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Commercial Logging of Timber Species Enhances Amazon (Brazil) Nut Populations: Insights from Bolivian Managed Forests

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Abstract: A typical case of multiple-use forest management (MFM) in Southwestern Amazon is the commercial harvesting of Amazon or Brazil nut (*Bertholletia excelsa*) seeds and of timber of other tree species. Although the Amazon nut is the most important non-timber forest product (NTFP) in the Amazon basin, the species is under serious threat due to deforestation and may also be affected by overharvesting. However, selective logging of other tree species coexisting with *Bertholletia* may positively affect *Bertholletia* populations, thus enabling a special case for MFM. For this research, we investigated the impact of the intensity of Amazon nut harvesting and timber logging on *Bertholletia* populations in the Bolivian Amazon. We used demographic data from 72 two-hectare transects located within 24 community-based household forests varying in the intensity of nut collection (0–100%) and timber logging (0–15% of logging-disturbed forest area). Simulated *Bertholletia* population size increased with logging intensity but decreased with Amazon nut harvesting intensity. *Bertholletia* populations were projected to grow at the average MFM harvesting scenario tested: 57.4% of nut harvesting, 5.3% of logging-disturbed area ($\lambda 100 = 1.011$). Our simulations also revealed that up to 89% of Amazon nut seeds can be harvested while sustaining *Bertholletia* populations, under 15% of logging-disturbed area, and applying liana cutting. Modest levels of timber logging and application of liana cutting may compensate for the negative effect of Amazon nut collection on *Bertholletia* populations for the next century. Our study demonstrates that Amazon nut and timber production could be combined in a sustainable MFM scheme, thus increasing the economic value of managed tropical forests and its promotion to reduce the increasing pressure by deforestation.

Keywords: Bolivian Amazon; multiple-use forest management; harvesting intensity; logging intensity; growth rate; survival rate; fecundity rate; liana cutting; population matrix model

1. Introduction

Multiple-use forest management (MFM) entails the provision of multiple goods and services within a forest management unit area [1,2]. As such, it has the potential to ensure the conservation of tropical forests in the face of increasing demand for food, changing land access rights, and trends in markets [2–4]. Harvesting of Amazon nut (*Bertholletia excelsa*, Lecythidaceae) seeds (considered a superfood) and timber of other tree species is a common market-oriented multiple use practice among rural communities in a significant part of the Bolivian, Peruvian, and Brazilian Amazon. Depending on the location, Amazon nut harvesting contributes to household income in the range of 12–71% [5]. Bolivia's export of Amazon nuts represents 25% of global exports and a third of it ends in EU markets [6].

However, price instability and coexistence of the Amazon nut with hardwood species are increasingly turning pressure on timber as well. The most recent study in the Bolivian Amazon found that commercial logging in managed and unmanaged forests together contribute 9% to peasant community household income [7]. The combined harvesting of both Amazon nuts and timber from other tree species may have synergic effects given that the majority of these species require higher light levels at early stages of their lifecycle, like the ones created by logging disturbance [8–12], and also because their harvesting seasons are complementary to each other [13,14]. However, MFM encompasses many (yet) unknown ecological feedbacks produced by the harvesting of timber and non-timber species that need to be understood to guarantee the future availability of the products and the income of rural families. The harvesting of multiple forest products can turn conflicting at times. This may happen when the harvesting of a multipurpose plant species requires killing the plant to extract one of its products or when the harvesting of a product disrupts the habitat of other provisioning species. In this research, we investigated the combined impact of Amazon nut seeds harvesting and logging of commercial timber species on Amazon nut demographic rates with the aim of understanding the nature of these ecological feedbacks around Amazon nut production.

The harvesting of forest products from timber and non-timber species alters reproduction and regeneration of plant species [15]. The extent of this effect depends on the harvesting intensity applied, harvesting method used, and size of harvested trees [16–18]. For instance, logging intensity favors seedling establishment and growth of light-demanding species by increasing light availability in the understory [19] but can also contribute to the local extinction of low-density occurring species when the species is intensively logged [17,20]. Although the harvesting of non-timber forest products has been commonly considered beneficial or neutral for forest communities, some studies have shown that NTFP harvesting may negatively affect the plant's survival, growth, or fecundity rate [21] due to the extraction of vital parts of the plant (e.g., fruits). However, liana cutting, i.e., a common management practice carried out by nut collectors, enhances Amazon nut fruit production [22] and may potentially improve *Bertholletia*'s population stability over the long run by increasing growth rates [23]. Population stability is determined by lambda (λ), which is the population growth rate once the population has reached stable size distribution [24].

A considerable amount of research has focused on studying the impact of harvesting on timber and NTFP species separately, but only few have assessed the effect of harvesting multiple products from the same species [25,26] or from more species [11,14,27,28] within an MFM scheme. However, most of these studies focus on a specific life stage (e.g., seedlings) or on a specific part (e.g., fruits) of a plant. The increasing rate of Amazon nut harvesting and logging occurring in the Bolivian Amazon as well as in the Brazilian and Peruvian Amazon regions calls for studying *Bertholletia*´s long-term population sustainability under an MFM scheme. We investigated this by asking two questions. First, we asked what the effects of Amazon nut harvesting and logging intensities on *Bertholletia* survival, growth, and fecundity rates are. We expected that logging intensity would increase *Bertholletia* growth and recruitment rates due to increased light availability [11,12,29] created by logging [11]. Additionally, we expected that logging intensity would decrease the survival rate of small *Bertholletia* individuals due to increased agouti predation of 1-year old recruits [30] and of large individuals due to increased susceptibility to wind caused by the logging of neighboring timber trees. Furthermore, we expected no effect of logging intensity on *Bertholletia* reproduction rate due to low logging intensity rates inherent to the region [14,31]. Finally, we expected that Amazon nut harvesting intensity would not have an effect on growth or survival rates because the harvesting of nuts does not imply as much habitat disturbance as logging. With regard to *Bertholletia* fecundity, *Bertholletia* reproduction rates would increase mainly due to the cutting of lianas applied by collectors during Amazon nut harvesting [7,32]. Second, we asked under which Amazon nut harvesting, logging, and liana cutting intensities could *Bertholletia* populations be sustained in the

future. We expected that the combined Amazon nut harvesting and logging of other timber species would contribute more to the increase in *Bertholletia* population growth rate ($\lambda 100$) than the harvesting of only Amazon nuts as well as that liana cutting would contribute to *Bertholletia* transient population growth rate by increasing fruit production.

2. Materials and Methods

2.1. Study Site

This study was carried out in the Department of Pando and the Vaca Díez Province in the Beni Department of the Bolivian Amazon region. Approximately 95% of the region is covered by the forest [33] comprising 30% of Bolivia's timber production forests, 8.8 out of 28.8 million ha [34]. Tree diversity ranges from 52 to 122 species ha^{-1} with the density between 544 and 627 trees ha^{-1} of trees $\geq$ 10 cm in diameter at 1.3 m above ground (DBH) [35]. Annual rainfall varies between 1774 and 1934 mm while the mean annual temperature differs slightly between the two main regional cities: Cobija (25.4 °C) and Riberalta (26.2 °C) [36]. The region presents a relatively dry season from May through September with < 60 mm of monthly rainfall. Its topography varies from upland "terra firme" to seasonally flooded forests. Terra firme forests grow on soils with low fertility (i.e., high aluminum toxicity), while seasonally flooded areas have relatively high nutrient-rich soils due to the sediments carried by rivers originating in the Andes [36].

The region has a long history of NTFP exploitation and a more recent history of timber exploitation [37]. Amazon nut is the most recent NTFP under exploitation and is the keystone of the regional economy, whereas timber is increasing in importance so that already 77% (189 communities out of 245) [38] of "campesino" communities are engaged in timber management (Bolivia's Forests and Lands Controlling Authority (ABT), unpublished data). For this study, we selected six campesino communities with relatively long-standing engagement in timber management under a community forest management plan (CFMP); see Appendix A for detailed information about the legal framework to log timber and harvest Amazon nuts in campesino communities. The harvesting of forest products at the household forest-level allowed us to account for household forest as our main sampling unit. Thus, we selected 24 household forests that represented a wide range of Amazon nut harvesting and timber logging intensities occurring in the region. Among the 24 household forests, we made sure to select an unlogged (control) household forest in each community.

2.2. Species Description

Bertholletia excelsa is a long-lived pioneer tree species that grows in the Amazonian upland forest. As a light-demanding species, *Bertholletia* needs disturbance for its germination and growth [12]. *Bertholletia* regeneration density (individuals $\leq$ 10 cm in DBH per hectare) ranges from 3–5 individuals in undisturbed forests [39,40], 5.8–7.6 individuals in logged forests [11] to 17–27 individuals in abandoned fallows [29,41]. The agouti (*Dasyprocta* spp.), a rodent that scatters and buries *Bertholletia* seeds as a food reserve, is the main seed disperser [12]. Agouties disperse seeds within 15–30 m from the parent tree, reaching the maximum of 60 m [42]. Occasionally, agouties forget buried seeds, which increases the chances of these seeds to germinate [12,42]. Seeds germinate within 1.5 years [12]. *Bertholletia* survival is high compared to most tropical tree species, and increases with tree size [12]. It can take > 100 years for *Bertholletia* individuals to reach the reproductive stage [40], whereas its reproductive stage can last over 150 years [12,43]. Its clustered distribution is attributed to past human manipulation [41,44,45].

2.3. Community Involvement in Data Collection (Participatory Research)

This research was supported by the six communities in which household forests were selected. Thus, community members´ involvement in data collection was imperative not only due to the selection of our research location, but also due to the amount of effort our research design required. At each field season, the principal investigator and two

research assistants (a biologist, a forester, and a Master's student) coordinated with the head of each community to present the research objectives at a community meeting. In most cases, the participating community members were selected at these meetings, while in other communities, the principal investigator could ask for support during visits to community households. By the end of the data collection period, over 120 community members got involved in data collection through an intensive knowledge exchange session prior to starting data collection in each community. Once the team proved sufficiently knowledgeable in the research tasks, they separated into smaller teams led by research assistants and the principal investigator to establish transects and collect data from a select number of tree species within these transects. The participatory framework of this research allowed for the last visit to share results with the six communities in which this research took place.

2.4. Study Design

In 2014, 72 transects were placed at the selected 24 household forests (three transects per household forest). Each transect was 500 m × 40 m (2 ha), totaling 144 ha of sampled area. Transects were established at random to account for the variability of *Bertholletia* populations across the Bolivian Amazon region. The distance between transects varied between 500 and 1000 m so as to comply with sampling independence within a household forest. Amazon nuts were harvested from all the selected household forests on a yearly basis, but only three household forests were solely harvested for Amazon nut seeds. Twenty-one household forests also underwent timber logging at least once over the last 10 years prior to data collection: eighteen were logged once under the legal framework of the 1996 Forestry Law and 12 were logged once during the two years of data collection under the small-scale timber logging operation modality (ABT Directive No. 001/2014). We did not account for the impact of small-scale timber logging operations in our analyses because their incidence within the research transects was minimal (only disturbed 0.06% of the total sampled area).

2.5. Collection of Demographic Data

At the moment of plot establishment, all the *Bertholletia* individuals ≥10 cm in DBH were inventoried, mapped, and tagged within the entire transect area; individuals ≤10 cm in DBH were sampled from within a quarter of the transect area (the inner 10 × 500 m). The height of the individuals ≤2.5 m was measured with a meter tape and height of the larger individuals was estimated following the eye-calibrated estimation practice with a laser range finder (Nikon Forestry Pro) at the start of each data collection day. DBH of the individuals ≥1.5 m in height was measured with a diameter tape and DBH of the individuals ≤5 cm was measured with a caliper. Categories of crown position, crown form [46], and degree of liana infestation were estimated for all trees. The reproductive status and evidence of liana cutting of trees ≥30 cm in DBH were also recorded. The description of the variables measured can be found in Table S1 in the Supplementary Information. All the individuals were remeasured in 2015, and new individuals were included. DBH of the trees measured at a different measurement height than the standard 1.3 m above ground were corrected following the equation of Metcalf et al. [47], the most reliable tapering approximation for tropical trees [48], further explained by Soriano et al. [7].

2.6. Evaluation of Amazon Nut Production and Harvesting Intensity

At the end of the 2013–2014 and 2014–2015 harvesting seasons, we counted all fallen Amazon nut fruits within the radius of 30 m around the trunk of each producing tree (trees > 30 cm in DBH, the size at which trees started to produce fruits at our study sites) encountered within the transects. Fallen fruits were classified in one of three categories: harvested by people (i.e., machete-opened fruits commonly found gathered near each tree), opened by *Dasyprocta* spp., or unharvested/unopened (i.e., fruits not found by collectors or seed dispersers). Harvested fruits and unopened fruits gathered next to a producing tree

(clearly intended for harvesting, too) were put together to calculate the percentage of fruits harvested per reproductive tree and per transect. The number of fruits left unharvested in the forest (unopened and agouti-opened fruits) was also used to investigate their role in the number of new recruits. We did not account for the fruits removed by agouties beyond the tree crown (6.3%) in our calculations [42] because this percentage can be lower in the Bolivian Amazon due to the fact that harvesters make frequent visits to the forest to harvest seeds, thus leaving fewer fruits for agouti dispersal. As the counting was performed at the end of the harvesting season (from the second half of February through July), we assumed that the percentage of uncounted fruits was very small. Thus, the average number of fruits produced and the percentage of harvested fruits over the two-year period were used as proxies for Amazon nut production and harvesting intensity, respectively.

2.7. Estimation of Timber Logging Intensity

We evaluated logging disturbance by measuring the areas of logging gaps, log landings, access roads, and skid trails occurring within the transects. Following the protocol of Contreras et al. [49], the area disturbed in logging gaps and log landings was estimated as described by Soriano et al. [11]. To calculate the area disturbed by access roads and skid trails, we measured the total length of those found inside the transects and measured their width at three randomly chosen points. The area disturbed was then calculated as the product of the length and the average width. The sum of all disturbed areas in each 2-hectare transect was extrapolated to calculate the percentage of disturbed area per transect. We also obtained other logging intensity measures such as the number of harvested trees and harvested volume per hectare and found that disturbed area is strongly correlated with both the number of logged trees (r = 0.70) and the harvested volume (r = 0.63). Percentage of disturbed area was preferred over the other two logging intensity measures because percentage of disturbed area can be a better indicator of light availability to which survival, growth, and recruitment respond more directly.

2.8. Modeling Effects of Tree Conditions, Harvesting Intensity, and Management on Bertholletia Vital Rates

We used backward regression analysis to determine effects of the variables related to tree size (e.g., diameter), tree condition (e.g., crown position), site-specific harvesting intensity (nut and timber), and management (liana cutting) on survival, growth, and fecundity (see Table S1). Categorical variables (e.g., crown position) were included as dummy variables.

Given that the effect of our selected explanatory variables on growth and survival rates may differ throughout a plant's lifecycle, we ran separate regression models for three broad size categories: ≤1 cm in DBH (seedlings), 1–50 cm in DBH (juveniles), and >50 cm in DBH (adults) (see Table S2). Survival probability was predicted using a logistic regression model, using the glm function in R [50]. However, juveniles and adults were combined to model survival rates because the initial size appeared to be the only predictor of survival. Three separate multiple linear regression models were ran to estimate *Bertholletia* growth rate because logging disturbance might be more important for the growth of seedlings [11] and juveniles [51] than for adults, whereas liana cutting might be more important for the growth of adults [23,52]. We included time since logging among the predictors of seedling growth in spite of its low significance level (*p* < 0.1) because logging intensity has a significant effect on seedling growth rate in the few years following logging [9,10]. All the analyses described here were performed in R [50].

Fecundity was calculated based on the probability of *Bertholletia* trees > 30 cm in DBH being reproductive, fruit production, and new recruits per unharvested fruits. The effect of size, size-squared, individual characteristics, and harvesting intensity on the probability of *Bertholletia* being reproductive was predicted using a logistic regression model under the glm function in R [50]. We assumed negative binomial distribution to predict *Bertholletia* fruit production due to the high variability found on fruit production among reproductive trees. For this, we used the glm.nb function developed under the MASS package [53] in

R [50]. We used the lrm function developed under the rms package [54] in R [50] to obtain the pseudo r^2 for our nonlinear models of survival, reproduction probability, and fruit production because these were not provided in the models' output.

2.9. Matrix Construction

We classified *Bertholletia* individuals in 26 size classes (see Table S2) to build two 26×26 size-structured matrices, one matrix (Table S3) to account for the effects of logging disturbance on the growth rate of seedlings during the first 4 years following logging and another matrix (Table S4) to exclude this effect over the remaining 16 years of a 20-year timber cutting cycle, i.e., the minimum timber cutting cycle legally allowed in Bolivia [52]. Such differentiation was not needed to incorporate the effect of Amazon nut harvesting intensity on any of *Bertholletia* vital rates because Amazon nuts are harvested on the yearly basis, which is equivalent to the transition period of the matrix elements. We also incorporated the effect of one-time application of liana cutting intensity into each matrix. Regression models for vital rates were used to calculate the matrix elements: progression, stasis, and fecundity. Progression elements (G) represent the probability of an individual to grow from one size class (G_i) to the next: $G_i = C_i \times r_i$, where C_i is the probability that a surviving individual in size class i grows to the next class ($i + 1$) and r_i is the annual survival probability in class i. $C_i = g_i/c_i$, where g_i is the height or DBH growth rate for class i, and c_i is the class width. Stasis elements (P) represent the probability that a surviving individual stays in the same size class: $P_i = r_i - G_i$. Fecundity elements (F) represent the production of new recruits per individual in a reproductive class: $F_i = r_i \times f_i$, where f_i is expressed as the new recruits produced by an individual in class i; $f_i = j_i \times k_i \times l_i$, where j_i is the probability of an individual in class i being reproductive, k_i is the number of unharvested fruits from an individual in class i, and l_i is the average number of observed new recruits per unharvested fruit; $k_i = ((P_{ki} \times m_i)/100) \times ((100 - h_i)/100))$, where P_{ki} is the observed percentage of unharvested fruits in class i, m_i is the number of fruits obtained from the regression analysis (Table 1) in class i, and h_i is the percentage of harvested fruits (harvesting intensity). We could determine the overall effect of Amazon nut harvesting intensity on the fruit production rate by incorporating the effect of harvesting intensity on the percentage of fruits left unharvested in the forest in the function of tree size. We then built transition matrices as the function of the effects of intensity of nut harvesting, logging, and liana cutting of reproductive Amazon nut trees on *Bertholletia* vital rates, around which we calculated population growth rate and simulated the population structure at different harvesting levels and liana cutting.

The first matrix was multiplied four times to account for the initial effect of logging on seedling growth rate (Table 1). Then, the resulting matrix was multiplied by the matrix not accounting for the effect of logging until completing the 20-year rotation cycle. Based on this final matrix, we simulated the population growth rate and population structure after 100 years upon accounting for the initial population structure after each rotation cycle. Thus, we used a 20-year periodic matrix model [24] for which we calculated elasticities for the average Amazon nut harvesting, logging, and liana cutting intensity following Zuidema and Boot's [12] procedure.

We simulated the following management scenarios: the average observed combination of Amazon nut harvesting (57.4%) and timber logging intensities (5.3%) and all possible combinations of three Amazon nut harvesting intensities (0, 75, 100%) and three timber logging intensities (0, 10, 15%). The simulated harvesting intensities were limited by the observed ranges at our sampled household forests. *Bertholletia* population growth rate values were obtained for each combination of harvesting intensity under 21% (observed average percentage of trees with lianas cut) and 90% (hypothetical assumption) of reproductive trees with lianas cut. In addition, for each liana cutting intensity tested, we searched harvesting intensity thresholds at which *Bertholletia* populations were stable by increasing and decreasing the percentages of timber and Amazon nut harvesting intensities by one factor.

Table 1. Models and corresponding significant predictors of *Bertholletia excelsa* vital rates. These regressions results were used to calculate the matrix elements. Significance levels are marked with asterisks: * *p*-value < 0.05, ** *p*-value < 0.01, *** *p*-value < 0.001. DBH = diameter at 1.3 m above ground.

Response	Size Class	R-squared	Significant Predictors	Estimate	*p*-Value
Survival	<1 cm in DBH	0.11	Intercept	0.617	0.145
			Initial height (m)	1.921	0.018 *
	>1 cm in DBH	0.40	Intercept	13.687	0.021 *
			Initial DBH (cm)	−0.056	0.074
Growth	<1 cm in DBH	0.08	Intercept	0.054	0.046 *
			Percentage of area disturbed due to logging	0.011	0.003 **
			Years since last logging	−0.008	0.064
	1–50 cm in DBH	0.2	Intercept	0.282	<0.001 ***
			Initial DBH (cm)	0.022	<0.001 ***
	>50 cm in DBH	0.15	Intercept	0.466	0.247
			Initial DBH (cm)	−0.007	0.002 **
			Full light	0.601	0.013 *
			Vertical light	0.313	0.279
			Perfect crown	0.614	0.039 *
			Good crown	0.302	0.297
			Fairly good crown	0.293	0.353
Probability of being reproductive	>30 cm in DBH	0.30	Intercept	−9.43	<0.001 ***
			Initial DBH (cm)	0.222	<0.001 **
Fruit production	>30 cm in DBH	0.55	Intercept	1.367	0.004 **
			Initial DBH (cm)	0.012	<0.001 ***
			Amazon nut harvesting intensity (% of harvested fruits)	0.033	<0.001 ***
			Liana cutting	0.497	0.037 *

3. Results

3.1. Effects of Amazon Nut Harvesting and Logging on Bertholletia Vital Rates

We found that the effect of Amazon nut harvesting, logging, and liana cutting intensities on *Bertholletia* vital rates varied with *Bertholletia* size, especially when it came to growth and reproduction (Table 1). Regarding survival, seedling survival probability ranged from 75 to 87% and was the only factor and positively affected by initial size ($r^2 = 0.11$, $p = 0.018$). The initial size also explained 40% of juvenile and adult survival ($p = 0.074$). We kept the initial size in the model even at the probability of <0.1 because it was the single most important predictor.

Logging increased *Bertholletia* seedling growth during only the first four years following logging. On average, the growth rate of seedlings increased with logging intensity ($p = 0.003$) but decreased with time since logging ($p = 0.064$). These two variables together explained little of the variation in the growth rate ($r^2 = 0.08$). On average, *Bertholletia* seedlings grew 1.7 cm year^{-1} more in height during the first four years after logging than during the subsequent 16 years of the timber cutting cycle (3.8 and 2.1 cm year^{-1}, respectively). The Initial DBH increased the juvenile growth rate ($r^2 = 0.20$, $p < 0.001$) but decreased the adult growth rate ($p = 0.002$). However, crown shape ($p = 0.039$, perfect crown) and crown position ($p = 0.013$, full light) counteracted the negative effect of the initial DBH. All the variables together explained 15% of the variation in adult DBH growth ($r^2 = 0.15$). The DBH growth rate peaked in the individuals between 40 and 50 cm in DBH (1.3 cm year^{-1}). They grew 1 cm more than the individuals >170 cm in DBH (0.23 cm year^{-1}; Table S5).

The initial DBH was also the only main predictor of the probability of the individuals >30 cm in DBH being reproductive ($r^2 = 0.30$, $p < 0.001$). The trees between 30 and 40 cm in DBH had 16% probability of being reproductive, whereas the trees > 60 cm in DBH had an over 99% chance of being reproductive (Table S5). The initial DBH ($p < 0.001$), Amazon nut harvesting intensity ($p < 0.001$), and liana cutting ($p = 0.037$) determined fruit production ($r^2 = 0.55$, Table 1). The results of our logistic regression analysis showed an exponential increase in fruit production with tree size: without nut harvesting and without liana cutting, the trees > 170 cm in DBH produced 179 more fruits per year^{-1} than the trees between 30 and 40 cm in DBH, 218 vs. 39 fruits per year^{-1}, respectively. In contrast,

the percentage of unharvested fruits per reproductive tree decreased with tree size: 100% of the trees between 30 and 40 cm in DBH, 51.3% of the trees between 50 and 60 cm in DBH, 9.4% of the trees between 100 and 110 cm in DBH, and 12.4% of the trees > 170 cm in DBH were left unharvested (Table S5). The number of new individuals per reproductive tree increased with tree size: the trees between 30 and 40 cm in DBH produced 0.17 new recruits, whereas the trees > 170 cm in DBH produced 0.72 new recruits (Table S5).

3.2. Bertholletia Populations under Amazon Nut Harvesting and Timber Logging Intensities

Bertholletia transient population growth rate ($\lambda 100$) appeared stable in most simulated scenarios with combined Amazon nut harvesting and timber logging intensities (Figure 1), but all the simulated population densities were unstable without logging disturbance (Figure 2). Simulated population size increased at higher logging intensity but decreased at higher Amazon nut harvesting intensity. *Bertholletia* population growth rate was projected to be stable after 100 years under the combination of average Amazon nut harvesting and timber logging intensities and with 21% (observed average) reproductive Amazon nut trees with lianas cut ($\lambda 100 = 1.011$, Figure 1a) as opposed to the unstable unharvested scenario ($\lambda 100 = 0.979$, Figure 1a). After 100 years, *Bertholletia* simulated population density was slightly lower in the scenario with average Amazon nut harvesting and timber logging intensities than in the unharvested one (10.4 and 12.8 individuals per ha^{-1}, respectively, Figure 2a). *Bertholletia* simulated population density increased by 31% under the average logging intensity and without the Amazon nut harvesting scenario ($\lambda 100 = 1.086$, Figure 1a; 16.8 individuals per ha^{-1}, Figure 2a) but decreased by 54% under the average Amazon nut harvesting intensity and without the logging scenario ($\lambda 100 = 0.928$, Figure 1a; 8.3 individuals per ha^{-1}, Figure 2a) compared to the unharvested population. Thus, the population under the highest logging intensity (15% of disturbed area) and lowest Amazon nut harvesting intensity (0% of fruits harvested) tested presented the largest simulated population size ($\lambda 100 = 1.208$, Figure 1a; 25.4 individuals per ha^{-1}, Figure 2a) after 100 years.

3.3. Liana Cutting Intensity Improves Bertholletia Population Growth Rate

Simulation results showed the favorable impact of liana cutting on *Bertholletia* population growth rate. This impact, however, decreased at higher nut harvesting and logging intensity. Simulated liana cutting of 21% and 90% of the reproductive Amazon nut trees allowed for an increase of 15% (i.e., from 62% to 73% of harvested fruits) and 4.5% (i.e., from 85% to 89% of harvested fruits) of Amazon nut harvesting intensity under the average logging disturbance intensities of 5.3% and 15%, respectively; the provided population growth rates were above 1 (Figure 2).

Elasticity analyses for year 20 (end of the first cutting cycle) showed that the asymptotic population growth of *Bertholletia* was more sensitive to changes in the progression and growth matrix elements than to those in reproduction (Figure 3).
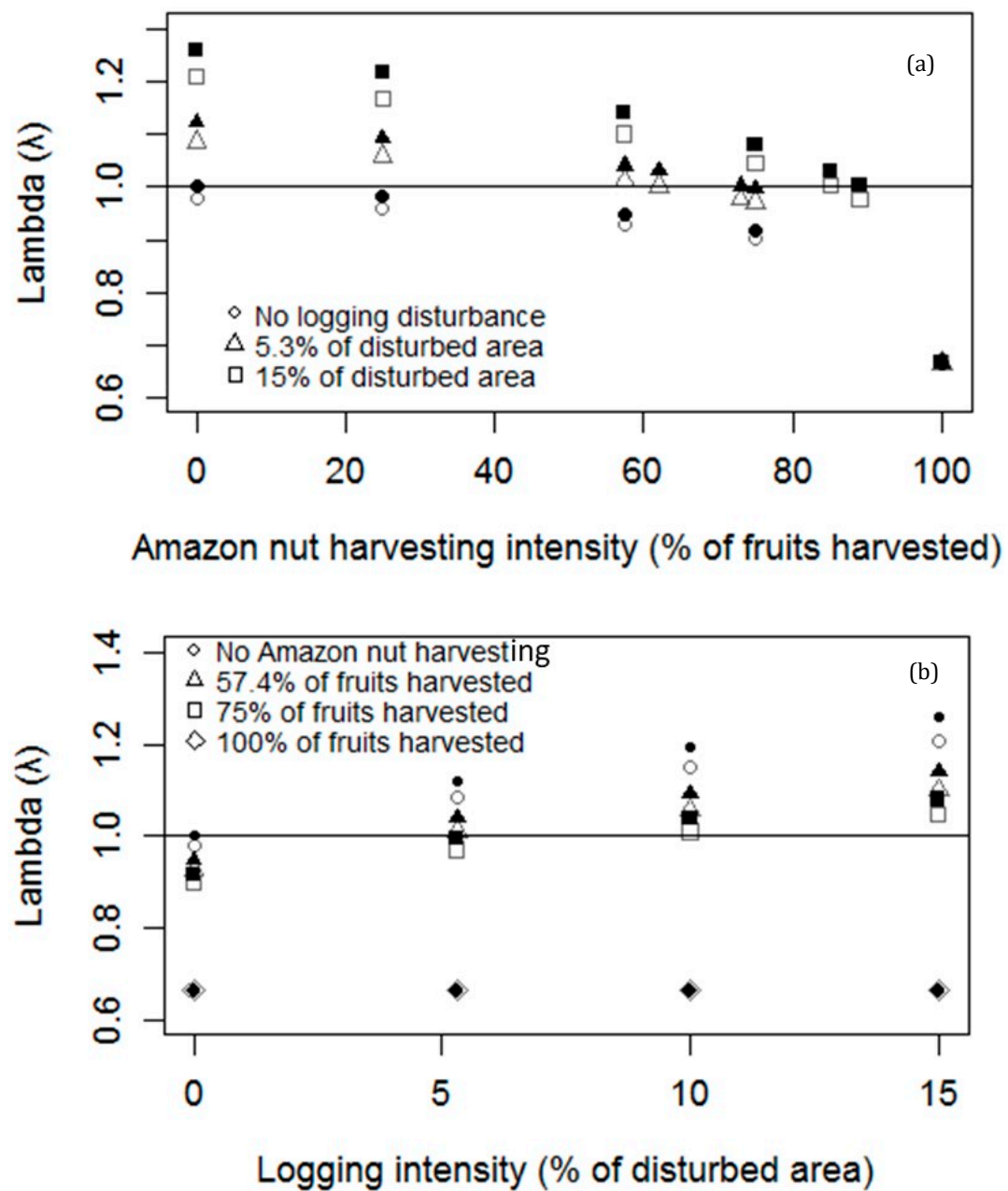
Figure 1. Impact of (**a**) Amazon nut (*Bertholletia excelsa*) harvesting and (**b**) logging intensity on *Bertholletia* transient population growth rate in the Bolivian Amazon. Empty and filled shapes are the population growth rate values for 100 years ($\lambda 100$) with lianas cut from 21% (average observed percentage from our studied populations) and 90% (hypothetical) of the reproductive trees, respectively.
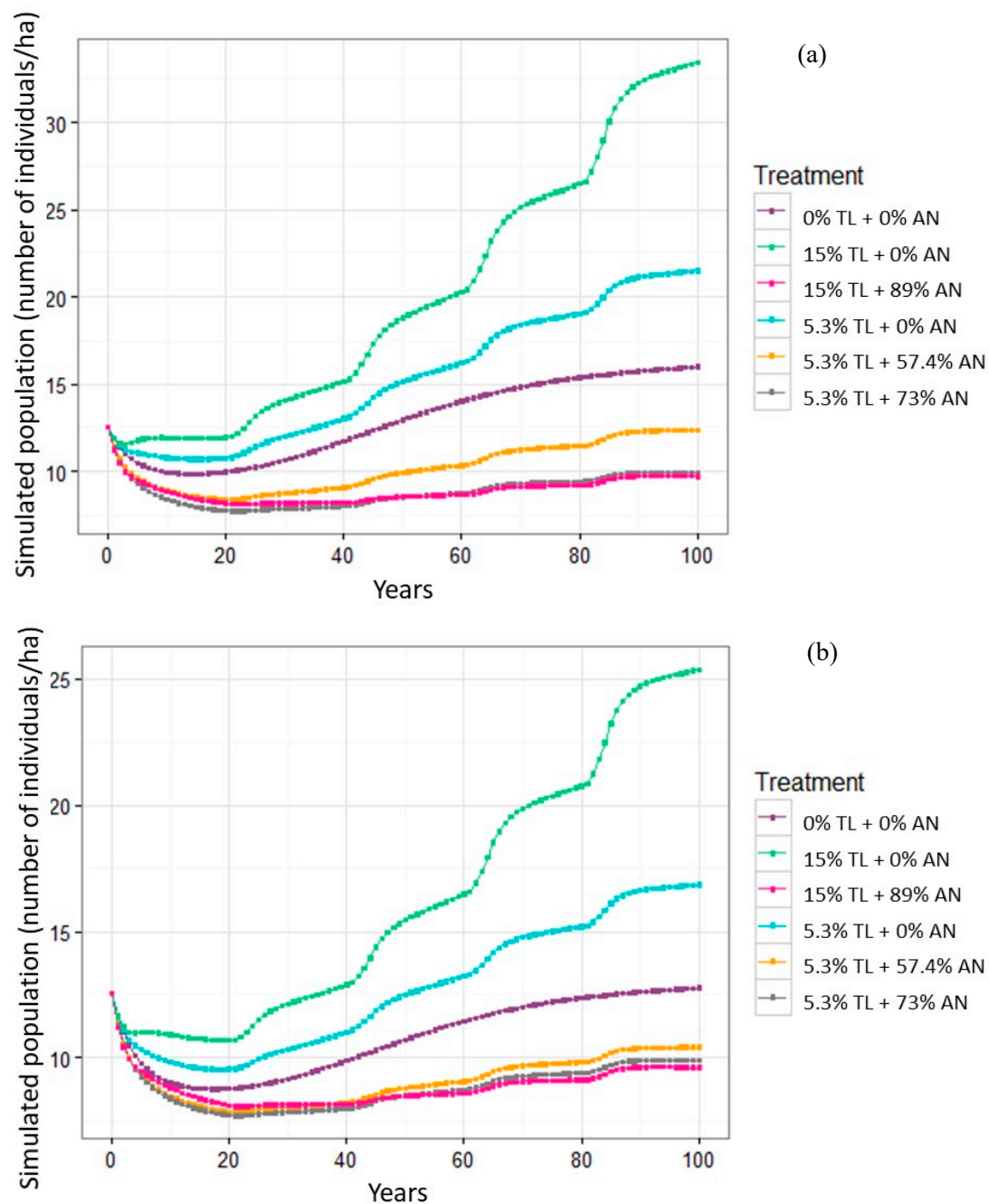
Figure 2. Simulated population densities of the Amazon nut (*Bertholletia excelsa*) under several combinations of logging and Amazon nut harvesting intensities in which *Bertholletia* transient population growth rate was equal to at least 1 after 100 years ($\lambda 100 > 1$) compared to the unharvested ($\lambda 100 = 0.979$) scenario (0% timber logging (TL) + 0% Amazon nut harvesting (AN) intensities). The scenarios of simulated populations are for the liana cutting intensity of (**a**) 21% (average) and (**b**) 90% (hypothetical) of the reproductive trees with lianas cut. The initial steep decrease of the simulated *Bertholletia* population is due to the initial population structure with the average Amazon nut harvesting and timber logging intensities.
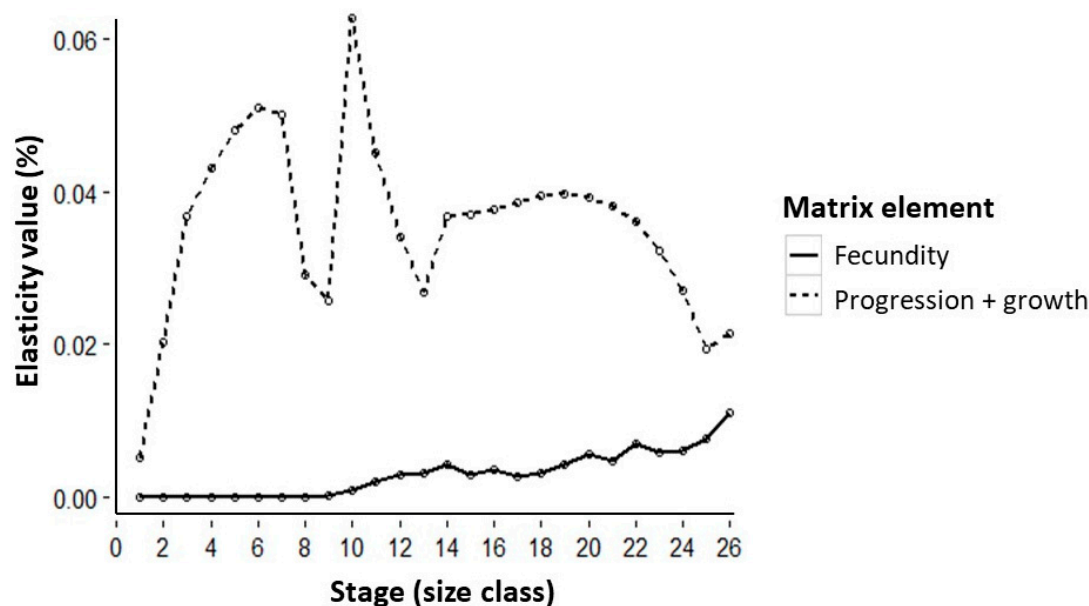
Figure 3. Elasticity values of *Bertholletia excelsa* populations under the average timber logging (5.3% of disturbed area) and Amazon nut harvesting (54.7% of harvested fruits) intensities, with lianas cut from 21% of the reproductive trees. Stages 1–6 correspond to seedlings, stages 7–12—to juveniles, and stages 13–26—to adults.

4. Discussion

The positive effect of logging disturbance intensity on *Bertholletia* seedling growth rate and of liana cutting on the fruit production rate played a key role in *Bertholletia* population growth rate after 100 years. This implies that Amazon nuts can be harvested more intensely under higher timber logging intensity (up to 15% of disturbed area, the maximum logging intensity found in the study area) and when lianas are cut from a larger percentage of reproductive trees (up to 90%).

We expected a positive effect of timber logging intensity on *Bertholletia* survival, growth, and recruitment rates, but only the seedling growth rate was positively affected (Table 1). However, the effect of logging was not significant after four years. Four years after logging, our predicted growth rate (growth at 4 years = 2.1 cm) approximated the average growth rate of two unlogged *Bertholletia* populations in the region ($\bar{x}$ = 2.40 cm) [40]. Our findings are consistent with growth patterns of planted *Bertholletia* seedlings in logging gaps [30] and are likely explained by an increase in light levels due to logging. The initial DBH was the only predictor of juvenile growth rate at our study sites, which differed from the study by Staudhammer et al. [51] who found that crown form and crown position are most critical for *Bertholletia* juvenile growth rate (5–50 cm in DBH). However, these two variables together with the initial DBH determined *Bertholletia* adult growth rate at our study sites (Table 1). We also expected that logging intensity may decrease *Bertholletia* survival, both of seedlings [30] and *Bertholletia* adult trees. We found, however, that the impact of logging intensity on *Bertholletia* survival was not detectable. The studies conducted in the Peruvian Amazon [14,31] found that low logging intensities (typical for the region) did not have an effect on *Bertholletia* fruiting and degree of damage to nut-producing trees. No effects of logging effects on *Bertholletia* survival at our study sites may as well be due to the low logging intensities.

Our estimates of reproduction probability for *Bertholletia* trees was higher than those found by Zuidema and Boot [12]. They found that trees > 40 cm in DBH had a 50% probability of being reproductive, whereas we found that the trees of similar size had a 63% probability of being reproductive. This variation is likely caused by differences in sample size and location of these studies and shows that *Bertholletia* reproduction capacity may vary within a region [55]. Despite the positive effect of Amazon nut harvesting intensity

on fruit production and upon accounting for the positive relationship between tree size and the percentage of unharvested fruits, Amazon nut harvesting intensity decreased the overall *Bertholletia* fecundity rate. However, liana cutting increased *Bertholletia* fecundity rate by increasing fruit production as predicted (Table 1). In line with our expectations, logging had no effect on Amazon nut production, probably due to the low logging intensity found at our research site and the fact that loggers avoid damaging large Amazon nut trees because those are easily recognizable [14].

Our population models projected growing *Bertholletia* populations under average Amazon nut harvesting, logging intensity, and liana cutting practices (Figure 1). The positive effect of logging intensity on *Bertholletia* population growth rate is likely related to its positive effect on seedling growth during the first four years since logging. This demonstrates that gaps created by logging play a positive role not only in improving *Bertholletia* regeneration density [11,28], but also in its long-term population stability. A higher logging (up to 15% of disturbed area) and liana cutting intensity (up to 90% of reproductive trees with lianas cut) could potentially allow harvesting a large percentage (up to 89%) of Amazon nut seeds and still ensure *Bertholletia* population stability. Even though the reported simulation results must be viewed and interpreted with caution, projections of the Amazon nut population's response to logging can be used to inform policies and practices. For instance, timber sourced from Amazon nut-rich managed forests at low logging intensity as it occurs in the Bolivian Amazon can make a special case for supplying timber to EU markets under the EUTR not only because it contributes to the maintenance of the forest cover of this biodiversity-rich ecosystem, a determining factor for EU timber imports [56], but also because the income sourced from timber is used by forest communities as an adaptation and mitigation mechanism to climate change and unstable Amazon nut prices in recent years.

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Appendix A

Legal framework to harvest Amazon or Brazil nuts (*Bertholletia excelsa*) and to log commercial timber species at community-managed forests in the Bolivian Amazon.

Timber logging under the community forest management plan (CFMP) in Bolivia is based on the general inventory of trees and identification of logging compartments and protection zones. To log timber from a logging compartment, it is required to carry a pre-logging census of timber trees > 40 cm in diameter at 1.3 m above ground (DBH), plan road infrastructure to extract trees, and leave sufficient seed trees to guarantee natural regeneration by leaving timber species with low abundance and at least 20% of trees $\geq$ the minimum diameter cutting (MDC) of harvestable species (Proyecto de Manejo Forestal Sostenible, 1997). The MDC varies between 50 and 70 cm in DBH depending on the species (Ministerio de Desarrollo Sostenible y Medio Ambiente, 2000). The most recent modality for logging timber in the Bolivian Amazon is the small-timber volume logging operation which allows each community household to log ~7 m^3 of timber six times a year following few management considerations in addition to the timber logged under the community forest management plan (CFMP) and prohibits the harvesting of timber species listed in CITES Appendices I and II (Bolivia's Forest and Lands Controlling Authority (ABT) Directive No. 001/2014; Integral Management of Forests and Lands Plan in Bolivia (Plan de Gestión Integral de Bosques y Tierras, PGIBT), ABT Administrative Resolution No. 250/2013). Currently, national policies enable the Integral Management of Forests and Lands Plan (ABT Administrative Resolution No. 250/2013), a landscape-level management approach that integrates the management of timber and non-timber forest products and agriculture and pasture lands altogether. The legal framework for Amazon nut management requires to leave 10% of the area under management unharvested (ABT Administrative Resolution No. 174/2008) and prohibits making a reentrance to harvest the remaining area under management (ABT Administrative Resolution No. 250/2013).

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