

REPORTS

Demographic Threats to the Sustainability of Brazil Nut Exploitation

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A comparative analysis of 23 populations of the Brazil nut tree (*Bertholletia excelsa*) across the Brazilian, Peruvian, and Bolivian Amazon shows that the history and intensity of Brazil nut exploitation are major determinants of population size structure. Populations subjected to persistent levels of harvest lack juvenile trees less than 60 centimeters in diameter at breast height; only populations with a history of either light or recent exploitation contain large numbers of juvenile trees. A harvesting model confirms that intensive exploitation levels over the past century are such that juvenile recruitment is insufficient to maintain populations over the long term. Without management, intensively harvested populations will succumb to a process of senescence and demographic collapse, threatening this cornerstone of the Amazonian extractive economy.

There is considerable interest in the promotion of nontimber forest products (NTFPs) as a tropical forest conservation strategy (1, 2). Brazil nuts are a classic NTFP and are the only internationally traded seed crop collected exclusively from natural forests (3). In the Brazilian Amazon alone, over 45,000 tons of Brazil nuts are collected annually, with sales of over U.S. \$33 million (4). Despite early warnings that the exploitation of this wild seed crop might

not be sustainable (5), it has generally been argued that current seed collection intensities may have little impact on the demography of natural populations (6, 7). Other reports, however, have noted that *Bertholletia excelsa* stands are often dominated by cohorts of large trees and lack juveniles (1, 8, 9), suggesting that the regeneration dynamics of natural populations have been undermined. Here we show that patterns of variation in population size structure are consistent with recruitment bottlenecks resulting from long-term harvest.

The Brazil nut tree *B. excelsa* (Lecythidaceae), the sole source of Brazil nuts, is a long-lived and widespread emergent tree in lowland Amazonian forests (Fig. 1). It produces extremely hard globose fruits (11 to 16 cm in diameter) with 10 to 25 seeds or "Brazil nuts" that remain encased after fruit fall, facilitating harvest. Under natural conditions, the fruits are typically gnawed open by agoutis [*Dasyprocta* spp. (10, 11)], which scatter-hoard the seeds [see (12, 13) and supporting online materials for further details on the regeneration ecology of *B. excelsa*].

We surveyed and measured all trees ≥ 10 cm in diameter at breast height (DBH) within 22 natural *B. excelsa* populations in the Brazilian, Peruvian, and Bolivian Amazon (Fig. 1 and table S1). Size structure data from one additional population (site 13) are restricted to the relative abundance of adults and juveniles. All populations had been subjected to different levels of seed exploitation but were otherwise located in structurally undisturbed

primary forests under varying degrees of hunting pressure (14). On the basis of size at first flowering and fruiting, juveniles were defined as trees < 60 cm DBH (15).

The history of seed exploitation at each site was documented using public records, interviews with local Brazil nut collectors, and/or systematic counts of fruits that had been opened by either human collectors or natural scatterhoarders in order to determine approximately (i) the proportion of fruits removed, (ii) the proportion of trees harvested, (iii) the length of the harvesting period since 1900, and (iv) how often the annual harvest had failed to take place during this period. A principal component analysis (PCA) was then used to class harvested stands into one of four broad levels of harvest pressure (figs. S1 and S2), with unharvested stands being defined as those where no systematic seed collection took place during the 20th century. For all forest sites, we compiled ranked data on forest type (reflecting canopy openness), soil nutrient availability, annual rainfall, degree of seasonality (number of dry months with < 50 mm of rainfall), and the level of hunting pressure (four classes) over the past 20 years. The main natural seed predator and seed dispersal agent (agoutis) and the main seedling herbivores were also assigned to one of four abundance classes.

The size of the trees and age structure of the stands were affected by the history of seed harvest. Persistently harvested stands were characterized by larger (and presumably older) trees and few or no juveniles (Fig. 2, A and B). Juveniles were most common in unharvested (range = 31 to 76% of all trees, $n = 5$ stands) and lightly harvested stands (10.6 to 47%, $n = 10$), uncommon to rare in moderately harvested stands (3.8 to 25%, $n = 5$), and virtually absent where seeds had been persistently collected (0.7 to 1.6%, $n = 3$). In the extreme, the only individuals < 60 cm DBH at Alto Cajari Extractive Reserve (site 6) were resprouts of trees broken by wind turbulence, which have no reproductive value (12).

We compared size distributions across sites using s^* , an index that measures the shape of the cumulative size distribution. High (or positive) values of s^* indicate populations with low median sizes (many juveniles) and a wide spread of sizes, whereas low (negative) values of s^* indicate populations with high median sizes (few juveniles) and little variance about the mean (16); that is, senescent populations (Figs. 1 and 2C). Because s^* explains most across-population variance in the relative abundance of juveniles ($R^2 = 0.87$, $F_{1,20} = 138.6$, $P < 0.001$), exploitation history can be used to predict the general shape of cumulative size distributions, from the least sinusoid curves, where juveniles are abundant, to the most sigmoidal curves, where juveniles are very rare or missing.

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The long-term correlates of seed removal were confirmed in step-down and step-up multiple regression models incorporating other variables that could potentially have affected the population dynamics of *B. excelsa*; these included the geographic coordinates of each stand, density of Brazil nut trees ≥ 10 cm DBH, soil nutrient availability, total rainfall, strength of the dry season, the abundance of natural seed predators and/or dispersers, the abundance of seedling/sapling herbivores, and classes of canopy openness. Most of these variables were excluded from models explaining either the proportion of juveniles occurring within a stand ($R^2 = 0.89$, $F_{5,17} = 24.9$, $P < 0.001$) or the s^* value of cumulative size distributions [$R^2 = 0.80$, $F_{3,18} = 23.5$, $P < 0.001$ (table S2)].

The only variables other than historical levels of seed collection retained by the models were site longitude, total rainfall, and the abundance of agoutis and large

herbivores. The significance of these variables could be explained by the gradual westward shift in large-scale Brazil nut harvest and trade over the past three decades. The significant relationship between large herbivore (and agouti) abundance and the percentage of juveniles (but not the s^* parameter) of different stands probably resulted from the key role played by (i) terrestrial browsers as seedling/sapling predators and (ii) large rodents as both seed predators and dispersers (10–13). However, the only key variable consistently retained in the regression models was the PCA score summarizing the history of seed harvest.

The conclusion that chronically exploited populations are experiencing a population bottleneck resulting from intensive harvest was tested using a matrix population model (17), which assumed that intense exploitation is applied to previously unexploited populations.

We simulated populations over a period of up to 200 years after the onset of exploitation, and estimated the parameters describing the size distributions (16). There is a close correspondence between the observed size distributions of the exploited populations and those predicted by the model assuming high levels of seed removal (Fig. 3). The model indicates that the simulated population bottlenecks, resulting from between 20 and 200 years of Brazil nut collection, are consistent with the patterns observed in real data. This is a powerful indicator that exploited populations may succumb to a recruitment bottleneck.

The model and field observations point to a dwindling number of increasingly older trees in persistently overexploited stands, which have not been adequately replaced by juveniles in recent decades. The clear message is that current Brazil nut harvesting practices at many Amazonian forest sites are not sustainable in the long

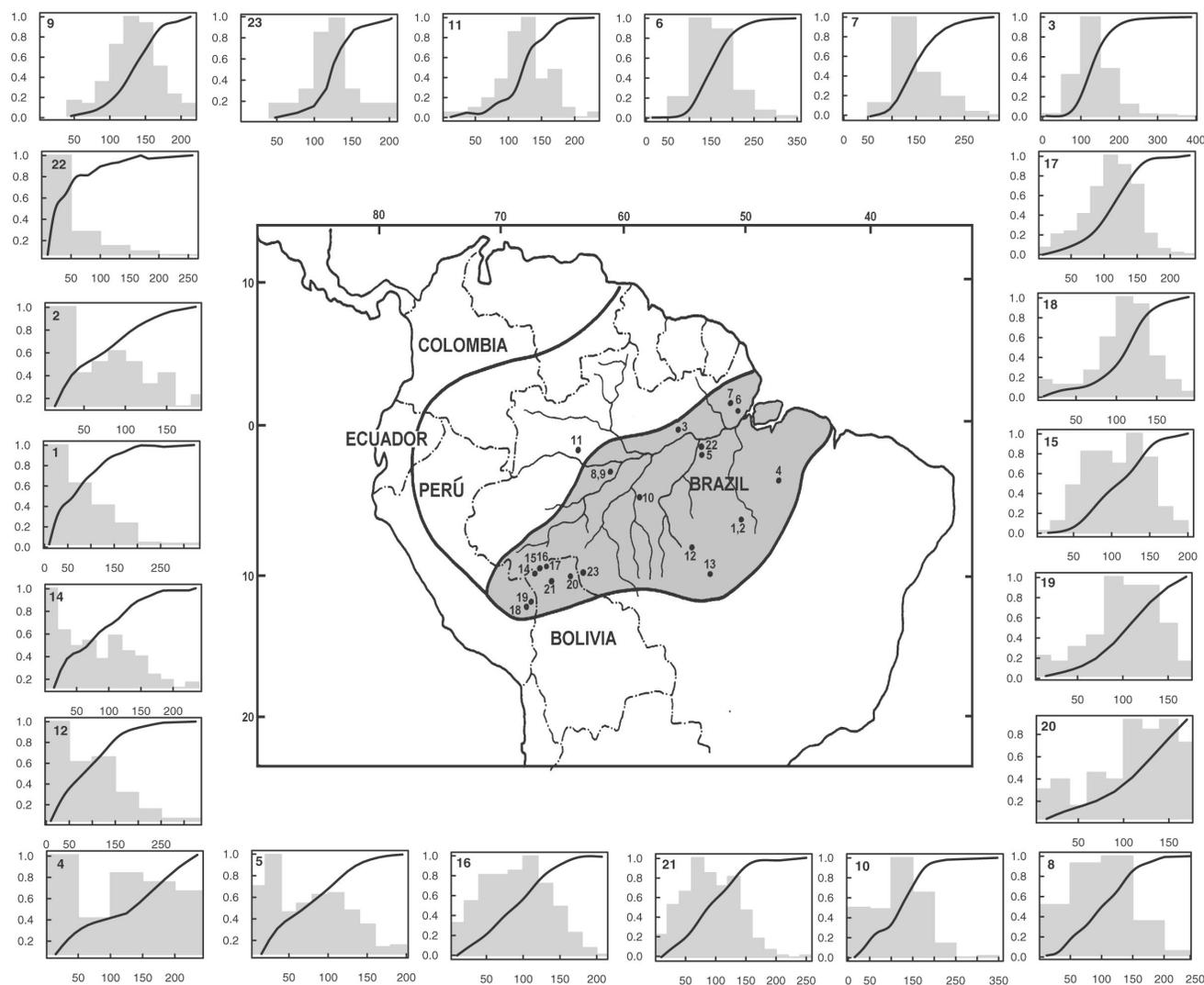


Fig. 1. Distribution of Brazil nut trees, *B. excelsa* (area surrounded by thick line on map), showing the cumulative size distribution of natural populations subjected to varying levels of seed exploitation. The shaded area indicates the region where adult trees may be locally abundant.

Numbers on map and histograms refer to the 23 populations surveyed (table S1). Histograms (DBH in cm) have been ordered clockwise, beginning at the top left, according to s^* , an index of the impact of harvesting on size structure (Fig. 2). Size structure data were unavailable for site 13.

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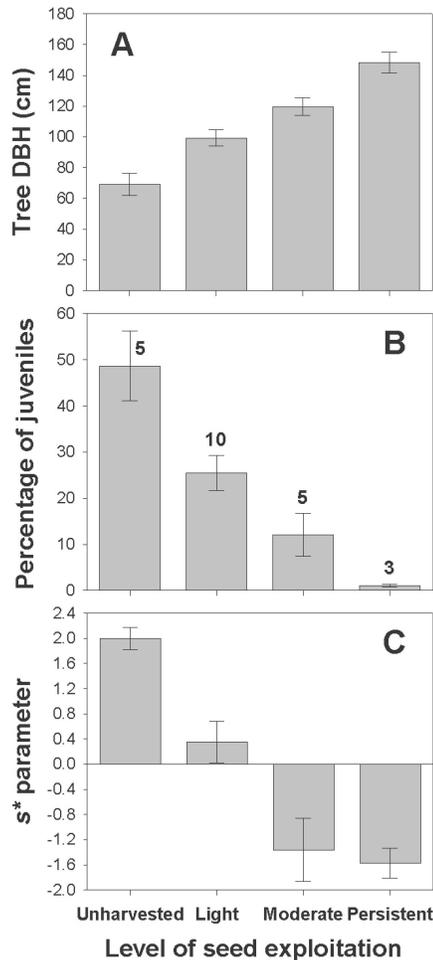


Fig. 2. Relationships between historical levels of Brazil nut collection and mean \pm SE (A) tree size measured as DBH; (B) percentage of juveniles (trees 10 to 60 cm DBH); and (C) the summary statistic s^* , which measures the shape of the cumulative size distribution of each population. Decreasing s^* values reflect populations characterized by high median DBHs and size distributions that are increasingly sigmoid in nature. Numbers next to error bars in (B) indicate the number of populations studied.

term. Over the next few decades, however, seed production can still be maintained because of the long reproductive life-span of Brazil nut trees [>150 years (7)]. Populations with a recent history of intensive exploitation should be monitored closely to avoid future regeneration failure, and strangled populations harvested for several decades should be managed to facilitate recruitment pulses. Low-cost methods to encourage recruitment within natural populations need to focus on increasing the supply of juveniles by managing the annual harvest quota (the percentage of seeds removed), planting viable seeds, or transplanting nursery-grown seedlings. The spatial structure of the harvest may also be manipulated over a supra-annual cycle to facilitate recruitment pulses by relaxing harvesting in annually rotated no-take areas. This would

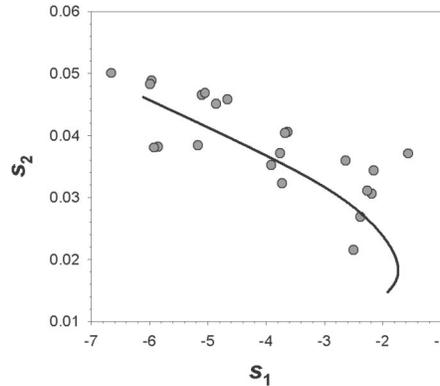


Fig. 3. Modeled and observed Brazil nut tree size structure summary statistics, which measure the median size of the population (s_1) and the slope of the cumulative density function for size at the median (s_2). Circles indicate the values estimated for all populations for which size information is available. The line represents population trajectories over 200 years for the s_1 and s_2 parameters after the commencement of harvesting predicted from a model (17).

increase the seed supply for natural seed predators and dispersal agents, which facilitate seedling recruitment most effectively when they are saturated by large seed crops (10, 12). Subsistence hunting pressure on both seed dispersers and large herbivores could also be controlled or manipulated within Brazil nut groves to maximize the probabilities of seed germination and seedling survival.

The long-term viability of traditional Brazil nut exploitation in the context of primary forests will not, however, depend solely on a healthy age structure and stable turnover of adult populations. More immediate threats to the sustainability of this extractive industry include deforestation and forest degradation (18), which are most prevalent in the highly seasonal southern arc of Amazonia, where high-density *Bertholletia* stands are currently concentrated. Both sound management of natural Brazil nut tree populations and protection of the larger primary forest matrix are required to avert demographic collapse, population decline, and the erosion of this cornerstone of the Amazonian economy.

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14. Supporting material on the study species, sampling sites, methods, and data analysis is available on Science Online.
15. This juvenile cutoff point was a powerful predictor of the proportion of trees <50 cm DBH ($r^2 = 0.97$) in the 23 populations considered in this study.
16. The size distributions were quantified using a logistic regression. Size distributions were expressed as cumulative distributions (as a function of DBH) and were logit transformed [$\text{logit}(p) = \log(p/(1-p))$]. The logit-transformed proportions were then regressed on DBH, fitting the equation $\text{logit}(p) = s_1 + s_2 \text{DBH}$. The parameters are the intercept s_1 , which is a function of the median size of the population, and the slope s_2 , which is related to variance in size. The fitted regression is effectively an estimate of the degree to which the fitted sigmoid function approaches a step function (high slope values) or a linear function (low slope values). s_1 and s_2 were found to be negatively correlated. As a single summary statistic of the nature of the size distribution, we therefore calculated the first axis score of the PCA for the two statistics measured across the 22-populations, and this is termed s^* .
17. This is a Lefkovich structured model [adapted from (7)] in which the population is divided into 17 stages based on size and stage. Census data were used by Zuidema and Boot (7) to estimate rates of transitions between size classes and reproduction. The estimates of model parameters ignored the effects of density dependence, which has been shown to be very important in models of tropical tree populations (19, 20). To account for this, we assumed that seedling survival was density dependent and reduced observed rates of survivorship to yield a population with a finite rate of population growth of 1. We only report results on size classes >10 cm DBH, hence we assume that density dependence acts before plants reach 10 cm DBH and is minimal thereafter. The model parameters were set using data on populations subject to harvesting (7), in which 93% of seeds may be removed. To account for this, we increased the rate of seedling production per tree to $1/0.07 = 14.3$ times the observed level. Because density dependence is assumed to act on seedlings, this modification has little effect on predictions of adult size distributions.
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Supporting Online Material
www.sciencemag.org/cgi/content/full/302/5653/2112/DC1
 Materials and Methods
 Figs. S1 to S3
 Tables S1 and S2
 References

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ERRATUM

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REPORTS: "Demographic threats to the sustainability of Brazil nut exploitation" by C. A. Peres *et al.* (19 Dec. 2003, p. 2112). The affiliations for Claudia Baider and Robert P. Freckleton were incorrect. For Claudia Baider, the affiliation is Departamento de Ecologia, Universidade de São Paulo, São Paulo–SP, 05508-900, Brazil, and The Mauritius Herbarium, MSIRI, Reduit, Mauritius. For Robert P. Freckleton, the affiliation is Department of Zoology, University of Oxford, Oxford OX1 3PS, UK.

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Materials and Methods

The study species

Bertholletia excelsa (Lecythidaceae) is a large emergent tree (up to 50 m tall) of widespread occurrence in lowland Amazonian terra firme (unflooded) forests (S1). Brazil nut trees are very long-lived and, in extreme cases, old individuals of up to 525 cm in DBH (S2) may sustain fruit production for over 500 yrs (S3), as suggested by carbon-dating studies (S4). *B. excelsa* trees produce extremely hard, woody, globose fruits or pyxidia (11-16 cm in diameter) that encase 10-25 large, nutritious seeds containing over 17% of protein and 72% of lipids (S5). Under natural conditions, a pyxidium is typically gnawed open by a large diurnal rodent (agouti, *Dasyprocta* spp.) occupying a home range containing one to several Brazil nut trees (S6). Seeds handled by agoutis are either eaten immediately or scatter-hoarded for later retrieval (S7), whereas >99% of the seeds remaining within unopened fruits die from fungal attack (S8). Subsequently, agoutis may fail to retrieve a minute fraction of the scatter-hoarded seeds which may eventually germinate to become seedling recruits (S8-S9).

Study areas

The *Bertholletia excelsa* populations examined here had been subjected to different levels of seed exploitation over the last century, but were otherwise located in structurally undisturbed primary terra firme (unflooded) forests that have experienced varying degrees of hunting pressure. The only exception was site 22 (Alter do Chão, Pará, Brazil) which had a recent history of recurrent surface fire disturbance (S10), which *B. excelsa* is largely immune to, but may kill a large proportion of other canopy tree species (S11). The atypically high proportion of Brazil nut tree juveniles [and lowest mean DBH (44.9 cm) and highest tree density (23.0 ind. ha⁻¹)] in this recently unharvested population (75.6%, *N* = 78) could therefore also be partly attributed to the

unusually open canopy structure of this forest site, which facilitates recruitment in this species (*S12–S14*). Considering all sites, level of hunting pressure was only weakly correlated with the level of Brazil nut exploitation ($r_s = 0.29$, $P = 0.195$, $N = 23$), so these variables were treated as independent in the multiple regression models.

Summary statistics on *Bertholletia excelsa* populations at all survey sites are presented in Table S1.

Population inventories

Exhaustive population inventories at different forest sites were conducted using either plot-based or plotless methods, and the diameter at breast height (DBH) of all individuals of at least 10 cm DBH were measured using a diameter tape accurate to the nearest mm. Brazil nut trees are unbuttressed so that DBH measurements for all trees were taken at ~136 cm above ground. The strip-width of forest area surveyed whenever a standard line-transect census method was used was truncated in the field to at most 20 m on either side of each transect. During line-transect censuses, two previously trained observers, walking together and slowly (~600 m/h), scanned opposite sides of the transect in search of Brazil nut trees of at least 5 cm DBH. In all cases, the total sampling area was measured, whether population surveys were based on plots, transects, or exhaustive inventories of entire natural clusters of adults and juveniles that are locally referred to as *castanhais* (Brazil) or *manchales* (Peru). Trees smaller than 10 cm DBH, in those populations with a minimum sampling cut-off point of 5 cm DBH, may also have been located and mapped but were later excluded from analyses to maximize comparability across all samples. In all cases, particular care was taken to search for small trees (e.g. 10–20 cm DBH), which could have been intrinsically less detectable than large trees, and therefore overlooked during census work. We are confident, however, that this potential size-dependent detectability bias was greatly reduced by the fact that field work in both harvested and unharvested areas was conducted with the assistance of local Brazil nut collectors who had well developed search images of Brazil nut trees of different sizes and were highly skilled in locating all stems down to small saplings. This search image is also aided by the highly distinctive and deeply fissured bark, crown architecture, and leaf characteristics of *Bertholletia excelsa*. In addition, census work was in most cases carried out over several days, weeks or months which facilitated the continuous combing by different research teams of trees which might have been previously undetected. Finally, we tested for a size-dependent detection bias in

those sites where a line-transect census method was used by examining the relationship between tree size (DBH) and the perpendicular distance (PD) from the transect line to each Brazil nut tree (measured with a Sonin[®] electronic distance measurer). In all five cases where this census method was used, there was no significant relationship between PD and tree size ($P > 0.4$ in all cases), suggesting that small trees farther away, but within a distance of 20 m, from the transect line were not intrinsically less detectable than larger trees.

Population classification in terms of the history of seed harvest

The *B. excelsa* seed exploitation categories were assigned using information on four key variables: (1) approximate (or estimated) number of years each population had been under a systematic regime of seed collection since 1900; (2) approximate percentage of mature fruits collected per tree; (3) approximate percentage of adult trees that were collected within a stand; and (4) approximate number of annual pulses of complete release of the seed crop from collection. These variables were entered into a principal component analysis (PCA). The first principal component explained 71% of the variance in these data. The scores for the first principal component were ranked (see Fig. S1), and based on these ranks, the populations were divided into four harvest categories.

PCA scores derived from the history of seed exploitation were strong predictors of the size structure and relative abundance of juveniles in each Brazil nut population (Fig. S2).

Other environmental variables

The long-term consequences of seed removal were also examined in multiple regression models incorporating other variables that could potentially also have affected the population dynamics of *B. excelsa*; these included the geographic coordinates of each stand, density of Brazil nut trees ≥ 10 cm DBH; soil nutrient availability, total rainfall, strength of the dry season, the abundance of natural seed predators and/or dispersers, seedling and/or sapling herbivores, and classes of canopy openness.

The only variables other than historical levels of seed collection retained by the models were site longitude, total rainfall, and the abundance of agoutis and large herbivores (Table S2). Surprisingly, canopy gap density was excluded from all models even though a high understory light environment in more open forests greatly accelerates the growth rate of saplings (S12) in this gap-dependent species (S13-S14).

The effect of site longitude and total rainfall are unlikely to be directly linked to the *B. excelsa* population size structure. The significance of these variables could be explained by the gradual westward shift in large-scale Brazil nut harvest and trade over the last three decades (S9, S26-S27). Commercial exploitation has slowly but steadily spread from higher rainfall areas in eastern Amazonia to more seasonally-dry forests of the Peruvian, Bolivian and southwestern Brazilian Amazon (notably Acre) that may be partly or entirely controlled by community-based extractive enterprises.

Table S1. Brazil nut tree (*Bertholletia excelsa*) populations examined in this study. Site numbers refer to those shown in Fig. 1. Area sampled corresponds to the aggregate area of forest plots and/or transect strip-width censused at each site. NA = data not available.

Site No.	Site locality	State, Country	Latitude, Longitude	Area sampled (ha)	Density (ind. ha ⁻¹)	Mean ± SE DBH (cm)	s^* ^a	% Juveniles	No. of trees sampled	Level of seed harvest ^b	K-S tests ^c	Data sources
1	Pinkaiti, Kayapó Indian Reserve	Pará, Brazil	7°46'S, 51°57'W	60	3.3	72.6 ± 3.8	1.886	43.3	224	U	2, 5, 12, 14	S8
2	Kranure, Kayapó Indian Reserve	Pará, Brazil	7°49'S, 51°55'W	16	3.4	65.7 ± 7.6	1.920	52.5	40	U	5, 12, 14	S8
3	Saracá-Taquëra National Forest	Pará, Brazil	1°45'S, 56°30'W	769	1.5	134.8 ± 1.4	-1.100	1.6	1165	P	9, 11	S15
4	Marabá	Pará, Brazil	5°12'S, 49°06'W	9	4.3	119.4 ± 11.7	1.572	33.3	39	L	8, 10, 11, 12	S16
5	Tapajós National Forest	Pará, Brazil	3°55'S, 55°28'W	100	0.7	73.8 ± 2.9	1.438	35.7	269	L	2, 12, 14	S17
6	Alto Cajarí Extractive Reserve	Amapá, Brazil	0°20'S, 51°43'W	23	12.0	156.4 ± 2.9	-1.850	0.7	272	P	7	S8
7	Iratapuru Sustainable Development Reserve	Amapá, Brazil	0°03'N, 52°30'W	25	9.4	154.1 ± 3.0	-1.779	0.9	230	P	6	S18
8	Aventura, Lago Uauaçú	Amazonas, Brazil	4°19'S, 62°30'W	25.8	6.8	102.3 ± 4.3	0.315	24.6	122	L	10, 12, 15, 16, 17, 19, 20	S19
9	Ussicanta, Lago Uauaçú	Amazonas, Brazil	4°21'S, 62°35'W	15.4	8.5	133.5 ± 3.04	-2.582	3.8	132	M	11	S19
10	Lago Cipotuba, Rio Aripuanã	Amazonas, Brazil	5°48'S, 60°13'W	114	1.8	116.6 ± 3.91	0.348	22.4	201	L	4, 8, 11, 21	S19
11	Amanã Sustainable Development Reserve	Amazonas, Brazil	2°21'S, 64°45'W	50	1.4	123.5 ± 4.1	-1.891	5.3	76	M	3, 4, 8, 10, 19	S20
12	Rio Cristalino	Mato Grosso, Brazil	9°28'S, 55°55'W	64	4.9	90.7 ± 6.1	1.691	40.7	113	U	1, 2, 4, 14, 16	S19
13	Cláudia	Mato Grosso, Brazil	11°30'S, 54°48'W	35	3.6	71.0 ± 4.5	NA	31.2	125	U	N/A	S19
14	Nova Esperança	Acre, Brazil	10°40'S, 68°30'W	51	3.1	73.9 ± 4.3	1.809	47.2	161	L	1, 2, 5, 12	S21
15	Colocação Tucumã	Acre, Brazil	10°51'S, 68°44'W	184.5	1.4	108.0 ± 2.4	-0.783	12.2	255	L	8, 18, 19	S22
16	Colocação Rio de Janeiro	Acre, Brazil	10°47'S, 68°40'W	378	1.4	89.8 ± 1.9	0.440	32.4	568	L	12, 17	S22
17	Encontro	Acre, Brazil	10°43'S, 68°50'W	211	1.4	91.4 ± 2.5	-1.029	25.1	295	L	8, 16	S22
18	Oculto	Madre de Dios, Perú	12°39'S, 68°56'W	925	0.7	109.9 ± 1.5	-0.974	10.9	613	L	15, 19	S23
19	Limón	Madre de Dios, Perú	12°32'S, 68°52'W	1350	0.1	108.2 ± 2.9	-0.587	10.6	160	L	8, 11, 15, 18	S23
20	El Tigre	Beni, Bolivia	11°30'S; 67°15'W	12	1.7	102.1 ± 3.0	0.162	25.0	20	M	8, 21	S24
21	El Sena	Pando, Bolivia	10°59'S, 65°43'W	7	3.3	111.3 ± 3.7	0.401	21.7	23	M	10, 20	S24
22	Alter do Chão	Pará, Brazil	2°33'S, 54°53'W	3	23.0	44.9 ± 5.3	2.509	75.6	78	U	2	S25
23	Rio Ouro Preto Extractive Reserve	Rondonia, Brazil	10°45'S, 65°30'W	12	2.0	127.7 ± 7.3	-1.917	4.5	22	M	3, 4, 9, 10, 11, 17	S25

^a s^* is an index that measures the shape of the cumulative size distribution (see text and Note 16).

^b Historical levels of seed harvest of different populations: (U) unharvested; (L) lightly harvested; (M) moderately harvested; (P) persistently harvested.

^c Refers to all possible pairwise comparisons with other populations that could be drawn from the same size distribution (Kolmogorov-Smirnov tests at $P=0.01$).

Table S2. Details of multiple step-down regression models examining the effects of environmental variables on (a) the relative frequency of juvenile Brazil nut trees ($R^2 = 0.89$, $F_{5,17} = 24.9$, $P < 0.001$), and (b) the s^* parameter of cumulative size distributions ($R^2 = 0.80$, $F_{3,18} = 23.5$, $P < 0.001$), across 23 natural populations throughout the Amazon basin. Independent variables are ordered from the most to the least important in the models according to their F -values.

(a) Dependent variable: Percentage of juveniles

Effect	Coefficient	Std Error	Std. Coef.	Tol.	df	F	P
Variables retained							
Seed harvest (PCA scores)	-0.441	0.052	-0.818	0.753	1	70.75	<0.001
Longitude	-1.453	0.306	-0.517	0.603	1	22.63	<0.001
Large herbivore abundance	-9.662	2.419	-0.440	0.587	1	15.96	0.001
Agouti abundance	-8.863	3.160	-0.307	0.594	1	7.86	0.013
Total rainfall	-0.020	0.007	-0.268	0.726	1	7.34	0.015
Variables excluded							
	Part. Corr.						
Hunting pressure	0.206	.	.	0.238	1	0.66	0.428
Forest canopy openness	0.201	.	.	0.389	1	0.63	0.438
<i>B. excelsa</i> tree density	0.201	.	.	0.421	1	0.63	0.440
Soil nutrient availability	0.125	.	.	0.103	1	0.24	0.631
Latitude	-0.142	.	.	0.085	1	0.31	0.587
Number of dry months	0.095	.	.	0.065	1	0.14	0.716
Sampling area	0.047	.	.	0.480	1	0.03	0.858

(b) Dependent variable: s^* parameter of the cumulative tree size (DBH) distribution

Effect	Coefficient	Std Error	Std. Coef.	Tol.	df	F	P
Variables retained							
Seed harvest (PCA scores)	-0.037	0.005	-0.876	0.877	1	59.59	0.000
Large herbivore abundance	-0.824	0.224	-0.482	0.657	1	13.55	0.002
Longitude	-0.097	0.027	-0.446	0.732	1	12.88	0.002
Variables excluded							
	Part. Corr.						
Rainfall	-0.355	.	.	0.847	1	2.44	0.136
<i>B. excelsa</i> tree density	-0.299	.	.	0.594	1	1.67	0.213
Forest canopy openness	0.258	.	.	0.717	1	1.21	0.286
Soil nutrient availability	0.241	.	.	0.765	1	1.05	0.320
Hunting pressure	0.161	.	.	0.271	1	0.45	0.509
Sampling area	-0.111	.	.	0.680	1	0.21	0.651
Number of dry months	0.110	.	.	0.860	1	0.21	0.654
Latitude	0.027	.	.	0.266	1	0.01	0.913
Agouti abundance	0.014	.	.	0.692	1	0.003	0.955

Fitted logistic models

The fits of the logistic model to the cumulative size data are shown in Fig. S3. We also fitted log-normal and gamma-distributions, but these performed worse. We note that the models are fitted to cumulative data and hence residuals are autocorrelated. However,

we did not perform any statistical tests on the fitted parameters, and there is no reason to expect autocorrelation to cause parameter bias. Indeed the fits of the logistic model were generally excellent. We also estimated the parameters of the logistic regression from the mean and variance of the data assuming a logistic distribution. However the fits of the model estimated in this way were generally worse, probably because the data are truncated at 10 cm DBH.

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Supporting Online Figures

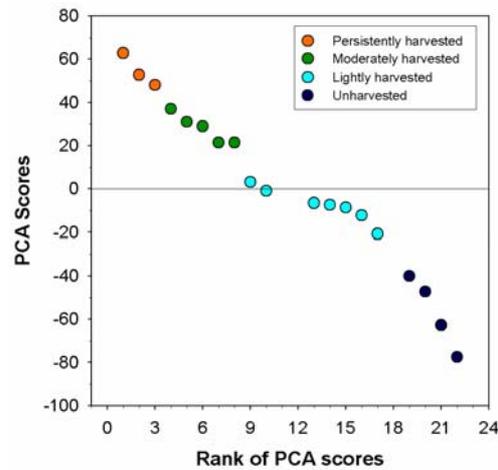


Fig. S1. Rank order of harvesting based on the first axis scores from a principal component analysis (PCA) using four key variables describing the history, intensity, and spatial scale of *Bertholletia excelsa* seed exploitation across all populations for which size distribution data were available. Data points, which are color-coded according to the history and intensity of seed collection, may overlap and therefore indicate more than one population.

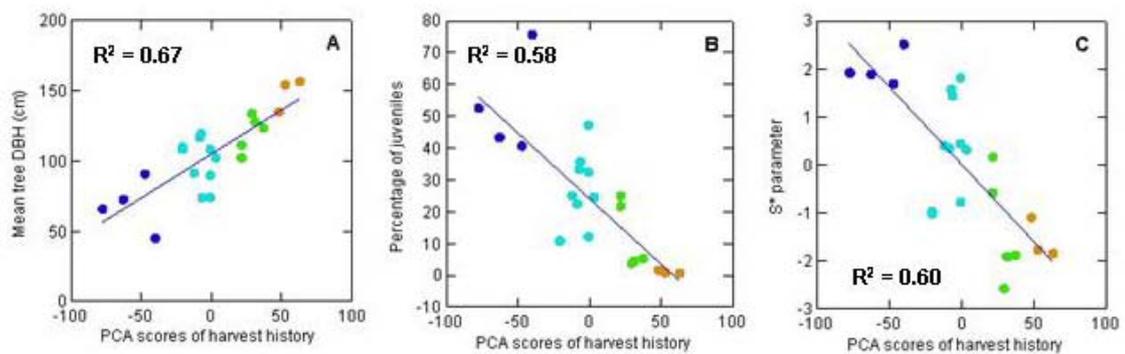


Fig. S2. Relationships between first axis scores from a PCA, summarizing the four key variables defining the historical levels of Brazil nut exploitation, and (A) mean tree DBH (cm); (B) percentage of juveniles; and (C) the s^* parameter describing the cumulative size distribution of all stands for which data were available. Data points are colored according to their class of seed harvest (see legend in Fig. S1). R^2 values are shown for each relationship.

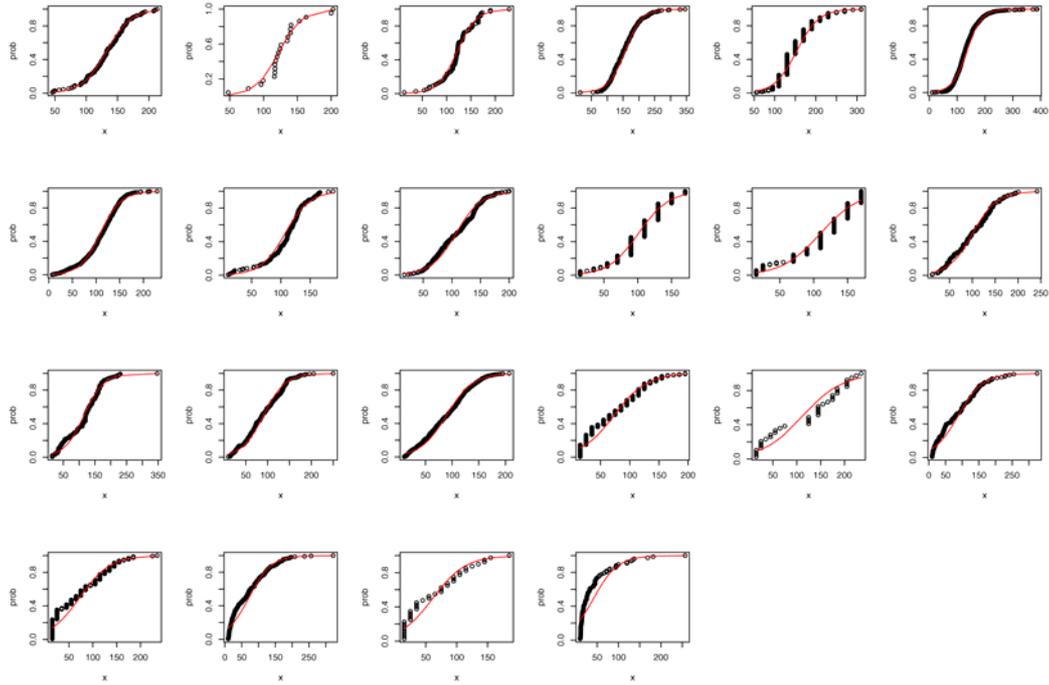


Fig. S3. The fitted logistic distributions, compared with the observed cumulative size distributions of 22 Brazil nut tree populations in Amazonian forests. The curves are drawn in order of decreasing s^* from top left to bottom right.