



Modeling bark thickness and probability of trunk cavity occurrence relative to tree size in *Araucaria angustifolia* trees

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Abstract

Key message Models of bark thickness and trunk cavity occurrence improve allometry assessments and provide good indicators of the probability of tree decay or vitality—knowledge useful for old-growth tree conservation and management.

Abstract This study aimed to model the attributes of *Araucaria angustifolia* that influence allometry assessments and its biomechanics. We used samples collected during dendrochronological studies to measure bark thickness and data from old-growth attribute surveys to assess the occurrence of trunk cavities (or hollows) associated with heartwood decay. First, nonlinear mixed-effects models were calibrated to predict bark thickness. Then the probability of hollow occurrence was evaluated with binomial regression using generalized linear models. Bark thickness increased with tree size, attaining an asymptote of 11.9 cm. This finding suggests that thickness above the asymptote may not offer additional protection to trees. Because bark has an influence on allometry assessments, we provide an accurate model to improve wood volume estimates. Hollows are associated with tree size and affect mechanical stability, and due to their empty space, it can cause bias in allometry assessment of biomass and wood volume. Suitable predictors of the probability of tree decay or vitality are provided. The predictors evaluated can also be used as a tree-level indicator of quality in selection systems. Our results highlight the importance of accounting for bark thickness and trunk hollows in carbon, conservation, and management surveys of *Araucaria* forests.

Keywords Allometry · Biomechanics · Tree bark · Hollow trunk

Introduction

Araucaria angustifolia (Bertol.) Kuntze is a native conifer to southern and southeastern Brazil that occurs in cold and humid highland plateaus (500–2400 masl), into Argentina and Paraguay (Hueck 1953; Wrege et al. 2017). It is an economically important species within its natural range and has been a source of timber and food for many decades (Eisfeld et al. 2020; Souza et al. 2012). *A. angustifolia* is a

key component of the mixed evergreen forest, also known as the Araucaria Forest, a forest type characterized by the dominance of this species. This forest type is mainly found in southern Brazil, where *A. angustifolia* has been described as a keystone species due to its role in maintaining the forest's ecological balance (Mattos 1994). However, due to its intense exploitation for wood products and conversion of forest land to agriculture, it is currently facing a critical situation. The species is restricted to a few populations related to each other, with low haplotype diversity, which expanded possibly from a single refugium with human aid (Lauterjung et al. 2018; Robinson et al. 2018). This status has led to the species being classified as critically endangered in the International Union for Conservation of Nature's Red List of Threatened Species (Thomas 2013). On the other hand, the wood of the species is highly valued for its quality and is used for a variety of purposes, including furniture making, construction, and paper production (Lorenzi 2002), while its pine nuts are one of the most important non-timber forest products in Brazil (Silva et al. 2020).

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Timber tree species are susceptible to a wide range of defects that can reduce the amount of wood with desirable qualities (Moreau et al. 2023). A common example of defect in *A. angustifolia* is trunk cavities or tree hollows, characterized as an attribute of old-growth trees (Scipioni et al. 2022). A hollow tree may fail if the cavity is $\sim \geq 70\%$ of the trunk radius (Mattheck et al. 2006; Mattheck 2007). Thus, hollows can compromise the mechanical stability of trees, making them more susceptible to breakage (Sterken 2005). Cavities also affect estimates of tree biomass and volume due to the empty space in trunks (Fearnside 1992). These biases are propagated to predictions at stand and landscape level, thereby compromising carbon assessments (Nogueira et al. 2006) and volume yield of timber harvested (Almeida et al. 2022). On the other hand, hollow trunks are microhabitats that provide ecological benefits and have positive effects on the biodiversity of forest ecosystems (Martin et al. 2022; Vuidot et al. 2011).

Thick bark is also a notable feature of *A. angustifolia*. Bark is all plant tissue external to the vascular cambium and includes conducting and non-conducting tissue (Roth 1981; Zimmermann and Brown 1980). As bark acts to protect living tissue, its thickness is thought to be mainly driven by its defensive function (Paine et al. 2010; Pausas 2015). Thus, the thicker bark in the Araucariaceae may be recognized as offering vital protection against insect attack, physical damage from abrasion or fire, and extreme weather events (Costa et al. 2021; Molina et al. 2016). Bark thickness influences both stem transpiration and respiration, reflecting strategies for growth and tolerance to water deficit (Loram-Lourenço et al. 2022), and is even associated with structural support and flexural rigidity of tree trunks (Niklas 1999). Another perspective is that bark can make up a large amount of the volume of a tree (Li and Weiskittel 2011). Although tree measurements are based on the diameter outside the bark, the volume of wood inside the bark is required for most forestry applications (Stängle et al. 2017); therefore, bark thickness and its relationships with tree diameter and volume must be accurately determined (Pemberton 1924; Muhairwe 2000).

As bark thickness and trunk cavities affect tree stability and cause uncertainties in biomass and wood volume estimation, they are essential knowledge both for conservation and management of timber species. The main aim of this study was to determine bark thickness and probability of trunk cavities occurrence in *A. angustifolia* as a function of tree size across young, mature, and old individuals. Therefore, we examined attributes at tree level that affect allometry assessments and biomechanics.

Materials and methods

Data collection and measurement

We used samples collected for dendrochronological studies (Scipioni et al. 2021) to measure tree bark thickness. Increment cores were collected from standing trees (Fig. 1d, e) and wood disks were extracted from fallen trees with preserved bark (Fig. 1f, g). Bark thickness was measured with a precision ruler later in the laboratory. These samples were collected at 9 sites, with 318 samples taken from 185 trees (Table S1). The diameter at 1.3 m above the ground (diameter at breast height [DBH]) of these trees was also measured in the field. To account for the probability of trunk cavities, we used data from old-growth attribute surveys (Fig. 1a, b, c) of 159 trees (Scipioni et al. 2022), of which 21 were visibly hollow, sampled at 13 sites (Table S1). DBH and total height (H) of these trees were measured using diametric tape and a laser dendrometer (Criterion RD 1000), and the number of reiterated trunks (NRT) was quantified visually (Fig. 1b). The dendrochronological samples (increment cores) were also used to assess possible trunk cavities not visible at the stem outer surface for all of the other sampled trees ($n=138$). Further information on data collection, measurements, and sampling site location are available in Table S1 and Scipioni et al. (2021, 2022).

Modeling bark thickness

We evaluated the relationships between tree size (DBH) and bark thickness (BT, cm) and percentage (BP, %) using scatter-plots. We then calibrated nonlinear biological models of bark thickness using tree diameter as a predictor. The data set was randomly categorized into training data (85%, 273 trees) and test data (15%, 45 trees) for calibration and model performance evaluation. Biophysical and growth rate models (Howell et al. 2022) were fitted for bark thickness modeling using the training data. We tested the following models: exponential (Eq. 1); Gompertz (Eq. 2); logistic (Eq. 3); Mitscherlich (Eq. 4); power (Eq. 5); and Weibull (Eq. 6).

$$BT = a - b.e^{-c.DBH} + \varepsilon, \quad (1)$$

$$BT = a.e^{(-e^{(b-c.DBH)})} + \varepsilon, \quad (2)$$

$$BT = \frac{a}{1 + e^{(b-c.DBH)}} + \varepsilon, \quad (3)$$

$$BT = a.(1 - e^{(b.DBH)}) + \varepsilon, \quad (4)$$

$$BT = a.DBH^b + \varepsilon, \quad (5)$$

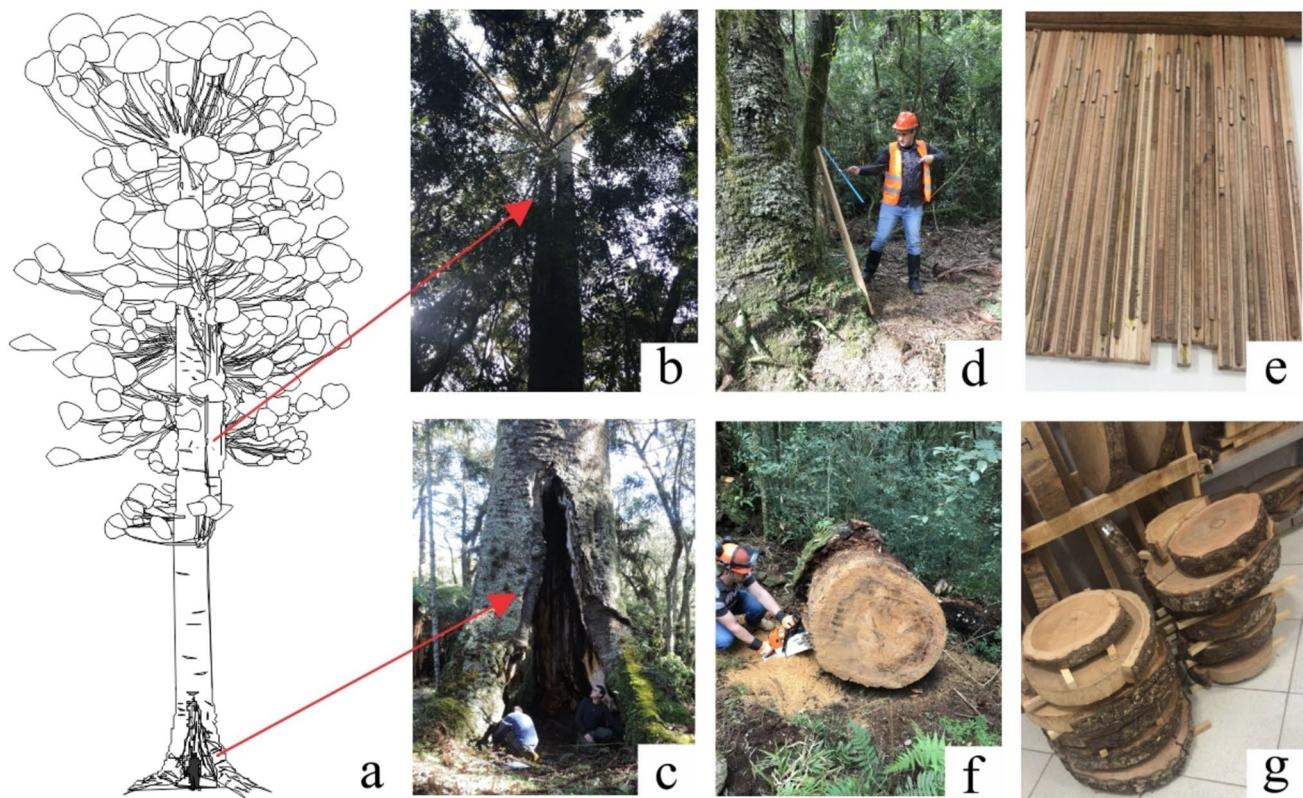


Fig. 1 **a** Old-growth attributes evaluated for *Araucaria angustifolia* trees, such as **(b)** reiterated trunks and **(c)** basal trunk cavities. **d** Increment cores and **(f)** wood discs were collected for **(e)** dendrochronological studies and **(g)** bark thickness measurements

$$BT = a \cdot \left(1 - e^{-(b \cdot DBH)^c}\right) + \varepsilon, \quad (6)$$

where BT was bark thickness (cm), DBH was diameter at breast height (cm), a , b , and c were parameter estimates, and ε was the residual error. The nonlinear models were calibrated with the maximum likelihood method using the *nls* function in the *nlme* package (Pinheiro et al. 2020) in R version 4.0.3 (R Core Team 2021).

The best model was selected based on the Akaike information criterion (AIC), root mean square error (RMSE), and coefficient of determination (R^2) computed using the square of the correlation between observed and estimated values. Therefore, the model that maximized R^2 and minimized AIC and RMSE was selected. In addition, graphical analysis was performed to verify whether the models provided adequate biological representation (Vanclay and Skovsgaard 1997) and to examine the assumptions of normality and homogeneity of variances.

After selecting the best model functional form, the random effect of sites was incorporated using nonlinear mixed-effects (NLME) modeling (Eq. 7) with the *nlme* function in the homonymous package in R.

$$BT = f(DBH) + \alpha_{\text{Site}} + \varepsilon, \quad (7)$$

where BT was bark thickness modeled as a non-linear function of DBH (f), α was site as random effect, and ε was the residual error. This procedure allows model parameters to vary between sites (Hulshof et al. 2015) and accounts for data non-independence (Banin et al. 2012). This provided a significantly better fit compared to the previous fixed-effects model (likelihood ratio test, $p < 0.001$). The final NLME model was also evaluated based on AIC, RMSE, R^2 criteria, and graphical analysis of statistical assumptions.

Bark thickness and diameter inside bark (DWB) measured for the test data were compared to estimates from the final NLME to examine model performance. To test whether BT and DWB differed significantly between measurements and estimates, we applied the non-parametric Wilcoxon rank-sum test ($\alpha = 0.05$). DWB was calculated by subtracting bark thickness multiplied by two from DBH (Muhairwe 2000).

Modeling the probability of trunk cavities

Binomial regression was used to determine the probability of trunk cavity occurrence in *A. angustifolia* trees. The presence of hollow trunks was categorized as a binary variable (0 = non-hollow and 1 = hollow). Then generalized linear models (GLMs) were calibrated to model the probability of cavity occurrence as a function of tree size attributes using the binomial distribution and the logit link function (Eq. 8).

$$\log(\text{HP}/1 - \text{HP}) = a + b \cdot (\text{X}) + \varepsilon, \quad (8)$$

where HP was the probability of hollow trunk, X was DBH, H, or NRT, a and b were parameter estimates, and ε was the residual error. Parameters of tree size—DBH, H, and NRT—were used as single predictors in the GLM. The model's performance was evaluated based on the AIC and the percentage of variance explained by the model. The significance of β_i coefficients indicated by the t -statistic was used to test the effect of predictors on the probability of hollowness. The GLMs were calibrated using base functions in R version 4.0.3 (R Core Team 2021).

We then used height–diameter allometry to examine the mechanical support capacity of trees with basal cavities. The height–diameter relationship may reflect a trade-off between growth and survival (King et al. 2006) and plays a key role in studies related to trees mechanical support (McMahon 1973). We fitted the power allometric model to height and diameter data for 159 trees, separately for non-hollow ($n = 138$) and hollow ($n = 21$) trees. NLME modeling was again applied to account for site effects as a random factor (Eq. 9) using the *nlme* function in the homonymous package in R language.

$$H = (a + \alpha_0) \cdot (\text{DBH})^{(b + \alpha_1)} + \varepsilon, \quad (9)$$

where H was total height (m) of non-hollow or hollow trees, DBH was diameter at breast height (cm), a and b were parameter estimates, α_0 and α_1 were random effect terms, and ε was the residual error. Lastly, we compared the estimated coefficients (b) with the predictions of metabolic theory (Niklas and Spatz 2004) that height increases consistently with diameter raised to $2/3$ power, and, therefore, the slope coefficient of the model is 0.667. The NLME power model fitting and evaluation followed the same statistical procedure used in NLME bark thickness models.

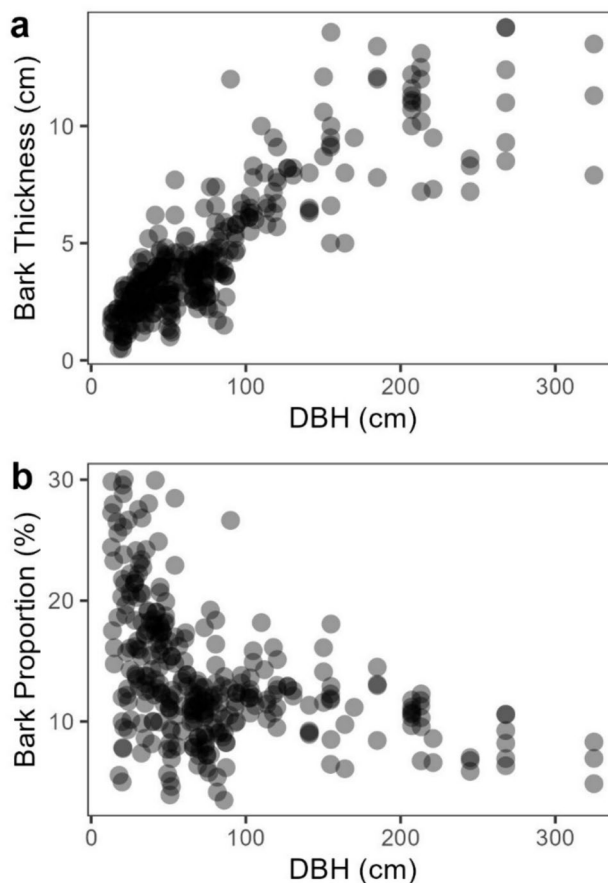


Fig. 2 Relationships between tree size (DBH) and (a) bark thickness (BT) and (b) bark percentage (BP) of *A. angustifolia* trees based on the entire data set

Results

Bark thickness

Bark thickness exhibited asymptotic growth as a function of tree size (Fig. 2a), with a tendency to stabilize in trees with DBH > 150 cm. The percentage of bark showed exponential decay (Fig. 2b), decreasing at a constant rate. Scatterplots indicated that some small trees had thick bark, and consequently, a high percentage of bark in DBH, while the percentage of bark of large trees was low even with thicker bark. Among the models tested, the logistic model (3) maximized R^2 and minimized AIC and RMSE (Table 1) and provided significant parameters ($p < 0.001$). In addition, the errors in this model were normally distributed (Fig. S1a) and the variance was homogeneous (Fig. S1b). Therefore, the logistic model was selected as the best for modeling bark thickness. The sigmoidal shape of the logistic model provided adequate biological representation and identified an asymptote of 11.9 cm for bark thickness as tree size increased (Fig. 3).

Table 1 Parameter estimates and goodness of fit of nonlinear models calibrated to bark thickness

Model	Parameter	Estimate	SE	<i>p</i> value	DF	AIC	<i>R</i> ²	RMSE
Exponential	<i>a</i>	23.940	6.343	<0.001	270	979	0.761	1.433
	<i>b</i>	23.250	6.145	<0.001				
	<i>c</i>	0.0025	0.0009	0.006				
Gompertz	<i>a</i>	13.567	0.901	<0.001	270	968	0.770	1.405
	<i>b</i>	2.397	0.093	<0.001				
	<i>c</i>	0.0106	0.0011	<0.001				
Logistic	<i>a</i>	11.896	0.487	<0.001	270	962	0.776	1.388
	<i>b</i>	7.073	0.568	<0.001				
	<i>c</i>	0.0194	0.0015	<0.001				
Mitscherlich	<i>a</i>	− 4.671	0.198	0.502	271	1004	0.753	1.561
	<i>b</i>	0.114	0.0048	0.454				
Power	<i>a</i>	− 2.796	0.196	<0.001	271	998	0.743	1.488
	<i>b</i>	0.474	0.0054	<0.001				
Weibull	<i>a</i>	38.172	31.435	0.358	270	983	0.758	1.443
	<i>b</i>	0.004	0.0028	0.191				
	<i>c</i>	0.8285	0.1020	<0.001				

SE standard error of parameter, *DF* degrees of freedom of model, *AIC* Akaike information criterion, *R*² coefficient of determination, *RMSE* root mean square error

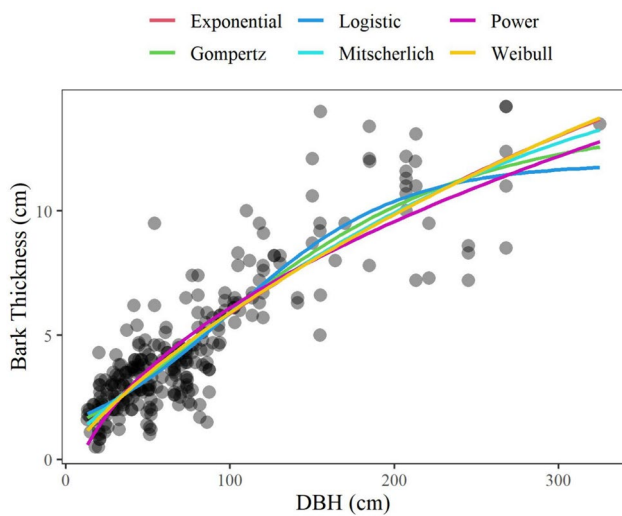


Fig. 3 Comparison of the performance of nonlinear models of bark thickness using training data

Table 2 Summary of the nonlinear mixed-effects model of bark thickness with site as a random effect

Parameter	Estimate	SE	<i>p</i> value	DF	Groups	AIC	<i>R</i> ²	RMSE
<i>a</i>	11.929	0.904	<0.001	262	9	929	0.822	1.237
<i>b</i>	9.532	1.043	<0.001					
<i>c</i>	0.022	0.001	<0.001					

SE standard error of model parameters, *DF* degrees of freedom of model; Groups, random factor levels, *AIC* Akaike information criterion, *R*² coefficient of determination, *RMSE* root mean square error (cm)

After the logistic model for bark estimation was applied, the random effect of site was significant (likelihood ratio test, *p* < 0.001), denoting a likely influence of location or sampling on predictions. The NLME logistic model, in addition to accounting for non-independence, improved predictions since it maximized *R*² and minimized AIC and RMSE (Table 2) compared to the previous fixed-effects model. The NLME model also fulfilled the assumptions of normality and homogeneity of variances (Fig. S1). In the tests of the model for new predictions (test data), we did not find differences between estimated and observed values of bark thickness (Fig. S2a, *p* = 0.91) and diameter without bark (Fig. S2b, *p* = 0.93), demonstrating its accuracy for assessing *A. angustifolia* trees.

Probability of trunk cavities

Binomial GLMs showed that tree size and reiterated trunks had a significant positive effect (*p* < 0.001) on the occurrence of basal trunk cavities (Table 3). Diameter was selected as the best predictor of trunk cavity occurrence (lower AIC and higher explained variance), followed by height and the

Table 3 Parameter estimates and goodness-of-fit statistics of generalized binomial models used to predict the probability of trunk cavities

Predictor	Parameter	Estimate	SE	<i>p</i> value	DF	AIC	Variance explained (%)
DBH	<i>a</i>	− 5.989	0.994	<0.001	157	66.5	46.1
	<i>b</i>	0.035	0.007	<0.001			
H	<i>a</i>	− 9.749	1.918	<0.001	157	70.7	42.5
	<i>b</i>	0.271	0.059	<0.001			
NRT	<i>a</i>	− 3.197	0.422	<0.001	157	80.2	34.3
	<i>b</i>	0.998	0.192	<0.001			

SE standard error of parameter, *DF* degrees of freedom of model, *AIC* Akaike information criterion, *DBH* diameter at breast height, *H* total height, *NRT* number of reiterated trunks

number of reiterated trunks. The probability of trunk cavity occurrence tended to increase with increases in all predictors (Fig. 4). Trees with DBH up to 70 cm did not have hollows, while trees with DBH > 200 cm showed a high probability of cavity occurrence (> 75%). Only trees over 25 m tall have a trunk basal cavity, with the probability of a cavity occurrence greater than 75% for those surpassing 40 m in height. Although the presence of reiterated trunks contributed less to explaining the presence of trunk cavities (higher AIC and lower explained variance), it still is a good predictor of the probability of cavity occurrence as it is easily assessed visually.

Only trees with a DBH of > 280 cm and six or more reiterated trunks showed the maximum probability of trunk cavity occurrence (Fig. 4). In fitting the NLME power model to test the influence of basal hollows on the mechanical stability of trees (Fig. 5), only trees without such basal cavities showed an allometric coefficient adhering to theoretical predictions of metabolic theory (0.667, $p < 0.001$). In contrast, trees with trunk cavities had a lower allometric coefficient than predicted (0.608, $p < 0.001$), denoting a lower rate of height growth.

Discussion

Relationship between bark thickness and tree size

According to the selected model, bark thickness tended to increase with tree size, reaching an asymptote of 11.9 cm that corresponded to an average DBH of 200 cm. Although the thickness pattern of *A. angustifolia* bark has been investigated previously (Costa et al. 2021), an asymptote has not been reported to date due to the small size of trees in previous studies compared to the sample in the present study (DBH range of 10–325 cm). An asymptotic increase in thickness is expected for tree bark, because beyond a certain limit, the additional thickness may not confer further survival advantages (Paine et al. 2010; Wilson and Witkowski 2003)—although the tree protection

mechanisms provided by bark are complex (Molina et al. 2016). Furthermore, the asymptotic bark thickness may be related to lower metabolic activity as trees grow (McMahon 1973, King 2006), limiting bark production due to lower phellogen activity. However, asymptotic growth is mainly expected in species with bark shedding (Roth 1981) such as *A. angustifolia* (Costa et al. 2021). In turn, the biologically realistic allometric functions (Howell et al. 2022) for the bark thickness × DBH relationship of this species had not yet been explored. Logistic and Gompertz growth rate models provided a better fit for and biological representation of this relationship, relative to Mitscherlich and Weibull models (which generated nonsignificant coefficients) and power model which indicated continuous growth. However, all models performed similarly in the case of smaller trees (DBH < 120 cm).

The results revealed that large trees have a low percentage of bark, unlike small trees whose bark is less thick but occurs at a higher percentage. This suggests that in *A. angustifolia*, the bark may have an important structural role in small trees (Niklas 1999) and greater protective capacity in large trees (Paine et al. 2010). These results also demonstrate that bark can affect allometric estimates of both large and small trees. However, the selected model showed high accuracy in training and test procedures, especially when site effects were accounted for by mixed-effects modeling. The site effects emphasize the need for a more comprehensive sampling across *Araucaria* forests, to produce model estimates applicable at larger spatial and environmental scales. Bark thickness can be influenced by several conditions at the tree and site level; thus, bark models are common in forest surveys to estimate inside-bark diameters (Stängle et al. 2017). Although these models have been applied to few tree species in the Brazilian Atlantic Forest, they are well known elsewhere for other timber species and stand types, such as European mixed-species and pure spruce stands (Stängle et al. 2017), Australian eucalyptus in natural and planted stands (Muhairwe 2000), and North American conifers in even-aged naturally regenerated stands (Li and Weiskittel 2011).

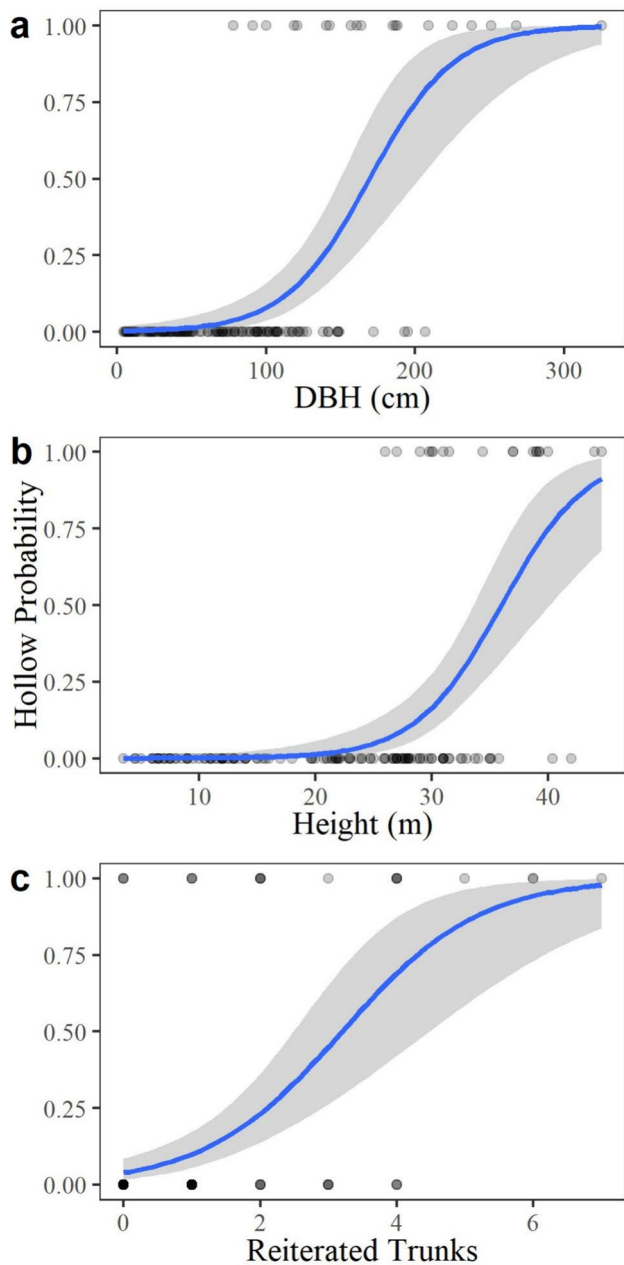


Fig. 4 Binomial regression computed with generalized linear models showing the effect of (a) tree size, (b) tree total height, and (c) the number of reiterated trunks on the probability of trunk cavity occurrence. Shaded areas represent confidence intervals with $\alpha=0.05$

Although bark thickness varies along the trunk according to height (Muhairwe 2000; Stängle et al. 2017), only bark measured at breast height was evaluated in the present study as the aim was to test its influence on diameter—the main forestry predictor of tree allometry (Chave et al. 2014). Other tree-level variables such as height, crown base height, branch arrangement, and sociological position can also affect *A. angustifolia* bark thickness (Costa et al. 2021). This highlights the need for further studies to elucidate the

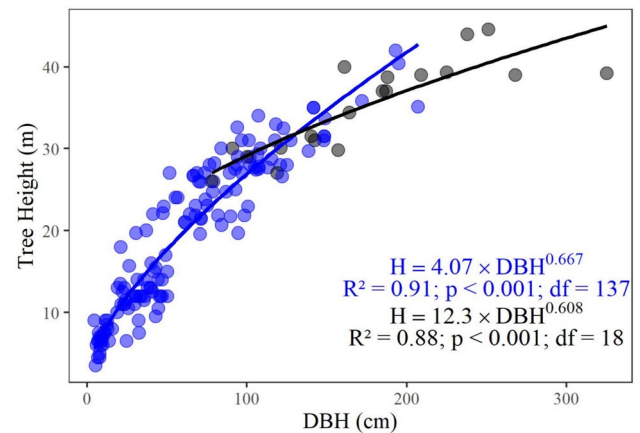


Fig. 5 Comparison of height–diameter allometry using the nonlinear mixed-effects power model to examine the effect of basal trunk cavities on mechanical support of trees. Circles in blue represent non-hollow trees and those in black hollow trees

environmental, ecological, and silvicultural drivers of *A. angustifolia* bark thickness, and its influences on biomass and wood volume estimation. In addition, we believe that *A. angustifolia* may be the species with the thickest bark in Brazilian humid forests; this emphasizes the importance of selecting an appropriate model for accurate estimates of bark thickness and diameter inside bark.

Relationships between probability of trunk cavities and tree attributes

Our results highlight that tree structural attributes such as trunk cavities and reiterated trunks become characteristic of large old-growth *A. angustifolia* trees (Scipioni et al. 2022), but are absent in smaller, younger trees; these findings are consistent with the hypothesis that the probability of a decline in wood quality increases as trees get old (Moreau et al. 2023). Thus, older age is an important driver of *Araucaria* cavity occurrence, since mature and old trees are strongly related to loss of vigor (reduced growth), greater wood decay, and mortality (King et al. 2006; Dey et al. 2017). The vigor reduction is also notable in *A. angustifolia*, which decrease its survival (Cysneiros et al. 2023) and relative growth rate for large and old trees (Stepka et al. 2021). Although tree size and age are the main drivers of trunk cavity occurrence, such hollows may originate from combinations of multiple factors not addressed in our analysis, such as the presence of crown damage, historical fire occurrences, unmanaged/stocked forests, higher average temperature (Moreau et al. 2023), spacing between neighboring trees, and bark damage (Vanclay 2022), in addition to species traits, such as wood density (Eleuterio et al. 2020) and vitality (Vuidot et al. 2011). Therefore, further studies considering the effects of competition (crown spacing, tree

damage, etc.) and environmental factors (climate, soil, susceptibility to wildfires, etc.) are still needed to explain the occurrence of trunk cavities in *A. angustifolia*.

Three theories about variations in tree height allometry (Banin et al. 2012; Hulshof et al. 2015) may partly explain the observed differences in *A. angustifolia* height:diameter relationships between smaller trees without trunk cavities and larger trees that commonly have basal trunk hollows. (1) The mechanical constraints theory states that trees may stop growing once reaching a certain height to avoid buckling (McMahon 1973); thus perhaps the population of *A. angustifolia* trees that is large and old enough to develop cavities has already almost reached their size limit as a strategy of not breaking or toppling under their own weight, and thus has a different tree height:diameter allometry than the population of smaller non-hollow trees. Further, a related direct explanation is that as older and larger-diameter trees become likely to develop basal cavities with heartwood decay, there are associated reductions in mechanical stability of basal trunks and roots that results in greater stem breakage and tip-overs during storm events, thereby eliminating some of the tallest trees from the population of trees with cavities, and flattening their height:diameter relationship. (2) The hydraulic limitation theory suggests that the challenges of maintaining hydraulic conductance in canopy leaves and lower availability of water in sapwood cross-sections restrict apical height growth of taller trees (McDowell and Allen 2015; Ryan et al. 2006), ultimately causing a height asymptote (Niklas and Spatz 2004); by extension, perhaps large *A. angustifolia* trees that have basal cavities may grow even less height-wise than undamaged trees due to reduced vertical water transport capacities from the reduced basal xylem area (Mattheck et al. 2006; Sterken 2005), thus the lower allometric coefficients for trees with basal hollows. (3) The metabolic theory predicts that tree height increases as a function of diameter (Niklas and Spatz 2004), in which lower allometric coefficients may indicate a decrease in the height growth capacity of old trees with trunk cavities, reflecting successful adjustments to long-term survival.

General implications

Our results provide useful information for allometry assessment of *A. angustifolia* since bark thickness (Cochran 1982; Muhairwe 2000) and trunk cavities (Nogueira et al. 2006) cause overestimation of biomass and wood volume (Fearnside 1992; Hauck et al. 2023). Furthermore, as trunk hollows compromise the mechanical stability of trees, their potential predictors can be used as indicators of wood production quality. The findings of this study can be used to prescribe a maximum tree size beyond which it may not be advantageous to keep the trees from an economic perspective, due to elevated risk of developing tree cavities and associated wood

defect (Dey et al. 2017; Mattheck et al. 2006; Moreau et al. 2023) and consequent reduction in forest timber stocks (Liu et al. 2013; Almeida et al. 2022). We found that in addition to diameter, the number of reiterated trunks was another predictor that can be used for tree quality assessment. Besides being able to be easily analyzed visually, it is an indicator of trees with a higher probability of developing cavities with decay, and thus is a potential indicator of commercial wood defect. These findings have significant implications for commercial tree management via selection systems (Moreau et al. 2023; Vanclay 2022).

However, it is also crucial to recognize the essential ecological roles of tree cavities and hollow trunks in providing unique and irreplaceable microhabitats that are necessary and beneficial for a wide range of biodiversity (Gibbons and Lindenmayer 2002; Martin et al. 2022; Michel and Winter 2009). Ecologically the reiterated trunks can be an indicator of high tree vitality after a top-damaging event, representing an old-growth structure related to crown recovery that also provides unique and rare microhabitats that are essential to support biodiversity (Scipioni et al. 2022). Cavities and reiterated trunks are such important forest structural features on the landscape that they must be recognized even in managed stands, as they provide increasingly scarce structural attributes in forest landscapes (Larrieu et al. 2018; Lindenmayer et al. 2012), particularly in *Araucaria* forests of south Brazil. In addition, the largest and oldest trees, despite being characterized by the presence of trunk cavities and other old-age commercial “defects” (Hauck et al. 2023), are well-known to store disproportionately large amounts of carbon in their woody structures (Lutz et al. 2018; Stephenson et al. 2014)—and reiterated trunks represent an additional tree carbon pool. Thus, managing forests to include conservation of old and large-diameter trees is an important way to enhance a variety of valuable ecosystem services (Lutz et al. 2018), from maintenance of irreplaceable biodiversity to acting as a climate nature-based solution to support forest carbon storage. Certainly, both the ecological benefits and economic trade-offs of tree cavities and hollow trunks must be considered in forest management and conservation.

Conclusion

Bark thickness of *Araucaria angustifolia* increased asymptotically with tree size, stabilizing only in large trees. Although thick bark provides effective protection against abiotic and biotic damage, tree biomass and wood volume estimates can be biased if bark is not considered. However, the model selected in this study provided accurate estimates of bark thickness to improve allometry assessments. Tree cavities and trunk hollows are associated with tree size and may affect tree biomechanics. The attributes evaluated in

this study (diameter at breast height, height, and number of reiterated trunks) are suitable predictors of the probability of tree decay and related essential biodiversity values. Finally, the tree-level indicators provided here can aid both timber management and forest conservation efforts, since these indicators can support decisions to retain or eliminate trees in selection forestry systems aiming that also aim to maintain important ecosystem services.

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Availability of data and materials The datasets generated during and/or analyzed during the current study are available from the authors upon request.

Declarations

Conflict of interests The authors declare they have no competing of interest.

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