Are Brazil nut populations threatened by fruit harvest?

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ABSTRACT

Harvest of Brazil nuts from the large, iconic tree *Bertholletia excelsa* generates substantial income for smallholders, providing a strong incentive to conserve the mature forests where it grows. Although much previous work has focused on the impact of nut harvest on new seedling recruits into *B. excelsa* populations, the connection between harvest rates and long-term population stability is still unclear. Moreover, there is additional uncertainty for Brazil nut management in terms of population response to climate change and other anthropogenic influences. We drew on 14 years of research in two sites in Acre, Brazil with different *B. excelsa* nut harvest intensities (39% and 81%), to produce stochastic and deterministic matrix population models which incorporated parameter uncertainty in vital rates. Adult abundance was projected to remain close to the current observed abundance or higher through the next 50 years. Elasticity analyses revealed that the asymptotic population growth rate (λ) was most sensitive to stasis vital rates in sapling, juvenile, and adult stages. Deterministic transition matrices calculated using diameter growth rates dependent on rainfall yielded average λ values around 1.0 under extreme high, extreme low, and average annual rainfall. While sustained high rates of Brazil nut harvest and climate change could potentially negatively impact *B. excelsa* populations, changes in human use of the forested landscape are more immediate concern. To reduce the risk of population decline, smallholders and managers of *B. excelsa* rich forests should focus on conservation of premature and mature individuals.

Abstract in Portuguese is available with online material.

Key words: Amazon; *Bertholletia excelsa*; demography; matrix population model; rainfall; sustainable harvest; tropical forest.

NATURAL RESOURCES THAT CAN BE HARVESTED REGULARLY AND IN-DEFINITELY FROM FORESTS PROVIDE INCENTIVES FOR CONSERVATION. Forest-dependent smallholders often possess local ecological knowledge and cultural practices that protect standing forests and accompany biodiversity (Camacho-Benavides *et al.* 2013). However, even seemingly benign extractive activities may have environmental consequences. Harvest of non-timber forest products (NTFP), such as leaves, bark, roots, and seeds, may impact populations of harvested species or the broader ecosystem (Hiremath 2004, Ticktin 2004). Thus, balance between utilization and conservation is required to achieve long-term sustainable relationships between people and resources. For long-lived organisms, such a balance may not be immediately apparent because of the temporal gap between harvest and population response.

The collection and sale of Brazil nuts, the seeds of *Bertholletia excelsa*, from mature forests of Brazil, Bolivia, and Peru provide up to 43% household income to Amazonian residents (Duchelle *et al.* 2011). A primary concern is whether harvesters leave enough *B. excelsa* seeds in the forest to allow for sufficient regeneration to replace reproductive adults. Of all tested variables from sample sites throughout the Amazon basin, Peres *et al.* (2003) reported that history of seed harvest was the most highly correlated with population structure. Since intensively harvested populations exhibited low proportions of juveniles, indicating declining populations, restrictions on nut harvest were recommended to avoid 'demographic collapse'. In contrast, more recent studies revealed positive or neutral relationships between nut harvest and regeneration. In Eastern Amazonia, a positive correlation was found between history of fruit collection over 20 years and seedling density (Ribeiro *et al.* 2014), while juvenile abundance was similar across a gradient of nut harvest intensities (Scoles & Gribel 2012). A 2-year demographic study in Western Amazonia which applied matrix models concluded that even under high seed collection rates (93%), both *B. excelsa* population stability and Brazil nut harvest were attainable (Zuidema & Boot 2002). Risks associated with overexploitation may be addressed through harvest management, but changes in rainfall patterns present another potential demographic threat.

Global climate change and regional land use are two main drivers that affect local precipitation patterns. One predicted climate change consequence is disruption in the El Niño Southern Oscillation (ENSO), which has been linked to reduced precipitation in the Amazon region (Li *et al.* 2011); future ENSO events

may occur with more frequency or last longer (Cai *et al.* 2014). Continued deforestation further interacts with predicted climate change. Since forest evapotranspiration accounts for about one-third of precipitation across the entire Amazon basin (Costa & Foley 1999), forest clearing reduces basin-wide precipitation and thus water availability to species critical to human livelihoods, such as *B. excelsa*.

Rainfall is a key factor in determining tree performance and demography. Following the 2005 and 2010 droughts, tree mortality in Amazonian forests sharply increased for individuals >10 cm diameter at breast height (1.3 m above ground level; dbh), with disproportionate increases for larger trees (Brienen *et al.* 2015). This is disconcerting for the giant *B. excelsa,* especially given that its growth is significantly and positively correlated with rainfall (Staudhammer *et al.* 2013) and that reproductive adults produce significantly fewer fruits following drought years (Kainer *et al.* 2007, Staudhammer *et al.* 2013). The predicted drier climate in Western Amazonia (IPCC 2014) could decrease growth and compromise recruitment, threatening the long-term stability of populations of long-lived, slow-growing tropical trees like *B. excelsa.*

An understanding of species demography, population structure, and change over time (Caswell 2001) is critical for developing forest policy and management practices which favor long-term sustained production. Matrix population models can help answer NTFP demographic questions by combining information about survival, reproduction, and development in distinct age- or size-defined classes from initial life stages to maturity. For example, Gaoue *et al.* (2013) applied a matrix model to African mahogany (*Khaya senegalensis*) to reveal that foliage and bark harvest affected time to reproductive maturity and life expectancy differently among climatic regions. Ten years of data informed the relative influence of a native hemiparasite, an invasive competitor, and harvest of medicinal 'amla' fruits on transient and long-term population dynamics of two *Phyllanthus* spp.(Ticktin *et al.* 2012). A related approach to demographic analysis, the integral projection model (IPM) defines continuous statistical relationships between each vital rate and the age or size of the individual (Rees *et al.* 2014). In this way, data from all individuals are used to define vital rates throughout a broader range of the life cycle, instead of limiting vital rate calculations to only one stage within a matrix. An IPM may therefore more precisely represent a species' demography than do matrix models, as Zuidema *et al.* (2010) demonstrate. Our study combined discrete and continuous relationships between vital rates and size classes within a matrix population model framework, as described by Morris and Doak (2002). This approach permitted a simpler application of the most characteristic advantage of an IPM. We used stochastic and deterministic matrix models to highlight critical areas of concern for *Bertholletia excelsa* (Bonpl., Lecythidaceae), a long-lived, slow-growing Amazonian species with high cultural, economic, and ecological importance. Our approach offers three novel contributions to the scientific understanding of *B. excelsa* demography: the models (1) incorporate data from the longest continuous monitoring effort for *B. excelsa* (up to 14 years for a key vital rate in one population); (2) build on detailed research of each component of the life cycle; and (3) include vital rate variation within two populations to estimate uncertainty in analyses of population growth rates and projections. In this study, we (1) test the hypothesis that the observed *B. excelsa* populations are stable given current rates of nut harvest; and (2) consider how a changing climate, particularly projected reduced rainfall in Western Amazonia (IPCC 2014), might influence *B. excelsa* demography.

METHODS

STUDY SPECIES.—*Bertholletia excelsa* is an iconic Amazonian tree, reaching up to 50 m tall and 3 m dbh (Zuidema 2003). It occurs in *terra firme* (non-flooded) forests throughout the basin (Mori & Prance 1990). In Eastern Amazonia, studies report that *B. excelsa* is clumped in 'groves' with average adult (>40 cm dbh) densities of 6.3 and 9.2 trees/ha, respectively (Scoles & Gribel 2011). In Western Amazonia, populations tend to exhibit more dispersed distributions, as in our two Acre sites and those in Madre de Dios, Peru, with densities of 1.01 (Wadt *et al.* 2008) and 1.58 adult trees/ha (unpubl. data) and 0.54–0.75 trees/ha (Rockwell *et al.* 2015), respectively. Fruits are spherical indehiscent capsules weighing 1–2 kg (Zuidema 2003) and contain approximately 10–25 seeds (Mori & Prance 1990). Fruit production is highly variable among individuals (Kainer *et al.* 2007), and variable among years (Kainer *et al.* 2014). For example, 40 percent of reproductive adults in one of our study sites produced fewer than 20 fruits per year over 5 years, while one produced 801 fruits in an exceptionally productive year (Kainer *et al.* 2007). Fruits are opened and seeds are dispersed primarily by agouti (*Dasyprocta* spp.) (Haugaasen *et al.* 2010), a scatter-hoarding rodent that buries them in predominantly single-seed caches away from the parent tree.

Bertholletia excelsa requires canopy gaps and/or clearings to reach the sapling stage and grow into adults (Zuidema & Boot 2002). According to our previous research, juveniles grow to 40–50 cm dbh and achieve canopy dominance, after which basal area growth rates stabilize and reproduction begins (Staudhammer *et al.* 2013). Fruit production then increases steadily, peaks when adults are in the 100–150 cm dbh size range, then falls as adults reach maximum size (Kainer *et al.* 2007), translating to a reproductive period lasting for at least 150 years. Tree ring analyses and repeated diameter measurements estimate individuals to reach 400 years or older (Schöngart *et al.* 2015), while radiocarbon dating has suggested a maximum lifespan of >1000 years (Vieira *et al.* 2005). *Bertholletia excelsa* reproductive ecology and longevity suggest that population vital rates may fluctuate dramatically among years while tree abundance and population structure change only gradually, indicating that long-term studies are essential to understand its demographic processes and trends.

STUDY SITES.—Filipinas and Cachoeira are former rubber estates located 30 km apart in the state of Acre, Brazil near the borders of Bolivia and Peru. Both are within federally designated areas where traditional peoples reside, extract forest resources, and

practice subsistence agriculture and small-scale cattle ranching. Filipinas forms part of the Chico Mendes Extractive Reserve (CMER), and Cachoeira is an agroextractive settlement project (officially known as PAE Chico Mendes). Cachoeira has generally had higher levels of forest disturbance than CMER due to a longer period of road access, more development projects, and legal timber harvest since 2001 (Stone 2003, Serrano 2005). Each location has similar forest composition and forest cover (92% and 90%, respectively) (SEMA 2010, Coopeagro 2001); however, Filipinas has greater liana presence. Average regional temperature is ~25°C, dropping to ~8°C in the June–August dry season (INMET 2015). Average annual rainfall between 1970 and 2014 in Rio Branco, 120 km away, ranged from 1770 to 1880 mm (Instituto Nacional de Meterologia 2015).

Commercial collection of Brazil nuts in the region likely started before 1933, the year in which a plant in Xapurí began processing them for export (Bakx 1988) although precise collection histories for our sites are unknown. Brazil nut extraction in both communities is a seasonal activity as fruits fall from mid-November to early February (de Faustino et al. 2014). Harvest intensity estimates from measured annual fruit production versus plot-based surveys of post-harvest fruit counts indicated differences between the sites (da Oliveira 2011). Between 2008 and 2010, an average of 25–53 percent of fruits produced was harvested in Filipinas versus 77–85 percent in Cachoeira (95% confidence intervals, da Oliveira 2011).

MODEL CONSTRUCTION.—We used matrix population models to quantitatively represent how the two B. excelsa populations change over time. Transition matrices, the essential components of matrix models, were comprised of three vital rates quantified for each stage in the life cycle of B. excelsa: (1) stasis, the probability of an individual surviving and remaining in its current size class after 1 year; (2) growth, the probability of an individual surviving and passing to the next largest or regressing to the next smallest size class after 1 year; and (3) fecundity, the average annual seedling production per individual in a given adult size class. We divided the populations of Filipinas and Cachoeira into 24 and 27 size classes, respectively. We defined the first two size classes as seedlings (<1.5 m height) and saplings (≥1.5 m height and <10 cm dbh) since they are biologically distinct phases of B. excelsa development. An assessment of the sensitivity to size class width revealed that the long-term population growth rate (λ) calculated from deterministic transition matrices changed by a magnitude of ≤0.001 for size classes 10 cm dbh or smaller, an amount smaller than the uncertainties in vital rates (Table S1). We therefore defined standard 10 cm dbh size classes for juveniles (10–40 cm) and reproductive adults (40–240 cm dbh for Filipinas, 40–260 cm dbh for Cachoeira). Model parameters were based on diverse observational studies focused on population structure, fruit yield, growth, and regeneration from a 420-ha landholding in Filipinas and a 192-ha area in Cachoeira (Tables 1 and 2).

Fecundity values applied to the transition matrices equaled the proportional fruit production by trees in each size class multiplied by the overall annual seedling recruitment rate per adult tree (Fig. 1). Fruit production was observed from samples of 136 and 141 reproductive trees in Filipinas (between 2002 and 2008) and Cachoeira (between 2010 and 2016), respectively. For each site, a generalized linear mixed model (GLMM) was fit to estimate annual production by tree size. We used dbh and dbh-squared as predictor variables and a random effect to account for the repeated measurements made on each tree. For Filipinas, we fit a quadratic function to marginal means of 50 cm dbh size ranges predicted by the fruit production GLMM developed by Staudhammer et al. (2013) (Fig. S1). Since marginal means are computed with all other model variables at their average levels, this had the effect of creating a production—dbh relationship for

TABLE 1. *Sources for estimation of vital rates for Filipinas.*

Parameter	Size classes	Metric	Mean	Standard deviation	Sample size[a]	Year(s)	References
Fecundity	Adults (>40 cm dbh)	Seedling recruitment per hectare	1.531	±0.520	108 subplots (6.75 ha total)	2007–2010	da Oliveira (2011)
		Reproductive adults per hectare	0.92	n/a	4 plots (36 ha total)	2003–2004	Wadt et al. (2008)
		Fruit production per reproductive adult	GLMM	n/a	136	2002–2008	Staudhammer et al. (2013)
Growth	Seedling	Mean height growth (m)	0.065	±0.129	51	2005–2006	da Oliveira (2011)
	Sapling	Mean dbh growth (cm)	0.215	±0.190	8	2007–2010	da Oliveira (2011)
	Juveniles and Adults (>10 cm dbh)	Mean estimated bai[b] (cm²)	See Table S3	See Table S3	190	2002–2008	Staudhammer et al. (2013)
Survival	Seedling	Proportion survived	0.814	±0.044	73	2007–2010	da Oliveira (2011)
	Sapling	Proportion survived	0.96	n/a	24	2007–2010	da Oliveira (2011)
	Juveniles and Adults (>10 cm dbh)	Proportion survived	See Table S5	See Table S5	516	2001–2015	Wadt et al. (2008), original data

[a]Number of trees, unless otherwise indicated.

[b]Basal area increment: the annual increase in cross-sectional area of the tree trunk at breast height (1.4 m).

TABLE 2. *Sources for estimation of vital rates for Cachoeira.*

Parameter	Size classes	Metric	Mean	Standard deviation	Sample size[a]	Year(s)	Reference
Fecundity	Adults (>40 cm dbh)	Seedling recruitment per hectare	0.938	±0.226	108 subplots (6.75 ha total)	2007–2010	da Oliveira (2011)
		Reproductive adults per hectare	1.67	n/a	4 plots (36 ha total)	2003–2004	Wadt *et al.* (2008)
		Fruit production per reproductive adult	See Table S2	n/a	141	2010–2016	Original data
Growth	Seedling	Mean height growth (m)	0.093	±0.121	12	2005–2006	da Oliveira (2011)
	Sapling	Mean dbh growth (cm)	0.234	±0.370	14	2007–2010	da Oliveira (2011)
	Juveniles and Adults (>10 cm dbh)	Mean estimated dbh increment[b] (cm)	See Table S4	See Table S4	174	2010–2016	Original data
Survival	Seedling	Proportion survived	0.626	±0.084	17	2007–2010	da Oliveira (2011)
	Sapling	Proportion survived	0.97	n/a	21	2007–2010	da Oliveira (2011)
	Juveniles and Adults (> 10 cm dbh)	Proportion survived	0.998	n/a	372	2008–2016	Wadt *et al.* (2008), original data

[a]Number of trees, unless otherwise indicated.

[b]Diameter at breast height increment.

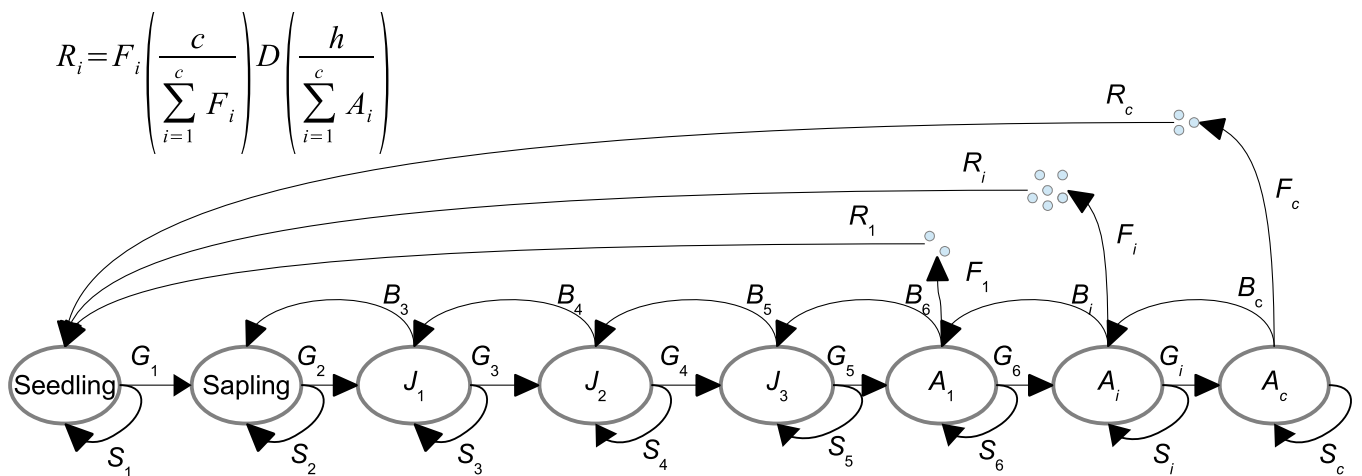$$R_i = F_i \left(\frac{c}{\sum_{i=1}^{c} F_i} \right) D \left(\frac{h}{\sum_{i=1}^{c} A_i} \right)$$

FIGURE 1. Life cycle diagram of the matrix population models. The population vector includes abundances of seedling, sapling, juvenile J_1 through J_3, and adult A_1 through A_c size classes. The transition matrix includes stasis S_i, the probability of advancing G_i to the next largest and of regressing B_i to the next smallest size class, and fecundity R_i dependent upon the predicted fruit production F_i for adults of a particular size, the inverse of average fruit production across all size classes $c/\Sigma_{i=1}^{c} F_i$, the average seedling recruitment per hectare D, and the abundance of adult trees $\Sigma_{i=1}^{c} A_i$ in the sample area of h hectares.

average year and average crown form conditions. For Cachoeira, we used unpublished data (F-statistic = 27.37, P-value <0.001, Table S2, Fig. S1). Model estimates were used to predict proportional fruit production of each of the 10 cm size classes. Annual seedling recruitment per adult tree was calculated by dividing seedling recruitment per hectare observed between 2007 and 2010 (da Oliveira 2011) by the number of reproductive adults per hectare (Wadt *et al.* 2008). Sampling uncertainty associated with seedling recruitment was incorporated into the fecundity rates in the transition matrix, but that of fruit production was not.

Seedling and sapling survival and growth rates were based on observations from 108 1/16 ha subplots within each study

site, surveyed annually between 2007 and 2010 (da Oliveira 2011). Average estimated diameter growth rates of trees >10 cm dbh at the Filipinas site were calculated from a growth function based on a sample of 140 adults and 54 juveniles observed quarterly over a 4-year and 3-year period, respectively. The model predicted basal area increment (bai) with a general linear mixed model which included diameter, rainfall, and reproductive status as covariates and a random effect to account for repeated measures on each tree (Table S3, Staudhammer *et al.* 2013). The rainfall effect was applied to the transition matrix by dividing annual rainfall measures by four. The reproductive status effect was applied assuming that trees <40 cm dbh had not begun fruiting,

while all those ≥40 cm dbh had. A separate GLMM of dbh increment was fit for trees in Cachoeira based on a subsample of 174 trees observed annually between 2010 and 2016, which included diameter and annual rainfall as fixed effects with normal error distributions, and individual trees as random effects (Table S4). The model with the lowest Akaike's Information Criteria (AIC) value was selected as the best fit (Akaike 1973). Growth rates were applied as the probability of advancing to the next largest or regressing to the next smallest size class within the transition matrices by dividing the predicted diameter increment by the width of the size class: 10 cm. The probability of advancing from the largest size class was set to zero to prevent trees from growing out of the largest size class.

Survival rates of trees in Filipinas >10 cm dbh were based on a logistic regression analysis of all 516 trees from the original 2001 census that could be accounted for in 2015, which included dbh, crown form, crown position, liana load, and liana cutting treatment as fixed effects, and individual trees as random effects (Table S5, Appendix S1). A similar analysis was not performed for the Cachoeira population because mortality of the 372 original trees of the 2008 census was near zero when reassessed in 2016. We therefore assigned the observed overall survival rate of juveniles and adults to all size classes (Table 2). Stasis probabilities in the transition matrix were equal to the survival rate minus the probability of growing out of that size class according to each site's dbh growth function.

We developed stochastic and deterministic transition matrices based on independent identically distributed random variables describing seedling recruitment, seedling growth and survival, sapling growth, >10 cm dbh growth functions (for both sites), and a > 10 cm dbh survival function (only for Filipinas). Values were randomly selected from normal (growth and adult survival), gamma (recruitment), or beta (seedling and sapling survival) distributions as appropriate for each average parameter estimate or coefficient within the functions. The mean dbh of each diameter size class was inserted into each of the variable growth and survival functions. Sapling survival at both sites and survival of trees >10 cm dbh in Cachoeira remained fixed for all iterations of the transition matrices.

KEY ASSUMPTIONS.—Matrix population models are based on population averages, resulting in key model assumptions. First, the rate that new seedlings enter the populations was assumed to depend only upon the number and distribution of reproductive adults. We were unable to include agouti activity or light conditions underneath the canopy into the model—variables known to influence seedling recruitment (Cotta *et al.* 2008). Second, all statistics for seedlings and saplings reflect survival, growth, and recruitment under mature forest conditions. Third, while tree growth parameters depended on rainfall inputs according to the fitted growth function for each site, model survival and fecundity rates did not change according to annual rainfall. Thus, any differences in population growth rate due to rainfall differences were through changes in the growth rate only, and not through changes in survival or reproduction rates. Finally, survival

parameters for saplings, juveniles, and adults in the Cachoeira model did not incorporate sampling uncertainty, thereby less accurately representing its source population than did the Filipinas model.

MODEL ANALYSIS.—Resultant analyses using matrix population models reveal (1) generation time, defined as the estimated time required for a new seedling to reach reproductive size (40 cm dbh for *B. excelsa* in our sites); (2) potential long-term population growth rate (λ) (Caswell 2001); (3) each vital rate and size class's contribution to the population growth rate (Otto & Day 2007); (4) comparisons between the stable stage distributions and observed distributions; and (5) projections of tree abundance. The value of λ is 1.0 for stable populations.

We produced estimated ranges of generation time based on model uncertainty by summing the expected growth rates in the pre-reproductive classes of 100 iterations of the deterministic transition matrix (assuming average rainfall) which incorporated parameter uncertainty. To assess the potential influence of rainfall on tree demography through distinct diameter growth rates, we ran 1000 iterations of the deterministic transition matrix including parameter uncertainty assuming estimated average diameter growth rates for the driest, the average, and the wettest years between 1970 and 2014 from weather station measurements in Rio Branco (933, 1907, and 2689 mm respectively, Instituto Nacional de Meterologia 2015). The dominant eigenvalue, λ, was calculated according to methods described by Caswell (2001). We compared the distributions of λ outputs using the median, 75% and 90% quantiles.

We reported the relative sensitivity of λ to perturbations of vital rates through elasticity analyses described by Caswell (2001) on fixed versions of the deterministic transition matrices for each site (which excluded parameter uncertainty in vital rates), assuming average rainfall in the growth functions. We excluded elasticity analyses reflecting parameter uncertainty in the deterministic transition matrix because similar elasticity matrices were produced.

The stable stage distribution, the right eigenvector of a transition matrix, is the asymptotic relative abundance of individuals in all classes (Caswell 2001). We compared the stable stage distribution from deterministic transition matrices (excluding parameter uncertainty) with the observed distribution, as differences between them can indicate fluctuating vital rates. We calculated Cohen's cumulative distance (Cohen's D_1) to quantify the distance between the stable stage and observed distributions (Cohen 1979).

Finally, for each site, we projected adult tree abundance 50 years into the future to illustrate transient population dynamics. Projections reflected model uncertainty by showing the range of 100 model runs of the stochastic transition matrices using randomly generated annual rainfall sequences from observations between 1970 and 2014.

We constructed and evaluated regression functions using the lme4 (Bates *et al.* 2014), and ResourceSelection packages (Lele & Keim 2006), calculated λ and performed elasticity analyses using the popbio package (Stubben & Milligan 2007), and calculated Cohen's D_1 using the popdemo package (Stott *et al.* 2012) in the R statistical environment (R Core Team 2015).

RESULTS

Staudhammer *et al.* (2013) reported a significant positive relationship between rainfall and bai for trees in Filipinas (*t*-value = 24.95, *P*-value <0.0001, Table S3, Fig. S2). Likewise, rainfall had a positive effect on dbh increment in Cachoeira (*t*-value = 2.474, *P*-value = 0.0135, Table S4, Fig. S2).

Survival rates differed dramatically between sites. In 2015, we found 530 of the 568 trees >10 cm dbh originally censused in Filipinas in 2001–2002. After 14 years, 50 trees had died within mature forest, and 14 were in clearings for electricity lines and pasture, but excluded from the survival analysis. Larger adults (>120 cm dbh) were the most likely to die, followed by juveniles (10–40 cm dbh) and finally smaller adults (40–120 cm dbh, Fig. S3). The most likely identified causes of mortality were wind (10 trees), a 2006 storm (4), fire (2), and liana infestation (2). Cachoeira presented lower mortality rates—only 1 juvenile of 69 and 3 adults of 303 died after 8 years of observation (Fig. S3).

Estimates of generation time were highly variable for both sites. The deterministic matrices including model uncertainty produced medians of 167 and 83 years, and the 25–75 percentile interval ranged between 126–200 years and 64–112 years for Filipinas and Cachoeira, respectively (Fig. S5). Deterministic transition matrix comparisons assuming estimated average growth rates under dry, average, and wet conditions revealed that the median λ values for each site and rainfall measure were within 0.998 and 1.044 for Filipinas, and within 1.007 and 1.010 for Cachoeira (Table 3). The 5–95 percentile interval of λ values for all rainfall assumptions fell between 0.997 and 1.058 for Filipinas, and between 0.998 and 1.025 for Cachoeira. For both sites, distributions of λ included values that were highest under wet conditions, lowest under dry conditions, and in between under average conditions.

The elasticity analyses confirmed that both populations exhibited little relative sensitivity to changes in diameter growth rates and fecundity rates (Fig. 2). Instead, stasis rates of individuals from the sapling size class and above most influenced λ (Fig. 2).

The observed distributions in both sites contained fewer juveniles and young adults and more adults >70 cm dbh than did their stable stage distributions (Fig. 3). The distance between the observed and stable stage distributions was larger for Filipinas (Cohen's D_1 = 36.89) than for Cachoeira (Cohen's D_1 = 9.62).

Projections of adult abundance reflected differences in demographic trends between the two observed sites. Adult density was projected to show a transient decline from 1.06 to about 1.00 trees per hectare (tph) by year 2030, after which it would increase at a rate approximating λ times the population size (Fig. 4). Cachoeira's adult density was projected to increase from 1.57 to about 1.75 tph by year 2058 (Fig. 4).

DISCUSSION

Our use of demographic models that incorporated long-term monitoring (up to 14 years) with detailed research on each life cycle component and variation in vital rates to estimate uncertainty provides one path to further illuminate population stability and sustainable NTFP harvest patterns and bottlenecks. Where large demographic data sets are available (>300 individuals), a matrix model may describe species demography as effectively as an IPM (Ramula *et al.* 2009). Our approach following Morris and Doak (2002) provides an example using data from each individual to define continuous functions and incorporate sampling uncertainty within methods already familiar to many ecologists. At the same time, robust demographic analysis of long-lived trees is challenging because accurate estimates of the three vital rates (survival, growth, and reproduction) require years of repeated measurements. Survival probability is particularly difficult to quantify, since mortality observations beyond the sapling stage are rare although more advanced approaches define tree survival more accurately where data are sparse (Metcalf *et al.* 2009, Sevanto & Xu 2016). The IPM method is likely the preferred option for demographic studies based on more modest data sets (Ramula *et al.* 2009, Zuidema *et al.* 2010).

Our comparison of two populations linked to communities with subtly different livelihoods and nut harvest intensities highlights that while demographic similarities exist, each population has its own dynamics. Analyses using our matrix models of both sites are consistent with earlier studies (Wadt *et al.* 2008, da Oliveira 2011), concluding that these populations are not in decline. However, the differences between the observed and stable stage distributions indicate that vital rates are not constant, causing transient dynamics to fluctuate over time, particularly in Filipinas.

Results from the elasticity analyses suggest that sapling and adult survival were the strongest determinants of long-term population stability, corroborating Zuidema and Boot's (2002) *B. excelsa* matrix models although sustained low seedling recruitment levels may produce negative long-term effects. Our estimates of generation time are consistent with other studies, which assert that the size at which most trees reach reproductive maturity, 40 cm dbh, can be achieved under the forest canopy from between 73 and 93 years (based on direct measurements in Pará

TABLE 3. *Distribution of λ values from the deterministic transition matrices incorporating parameter uncertainty.*

Site	Rainfall	Quantiles				
		0.05	0.125	Median	0.875	0.95
Filipinas	Dry	0.997	0.997	0.998	1.020	1.026
	Average	0.998	0.999	1.030	1.041	1.046
	Wet	1.028	1.034	1.044	1.054	1.058
Cachoeira	Dry	0.999	0.999	1.007	1.014	1.017
	Average	0.999	1.000	1.009	1.018	1.021
	Wet	0.998	0.999	1.010	1.021	1.025

Quantiles from the distribution of λ outputs from 1000 iterations of the model assuming estimated average diameter growth rates for dry (933 mm), average (1907 mm), and wet (2689 mm) years.
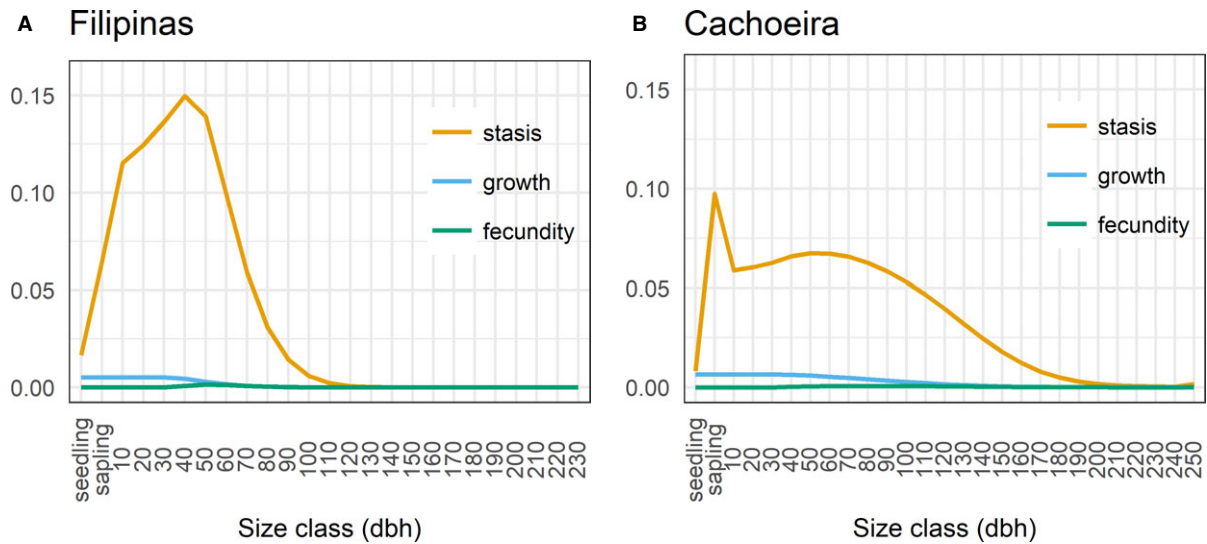
FIGURE 2. Elasticity analyses of the deterministic transition matrices without incorporating sampling uncertainty and assuming average rainfall.
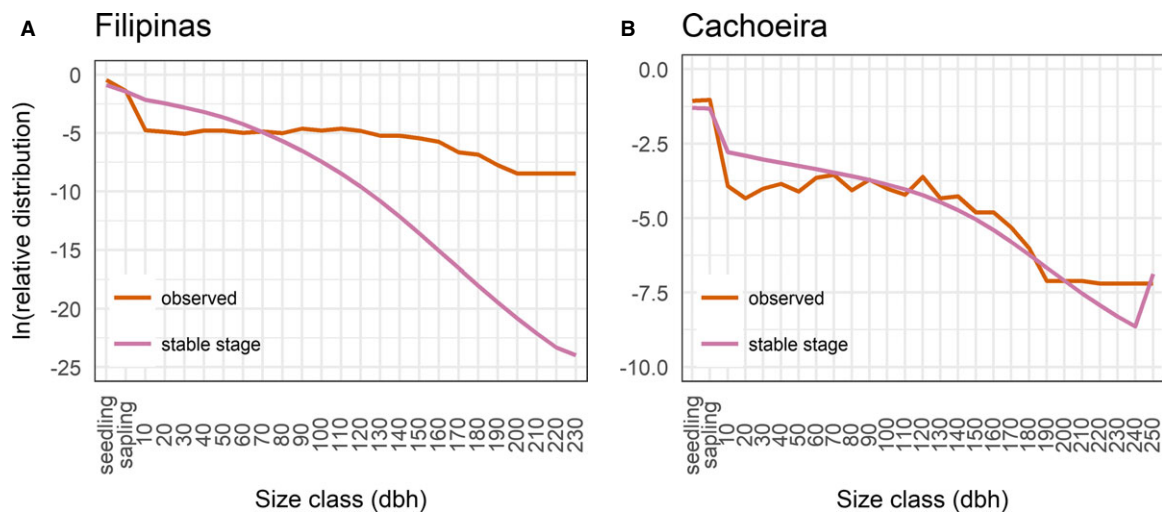

FIGURE 3. Natural log-transformed comparisons between observed distributions and stable stage distributions calculated from deterministic transition matrices without incorporating sampling uncertainty.

and Amazonas, Brazil; Schöngart *et al.* 2015), to approximately 100 years or more (based on tree ring measurements from Pando and Beni, Bolivia; Brienen & Zuidema 2006). This long-lasting juvenile period and the high sensitivity of population growth rate to stasis rates of trees from the sapling to adult stages imply that a focus on protecting pre-reproductive and mature individuals is paramount for future generations.

POPULATION STABILITY IN THE PRESENCE OF FRUIT HARVEST.—Harvest of wild fruits reduces the amount available to animal seed dispersers. Yet, recent studies have shown that factors such as destructive harvest methods, cattle ranching, and vegetation thinning are more responsible for decline in abundance of certain NTFPs than are the targeted fruit harvests (Giroldo & Scariot

2015, Isaza *et al.* 2016). What is still unclear for *B. excelsa* is which levels of nut harvest might induce a cascading effect of fruit scarcity for agouti (*Dasyprocta* spp.), resulting in fewer buried seeds and reduced germinants. Differences between our two sites permit more nuanced interpretation of the relationship between fruit harvest intensity and long-term population stability. Scatter-hoarders open more unharvested fruits in Cachoeira than in Filipinas (average of 96 vs. 63 open fruits per ha per year between 2008 and 2010, p < 0.001, da Oliveira 2011), but more seedlings are recruited from those remaining fruits in Filipinas (Tables 1 and 2). Relative seedling density per reproductive tree in our sites (6.1 in Filipinas, 2.0 in Cachoeira) is comparable to those found by Zuidema and Boot (2002) (approximately 3.0 in El Tigre and 2.4 in El Sena) in sites where population stability
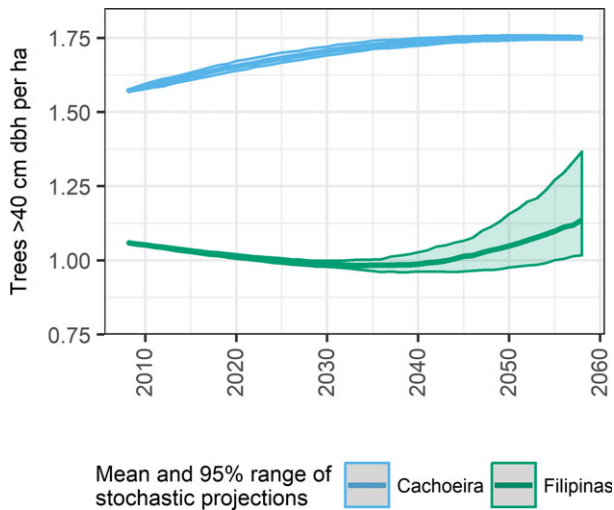
FIGURE 4. Projected adult abundance (>40 cm dbh) for 50 years using stochastic transition matrices incorporating sampling uncertainty, respectively.

was demonstrated through population matrix models, despite high seed harvest rates. Thus, we offer no evidence to suggest a relationship between rates of nut harvest and long-term population stability. Moreover, the long-term population growth rate of a transition matrix assumes constant environmental conditions and that the population structure reflects its stable stage distribution. Species with long generation times are unlikely to ever reach their stable stage distributions before environmental change occurs, potentially altering vital rates. In the *B. excelsa* case, while our projections indicate stable populations for several decades, we are not confident that environmental and management conditions under which these populations were modeled would be unchanged in subsequent decades.

Still lacking, however, is more knowledge on fruit and seed fate and potential changes in animal disperser behavior in response to various harvest rates. Detailed investigations of seed caching and dispersal (Haugaasen *et al.* 2010) and of fruit fate (de Faustino 2012) already provide useful guidance, but further research on the processes connecting fruit availability, seed dispersal, and seedling establishment is needed before imposing harvest restrictions, which immediately affect family income and potentially, motivations to conserve standing forest.

POTENTIAL EFFECTS OF REDUCED RAINFALL.—Lower annual rainfall is projected to reduce plant productivity in the Amazon (Hilker *et al.* 2014). Our matrix models produced distributions of the long-term population growth rate λ which were centered above 1.000 under expected diameter growth rates in dry, average, and wet years, except in Filipinas under dry conditions (Table 3). This result does not reflect all potential demographic sensitivity to changes in rainfall since survival and fecundity rates in the models did not reflect rainfall variation. Still, we found no evidence that isolated years of low rainfall in our sites were a threat to population stability. According to our elasticity analysis, survival

rates for individuals in the sapling size class and larger would have the largest impact on *B. excelsa* demography, but we were unable to determine the relationship between rainfall and survival because of our limited sample size; studies of thousands of individuals (Holzwarth *et al.* 2013) or those focused on physiological traits (Sevanto & Xu 2016) are better suited to examine mortality in long-lived organisms. The 18 of 50 Filipinas mortality cases we could identify with certainty were due to factors unrelated to water availability. Furthermore, the vast majority of trees in Cachoeira survived the 8-year observation period which included the 2010 drought, indicating that isolated years of low rainfall may not pose a threat to *B. excelsa*. However, the probability of tree mortality for Amazonian tree species increases after multiple years of low rainfall (Brienen *et al.* 2015), and climatic futures are uncertain.

MANAGEMENT IMPLICATIONS.—After 80 years of attempts at Brazil nut production in modern plantations, only an estimated 2 percent of Amazonian commercial harvests are produced on several thousand hectares of plantations (Homma *et al.* 2014). This suggests that Brazil nut harvest from existing old-growth forests will continue to play a critical role in the extractive economy and culture of the Amazon. Our findings indicate that it is the survival of these existing trees that is a more pertinent risk to *B. excelsa* demography than the fate of most seeds produced. Our populations and models do not provide evidence that drought is a current threat, but more information is needed to accurately assess the possibility of increased drought occurrence. Finally, changes in human use of the forested landscape are of more immediate concern than rates of fruit harvest or climate change. Continued forest loss is expected as infrastructural improvements expand into more remote portions of the Amazon (Arima *et al.* 2008). However, legally designated sustainable use areas, such as our study areas, have been shown to substantially reduce deforestation even as road networks expand (Barber *et al.* 2014). They also permit reserve residents to derive income and subsistence benefits from NTFP species housed within these forests. In the face of potential shifts in land use and livelihood strategies throughout the Amazon, more attention should be allotted to avoid damage to existing valuable NTFP tree species from the sapling stage and beyond. Managing for stable or growing populations of valuable, long-lived tropical species like *B. excelsa* depends on an understanding of the entire life cycle, a timeframe which includes anthropogenic pressures and change.

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DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.br360 (Bertwell *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Survival probability analysis for Filipinas.

TABLE S1. *Sensitivity of long-term population growth rate λ to size class width, calculated from deterministic transition matrices.*

TABLE S2. *Best-fit annual fruit production model for Cachoeira.*

TABLE S3. *Estimated fixed effects from annual bai model for Filipinas (Staudhammer* et al. *2013).*

TABLE S4. *Estimated fixed effects from annual dbh increment model for Cachoeira.*

TABLE S5. *Best-fit survival model for Filipinas.*

FIGURE S1. Average annual fruit production by tree size as predicted by models for Filipinas and Cachoeira, respectively.

FIGURE S2. Average annual basal area increment in Filipinas and Cachoeira by tree size, as predicted by models for wet, average, and dry years.

FIGURE S3. Distribution of mortality across the entire study sites in Filipinas and Cachoeira.

FIGURE S4. Logistic regression model for survival probability for Filipinas.

FIGURE S5. Boxplot of generation times, defined as the estimated time required for a new seedling to reach reproductive size.

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