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Modeling Tree Diameter Growth of *Bertholletia excelsa* Bonpl. in the Brazilian Amazon

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Abstract: Modeling the growth of *Bertholletia excelsa* Bonpl. (*B. excelsa*) trees in natural forests is important for understanding the species' ecology and for better defining site-specific management. In this sense, this study aimed to model the diameter growth rate of *B. excelsa* trees in contrasting forest environments in the Brazilian Amazon. This study was conducted in the Extractive Reserve Rio Cajari (RESEX Cajari). Growth models were fitted at species level to predict diameter growth rate in the two Amazonian forest environments. Subsequently, the age at which the *B. excelsa* tree in each forest environment reaches the minimum diameter for seed production was calculated by integrating the growth models. In each forest environment, the negative exponential behavior of the diametric growth rate of the tree species was fitted by an appropriate model. The time required for *B. excelsa* trees to reach the minimum diameter was shorter in the secondary forest environment when compared with that of the old growth terra firme forest (47 and 78 years to reach the diameter of 25 cm in the secondary and old growth terra firme forest, respectively). While the average growth pattern indicated higher diameter growth rates of *B. excelsa* in the secondary forest environment, the high level of uncertainty in the model's estimation makes this inference complex. In conclusion, the secondary forest seems a favorable forest environment for the growth of *B. excelsa* trees, which may be an indicator of the potential for secondary forest environments to produce *B. excelsa* seeds in the future.

Keywords: growth modeling; forest environments; seed production

1. Introduction

Growth studies are relevant since they can be used to reveal the current productivity of a given tree species [1]; to gain a better understanding of growth–climate relationship [2]; to better define site-specific management of timber resources [3]; for ecological and conservation insights [4]; and to understand carbon accumulation capacity [5], among others. Timber resources are abundant in the Amazon rainforest, but the lack of understanding with respect to ecological and management factors for certain tree species highlights the importance of growth studies in this biome.

The Amazon rainforest is a great source of natural resources, including valuable non-timber forest products (NTFP), such as the Brazil nut (*Bertholletia excelsa* Bonpl., *B. excelsa*). In 2014, for instance, this NTFP production resulted in a market value of USD 40.0 million [6]. *B. excelsa* nut production

relies on the extractive system, where seeds are almost exclusively collected from trees in natural forest environments in the Amazon [7]. The product is commercialized in domestic and international markets, with Bolivia, the United States of America, China, the European Union, and Peru being the greatest importers [8]. Although the largest number of *B. excelsa* trees is in the Brazilian Amazon, the tree species' occurrence is also high in other countries in South America, such as Venezuela, Colombia, Peru, Bolivia, Suriname, Guyana, and French Guiana [9].

Despite the importance of *B. excelsa* in the natural forest environment of the Amazon region, little is known about how the extractive system impacts the natural regeneration of these forest environments [10,11]. According to [12], the intense seed (nut) collection significantly compromises the natural regeneration of *B. excelsa* forests. Nevertheless, other studies have verified that the extractivism carried out in natural *B. excelsa* forests with a long history of exploitation does not affect the establishment of *B. excelsa* trees [7,13,14].

It is assumed that the effect of cutting and burning in *B. excelsa* natural forest environments, a well-known activity in extractivist communities, results in higher regeneration levels in these forests (secondary forest environments) than in old growth terra firme forest environments [13]. Naturally, the density of the natural regeneration of *B. excelsa* in these secondary forest environments is higher than in non-flooded forests (old growth terra firme forest environments) [15,16]. This fact may be related to the greater availability of light and greater involuntary seed dispersal (mainly by humans and animals) [7,17]. For instance, agoutis, a species of rodent, bury seeds in secondary forest environments due to the forests' low understory density [15]. In addition, fire also has a positive effect on Brazil nut regeneration [16,18].

In addition to their higher natural regeneration rate, seed productivity potential is also suggested to be higher in secondary forest environments [11]. This fact is due to the earlier seed production of the tree species in secondary forests than in old growth terra firme forest environments [10,16]. Hence, research to quantify *B. excelsa* tree growth in secondary forest environments can provide an opportunity to expand seed production areas and to enhance sustainable seed production.

For this purpose, it is suggested that diameter can be used as a proxy for seed production [1], in which a larger tree diameter is indicative of more resources being allocated to each tree and therefore more likely to indicate seed production [13,19]. Hence, knowledge of the diameter growth of *B. excelsa* trees in both secondary forests and old growth terra firme forests is crucial. This information can be used in growth models to predict *B. excelsa* tree growth from a natural regeneration perspective, which is key information for decision-making about management and/or conservation strategies for this tree species [1]. Of course, the growth response of *B. excelsa* and how seed production is related to that is based on several factors such as weather fluctuation, stand density and individual tree variability, for instance [7].

At present, growth models have been developed to predict tree species' growth in natural forest environments [20–22] and in commercial plantation conditions [23,24]. The study of [23], for instance, applied an individual tree growth model to simulate the dynamics of leaf area index, woody biomass and carbon fluxes in a Malaysian tropical forest. Through the use of a non-linear mixed effect model, [24] developed diameter growth models for natural black spruce and jack pine forests in Canada. Climate–diameter growth relationships of two species in boreal forests were addressed by [25], while [26] studied the radial growth response of black spruce stands. Finally, it is also possible to highlight the study of [27], who reported a modeling approach to simulate management regimes in native *Araucaria* forests.

Long-term datasets are commonly unavailable for tropical forest environments [28] and growth models with biologically sound properties [29] are required in order to properly predict and understand *B. excelsa* tree growth in the Brazilian Amazon. [1] developed a method to estimate diameter growth for tree species in the Brazilian Atlantic Forest that helps to bridge the scarcity of species-specific growth information. The method consists of the use of an exponential growth model formulated to indicate the time required for a unique tree species to reach a given diameter. The method presented by [1]

allows for the identification of tree species with higher growth potential for timber production and the recovery of degraded areas. Hence, considering the lack of results with respect to the growth of Amazonian tree species, studies on the diameter growth trajectory of *B. excelsa* trees in secondary forest and old growth terra firme forest are important for revealing the current productivity of this tree species.

Thus, this study aimed to: (1) model the diameter growth rate of *B. excelsa* trees in two forest environments (secondary forest and old growth terra firme forest) in the Brazilian Amazon; (2) verify the diameter growth of *B. excelsa* trees over time in these two forest environments; and (3) determine if the secondary forest is indeed a favorable environment for increasing *B. excelsa* growth with respect to time. The study's hypothesis is that the productivity of *B. excelsa* trees is higher in secondary forests than in old growth terra firme forests, which favors the management of secondary forest environments for seed production.

2. Materials and Methods

2.1. Characterization of the Study Area

The state of Amapá covers an area of 142,828 km², which corresponds to 3.9% of the North Region of Brazil, and 1.65% of Brazil as a whole. Approximately 73% of the Amapá state area is under federal protection, with 19 conservation units classified as part of the Brazilian System of Nature Conservation Units [30].

The area being studied is located in the Rio Cajari Extractive Reserve (RESEX Cajari) in the southern-most part of the Amapá state, comprising an area of 5017.7 km². RESEX Cajari is classified as part of the Brazilian System of Nature Conservation Units and is also classified as an area used by traditional extractivist communities; the activities of these communities include agriculture and small animal husbandry.

RESEX Cajari's climate is at the transition point between tropical savanna climate (Aw) and tropical monsoon climate (Am), according to the Köppen classification system [31]. The region presents a mean annual temperature of 25 °C and the annual rainfall is 2300 mm, with a dry season (rainfall < 100 mm per month) from September to November [32]. According to the Brazilian Soil Classification System, RESEX Cajari mostly presents Oxisols [33], and its elevation is approximately 150 m above sea level.

2.2. Database and Sampling

The study area is located in a high-density region of *B. excelsa* trees that is subject to intense seed collection [16]. A total of 48 sample plots were installed in the old growth terra firme forests, in which they were randomly located across 6 stands (Figure 1). A second forest environment, popularly known as "capoeiras" (secondary forests), was also sampled in RESEX Cajari. The sites are in agroextractivist communities (Figure 1). For the secondary forests, a total of 9 stands were sampled, with areas ranging from 0.5 to 2 ha.

The inventory in the two forest environments included all *B. excelsa* trees with a height greater than 1.5 m (to facilitate species recognition) and diameter at 1.30 m aboveground (DBH) \geq 2.5 cm. Individual trees were georeferenced using a Global Positioning System (GPS). The first inventory was conducted in 2011, with remeasurement of the surviving trees conducted in 2013.

Descriptive statistics of *B. excelsa* trees are displayed in Table 1, in which it is possible to verify the high dataset variation. It is also possible to verify that trees in the secondary forest grow faster on average than in the old growth terra firme forest environment.

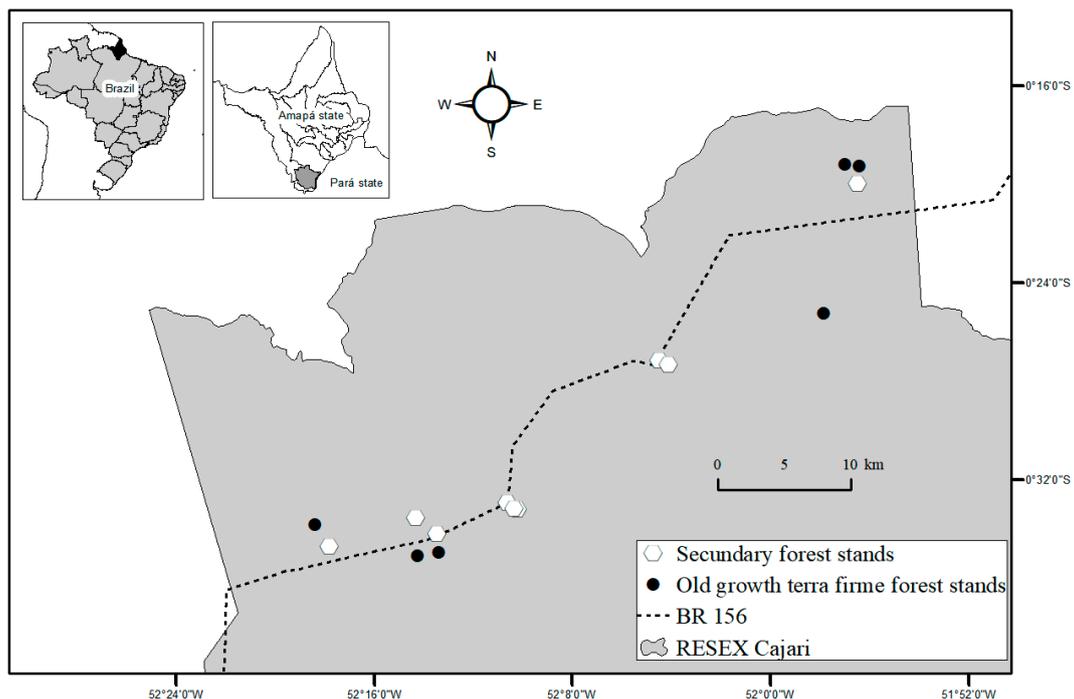


Figure 1. RESEX Cajari in southern Amapá, Brazil.

Table 1. Mean DBH growth rate ($\ln(\text{cm})\cdot\text{year}^{-1}$); coefficient of variation of the diametric growth rate (CV—%); average trees per hectare (TPH/ha), and mean density of *Bertholletia excelsa* Bonpl. trees (DR—TPH/ha) for the different forest environments.

Forest Environment	Mean DBH	CV (%)	TPH	DR
Old growth terra firme	0.069	94.3	1300	25
Secondary forest	0.107	76.3	1105	34

2.3. DBH Growth Rate Modeling

2.3.1. Growth Model

The methodology proposed by [1] was applied to estimate the age at which the *B. excelsa* tree in each forest environment (old growth terra firme forest and secondary forest) can reach the minimum diameter for seed production. This method allows us to infer the diametric growth rate pattern at species level. The great advantage of this method is the possibility of inferring diametric growth from short-term data collection.

Firstly, the method calculates the diameter growth rate (g). This growth rate is calculated by the natural logarithmic ratio between the diameter in the second measurement (DBH_2) and the first measurement (DBH_1), and this ratio is divided by the time period (t) between the measurements:

$$g = \left[\frac{\ln\left(\frac{DBH_2}{DBH_1}\right)}{t} \right] \quad (1)$$

where g is the growth rate; DBH_1 is the diameter measured in the first inventory (cm); DBH_2 is the diameter remeasured in the second inventory; t is the time period between the inventories (years); \ln is the natural logarithm.

After calculating g for all the trees, a regression was fitted for each forest environment in order to estimate the diameter growth rate of *B. excelsa* trees. The negative exponential model was selected

since this model is well suited to represent the diameter growth rate behavior of a typical natural tropical forest (inverted J) [1].

$$g = a e^{bDBH_1 + \varepsilon} \quad (2)$$

where a and b are the parameters to be estimated; ε is the random error associated with the model.

We assessed the precision of the mean estimates generated by the growth models through the mean bias (B) and graphical analyses using R software [34].

$$B = \frac{1}{n} \sum_{i=1}^n (Obs - Pred) \quad (3)$$

where $Pred$ is the predicted values; Obs is the observed values; n is the number of observations.

2.3.2. Diameter Growth over Time

The trajectory of the diameter over time (t) for each forest environment is obtained by Equations (4) and (5). These trajectories provide estimates of the mean time required for the tree species to reach a certain DBH value from a predetermined minimum DBH [1]. For this study, the minimum pre-determined DBH was 2.5 cm, which was the minimum DBH measured in the forest inventories.

$$t = \frac{1}{\hat{a}} \left(\ln(DBH) + \left(\frac{-\hat{b} \times DBH}{1} \right) + \left(\frac{(-\hat{b} \times DBH)^2}{4} \right) + \left(\frac{(-\hat{b} \times DBH)^3}{18} \right) - m \right) \quad (4)$$

$$m = \left(\ln(DBH_{\min}) + \left(\frac{-\hat{b} \times DBH_{\min}}{1} \right) + \left(\frac{(-\hat{b} \times DBH_{\min})^2}{4} \right) + \left(\frac{(-\hat{b} \times DBH_{\min})^3}{18} \right) \right) \quad (5)$$

where t is the time (age in years) after the minimum diameter; m is the constant that zeroes the growth at $t = 0$ to reach the minimum diameter (DBH_{\min}); DBH_{\min} represents the minimum diameter of tree n ; DBH represents the projected diameter; \hat{a} and \hat{b} are the estimated parameters from Equation (2).

2.3.3. Uncertainty Analysis

We acknowledge that an average output from a fitted growth model may impact decision making. Especially in this study, the high variation of *B. excelsa* diameter growth rates within this dataset must be taken into account when reaching any conclusion. For that purpose, we decided to assess the uncertainty effect on the predictions by applying a nonparametric bootstrapping approach (using R software [34]), such as suggested by [35].

Hence, the original dataset in each forest environment was sampled through nonparametric bootstrapping with replacement generating 10,000 unique datasets. Each dataset was used then to fit Equation (2). Hence, the estimated parameters of the 10,000 fitted growth models for each forest environment were applied in Equations (4) and (5) to generate confidence intervals around the mean time required for the tree species to reach a certain DBH value. This strategy was used to deal with all uncertainty around the mean DBH growth rate in each forest environment and serves as a statistical test to validate if the secondary forest is indeed a favorable environment for seed production with respect to time.

3. Results

3.1. Fitted Growth Rate Model of *B. excelsa* Trees in the Different Forest Environments

The fitted growth equations displayed significant coefficients (at $\alpha = 0.05$) (Table 2) and estimates with low degree of bias (secondary forest = -0.001 (ln(cm)·year⁻¹) and old growth terra

firme forest = $-0.002 (\ln(\text{cm})\cdot\text{year}^{-1})$). The fitted equations imply that DBH growth rate decreases over time for larger trees as expected.

Table 2. Fitted parameters of the exponential model for each forest environment (secondary forest and old growth terra firme forest) for *Bertholletia excelsa* Bonpl. trees in RESEX Cajari, southern Amapá.

Species	<i>a</i>	<i>b</i>
Old growth terra firme forest	0.1280 *	-0.0955 *
Secondary forest	0.1674 *	-0.1057 *

* Significant at 5%.

It is worth mentioning that the DBH growth rate variation of each forest environment is high (Table 1). However, the fitted growth equations were still able to properly capture the mean tree species growth pattern in each forest environment (Figure 2). Figure 2 reinforces this behavior since the average DBH growth rate in each forest environment was modeled successfully.

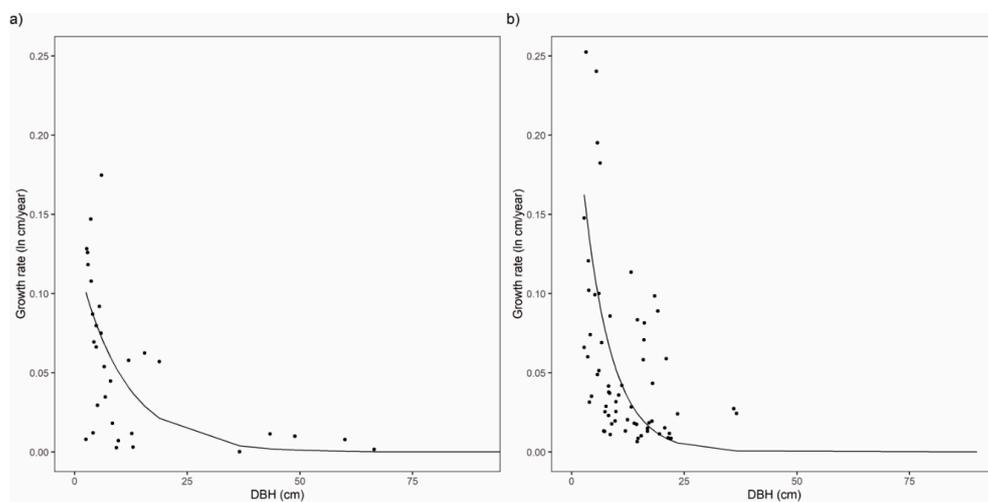


Figure 2. Mean diameter growth rate curve fitted for *Bertholletia excelsa* Bonpl. trees: old growth terra firme forest (a), and secondary forest (b).

3.2. Growth Time in the Different Forest Environments

B. excelsa trees, on average, reach certain diameters sooner in the secondary forest than in the old growth terra firme forest environment. For the secondary forest, *B. excelsa* trees are estimated to reach a diameter of 25 cm at approximately 47 years. For the old growth terra firme forest, the estimate for the same diameter is 78 years (Table 3).

Table 3. Mean and 95% confidence intervals of the age required for the *Bertholletia excelsa* Bonpl. tree species to grow from 2.5 cm to 25 and 38 cm in each forest environment.

Forest Environment	DBH of 25 cm			DBH of 38 cm		
	2.50%	Mean Age	97.50%	2.50%	Mean Age	97.50%
Old growth terra firme forest	47	78	131	76	174	350
Secondary forest	36	47	63	60	88	142

The secondary forest reaches a DBH of 25 cm faster on average when compared to the old growth terra firme forest. The main reason for this is the lower stand density in the secondary forest (Table 1), which naturally favors tree growth due to the decrease in tree competition in this forest environment.

When we account for the uncertainty involved in the DBH growth rate estimation, however, it is possible to verify an overlap between the confidence intervals generated for the time required for *B. excelsa* trees

to reach certain diameters (DBH of 25 cm, for instance—Table 3). The large variability results in a non-statistical difference occurring with respect to the DBH yield over time for this tree species in the different forest environments (as noticed in Figure 3).

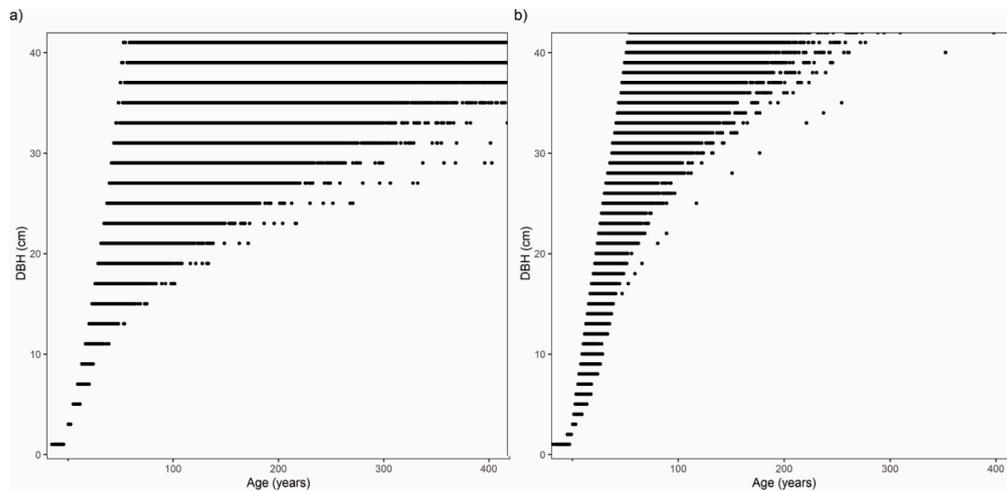


Figure 3. Simulation of diametric yield of *Bertholletia excelsa* Bonpl. trees in the different forest environments over time: old growth terra firme forest (a) and secondary forest (b).

4. Discussion

4.1. Growth Rate of *B. excelsa* Trees in the Old Growth Terra Firme and Secondary Forests

This study involved the development of models to express *B. excelsa* tree growth in the Brazilian Amazon rainforest. To our knowledge, this is the first effort to model the growth of this key tree species in the Amazon rainforest. The biologically sound properties of these growth models ensure that data can be reliably extrapolated from them. The findings of [21] indicated similar productivity for *B. excelsa* trees in the old growth terra firme forest to the results shown in this study, which also reinforces the validity of our findings.

While there are several growth studies addressing a variety of questions in natural forests [2,3,36–38], studies focused on understanding *B. excelsa* tree growth are scarce. A set of stand-level growth equations were already developed by [36] in the Tapajós region for secondary forests. Meanwhile, [2] studied the growth–climate relationship in Canadian forests and [3] applied growth models to better define site-specific management for *Calophyllum brasiliense* in several Brazilian biomes (Amazon, Atlantic forest, Savannah and Pantanal).

The attractiveness of the growth modeling approach used in the study was discussed by [1], since it can be reliably used to predict *B. excelsa* tree growth where long-term data collection is still unavailable. Hence, this study represents an important step towards the better understanding of the ecological behavior of the *B. excelsa* tree species. This fact reveals how critical it is to have appropriate growth models to better manage and plan decisions in *B. excelsa* stands.

4.2. Assessing the Uncertainty Effect on the Growth Equations

The productivity of *B. excelsa* trees in the secondary forest environment is higher, on average, than in the old growth terra firme forest [10]. The high uncertainty in the model estimation, however, implies a non-statistical difference with respect to the DBH yield over time for this tree species in the different forest environments.

Understanding the uncertainty around the mean response generated from a growth model is key for decision making. Indeed, uncertainty analysis demonstrated that while the set of growth equations developed by [39] was able to well estimate the mean productivity of eucalypt stands in the southern

United States, the large variability around those mean estimates implied that the growth equations should be used with caution for future inferences.

The studies of [9,10] reported an assumption that while seed production begins at 25 cm in DBH in the secondary forests, this seed production begins only at 38 cm in DBH in the old growth terra firme forests. When this assumption is made, it is possible to verify a statistical difference with respect to the DBH growth over time for this tree species in the different forest environments (as noted in Table 3). This allows us to imply that managed forests have a shorter time to seed production at this point.

4.3. Management Perspectives and Future Research

The productivity of *B. excelsa* trees in the secondary forests suggests the important role of traditional communities in the maintenance of *B. excelsa* populations [10,17,40,41]. In addition, it is worth highlighting how secondary forest environments help the economic development of traditional communities.

Secondary forests are easier to manage than the old growth terra firme forests, since their structures are simpler [42]. Another indication of the potential of the secondary forests is the abundance of the natural regeneration of the *B. excelsa*, which is superior in these forests when compared to other environments [10].

Finally, it is worth mentioning that the data are limited to short-term records, which could potentially be reflected in the inference properties of the growth model. The database used in this study limits the accuracy of the estimation of diameter growth rates, which could be dramatically increased by future field data collections. We recommend future exploration of the growth response as a function not only of DBH, but also of extra covariates that influence tree growth over time, such as weather fluctuation, stand density and individual tree variability [43]. In conclusion, it is clear how gathering larger datasets is important in order to offer management and conservationists guidance for the Amazon region, especially to optimize *B. excelsa* tree diameter growth in the secondary forest environment [44].

5. Conclusions

We successfully developed growth models to contrast *B. excelsa* tree diameter growth in two different forest environments in the Brazilian Amazon. The models produce biologically sound outputs that enable the better understanding of *B. excelsa* tree growth in old growth terra firme and secondary forests.

The conservation and management of secondary forests can indeed be considered as an essential component of, and of great potential for the perpetuation of the sustainable extractivism of *B. excelsa* stands in the Amazon region.

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