth strategies in relation to life-history trajectories, light competition and environmental restrictions. Scaling exponent and asymptotic heights obtained from height–diameter (HD) models may elucidate how trees optimise growth strategies and the potential drivers that influence tree height. Our main objective was to explore how the HD relationship in Bracatinga (Mimosa scabrella) varies along stands chronosequence and life history. The study was carried out in discontinuous stands located across the metropolitan region of Curitiba, southern Brazil. We used HD data from 300 temporary plots in chronosequences dating from a disturbance, which represented stand development after intervention, covering the life history of the species. Power and exponential models were fitted to data to describe the HD relationship over time. Mixed-effects models were applied to explain the height variations by stand characteristics. We found that tree height and allometry were influenced by stand development phase and tree life stage along the chronosequence. Changes in tree height were also driven by light competition related to certain stand characteristics, such as basal area, stem density and species diversity. We concluded that growth strategies are conditioned by interactions between light requirements along a tree’s life history and successional stand evolution. The results revealed that gradual changes in tree development might be recognised by stationary data along chronosequences. Quantifying changes in HD allometry has ecological and practical applications for explaining the strategies and drivers underpinning tree growth and providing useful knowledge for improving growing stock predictions and stand management.

Keywords: height–diameter relationship, managed ecosystems, secondary succession, tree life history

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Height growth strategies of *Mimosa scabrella* along a chronosequence

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**Abstract**

Assessing variations in tree allometry is useful for understanding height growth strategies in relation to life-history trajectories, light competition and environmental restrictions. Scaling exponent and asymptotic heights obtained from height–diameter (HD) models may elucidate how trees optimise growth strategies and the potential drivers that influence tree height. Our main objective was to explore how the HD relationship in Bracatinga (Mimosa scabrella) varies along stands chronosequence and life history. The study was carried out in discontinuous stands located across the metropolitan region of Curitiba, southern Brazil. We used HD data from 300 temporary plots in chronosequences dating from a disturbance, which represented stand development after intervention, covering the life history of the species. Power and exponential models were fitted to data to describe the HD relationship over time. Mixed-effects models were applied to explain the height variations by stand characteristics. We found that tree height and allometry were influenced by stand development phase and tree life stage along the chronosequence. Changes in tree height were also driven by light competition related to certain stand characteristics, such as basal area, stem density and species diversity. We concluded that growth strategies are conditioned by interactions between light requirements along a tree’s life history and successional stand evolution. The results revealed that gradual changes in tree development might be recognised by stationary data along chronosequences. Quantifying changes in HD allometry has ecological and practical applications for explaining the strategies and drivers underpinning tree growth and providing useful knowledge for improving growing stock predictions and stand management.
Bracatinga (*Mimosa scabrella* Benth.) is the most important, fast-growing native tree species used for supply of firewood and charcoal in southern Brazil. It is a light-demanding and short-lived species (Machado et al. 2011), with a pioneer-tree behaviour (Whitmore 1989). When induced by common swidden–fallow practices, such as clear-cutting, soil tilling and burning, *M. scabrella* tends to form monodominant stands (Somarriba and Kasai 2001; Machado et al. 2006). Therefore, it is the main source of income for settled families and small farmers in southern Brazil, emphasising the social and economic importance of the management of the species (Urbano et al. 2021; Silva et al. 2016a; Steenbock et al. 2011). It is also an alternative to land use that avoids the replacement of vegetation by monocultures of non-native species (Fantini et al. 2019; Steenbock et al. 2011), playing a prominent ecological role by providing landscape-use sustainability through forest management. In addition, the species is a facilitator in the forest succession process, providing shade, rapid soil cover, humidity retention and nutrient cycling (Gerber et al. 2021; Ferreira et al. 2017). However, it is gradually replaced by other species due to canopy shading.

Major environmental disturbances result in the complete or near-complete removal of vegetation, leading to the establishment of even-aged regrowth stands (Chazdon et al. 2007). In this context, secondary succession conducts vegetation through a sequence of stages characterised by changes in structure, composition and function, following the previous non-forested state (McNicol et al. 2015; Chazdon et al. 2007). Although secondary succession in natural forests may follow several trajectories associated with land-use characteristics, disturbance and the surrounding landscape, some chronological trends can be expected, such as increased basal area, biomass accumulation, tree size, species diversity, similarity to surrounding mature forests and species turnover, together with decreased stem density and pioneer-species dominance (Gomes et al. 2020; McNicol et al. 2015; Guariguata and Ostertag 2001). Most references regarding secondary forest succession are derived from chronosequence studies, in which temporal changes in the stand are inferred from a single point in time at different ages, and thus emphasise the cumulative effects of ecological processes (Chazdon et al. 2007).

Owing to human interventions in conducing successional processes, *M. scabrella* stands are managed systems, distinct from secondary forests, mainly because of their demographic structure and species diversity (Steenbock et al. 2011). However, their evolution to late stands is consistent with secondary succession (Silva et al. 2016a,b). In this sense, changes in stand structure caused by successional advance can be expected to result in different tree allometric strategies. Our main aim was to explore how the HD relationship of *M. scabrella* varied along life history. We assessed: (1) whether changes in tree-height patterns were related to the forest succession; and (2) whether stand structure, dominance and species diversity could explain variations in the HD relationship. We fitted power and exponential three-parameter models to the HD data for different stand ages that covered the life history of the species. Additionally, we associated the allometric relationship and tree height with the stand development phases and their attributes, such as structure, competition, diversity and dominance.

### Material and methods

#### Study area and data collection

This study was carried out in discontinuous *M. scabrella* stands across the metropolitan region of Curitiba, southern Brazil, located in Atlantic Forest biome (24°58’11”–25°55’44”S; 49°29’09”–49°03’58”W). The sampling was conducted primarily in the northern region of the First Paraná Plateau, where *M. scabrella* stands occur with high frequency. The local climate type is Cfb or subtropical, characterised as a temperate, humid and mesothermal climate, without hydric stress (Alves et al. 2013). The annual temperature ranges from 11 to 24 °C and the total annual precipitation from 1 400 to 1 600 mm. The Atlantic Orogenic Belt is the predominant geological domain, in which the First Paraná Plateau is a morphostructural unit (Maak 2002). On the plateau, the northern region is characterised by mountainous landscapes comprising low-grade metamorphic and metavolcanic rocks, granitic intrusions and diabase dikes (Pereira et al. 2013). The soils are mostly Alic Cambisols and Latosols with different degrees of depth, fertility and texture.

We used a large dataset of *M. scabrella* from chronosequences dating from a disturbance, representing stand development following human intervention (clear-cutting, burning and thinning in the first year). In this context, 300 temporary plots, from 100 to 600 m², were randomly distributed in stands aged from 3 to 20 years (Urbano et al. 2021; Silva et al. 2016a). A total of 11 216 *M. scabrella* trees with diameters at breast height (DBH) > 5 cm were measured. The total tree heights and DBHs were measured using a graduated rule and a metric tape, respectively. The stand age in each plot was estimated based on landowner and resident interviews and by dendrochronological methods (Silva et al. 2016b). The sample details and allometric characteristics by stand age are presented in the Supplementary Material (Table S1).

#### Modelling of height–diameter relationship

We use nonlinear models to describe the HD relationship of *M. scabrella* trees. Firstly, we fitted the power model (Equation 1) in which coefficients denoted the scale parameter (a) and the parameter that described the growth rate (b). On a log–log scale, these, respectively, denote the intercept and scaling exponent or slope (Hulshof et al. 2015). Although log–log transformations are common in allometric modelling (Feldpausch et al. 2011), nonlinear models with no variable transformations provide more biological plausibility for data containing homoscedastic and normal error (Xiao et al. 2011). The power model fit allowed testing the MST predictions.

\[
H_i = a_i \times DBH_{ij}^b 
\]  

(1)

where \(H\) is the total tree height and \(DBH\) is the diameter at age class level \(i\) and for observation \(j\), respectively, and \(a\) and \(b\) are the estimated regression coefficients or parameters.

Secondly, the three-parameter exponential model was fitted (Equation 2) in which estimated regression coefficients represented the asymptotic maximum height or asymptote (\(a\)), the range of tree height values (\(b\)) and the shape of the HD curve (\(c\)) (Banin et al. 2012):
\[ H_i = a_i - b_i \exp(-c_i \text{DBH}_j) \]  \hspace{1cm} (2)

where \( a, b, \) and \( c \) are the estimated regression coefficients or parameters. Despite \( c \) being indicative of stem allometry, its sensitivity is dependent on the parameterised asymptote (Zhao et al. 2021; Banin et al. 2012). In this study, the power model was used as an indicator of tree allometry (growth rate) while the exponential model was used as an indicator of potential maximum height (asymptote).

Nonlinear models were fitted with all parameters varying by age class. Therefore, we explored the changes in relationship patterns along stand ages that encompassed the life history of the species (except seedling phase). In order to describe how the HD relationship varied along the chronosequence, we assessed changes in the scaling exponent (power model) and the asymptotic maximum tree height (exponential model). In preliminary analyses, we observed non-convergence in models fitted by age due to less-evident patterns in young stands and too few samples representing advanced ages (Figure S1). To solve this problem, we classified the plots in chronological order of stand age thus: 3–4, 5–6, 7–8, 9–10, 11–12, 13–14, 15–16, 17–18 and 19–20 years. Based on the size growth rate (scaling exponent) and maximum tree height (asymptote), three distinct phases were found along the chronosequence. The stands were therefore categorised into the following phases: early (3 < 10 years), middle (11 < 16) and late (17 < 20). We refitted the nonlinear models (Equations 1 and 2) by stand phase to test whether allometry were indeed distinct.

Influence of stand characteristics

We associated the changes in height allometry with the stand characteristics in order to explain the relationship between tree height and forest succession. To examine whether allometric patterns could distinguish development phases, we computed the stand structure, species diversity and dominance for all plots. The stand structure was described by computing its general attributes, such as stem density (stems ha\(^{-1}\)), basal area (m\(^2\) ha\(^{-1}\)) and the quadratic mean diameter (m). These attributes also denoted competition in the stands and exerted a strong influence on tree allometric relationships. As decreasing dominance and increasing diversity are expected to represent the evolution of \( M. \) scabrella stands, we used these as descriptors for the successional development of the stands. We tested two plot-level dominance indices for \( M. \) scabrella, calculated using the ratio between stem density and basal area in relation to all other species. These indices varied between 0 and 1, where values close to 1 indicated greater dominance. We calculated the Shannon (\( H' \)) and Simpson (\( D' \)) indices to describe plot-level species diversity, and the Pielou index (\( J' \)) to determine the evenness (Magurran 2004).

The plot-level explanatory variables were incorporated into linear mixed-effects models to explain the variations in tree height. Too many local sources of such variation can affect the modelling of allometric relationships. Owing to the site conditions, the trees tended to be more similar within the same site; therefore, it was expected that the model’s residuals would also be site dependent (Kearsley et al. 2017; Calama and Montero 2004). In practice, this dependence can be corrected for when modelled as a random effect in mixed-effects models (Robinson and Hamann 2011). To describe the local variability, plots were included as random effects in all models. Thereby, variability among the plots was modelled by introducing random parameters (Sharma and Parton 2007). In this study, the height and DBH data were transformed to a log–log scale, which has been commonly used to describe this relationship (Zhao et al. 2021; Feldpausch et al. 2011), and is useful for achieving residual statistical assumptions of normality and homoscedasticity (Hulshof et al. 2015).

The explanatory variables were tested in the mixed-effects model by groups following the order: (1) only tree-level DBH; (2) stand structure (basal area, stem density and quadratic mean diameter); (3) diversity (Shannon, Simpson and Pielou indices); and (4) dominance (basal area and stem density). Finally, we tested all the variables in a generic model. We retained DBH as the main predictor at the tree level in all the fitted models. Basal area and stem density were modified in order to assess competition, subtracting the values of the subject tree, because a given tree would not exert competition on itself (Fortin et al. 2019). For the performance comparison of the explanatory variables, both were standardised to a mean of zero and a standard deviation of one. This transformation did not change the slopes of the relationships, resulting in interpretable intercept models (Feldpausch et al. 2011).

We repeated running the selected models by variable group, retaining stand development phase as a factor to test whether the stand attributes removed the forest-succession effects. We also explored the influence of tree size and life history on the height variation. The trees were classified as juvenile/small (DBH < 20 cm) and adult/large (DBH > 20 cm), respectively. To test whether the stand characteristics distinctly affected the HD relationship over time, we reported the interactive effects between the development phases and life stages with selected explanatory variables.

Data analyses

The evaluation and comparison of the nonlinear models were based on the Bayesian information criterion (BIC) and the root mean square error (RMSE). Residual analysis was conducted to verify the statistical assumptions of normality and homoscedasticity. Analysis of variance (ANOVA) was applied to test the changes in the scaling exponent and asymptote along the stand ages and development phases. Likelihood ratio tests were used to compare the coefficients of the models. The Kruskal–Wallis rank sum test was applied to test whether structure, species diversity and/or dominance differed among the stand development phases. Significant differences were identified by the post-hoc Dunn test, a nonparametric pairwise multiple comparison procedure for when the null hypothesis of the Kruskal–Wallis test is rejected. The tests were performed with a 5% significance level.

Regarding the variable selection procedure, a given explanatory variable was maintained in the mixed-effects models if: (1) the fixed-effect term was significant (\( p < 0.01 \)); (2) the likelihood ratio statistics indicated a significant model improvement; (3) the BIC of the model decreased by at least two units; and (4) it did not inflate the variances of the regression coefficients (VIF < 5). After variable selection, the models were compared based on the BIC, variance of fixed
effects (marginal $r^2$) and variance of fixed and random effects (conditional $r^2$). A residual analysis was conducted to verify the statistical assumptions. Initially, the mixed-effects models were fitted using the maximum likelihood (ML) method to compare the models according to the BIC. After variable selection, the models were refitted using the restricted ML (REML) method to obtain more robust parameter estimates (Zuur et al. 2009; Hulshof et al. 2015). The nonlinear and mixed-effects models were fitted using the nlme R package (Pinheiro et al. 2021).

Results

The three-parameter exponential model performed better than the power model based on the BIC and RMSE values (Table 1), but both achieved the statistical assumptions (Figure S2). The parameters estimated by the nonlinear models varied significantly along the stand ages (ANOVA, parameters by age $\times$ generic parameters; $p < 0.001$ for all parameters). Changes in the scaling exponent and asymptote showed three distinct patterns of HD relationships in the chronosequence (Figure 1). The scaling exponent increased continuously from 3 to 10 years, defining an early phase for the *M. scabrella* stands. In the middle phase, this exponent tended to decrease from 11 to 16 years, with an evident increase to late stands after 17 years. The asymptote followed a similar pattern to the scaling exponent in the early and middle phases, showing a strong reduction, however, in the late stands. For a given diameter, trees at the beginning of the late phase were taller (asymptote in Figure 1).

When refitting the nonlinear models by stand development phase, we confirmed distinct allometric relationships (Figure 2) (ANOVA, $p < 0.001$). However, these models also showed that the relationships varied with tree life history. For example, both juvenile and adult trees exhibited constant growth between the early and late stands, whereas the juvenile trees showed higher growth in the middle stands, where there was an evident decrease in adult tree growth (power model). Similarly, juvenile trees had greater asymptotic heights in the middle stands, while the adult trees were taller in the late stands (exponential model). For all stand ages and phases, *M. scabrella* height allometry was considerably lower than the 0.667 predicted by MST (Table 1).

The results show that changes in the HD relationship are related to successive phases of stand development. The mean, median and range of the stand characteristics by phase are presented in Figure 3. Early stands are characterised by a high dominance and density of small trees. In middle stands, dominance and stem density decrease, while diversity and other structural attributes increase. Finally, in late stands, stem density tends to stabilise, exhibiting greater species diversity and low *M. scabrella* dominance. All stand characteristics showed significant differences in the early stands in relation to the other phases (Dunn test, $p < 0.05$). On the other hand, only the dominance indices differed significantly between all the phases. Although the middle and late stands did not differ in structure and diversity (Dunn test, $p < 0.05$), observed trends showed a successional development (Figure 3).

Regarding the explanatory variables, some variation in tree height was explained by stand structure and species

| Stand age (years) | Power Coefficient | Power Coefficient | Power Coefficient | Power Coefficient | Power Coefficient | Power Coefficient | Power Coefficient | Power Coefficient |
|------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| 03–04            | 0.61 (0.21)       | 4.94 (0.11)       | 4.83 (0.10)       | 4.63 (0.11)       | 4.59 (0.14)       | 4.83 (0.21)       | 4.83 (0.21)       | 4.83 (0.21)       |
| 05–06            | 0.26 (0.02)       | 3.8 (0.01)        | 0.39 (0.01)       | 0.39 (0.01)       | 0.41 (0.01)       | 0.33 (0.01)       | 0.41 (0.01)       | 0.41 (0.01)       |
| 07–08            | 0.76 (0.23)       | 15.15 (0.63)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      |
| 09–10            | 1.11 (0.23)       | 15.15 (0.63)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      |
| 11–12            | 1.11 (0.23)       | 15.15 (0.63)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      | 14.52 (0.27)      |
| 13–14            | 15.25 (1.23)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      |
| 15–16            | 15.25 (1.23)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      |
| 17–18            | 15.25 (1.23)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      |
| 19–20            | 15.25 (1.23)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      | 19.88 (1.75)      |

Table 1: Estimated parameters and fit statistics for power and exponential three-parameter models fitted to describe the *Mimosa scabrella* HD relationship along the chronosequence. Standard errors are given in parentheses for all estimated parameters; a, b, and c are the model’s parameters.
demonstrated that the accounted stand explanatory variables did not entirely explain the variation in tree height along the chronosequence. Moreover, the stand effect on tree height varied according to development phase and tree life history (Table 3). Basal area had a significantly positive influence on tree height only in the middle stands \((p < 0.05)\). However, it presented a similar influence between the tree life stages. Unlike our findings for the entire dataset, stem density in middle stands positively affected tree height and did not influence adult trees \((p > 0.05)\). Similarly, species diversity negatively affected tree height in middle stands and did not influence adult trees.

## Discussion

### Changes in the height–diameter relationship

The scaling exponent evidenced changes in tree allometry together with asymptotic height along the assessed chronosequence (Table 1, Figure 1). A continuous increase was found in the scaling exponent and asymptote in the early phase because trees invest in height growth where competition is intense, as is the case in early successional stages (Sun et al. 2017). As light is a limiting factor in the life cycle of pioneer species (Whitmore 1989), this increase followed the gradual canopy shaping in a gradient of light competition. Meanwhile, both parameters decreased in the middle stands, suggesting a dominant canopy position was attained, in light competition terms. In late stands, the abrupt reduction in the asymptote suggests tree senescence since this characteristic emerges as the tree approaches maximum height (Xu et al. 2016). Moreover, taller trees with greater scaling exponents suggest that trees grow close to their critical buckling limit (Banin et al. 2012), thus making them less stiff and more vulnerable to physical damage (Zhao et al. 2021).

In general, very shade-intolerant trees have higher asymptotic heights and allometric curves, indicating a strategy to maximise vertical growth (Hulshof et al. 2015). We found that *M. scabrella* also changed its growth strategy between life stages because juvenile trees in the understory grow differently from adult trees in the canopy (Figure 2). Although each tree has its own light trajectory, from seed to adult, species change their light requirements in different life-cycle stages (Poorter et al. 2005). The results agree with the flexible phenotypic responses of height to heterogeneous light conditions, in which species stature determines, at least in part, a tree’s light availability and growth efficiency (Zhao et al. 2021).

### Stand development and tree height

In early stands, *M. scabrella* invests in colonisation through high dominance and stem density (Figure 3), together with continuous height growth (Figure 1). High density is related to the recent exposure of light to the seed bank, inducing their germination and colonisation of open areas (Ferreira et al. 2017; Somarriba and Kass 2001). This line of evidence explains *M. scabrella*’s dominance through a high density of small stems in early stands. The high overlapping of niches results in strong interactions, which enhance competitive exclusion (Webb et al. 2002), causing an abrupt
Figure 3: Stand characteristics along development phases. Ds – stem density, Ab – basal area, Dq – mean quadratic diameter. A, B and C are the same where the means do not differ significantly (post-hoc Dunn tests; p > 0.05)

Table 2: Mixed-effects models selected by variable group to explain variations in *Mimosa scabrella* height, with tree-level variables, stand structure and diversity as fixed effects and plot as a random effect

| Parameter       | Tree level    | Diversity | Structure | All variables |
|-----------------|---------------|-----------|-----------|---------------|
| BIC             | -35 969       | -35 982   | -35 992   | -36 011       |
| Marginal $r^2$  | 0.2677        | 0.3558    | 0.4030    | 0.4301        |
| Conditional $r^2$| 0.7929        | 0.8068    | 0.8286    | 0.8301        |

Fixed effects

- **Intercept**: 0.7505* 0.009 0.7462* 0.009 0.7398* 0.009 0.7372* 0.009
- **log(DBH)**: 0.3264* 0.008 0.3229* 0.008 0.3305* 0.008 0.3303* 0.008
- **J’**: – – 0.0165* 0.003 – – 0.0289* 0.003
- **Ab**: – – – – 0.0203* 0.003 0.0239* 0.003
- **Ds**: – – – – –0.028* 0.004 – –

Random effects

- **Intercept**: 0.1331 0.1328 0.1398 0.1353
- **log(DBH)**: 0.1182 0.1199 0.1203 0.1202
- **Correlation**: -0.852 -0.865 -0.872 -0.871

* = Significant at the 5% level  
BIC = Bayesian information criterion  
J’ = Pielou index  
Ab = basal area (standardised)  
Ds = stem density (standardised)  
SE = standard error
reduction in small *M. scabrella* trees with increasing age (Steenbock et al. 2011; Machado et al. 2006). Species turnover along secondary successions reveals a gradual replacement of pioneer/light-demanding species, which, after canopy shaping, are unable to reproduce and regenerate, becoming compensated for by secondary/shade-tolerant species (Guariguata and Ostertag 2001; Whitmore 1989). As *M. scabrella* is replaced, its pattern changes from aggregate to random, due to intraspecific competition (Ferreira et al. 2016; Silva et al. 2016a), providing space for more shade-tolerant species, mostly when stands are not subjected to new management practices.

In middle stands, the species presented demographic stability by occupying a dominant canopy position because it no longer needs to invest in height growth (Figures 1, 2), while diversity increases (Figure 3) due to the recruitment of understory and shade-tolerant species, which are favoured by the shading provided by *M. scabrella*. In turn, this shading inhibits its recruitment and regeneration (Ferreira et al. 2017), beginning its replacement in the understory. In late stands, higher growth rates and tree heights (Figure 1) reflect a strategy to avoid shading, indicating their replacement in the canopy by other species once diversity also increases. This leads to taller and more slender trees, which are more susceptible to physical damage, such as buckling (Zhao et al. 2021). The mechanical constraints provided by tree senescence and *M. scabrella*'s short life cycle cause low abundance in late stands, which may be similar to natural mixed-forest regarding species diversity (Silva et al. 2016a). Although the *M. scabrella* population declines over time, the stand characteristics follow general successional trends as they are compensated for by secondary species.

Regarding the significant differences between the early stands compared with the other phases (Figure 3), the initial successional stages are more characteristic and predictable, dominated by light-demanding species (Gomes et al. 2020; McNicol et al. 2015). In this study, the early stands were distinguished by high *M. scabrella* dominance and density, reflecting human intervention via management practices (Steenbock et al. 2011), local patterns of species colonisation and the effects of remnant vegetation (Chazdon et al. 2007).

### Table 3: Interactive effects of stand explanatory variables with development phases and life stages to explain variations in tree height. SE = standard error

| Interaction     | Parameter | Estimate | SE   | p-value |
|-----------------|-----------|----------|------|---------|
| **Development phase** |           |          |      |         |
| Stem density    | Intercept | 0.745    | 0.009| < 0.001 |
|                 | DBH       | 0.326    | 0.008| < 0.001 |
|                 | Early     | −0.018   | 0.004| < 0.001 |
|                 | Middle    | 0.039    | 0.011| < 0.001 |
|                 | Late      | −0.032   | 0.008| < 0.001 |
| Basal area      | Intercept | 0.749    | 0.009| < 0.001 |
|                 | DBH       | 0.332    | 0.008| < 0.001 |
|                 | Early     | 0.004    | 0.004| 0.404   |
|                 | Middle    | 0.069    | 0.009| < 0.001 |
|                 | Late      | −0.003   | 0.005| 0.555   |
| Species evenness| Intercept | 0.749    | 0.009| < 0.001 |
|                 | DBH       | 0.326    | 0.008| < 0.001 |
|                 | Early     | 0.029    | 0.005| < 0.001 |
|                 | Middle    | −0.027   | 0.007| < 0.001 |
|                 | Late      | 0.019    | 0.004| < 0.001 |
| **Life stage**  |           |          |      |         |
| Stem density    | Intercept | 0.731    | 0.009| < 0.001 |
|                 | DBH       | 0.342    | 0.008| < 0.001 |
|                 | Juvenile  | −0.016   | 0.004| < 0.001 |
|                 | Adult     | 0.001    | 0.005| 0.837   |
| Basal area      | Intercept | 0.747    | 0.009| < 0.001 |
|                 | DBH       | 0.331    | 0.008| < 0.001 |
|                 | Juvenile  | 0.010    | 0.003| 0.003   |
|                 | Adult     | 0.012    | 0.004| 0.002   |
| Species evenness| Intercept | 0.734    | 0.009| < 0.001 |
|                 | DBH       | 0.335    | 0.008| < 0.001 |
|                 | Juvenile  | 0.017    | 0.003| < 0.001 |
|                 | Adult     | 0.008    | 0.004| 0.023   |

**Stand influence on tree height**

The influence of stand on HD relationships (Table 2) is consistent with the findings of several previous studies (Sharma and Parton 2007; Wang et al. 2006; Calama and Montero 2004). Tree growth, recruitment and mortality are influenced by stand density and basal area, while species diversity reflects community turnover processes (Chazdon et al. 2007). Often, these characteristics are used to report competition in stands and their influence on tree height (del Rio et al. 2019; Fortin et al. 2019; Forrester et al. 2017). Thus, competition presented a distinct effect on tree height, positive by basal area and negative by stem density. This may suggest that the presence of larger trees induces a competitive effect (Banin et al. 2012). Although large trees
were not sampled in the chronosequence, the presence of larger trees may indicate that competitive effects are also induced by increase in tree size.

The joint increase in diversity, basal area and tree size, followed by a decrease in dominance (Figure 3) suggests the influence of interspecific competition in late stands, unlike the intraspecific competition in early stands. A positive influence of diversity on tree height was found (Table 2), confirming a growth strategy to avoid shading caused by interspecific competition in the canopy of late stands. Although species diversity had less effect on the allometric relationships than competition (Forrester et al. 2017), tree allometry varied in response to both intra- and interspecific interactions, which were related to species shade tolerance (del Río et al. 2019).

The effects of stand development phase and tree life stage persisted, even after accounting for the stand characteristics; therefore, they are mechanisms shaping the HD relationship of M. scabrella in the chronosequence. Because tree height allometry is related to stand characteristics, and both changed along the chronosequence, they related distinctly over time. In early and late stands, there was a variable influence of stand characteristics because these are more dynamic, with early stands being influenced by high mortality from intraspecific competition and late stands by M. scabrella replacement due to interspecific competition (Ferreira et al. 2017; Machado et al. 2006). This also explains the constant growth between juvenile and adult trees in these stands (Figure 2), both driven by competition. In general, high competition levels decrease the crown projection area and increase height and the live-crown length (Forrester et al. 2017). Regarding tree life stage, stand density and species diversity influenced only juvenile trees, whereas basal area had a significant influence on all life stages. Therefore, the influence of the stand on tree height and allometry was also conditioned by different stand development phases and tree life stages.

Variations in the HD allometry indicate the way in which the trees modified their growth conditions, elucidating the drivers of development (Forrester et al. 2017) and providing insights into their life-history strategies and limitations (Hulshof et al. 2015). Our findings are in agreement with other reports on tree allometric strategies across light competition gradients associated with a species life history, stature and canopy position (Zhao et al. 2021; del Río et al. 2019; Forrester et al. 2017; Sun et al. 2017; Poorter et al. 2005) and support the strong effect of canopy cover on the dynamics of M. scabrella populations (Ferreira et al. 2017).

Regarding practical applications, quantifying and understanding the variation in HD allometry is critical to improving biomass and carbon predictions (Hulshof et al. 2015; Banin et al. 2012). The improvement of predictions is required, since early-growth forests show great potential for carbon sequestration due to their higher growth rates compared to late-successional forests (Sun et al. 2017), while re-establishing forests on land previously used for agriculture represents the most common type of successional forest in the tropics (Chazdon et al. 2007). This applies to M. scabrella stands because it is a dominant, fast-growing species that covers post-disturbance and fallow areas in southern Brazil (Steenbock et al. 2011; Machado et al. 2006). The allometry differences between stand phases and tree life stages indicate that they should be quantified to enable predictions that are more accurate. Furthermore, incorporating stand characteristics into allometric models allows the development of a general equation to the application in a wider range of stands (Forrester et al. 2017). Likewise, our findings can be useful to management practices, since silvicultural interventions, such as liberation thinning, are improved by knowledge of the appropriate ontogenetic stage for their application (Poorter et al. 2005). We verified the greater sensitivity of juvenile trees and middle stands to the influence of stand characteristics, indicating a possible advantage for management implementation.

Conclusions

We found that changes in the HD relationship along a chronosequence reveal distinct height growth strategies in the M. scabrella life history. We conclude that variations in tree height in our chronosequence were driven by light competition, with the influence of successional stand evolution and tree life stages. Our results support the theory that tree allometric relationships are plastic rather than fixed, even when assessing species-specific allometry on more restricted scales. Finally, we found that gradual changes in tree development may also be recognised in stationary data along chronosequences.

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