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ORIGINAL ARTICLE

Strong El Niño reduces fruit production of Brazil-nut trees in the eastern Amazon

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ABSTRACT

The Brazil-nut tree (*Bertholletia excelsa*) is native to the Amazon rainforest, and its fruit production varies naturally with climatic conditions. Our aim was to evaluate the temporal variation in Brazil-nut production associated with climatic variables, including the strong El Niño of 2015/2016. The study was carried out in two 9-ha permanent plots in the northeastern Brazilian Amazon from 2007 to 2018: one in forest (12-year monitoring) and the other in savannah/forest transition (eight years). Overall, we monitored fruit production of 205 trees with diameter at breast height ≥ 50 cm. Annual fruit production was related to temporal series (2005-2018) of climatic data (the Oceanic Niño Index; and precipitation and air temperature from two local meteorological stations). Average fruit production per tree in 2017 was eight times lower than in 2015 and two times lower than the general average for both sites, and was significantly associated to the El Niño of 2015/2016, that increased average maximum monthly temperature and reduced the precipitation in the region, extending the dry season from three to six months. Years with higher and lower fruit production per tree coincided in both sites. Annual fruit production was significantly and negatively correlated with thermal anomalies that occurred in the third semester prior to harvest monitoring. Years with higher production were related with predominance of neutrality or the La Niña phenomenon at the global scale, and higher rainfall at the local scale. The relationship of fruit production with climate was independent of the local habitat.

KEYWORDS: *Bertholletia excelsa*, climate variability, Oceanic Niño Index (ONI), productivity

Forte El Niño reduz a produção de frutos de castanheiras na Amazônia Oriental

RESUMO

A castanheira-da-amazônia (*Bertholletia excelsa*) é nativa da floresta amazônica e sua produção de frutos varia naturalmente com as condições climáticas. Nosso objetivo foi avaliar a variação temporal na produção de frutos da castanheira associada a variáveis climáticas, incluindo o forte El Nino de 2015/2016. O estudo foi realizado em parcelas permanentes de 9 ha de 2007 a 2018, uma localizada em floresta (12 anos de monitoramento) e a outra em transição floresta/savana (oito anos). Em total, monitoramos 205 castanheiras com diâmetro à altura do peito ≥ 50 cm. A produção anual de frutos foi relacionada a séries temporais (2005-2018) de dados climáticos (o Índice Oceânico Niño; e a precipitação e temperatura do ar de duas estações meteorológicas locais). A produção média por castanheira em 2017 foi oito vezes menor que em 2015 e duas vezes menor que a média geral nos dois sítios, e foi significativamente associada ao El Niño de 2015/2016, que causou aumento na temperatura máxima mensal e redução na precipitação regional, prolongando a estação seca de três para seis meses. Os anos com maior e menor produção média por castanheira foram os mesmos nos dois ambientes. A produção anual de frutos foi significativa e negativamente correlacionada com as anomalias térmicas ocorridas no terceiro semestre antes da colheita. Anos de maior produção foram relacionados com predominância de neutralidade ou do fenômeno La Niña em escala global, e aumento da precipitação em nível local. A relação entre produção de frutos e clima foi independente do ambiente local.

PALAVRAS-CHAVE: *Bertholletia excelsa*, variação climática, índice oceânico do Niño, produtividade

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INTRODUCTION

The Brazil-nut tree (*Bertholletia excelsa* Bonpl.) has been undergoing a process of domestication by amerindian peoples in the Amazon region since pre-Columbian times (Levis *et al*. 2018), and has great socioeconomic and cultural importance in the region today (Salomão 2014). Many extractive communities in the region depend on Brazil nut and its sub-products for family income (De Jesus and Guedes 2017).

The species has a long and synchronous flowering period that occurs during six months (Rathcke and Lacey 1985), normally in the dry season (Tonini 2011). The flower buds yield yellow, hermaphroditic flowers that are pollinized only by specific bees that are able to reach the pollen (Maués *et al*. 2015). The period between the emission of the first floral buds and maturation of the fruits is about 15 months and fruit dispersion occurs during the rainy season (Moritz 1984; Tonini 2011; Wadt *et al*. 2018).

There is a large intrapopulational and intraindividual yearly variation in fruit production (Kainer *et al*. 2006; Pedrozo *et al*. 2015), which may be due to crown characteristics such as sociological position and vine infestation (Wadt *et al*. 2015), tree age and size, mainly stem diameter (Neves *et al*. 2015), soil nutrients (Costa 2018), spatial location of trees and support capacity of different forest typologies (Batista *et al*. 2019), or interaction with pollinators and climate factors such as rainfall (Wadt *et al*. 2018).

The rainfall can directly interfere with flowering by affecting flower production, or indirectly by affecting pollinators (Rathcke and Lacey 1985), so that fruit production depends on climatic conditions of the previous year that affect flowering (Tonini 2011). In some species, fruit production is higher in some years and synchronized across large areas, and this can be related to specific climatic conditions during the years preceding the reproductive period (Bogdziewicz *et al.* 2019). Climate influence can be particularly significant considering scenarios of climate change, with increase of anomalies and frequency of extreme weather events.

The interannual variation in Brazil-nut production directly affects its market supply, price and economic viability. In 2017, the low production of fruits increased the price of an 11-kg can (the reference unit for commercialization) to R$ 120 (USD 22 according to the 2021 exchange rate), in some regions, compared to the average price of R$ 50 (USD 9) in 2016. In the northeastern Brazilian Amazon, the 11-kg can was sold for R$ 200 (USD 38) (Embrapa 2017).

In order to test the hypothesis that the drastic decrease in fruit production of Brazil-nut trees in 2017 was associated with the effects of a strong climatic anomaly, the 2015/2016 El Niño phenomenon, we evaluated Brazil-nut tree production across a series of years (2007-2018). Two Brazil-nut tree populations located in different habitats (forest and savannah/forest transition) were monitored in the northeastern Brazilian Amazon. Our aims were to: (1) characterize the effect on local climatic conditions of the 2015/2016 El Niño; (2) quantify the average annual production of Brazil nuts in the two populations and relate the yearly variation in production with climatic variables; and (3) evaluate whether the effect of the El Niño on fruit production was affected by the local habitat.

MATERIAL AND METHODS

Study area

Data were collected in the Extractivist Reserve of the Cajari River (Resex Cajari), a sustainable-use conservation unit located in the eastern Brazilian Amazon, in the south of the state of Amapá (Funi and Paese 2012) (Figure 1).

In the upland areas of the reserve, clustered Brazil-nut stands naturally occur in vast extensions of rainforest (referred as forest from here on) and transition areas between Amazon rainforest and typical savannah vegetation (savannah with gallery forest) (referred as savannah/forest transition from here on) (IBGE 2012). The climatic typology of the region is Am3, according to the adaptation of the Köppen classification (Martorano *et al.* 1993).

In the study area, the average annual air temperature is about 25 °C and average annual rainfall is 2,300 mm, distributed in two distinct seasons: a rainy season (January to July), and a dry season (August to December), when rainfall is lower and may lack completely in some months. September through November is the period with the lowest average rainfall (< 100 mm per month), and includes prolonged

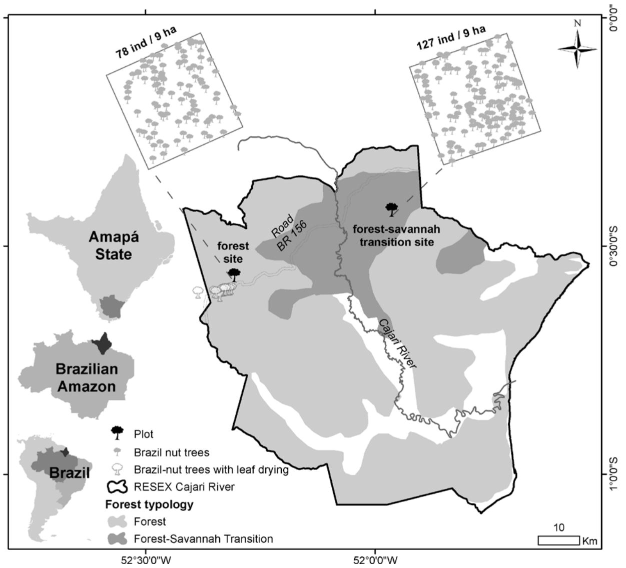

Figure 1. Location of the study area in the Brazilian Amazonian state of Amapá. The larger area represents the contour of the Extractive Reserve of the Cajari River (Reserva Extrativista do Rio Cajari) (Resex Cajari), showing the location of the two 9-ha permanent sampling plots within natural stands of Brazil-nut tree (*Bertholletia excelsa*) in an area of forest and an area of savannah/forest transition.

drought periods with no rainfall (Da Cunha *et al.* 2010). The main soils in the region are red-yellow dystrophic oxisols with a clayey texture, yellow dystrophic oxisols with a loamy texture, and red-yellow ultisols (RadamBrasil 1974). The soil was classified as eutrophic red-yellow ultisol in the forest plot and as red-yellow petroplintic dystrophic oxisol in the savannah/forest transition, which has lower support capacity (Oliveira Jr. *et al.* 2021).

Brazil-nut fruit yield

Data were collected in two permanent plots of 9 ha each (300 m x 300 m), one located in natural forest (monitored from 2007 to 2018) and the other in natural savannah/forest transition (monitored from 2010 to 2018, except 2012). All Brazil-nut trees in each plot with ≥ 31 cm circumference at breast height – CBH (at 1.3 m above the soil) were identified and mapped. CBH was measured in 2018 using a metric tape with a precision of 1 mm, and values were converted to diameter at breast height (DBH = CBH/π). The inclusion criterion for this study was DBH ≥ 50 cm, as Brazil-nut trees of this size are considered to have production potential (Wadt *et al.* 2005). Productive trees were classified into DBH classes, which are assumed to be related to age: Class I = DBH 50 - 100 cm; II = 100.1 - 150 cm; III = 150.1 - 200 cm, and IV = > 200.1 cm (Wadt *et al.* 2005).

Both populations are explored by local agroextractivist communities, who harvest fallen fruit each year. The monitored trees were visited annually after the period of fruit fall (second half of February). For safety reasons, the agroextractivists do not enter the Brazil-nut tree stand while the fruits are falling from the trees. Before collection, we assumed that only native fauna (mainly agoutis) removed the fruits (Wadt *et al.* 2018). From the end of fruit-falling onwards, we accompanied the extractivists into the plots during fruit collection. We monitored the effective production, i.e. the number of fruits available for collection by the extractivists after the fruits stopped falling from the trees, referred from here on as fruit production.

The fruit production of each individual tree was quantified by collecting all healthy fruits on the ground under the projection of the crown (Supplementary Material, Table S1). We excluded immature fruits (small and light), fruits damaged by animals (with tooth marks from agoutis and beak marks from macaws) and fruits from the previous year's harvest (much lighter then freshly fallen fruits and without bark).

Meteorological variables

A historical series (from 2005 to 2018) of monthly mean air temperature, maximum temperatures and precipitation were obtained from Instituto Nacional de Meteorologia (the Brazilian National Meteorological Institute), from meteorological station nr. 82098 located in Macapá, the capital of Amapá (INMET 2021a). This station is the nearest to Resex Cajari (121 km in a straight line) that contains a long series of data. Data collected at a station installed in the Resex Cajari and monitored by Sobrinho (2017), from April 2015 to March 2016 March were also used.

To analyse the effect of climate anomalies, we used the Oceanic Niño Index (ONI), which is calculated using data from floating monitoring stations installed in the Equatorial Tropical Pacific Ocean, in the region of Niño 3.4, between the latitudes 5ºN and 5ºS, and longitudes 120° to 160°W. The data are available for overlapping quarterly periods from the US National Aeronautics and Space Administration (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php). Positive anomalies (> 0.5 ˚C) in the sea surface temperatures (SST), which are characterized as an El Niño on a global scale, occurred between October 2015 and June 2016. These anomalies were ≥ 2.5 ˚C during the quarters Oct-Nov-Dec 2015 (OND2015), Nov-Dec-Jan 2016 (NDJ2016) and Dec-Jan-Feb 2016 (DJF2016).

In order to standardize our local metreorological data with the ONI, we calculated the three-month running mean of rainfall and mean and maximum air temperature for the same periods used for the ONI.

Statistical analyses

The fruit production data did not comply with the requirements of homogeneity of variance and normal distribution according to the Levene and Shapiro-Wilk tests, respectively.

The association of annual fruit production per plot with the quarterly averages of the climatic variables (ONI, maximum temperature, and rainfall) and the maximum temperature and rainfall averages in the first to fourth semester preceding harvest was analyzed by Pearson correlation. In each correlation, the values of annual fruit production per plot (12 values for forest and 8 values for forest/savannnah) were correlated with quarterly or grouped semiannual periods prior to the year of each harvest. For example, for the production of 2007, the corresponding values of the climatic variables used in correlations ranged from the quarters Dec 2006-Feb 2007 to Jan-Mar 2005, while for the production of 2018, in the same way, the values ranged from the quarters of Dec 2017-Feb 2018 to Jan-Mar 2016.

We used generalized linear models (GLM) to test for differences in average fruit production per tree among the years with data for both areas, considering two prediction factors (habitat and DBH class). The Mann-Whitney U test was used to compare the production per tree between the two sites in 2017 (the year with the notable decrease in production) and in 2018 (when production increased again). The difference between the distribution of diametric classes in the two habitats was tested using a chi-square test.

All analyzes were done using the R software (R Core Team 2020). For the Levene and Shapiro-Wilk tests, we used the car package (Fox and Weisberg 2019), for the GLM, we used the tidyverse package (Wickham *et al*. 2019), for the Pearson correlations, we used the PerformanceAnalytics (Carl and Peterson 2020) and ggpubr packages (Kassambara 2020), for the Mann-Whitney U test, we used the dpylr (Wickham *et al*. 2021) and rstatix packages (Kassambara 2021).

RESULTS

Characterization of the El Niño in the study area

The local increase in the average maximum monthly temperature during the second semester of 2015 and the first months of 2016 in the study area corroborate the description of this period as a strong El Niño. During this period, the monthly maximum temperatures were always higher than in any other year of the monitoring period and were also higher than the normal climatological pattern from 1961 to 1990 for the Macapá meteorological station (INMET 2021b) (Figure 2).

The average monthly of the maximum temperature in 2015/2016 (32.6 °C) was 2.1 °C higher, and the monthly average of the minimum temperature (22.9 °C) was 0.3 °C lower than in the other years. The precipitation regime was also altered. In 2015, the drought period (precipitation < 100 mm month^{-1}), which normally lasts three months, lasted six months, from July to December, with more than 100 continuous days without rain. There was a similar variation pattern in precipitation and temperature data from the weather stations in Resex Cajari and Macapá (Figure 3).

The total accumulated rainfall in one year (April 2015 to March 2016) at the Resex Cajari station was 2,818 mm (Sobrinho 2017), and 2,564 mm for the same period at the Macapá station (INMET 2021a). Despite being near the climatological normal, the precipitation was more irregularly distributed than normal, amplifying the drought effect through the reduced rainfall in the second semester of 2015, in association with the El Niño that occurred in this period.

Relationship of fruit production with climatic variables

There were significant negative correlations of fruit production with the Oceanic Niño Index and monthly maximum temperatures, mainly during the third semester before harvest (Table 1).

The significant correlation with monthly maximum temperatures started in the quarter beginning with July in the second year before harvest and up to the quarter beginning with June in the year before harvest. The begin and end of the negative relationships occurred first with the temperature anomaly in the Pacific Ocean (ONI), than with maximum temperature and precipitation. Comparing the beginning and end of significant correlations of production with ONI, there was a 2-month delay at the beginning and a 4-month delay at the end of the period when the local temperature was significantly correlated.

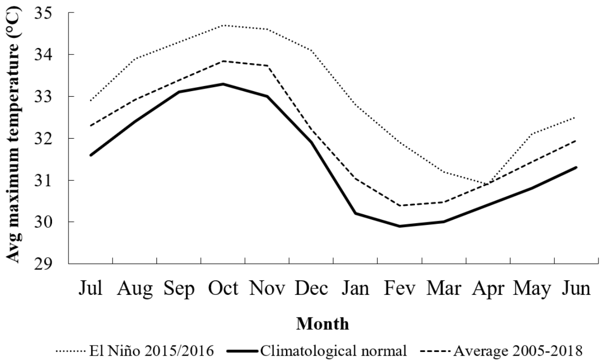

Figure 2. Monthly maximum temperature in the study region in southern Amapá state (Brazil) from July to June during the 2015/2016 El Niño, averaged for the whole study period (2005-2018) and for the period used to calculate the climatological normal (1961 to 1990). Source: INMET (2021b)

There was a significant negative correlation (r = -0.60, p= 0.004, n = 20) of the total annual fruit production per plot with the ONI during the less-rainy period in the third semester before harvest (Figure 4).

The year with the lowest fruit production in both areas (2017) was associated with an increase of more than 2 °C in the temperature of the ocean during the dry season of 2015, characterized as the strong El Niño. The years of greatest production (2012, 2015 and 2018) were related to previous periods of normal or negative ONI values.

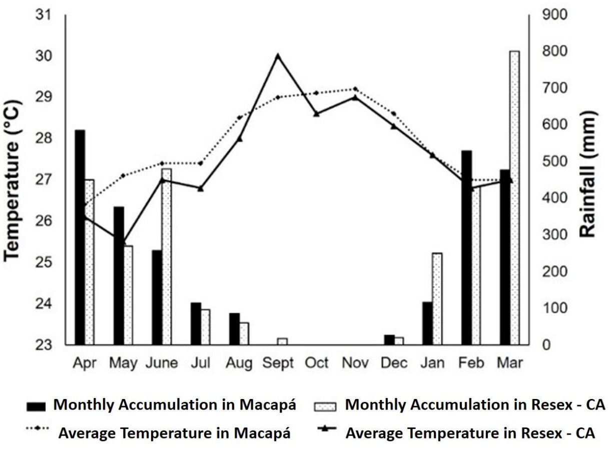

Figure 3. Monthly rainfall and temperature average from April 2015 to March 2016 at meteorological stations in Resex Cajari and Macapá, in Amapá state, Brazil. Source: Sobrinho (2017); INMET (2021a).

Table 1. Pearson correlation coefficients and p-values for the relationship between annual fruit production of Brazil nut trees (*Bertholletia excelsa*) in a natural forest stand (from 2007 to 2018) and a forest/savannah transition area (2010, 2011 and 2013 to 2018) (n = 20) in southern Amapá, in the eastern Brazilian Amazon, with quarterly running averages of Oceanica Niño Index, quarterly running averages of maximum temperature (T max) and quarterly running averages of precipitation in the study area in the two years prior to fruit harvest. The quarterly values are grouped by semester. The number in the code for correlation period indicates whether it is the first, second, third or fourth semester prior to harvest. The three letters indicate the three months that compose each quarter period (e.g. DJF = December, January, February; NDJ = November, December, January; and so on); acc = accumulated value for the semester; average = averaged value for the semester. Significant values are in bold.

Correlation period	ONI (°C)		T max (°C)		Precipitation (mm)	
1 DJF	0.05	p = 0.820	0.41	p = 0.069	-0.47	p = 0.067
1 NDJ	0.09	p = 0.707	**0.53**	**p = 0.015**	-0.45	p = 0.078
1 OND	0.10	p = 0.664	0.11	p = 0.639	-0.21	p = 0.429
1 SON	0.09	p = 0.691	-0.18	p = 0.440	0.22	p = 0.406
1 ASO	0.11	p = 0.647	-0.27	p = 0.250	0.22	p = 0.422
1 JAS	0.10	p = 0.674	-0.32	p = 0.169	0.35	p = 0.178
1 acc	–	–	–	–	-0.25	p = 0.348
1 average	–	–	0.15	p = 0.525	**0.62**	**p = 0.010**
2 JJA	0.07	p = 0.772	**-0.42**	**p = 0.063**	**0.64**	**p = 0.003**
2 MJJ	0.04	p = 0.860	**-0.52**	**p = 0.019**	0.33	p = 0.210
2 AMJ	-0.14	p = 0.566	**-0.49**	**p = 0.028**	0.07	p = 0.795
2 MAM	-0.40	p = 0.084	**-0.59**	**p = 0.006**	0.25	p = 0.350
2 FMA	-0.57	**p = 0.009**	**-0.68**	**p = 0.001**	0.19	p = 0.484
2 JFM	**-0.61**	**p = 0.004**	**-0.76**	**p < 0.001**	0.46	p = 0.072
2 acc	–	–	–	–	0.13	p = 0.624
2 average	–	–	**-0.64**	**p = 0.002**	0.04	p = 0.888
3 DJF	**-0.61**	**p = 0.005**	**-0.71**	**p < 0.001**	0.04	p = 0.895
3 NDJ	**-0.60**	**p = 0.006**	**-0.66**	**p = 0.002**	-0.04	p = 0.874
3 OND	**-0.58**	**p = 0.008**	**-0.64**	**p = 0.002**	0.37	p = 0.161
3 SON	**-0.58**	**p = 0.007**	**-0.71**	**p < 0.001**	0.40	p = 0.128
3 ASO	**-0.61**	**p = 0.004**	**-0.62**	**p = 0.004**	0.18	p = 0.514
3 JAS	**-0.62**	**p = 0.004**	**-0.59**	**p = 0.006**	0.04	p = 0.870
3 acc	–	–	–	–	0.01	p = 0.974
3 average	–	–	**-0.77**	**p < 0.001**	0.36	p = 0.175
4 JJA	**-0.64**	**p = 0.002**	-0.29	p = 0.207	0.46	p = 0.073
4 MJJ	**-0.56**	**p = 0.010**	0.04	p = 0.855	0.18	p = 0.503
4 AMJ	-0.25	p = 0.282	0.26	p = 0.270	-0.23	p = 0.392
4 MAM	0.05	p = 0.818	0.30	p = 0.198	0.22	p = 0.412
4 FMA	0.26	p = 0.269	0.26	p = 0.262	-0.25	p = 0.348
4 JFM	0.31	p = 0.185	0.22	p = 0.351	0.46	p = 0.072
4 acc	–	–	–	–	0.18	p = 0.514
4 average	–	–	0.16	p = 0.491	0.22	p = 0.412

The strongest negative correlation of fruit production ($n= 20$, $r = -0.77$, $p < 0.001$, $n = 20$) at the local scale was obtained with average maximum temperature (Table 1; Figure 5a) during the dry period in the third semester before harvest, when the trees were flowering and forming new fruits. Average rainfall was positively and significantly ($r = 0.64$, $p = 0.003$, $n = 20$) correlated with fruit production in the first semester and first quarter of the second semester before harvest (Table 1; Figure 5b).

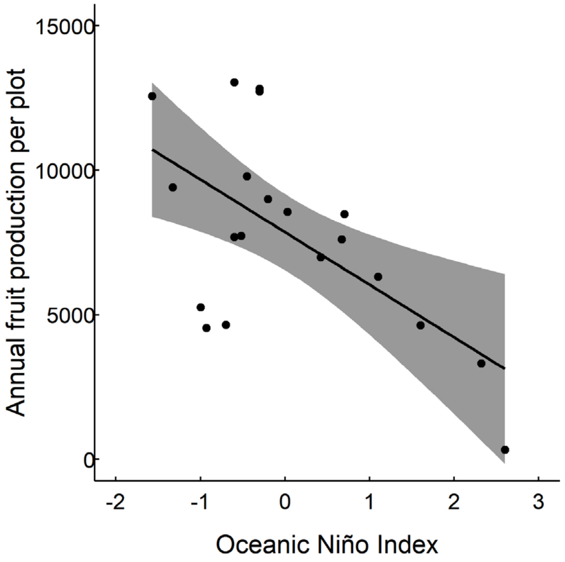

Figure 4. Correlation of total annual fruit production per plot in two natural stands of Brazil nut trees (*Bertholletia excelsa*) (n = 20) with the Oceanic Niño Index during the third semester before harvest. Data from extractivist harvest monitoring for 12 years in a forest area (2007 to 2018) and for eight years in a forest/savannah transition area (2010, 2011 and 2013 to 2018) in southern Amapá (eastern Brazilian Amazon). The grey area indicates the 95% confidence interval.

Comparison between sampling sites

The fruit production per tree was differed significantly among the years with data for both areas, considering habitat and DBH class as prediction factors ($F = 2940.2$, $df = 1719$, $p < 0{,}001$. Fruit production per tree was significantly lower in the forest/savannah site than in the forest site in 2017 ($W = 10222$, $p < 0.001$), when overall production in the forest/savannah site was 97% lower than in 2016, while it was only 53% lower in the forest site (Figure 6a). Fruit production per tree was slightly higher in the savannah/forest site than in the forest site in 2018, but the difference was not significant ($W = 5826.5$, $p = 0.366$) (Figure 6b).

The frequency distribution of trees in the diametric classes differed significantly between the populations (X-squared = 1498.5, $df = 174$, $p < 0.001$) (Figure 7a). Average fruit production per tree was higher in all diametric classes in the forest than in the forest/savannah (Figure 7b). Fruit production was highest in intermediate-sized trees of the 100-150-cm DBH class in the forest/savannah transition, and in older and larger trees of the 150-200-cm DBH class in the forest. In both habitats, maximum average fruit production occurred in intermediate-sized trees (figure 7a,b). In 2017, average fruit production per tree in the forest was similar to the interannual average production in all size classes, while there was a sharp drop in this parameter in all size classes in the savannah/forest transition (Figure 7c).

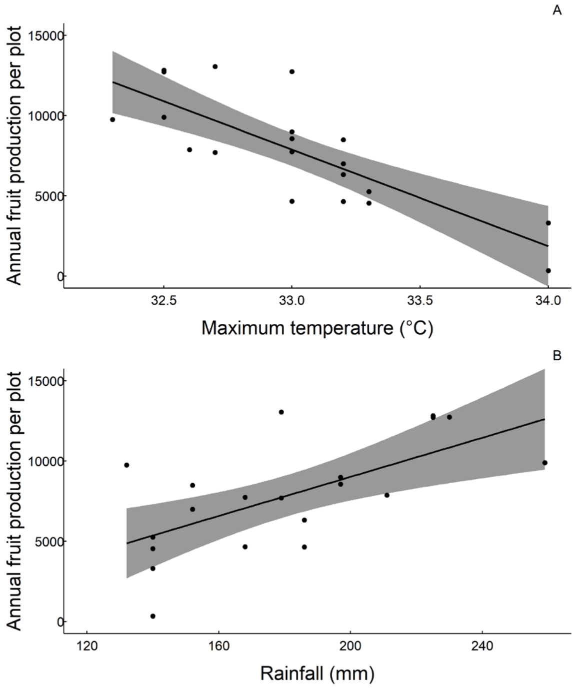

Figure 5. Correlation of total annual fruit production per plot in two natural stands of Brazil-nut trees (*Bertholletia excelsa*) (n = 20) with average local maximum temperature in the third semester before harvest (A); and with local precipitation in the quarter June-July-August of the year before harvest (B). Data from extractivist harvest monitoring for 12 years in a forest area (2007 to 2018) and for eight years in a forest/savannah area (2010, 2011 and 2013 to 2018) in southern Amapá (eastern Brazilian Amazon). The grey area indicates the 95% confidence interval.

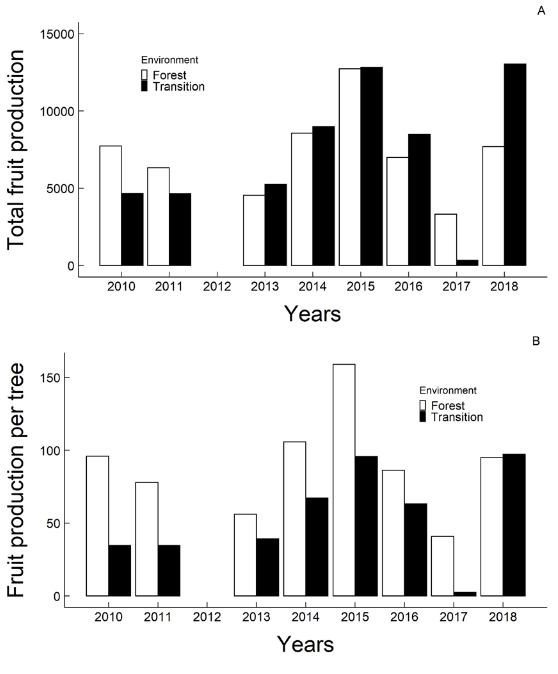

Figure 6. Total production per plot (A) and average fruit production per tree (B) of Brazil nut in 2010, 2011 and 2013-2018 in two 9-ha permanent sampling plots in a forest site and a savannah/forest transition site in Resex Cajari, southern Amapá, eastern Brazilian Amazonia.

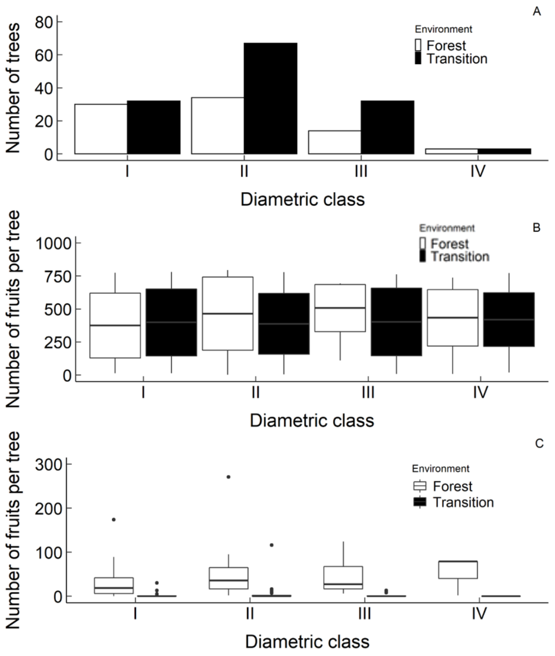

Figure 7. Number of productive Brazil-nut trees (A); interannual average fruit production per tree (2010, 2011, 2013-2018) (B); and average fruit production per tree in 2017 (C) per DBH class in two 9-ha permanent sampling plots in a forest site (78 trees) and a savannah/forest transition site (127 trees) in Resex Cajari, southern Amapá, eastern Brazilian Amazonia. DBH classes: I = 50.1 – 100 cm; II = 100.1 – 150 cm; III = 150.1 – 200 cm; IV = > 200.1 cm. The within-box line represents the average value (B) or median value (C), the box the *standard deviation (B) or* the *50% percentile (C)*, and the bars the confidence interval. The dots indicate outlier values.

DISCUSSION

Characterization of El Niño in the study area

The observed increase in air temperature in the Cajari and Macapá meteorological stations is in agreement with the increase in average temperatures recorded around the world in 2015, possibly in association with the El Niño phenomenon (Fonseca *et al*. 2017). The 2015/2016 El Niño was the strongest of the last 50 years, and affected the entire Amazon region (Vogt *et al*. 2016). Another study conducted in Amapá related the 2015/2016 El Niño with decreases in regenerating individuals (DBH < 5 cm) density and with physiological stress of another native tree species, *Mora paraensis* (Miranda *et al*. 2018). We also observed the drying and senescence of leaves of Brazil-nut trees in the forest area (see Figure 1) in the years following the El Niño, until the beginning of 2018, a period of strong rainfall, which is not the normal period for leaf abscission and resprouting in this species.

Extreme climatic events such as droughts associated with temperature anomalies in the equatorial Pacific Ocean occur with distinct frequencies in different regions of the planet. In the Amazon, these events occur approximately every five years. Besides 2015, there were severe droughts in the region in 2005 and 2010 (Marengo 2007; Zaho *et al*. 2017; Zeng *et al*. 2008). The negative effect of the 2010 drought, which occurred due to increased SST of the tropical North Atlantic (Marengo and Espinoza 2016; Aragão *et al*. 2018), on the fruit production in 2011 was also observed in our study area (see Figure 4). After 2017, 2011 was the year with the second lowest Brazil-nut production.

The eastern Amazon is more sensitive to climate change than other Amazon regions and is predicted to suffer most alterations due to its effects (Nobre 2008). However, strong climatic variations such as those in 2010 and 2015 can have pan-Amazonian effects on three large epicenters in southwestern Amazonia, north-central Bolivia, and Brazil's Mato Grosso state (Lewis *et al*. 2011; Vogt *et al.* 2016), and can thus affect the basin-wide fruit production of Brazil nut or other species that have great importance for the economy and food security in Amazonia.

The reduction in production, and the resulting low supply of Brazil nuts in a strong market with rising prices increased social pressure and conflicts in the extractivist units. In Resex Cajari, the value of the standard measure unit of 11 kg of Brazil nut incresed from USD 10 in 2016 to USD 38 in 2017 (pers. obs. by the authors). There were reports of invasions of collection areas by non-residents of the Resex Cajari, which had never happened before, and of clandestine gold mining in the Jari Ecological Station (ESEC Jari) located near Resex Cajari. Furthermore, there were reports of theft of Brazil nuts that had already been bagged and placed along forest roads ready for transport to market, which increased the level of danger in traditional communities and reduced the income of many families who are dependent on Brazil-nut extractivism.

Relationship of fruit production with climatic variables

In 2017 there was a drastic decrease in Brazil-nut production across the Amazon region, with a total of 21,651 tons that was 37% below the 10-year average (2010-2019) (IBGE 2021). This unprecedented decrease occurred in all states of the Brazilian Amazon, and in the Amazon region outside Brazil (EMBRAPA 2017).

Our results showed that Brazil-nut fruit production decreased drastically in 2017 and was associated with temperature anomalies. Maximum temperature is the most important predictor of biomass productivity reduction and has a greater impact per °C in the hottest forests (> 32.2 °C) (Sullivan *et al*. 2020), as was the case in our forest plots, where we recorded values near 35 °C and increases of more than 2 °C in maximum temperature during the El Niño.

The development, maturation, and dispersion of Brazil-nut fruits takes up to 15 months (Moritz 1984), thus the fruits harvested in 2017 initiated their formation in the second semester of 2015, when the El Niño occurred, which explains the association of the low fruit production in 2017 with this semester. As flowering occurs in the second semester (Maués *et al.* 2015), the temperature increase can cause an increase in respiration above the normal level needed for photosynthesis, leading to the consumption of carbohydrate reserves, flower abscission and consequent reduction in fruit production and fruit sweetnesss (Matos *et al*. 2019).

Higher temperatures in the phenological activity period can also affect pollinator survival (Rathcke and Lacey 1985). There is evidence of recent declines in the abundance and richness of pollinator species, mainly of bees (Novais *et al.* 2016), which are polinators of Brazil nut (Maués *et al*. 2015; Santos and Absy 2012). The decline in pollinators has been shown to be associated with temperature increases (Becker *et al*. 2018).

The positive correlation of fruit production with rainfall in the eight months preceding harvest is likely related to that these months correspond to the period of final growth and maturation of fruits that will be dispersed in the beginning of the following year. Higher rainfall rates during this period can accelerate the final maturation of fruits and aid in the process of breaking off from branches. Thus, when the rainy season is prolonged until August and there is more rain in the quarter June-July-August, during the final phase of maturation of fruits, fruit production improves. The years of greater fruit production (2012, 2015 and 2018) were related to previous periods characterized as a La Niña at a global level, which is associated with higher rainfall in the eastern Amazon (Villar *et al*. 2008). Likewise, in the state of Roraima (Brazil), during monitoring of Brazil-nut fruit production from 2006 to 2012, a much higher production was observed in 2012 (Tonini and Pedrozo 2014). The latter authors report that Brazil-nut trees appear to have years of peak production (mast years) and emphasize that long-term studies are needed for species with masting behavior, as they are particularly sensitive to climate changes that can alter the frequency of fruit production (Tonini and Pedrozo 2014).

In the state of Acre (Brazil) and in Bolivia, significant reductions in Brazil-nut fruit production were also related with decrease in rainfall and prolonged drought in previous years (Kainer *et al*. 2007), and in the state of Roraima, higher rainfall in September had a positive effect on Brazil-nut fruit production (Tonini 2011), corroborating our results on the effect of rainfall.

Comparison between sampling sites

Although the temporal variation in fruit production followed a similar pattern in both study sites, average fruit production per tree was generally higher in the forest, so that total fruit production was frequently similar or higher than in the forest/savannah plot, despite the fact that there were 38% less trees and a higher proportion of young trees (at an early stage of reproduction) in the forest plot. This indicates that the forest habitat has greater support capacity for Brazil-nut trees. The soil in the forest area has better soil quality, with higher levels of soil organic matter and nutrient availability that in the forest/savannah transition soil, which has higher acidity and concentration of lateritic concretions (Oliveira Jr. *et al.*, 2021; Sobrinho 2017).

The greater support capacity of the forest likely also favored the higher average fruit production in larger and older trees. The trees in the forest/savannah transition had maximum fruit production at intermediate sizes of 100-150 cm DBH, as was also reported for Brazil-nut trees by Neves *et al.* (2015). Another factor that may contribute to higher individual productivity is the lower density of Brazil-nut trees in the forest habitat. The higher density of Brazil-nut trees in the forest/savannah transition increases the intraspecific and interspecific competition for nutrients and, consequently, the rate of exported nutrients in the previous harvest (Oliveira Jr. *et al.* 2021).

Our results indicate that Brazil-nut trees respond with a significant decrease in fruit production to extreme El Niño events, and that this response (but also the ensuing recovery) is more pronounced in enrironments with lower support capacity. In this context, the prospect of an increase in the frequency of extreme climatic events that affect the stability and functioning of ecosystems (Meir *et al.* 2015) can have a significant negative impact on Brazil-nut productivity and, consequently, on the livelyhood of extractivist communities that depend on it. It is thus important to further understand and monitor the effects of future frequency and magnitude of El Niños on the Brazil nut production chain, as well as on the behavior and survival of *B. excelsa* trees and their forest habitat.

Although fruit production declined in both sampling areas in 2017, the intensity of the decline was greater in the savannah/forest transition, but capacity for recuperation in this area the next year was also relatively higher, as average production per tree was equivalent to that in the forest in 2018, when it had been below average productivity in the forest in all previous years. This striking recovery capacity of fruit production in Brazil-nut trees in the transition site may be due to that there was very little nutrient export in 2017, allowing for internal accumulation in the trees and subsequent increased cycling of nutritive elements used to form fruits for the next harvest (Fenner 1998). This suggests that there is proportionality between decrease and recovery in Brazil nut productivity in both habitats in response to major climatic impacts, and that the recovery rate is more related to habitat conditions during the previous than the current harvest, depending on the support capacity of the habitat.

CONCLUSIONS

A strong El Niño in 2015/2016 was associated with a significant increase in maximum air temperatures in the eastern Brazilian Amazon, which in turn was associated with a reduction in Brazil-nut fruit production in the following harvest. In a series of 12 years of harvest monitoring, years with greater fruit production were related to preceding periods of normal or lower-than-normal temperatures, associated with predominance of La Niña at a global level, and higher rainfall at a local level. Brazil-nut trees within forest had higher individual productivity than trees in savannah/forest transition, but trees in both habitats responded in the same way to climatic variability.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

Pastana *et al*. Strong El Niño reduces fruit production of Brazil-nut trees in the eastern Amazon

Table S1. Annual fruit production (fresh, undamaged fruit fallen on the ground below the crown projection, available for harvest in February) of Brazil-nut trees monitored in two 9-ha plots in natural stands in a forest area and a savannah/forest-transition area in the Cajari Extractivist Reserve (Resex Cajari), in southern Amapá state, eastern Brazilian Amazon. Zero (0) indicates that fruit production was monitored but no fruit was found; a dash (–) indicates that there was no monitoring in this year. DBH = diameter at breast height; STATUS: P = productive; NP = not productive throughout the study period.

ID	DBH (cm)	STATUS	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Forest plot														
1	50.00	P	3	24	29	0	16	11	1	22	46	8	7	5
2	52.55	P	0	0	0	217	124	266	27	50	26	37	22	17
3	52.87	P	0	7	18	0	28	14	12	28	55	54	3	46
4	58.28	P	0	3	9	0	0	0	3	0	0	1	0	0
5	68.47	P	9	34	34	0	7	12	34	16	0	0	6	54
6	71.66	P	98	97	107	33	34	199	4	100	85	26	26	174
7	74.52	P	248	190	200	134	144	209	93	0	211	132	174	127
8	75.80	P	107	189	200	66	140	140	70	100	177	101	31	80
9	76.43	P	132	14	14	0	0	35	5	50	37	52	8	50
10	81.21	P	0	37	40	71	52	66	38	50	57	71	22	41
11	81.53	P	146	138	157	152	75	129	80	150	184	144	89	198
12	81.53	P	50	54	56	98	79	81	93	75	145	137	33	105
13	81.85	P	133	46	60	0	59	159	41	200	171	115	15	114
14	81.85	P	36	4	19	5	0	0	7	0	7	0	2	0
15	83.12	P	156	130	196	68	120	307	28	200	156	88	65	153
16	85.99	P	107	134	137	150	83	170	115	100	233	134	89	166
17	88.85	P	0	52	52	49	30	35	41	25	109	103	41	110
18	91.40	P	0	41	46	7	5	43	7	18	35	12	10	19
19	94.27	P	5	1	9	7	19	27	9	0	20	24	2	3
20	94.90	P	0	115	134	122	220	0	142	0	158	227	56	360
21	95.54	P	72	38	41	63	0	38	14	9	188	25	35	94
22	95.54	P	27	20	27	18	22	53	67	0	11	43	1	14
23	97.13	P	0	17	22	0	33	71	39	75	70	49	9	26
24	97.13	P	115	74	96	68	80	201	84	150	277	53	42	137
25	97.77	P	171	156	175	205	186	112	49	200	315	88	80	175
26	98.73	P	347	229	236	59	155	234	38	250	223	111	64	230
27	98.73	P	0	0	0	0	0	0	0	0	39	28	0	0
28	98.73	P	155	121	146	124	50	172	43	75	149	59	53	115
29	99.36	P	0	146	161	58	0	112	31	200	559	33	48	93
30	99.68	P	8	109	110	47	74	70	34	150	104	58	4	31
31	101.91	P	174	90	126	71	64	238	28	150	142	92	50	210
32	101.91	P	97	105	117	48	27	141	4	150	229	56	27	111
33	103.50	P	0	0	0	0	46	0	18	0	0	0	16	0
34	104.46	P	41	45	53	14	0	14	5	50	106	12	2	46
35	105.10	P	200	63	63	247	128	156	69	200	150	113	65	46
36	105.73	P	0	115	134	121	127	0	115	0	134	187	95	20
37	107.64	P	160	68	81	153	192	201	96	225	192	140	60	161
38	109.87	P	46	41	43	31	0	45	98	50	53	53	26	79
39	110.51	P	106	88	88	50	31	112	80	100	160	52	64	164
40	111.46	P	49	30	61	41	33	103	28	50	68	48	10	39
41	112.10	P	56	25	47	39	0	6	32	50	22	44	34	0
42	112.10	P	133	112	119	74	34	265	13	150	136	44	41	117
43	114.65	P	13	22	22	30	12	20	61	2	37	25	11	16
44	121.02	P	402	51	68	48	71	105	35	2	190	62	24	87
45	124.52	P	51	131	158	58	128	330	18	6	7	97	78	43
46	125.16	P	619	478	516	162	241	681	142	400	506	285	271	375
47	136.31	P	137	106	114	73	64	71	24	100	200	41	13	97
48	136.31	P	219	190	190	156	192	131	12	150	331	223	78	120
49	136.94	P	26	4	9	1	4	58	5	0	53	17	3	9
50	137.26	P	164	94	102	13	232	287	161	150	300	148	53	30
51	138.54	P	148	86	122	173	115	215	100	200	152	107	86	146

Table S1. Continued

ID	DBH (cm)	STATUS	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
52	138.54	P	212	141	193	454	154	334	240	200	349	191	78	98
53	140.13	P	198	187	221	217	141	266	71	150	295	140	35	137
54	140.13	P	48	57	58	30	12	72	53	50	54	82	36	28
55	140.76	P	0	79	220	211	40	285	182	200	315	297	88	123
56	140.76	P	169	138	154	237	147	104	250	100	176	172	68	50
57	142.36	P	33	23	45	17	7	61	13	20	55	21	4	19
58	143.31	P	0	7	20	114	100	306	42	250	323	127	11	253
59	144.90	P	48	35	37	28	27	55	49	50	66	69	19	33
60	146.18	P	151	75	77	53	14	193	9	22	197	50	23	31
61	146.82	P	20	45	53	202	33	102	70	50	155	40	19	61
62	152.87	P	202	25	83	237	110	243	113	200	161	79	41	75
63	152.87	P	282	79	179	162	194	267	84	250	113	229	96	60
64	161.15	P	295	268	270	173	171	285	36	250	165	176	12	152
65	162.10	P	135	90	110	143	157	298	126	100	265	62	99	128
66	165.61	P	122	112	116	95	110	94	30	150	34	201	16	118
67	165.61	P	181	213	226	113	20	193	69	100	316	55	20	174
68	165.92	P	112	14	138	37	87	193	16	16	66	24	26	39
69	166.24	P	363	110	316	110	192	204	24	100	489	74	19	15
70	172.61	P	211	172	210	47	81	278	42	150	286	103	38	199
71	175.16	P	98	47	48	103	105	257	24	50	193	46	6	48
72	177.39	P	0	0	0	0	0	0	149	0	417	181	28	116
73	178.34	P	1027	788	879	191	292	935	61	950	600	148	124	661
74	183.44	P	96	17	54	19	22	60	28	14	66	12	6	23
75	202.55	P	293	142	331	263	207	483	44	250	0	129	76	158
76	226.75	P	213	224	225	458	153	300	190	250	376	264	79	83
77	247.13	P	83	10	17	200	22	89	23	0	18	0	2	0
78	280.25	P	210	295	295	358	114	321	47	150	296	111	79	74
Forest/savannah-transition plot														
1	51.57	P	–	–	–	67	71	–	45	237	155	143	0	204
2	55.70	P	–	–	–	0	0	–	4	31	31	4	0	2
3	57.30	P	–	–	–	0	0	–	10	0	5	25	0	70
4	62.07	P	–	–	–	0	9	–	4	13	15	36	0	30
5	63.03	P	–	–	–	2	12	–	7	12	79	26	0	24
6	63.66	P	–	–	–	21	8	–	54	21	125	33	1	107
7	64.62	P	–	–	–	32	16	–	4	55	74	28	2	16
8	65.89	P	–	–	–	12	28	–	26	45	170	19	0	41
9	66.84	P	–	–	–	149	183	–	98	301	321	182	1	46
10	67.48	P	–	–	–	73	75	–	70	103	216	138	0	223
11	68.12	P	–	–	–	16	38	–	4	67	23	88	0	1
12	71.62	P	–	–	–	0	17	–	0	6	27	8	0	17
13	72.57	P	–	–	–	0	0	–	8	9	32	10	0	0
14	76.39	P	–	–	–	110	132	–	183	321	254	190	11	394
15	76.39	P	–	–	–	15	0	–	6	0	78	2	0	71
16	77.03	P	–	–	–	11	0	–	19	31	96	31	0	153
17	78.94	NP	–	–	–	0	0	–	0	0	0	0	0	0
18	79.58	P	–	–	–	19	23	–	56	97	85	27	16	243
19	81.81	P	–	–	–	0	0	–	0	8	55	7	0	0
20	82.76	P	–	–	–	77	15	–	36	148	69	87	0	231
21	83.72	P	–	–	–	17	0	–	4	57	156	70	30	37
22	84.03	P	–	–	–	9	0	–	0	0	48	19	4	0
23	85.94	P	–	–	–	57	15	–	17	26	161	19	0	2
24	86.58	P	–	–	–	19	6	–	62	88	45	19	2	150
25	86.58	P	–	–	–	0	39	–	13	60	43	4	0	7
26	87.85	P	–	–	–	14	0	–	22	69	72	78	2	287
27	89.13	P	–	–	–	70	37	–	109	99	15	107	1	15
28	92.31	P	–	–	–	3	3	–	20	48	56	48	0	172
29	92.31	P	–	–	–	45	121	–	47	140	94	154	7	227
30	93.58	NP	–	–	–	0	0	–	0	0	0	0	0	0
31	93.90	P	–	–	–	46	77	–	0	96	260	32	3	136
32	97.40	P	–	–	–	50	45	–	19	53	27	27	1	69

Table S1. Continued

ID	DBH (cm)	STATUS	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
33	97.72	P	–	–	–	62	55	–	133	79	160	137	11	201
34	98.68	P	–	–	–	54	86	–	107	137	207	27	5	138
35	98.68	P	–	–	–	21	42	–	14	27	45	62	2	207
36	102.81	P	–	–	–	14	14	–	3	3	19	8	0	39
37	104.09	P	–	–	–	0	0	–	0	0	9	0	0	4
38	104.09	P	–	–	–	43	2	–	105	52	57	17	1	5
39	105.04	P	–	–	–	218	64	–	194	158	145	327	1	568
40	105.68	P	–	–	–	54	39	–	8	44	71	31	2	93
41	106.00	P	–	–	–	106	13	–	32	114	18	95	0	160
42	106.63	P	–	–	–	1	0	–	4	27	16	36	1	25
43	107.59	P	–	–	–	2	6	–	1	10	72	5	0	0
44	110.13	P	–	–	–	62	24	–	0	40	55	13	0	50
45	111.41	P	–	–	–	14	21	–	0	50	30	79	0	0
46	111.41	P	–	–	–	139	5	–	26	246	130	286	10	1
47	112.68	P	–	–	–	23	31	–	78	11	92	76	0	23
48	113.00	P	–	–	–	5	3	–	7	0	63	7	3	40
49	113.64	P	–	–	–	39	300	–	260	543	294	285	0	361
50	113.95	P	–	–	–	11	39	–	18	43	130	14	0	175
51	114.59	P	–	–	–	4	10	–	60	10	28	28	1	0
52	114.59	P	–	–	–	65	4	–	172	6	6	43	1	191
53	114.91	P	–	–	–	64	102	–	39	171	186	56	1	174
54	116.18	P	–	–	–	0	2	–	0	10	63	35	0	0
55	116.18	P	–	–	–	13	0	–	81	13	26	7	0	5
56	117.14	P	–	–	–	15	86	–	72	145	218	146	5	128
57	118.41	P	–	–	–	148	70	–	174	273	93	305	0	0
58	119.05	P	–	–	–	89	9	–	4	109	64	247	0	2
59	119.05	P	–	–	–	25	99	–	149	166	87	55	0	196
60	120.32	P	–	–	–	17	33	–	38	30	66	75	1	154
61	121.59	P	–	–	–	0	4	–	4	6	39	11	0	0
62	121.91	P	–	–	–	84	33	–	32	91	70	28	0	197
63	122.55	P	–	–	–	0	21	–	12	4	96	32	0	28
64	124.14	P	–	–	–	36	2	–	22	51	2	56	1	2
65	124.14	P	–	–	–	45	1	–	0	19	41	71	1	0
66	124.14	P	–	–	–	4	25	–	1	64	108	43	0	30
67	124.78	P	–	–	–	0	0	–	0	0	0	0	0	7
68	124.78	P	–	–	–	79	195	–	87	123	268	98	5	294
69	125.10	P	–	–	–	84	30	–	6	32	175	125	0	347
70	126.37	P	–	–	–	156	328	–	193	548	185	694	0	471
71	126.69	P	–	–	–	7	60	–	38	27	30	21	2	66
72	127.32	P	–	–	–	11	4	–	0	39	87	10	0	89
73	127.32	P	–	–	–	9	1	–	4	6	13	0	0	1
74	127.32	P	–	–	–	24	0	–	49	171	90	97	0	0
75	128.28	P	–	–	–	1	60	–	30	33	69	13	2	48
76	128.92	P	–	–	–	18	50	–	9	12	63	15	0	30
77	131.14	P	–	–	–	27	4	–	9	55	42	26	2	75
78	131.14	P	–	–	–	42	21	–	6	40	63	130	0	156
79	132.10	P	–	–	–	41	11	–	256	28	67	20	13	92
80	132.10	P	–	–	–	68	134	–	115	236	110	76	7	117
81	132.73	P	–	–	–	9	5	–	26	16	56	2	0	7
82	133.69	P	–	–	–	23	21	–	28	8	22	4	0	12
83	135.28	P	–	–	–	3	0	–	7	6	33	14	0	6
84	135.92	P	–	–	–	0	41	–	0	32	128	21	5	121
85	136.87	P	–	–	–	16	2	–	2	6	6	54	0	9
86	137.83	P	–	–	–	134	54	–	157	176	345	79	13	350
87	138.15	P	–	–	–	35	77	–	4	40	293	14	0	25
88	138.46	P	–	–	–	17	26	–	1	39	102	27	0	122
89	140.06	P	–	–	–	131	62	–	185	154	302	337	0	360
90	140.06	P	–	–	–	6	6	–	13	26	70	35	0	45
91	140.37	P	–	–	–	19	10	–	0	11	88	10	0	82
92	143.24	P	–	–	–	24	11	–	7	17	79	63	0	0

Table S1. Continued

ID	DBH (cm)	STATUS	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
93	143.24	P	–	–	–	23	0	–	2	11	20	1	0	18
94	143.24	P	–	–	–	7	38	–	22	26	80	32	0	57
95	143.88	P	–	–	–	10	47	–	24	74	119	53	8	134
96	148.01	P	–	–	–	4	15	–	45	60	221	27	0	112
97	148.01	P	–	–	–	27	10	–	26	31	210	12	0	65
98	149.61	P	–	–	–	24	13	–	28	77	91	46	1	86
99	149.61	P	–	–	–	0	0	–	0	8	13	15	0	0
100	149.61	P	–	–	–	10	3	–	19	27	85	68	0	41
101	151.20	P	–	–	–	10	11	–	45	46	78	4	0	29
102	152.79	P	–	–	–	28	3	–	9	19	0	60	0	16
103	152.79	P	–	–	–	18	0	–	12	6	174	37	1	145
104	154.38	P	–	–	–	97	33	–	56	57	84	127	0	36
105	154.38	P	–	–	–	18	10	–	1	44	30	27	0	13
106	154.38	P	–	–	–	183	186	–	159	262	235	183	116	315
107	155.33	P	–	–	–	24	6	–	129	19	50	26	0	129
108	155.97	P	–	–	–	2	20	–	22	23	82	15	0	59
109	159.15	P	–	–	–	7	0	–	0	0	0	0	0	0
110	159.15	P	–	–	–	53	8	–	33	13	22	32	0	41
111	159.15	P	–	–	–	22	21	–	14	22	56	50	4	42
112	159.15	P	–	–	–	0	0	–	0	0	24	15	0	44
113	161.06	P	–	–	–	0	2	–	21	3	62	6	0	3
114	163.61	P	–	–	–	52	114	–	129	13	124	263	1	178
115	164.25	P	–	–	–	49	61	–	8	67	94	20	0	67
116	167.75	P	–	–	–	35	0	–	0	0	33	88	2	0
117	169.34	P	–	–	–	30	81	–	7	118	238	81	0	208
118	170.61	P	–	–	–	49	31	–	7	40	65	40	2	121
119	171.89	P	–	–	–	8	6	–	6	93	9	80	0	0
120	171.89	P	–	–	–	131	36	–	18	49	125	47	1	42
121	175.07	P	–	–	–	7	7	–	2	14	96	6	0	2
122	181.44	P	–	–	–	18	14	–	15	12	56	32	0	68
123	183.98	P	–	–	–	5	2	–	28	41	9	32	0	17
124	189.39	P	–	–	–	9	26	–	8	0	34	7	0	14
125	203.72	P	–	–	–	11	66	–	6	67	31	88	0	242
126	211.68	P	–	–	–	6	5	–	4	13	82	8	0	177
127	222.82	P	–	–	–	16	18	–	30	33	92	42	0	48