Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia

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ABSTRACT. Seeds of the Brazilnut tree (*Bertholletia excelsa* Humb. & Bonpl., Lecythidaceae) sustain one of the most important extractive industries in neotropical forests. Yet little is known about the demography and seed dispersal ecology of *Bertholletia*, particularly in natural stands which have not been previously harvested. This study presents data on the population density, spatial distribution, and seed dispersal ecology of Brazilnut trees at a pristine stand located within the Kayapó Indian Area of southeastern Amazonia, Pará, Brazil. Brazilnut trees were primarily found within groves (*castanhais*) of 75 to 149 trees, with a few isolated trees in between. Although the density of trees $\geqslant$10 cm in diameter at breast height (hereafter, dbh) at two groves was 4.8 to 5.1 trees ha^{-1}, the overall density for the entire study area of *c.* 950 ha was estimated at 1.3 tree ha^{-1}. Within-grove nearest neighbour distances averaged 21 m and were markedly skewed towards even shorter distances. Seed dispersal experiments using 709 marked seeds indicated that this pattern can be largely explained by the highly restricted seed shadows imparted by the main seed dispersal agents of *Bertholletia* at this site, the red-rumped agouti (*Dasyprocta leporina*). Agoutis on average scatterhoard *Bertholletia* seeds to an average distance of 5 m, and rarely beyond 20 m, from seed stations. We suggest that, once edaphic and climatic conditions are suitable, the highly contagious spatial distribution of *Bertholletia* trees at the landscape level can be largely accounted for by the quantitatively dominant effect of short-distance dispersal by caviomorph rodents, and rare events of long-distance dispersal provided by other vectors. This mechanism of grove formation need not resort to untested conjectures of human dispersal and intentional planting in prehistoric and historic times as it has often been suggested in the literature.

KEY WORDS: Brazil-nuts, *Bertholletia excelsa*; seed dispersal, seed predation, *Dasyprocta*, spatial distribution, Amazonia.

RESUMO. Semestes da castanheira do pará (*Bertholletia excelsa* Humb. & Bonpl., Lecythidaceae) são a base de uma indústria extrativista de alta importância socioeconômica em florestas neotropicais. Apesar disso, sabe-se pouco a cerca da demografia da espécie e da ecologia da dispersão de suas sementes. Este estudo mostra dados relativos a densidade populacional, a distribuição espacial, e a ecologia de dispersão de sementes de uma população natural de *Bertholletia* localizada na Área Indígena Kayapó, sudeste da Amazônia, Pará, Brasil. Castanheiras com diâmetro a altura do peito (dap) $\geqslant$10 cm foram encontradas em agregados naturais (ou castanhais) com 75 a 149 árvores, com alguns indivíduos isolados entre eles. A densidade de indivíduos em dois castanhais variou entre 4.8 e 5.1 ind. ha^{-1}, enquanto que a densidade em toda a área de estudo (*c.* 950 ha) foi estimada em 1.3 ind. ha^{-1}. Dentro de um castanhal, a distância média ao vizinho mais próximo foi de 21 m, com um forte desvio a distâncias ainda mais curtas. Um experimento de dispersão de sementes, baseado em 709 sementes marcadas, mostrou que isso pode ser decorrente do alcance restrito da dispersão efetivada por cotias (no caso *Dasyprocta leporina*), o principal agente dispersor de sementes de *Bertholletia*. Em média, cotias enterraram as sementes a 5 m do ponto

amostral, e raramente ultrapassando 20 m. Nós sugerimos que, uma vez que as condições edáficas e climáticas sejam adequadas, a distribuição altamente agregada de *Bertholletia* pode ser perfeitamente explicada por um padrão de dispersão a curta distância ocasionado por roedores caviomorfos, sendo raros os eventos de dispersão a longa distância decorrente de outros agentes. Dessa forma, o mecanismo de formação de agregados naturais não precisaria ser explicado por dispersão humana, através de plantios acidentais ou intencionais, como tem sido sugerido na literatura.

INTRODUCTION

The Brazilnut tree (*Bertholletia excelsa* Humb. & Bonpl., Lecythidaceae) represents a monotypic genus of forest emergents occurring throughout Amazonia and the Guianan Shields (Mori & Prance 1990a, b). Seeds of this species are often hailed as one of the most important non-timber tropical forest products in Amazonia, and sustain one of the largest extractive industries in neotropical forests, which involves some 200,000 people and 1.7–3.5% of the international raw edible nut trade estimated at US\$2.3 billion y^{-1} (Clay 1995, LaFleur 1991). Indeed Brazil-nuts harvested from wild stands are now the central focus of several market-oriented initiatives comprising the most important source of income for many Amazonian extractive and indigenous reserves (Clay 1992, Mori 1992).

Yet despite an extensive bibliography of nearly 300 papers on this species (Vaz Pereira & Costa 1981, Müller 1981, Mori & Prance 1990b), almost nothing is known about the population structure and regeneration ecology of either harvested or unharvested natural populations of *Bertholletia*. Apart from anecdotal information on its seed dispersers (Huber 1910, Prance & Mori 1978), and a detailed study in Madre de Dios, eastern Peru (E. Ortiz, unpubl. data) little is known about the reproductive biology of wild Brazilnut trees, particularly at their seed-seedling stage.

The large seeds of *Bertholletia* (47 mm × 21 mm) could represent one of the most important demographic bottlenecks in harvested stands as they are often heavily depleted by Brazil-nut extractivists on a long-term basis, who tend to leave few seeds behind for recruitment. Seed survival is, however, likely to be low even in unharvested stands because of (i) the functional indehiscence of the heavily armored *Bertholletia* fruits, which are unique in the Lecythidaceae (Mori & Prance 1990b), (ii) an intense reliance on a key caviomorph rodent dispersal agent, and (iii) high levels of post-dispersal seed predation (Terborgh *et al.* 1993, Peres *et al.* 1997). Unfortunately, the opportunities to carry out unbiased studies on the population ecology of *Bertholletia* in the absence of chronic seed harvesting are becoming increasingly narrower because intensively collected stands – in the form of commercially-leased concessions and extractive reserves – are now the rule rather than the exception throughout Amazonia.

In this paper we present preliminary data on the spatial distribution and size structure of Brazilnut trees from an entirely undisturbed and unharvested stand in a headwater region of southeastern Amazonia. Population density

estimates are presented for the species within natural tree groves and over the wider study area. Nearest-neighbour data on the dispersion of adults and juveniles within a grove are then related to experimental data from *in situ* seed dispersal experiments quantifying the distance at which seed caches were placed from seed sources (hereafter, dispersal distance). We then speculate on some of the biotic reasons determining the highly clumped distribution of Brazilnut trees in our study area, which confirms popular knowledge of the dispersion of this species in Amazonian forests. Finally, we compare the size distribution of *Bertholletia* trees of the unharvested stand with that of a harvested population from western Amazonia. This has important management implications because it has been implied that the conspicuous absence of smaller size classes in mature stands, which may be typical of this species (Pires 1984), could result from the lack of adequate number of seeds, seedlings, and saplings in replacing the larger size classes. Unsustainable exploitation of seeds might, therefore, eventually lead to stand senescence (Nepstad *et al.* 1992, Boot & Gullison 1995) and generalized collapse of the extractive industry in harvested areas. Support for this 'seed bottleneck hypothesis' should therefore be expected if unharvested stands of Brazilnut trees exhibit a more skewed distribution towards small size classes than those of harvested stands.

NATURAL HISTORY AND SEED DISPERSAL OF *BERTHOLLETIA*

Bertholletia is an exceptionally large emergent tree (40–50 m in height) occurring throughout seasonally dry, unflooded (hereafter, terra firme) forests of Amazonia receiving between 1400 and 2800 mm of annual rainfall (Diniz & Bastos 1974). The species is found mainly on nutrient-poor, well-drained oxysol and utisol soils (Clement 1993, Miller 1990), and is considered to be a light-dependent (gap) specialist (Müller & Calzavara 1989, Pires 1984), although seedlings can be found in the shaded understorey (C. Baider & C. Peres, unpubl. data). The Brazil-nut is actually a seed rather than a nut, although we adopt the popular usage for the purposes of this paper. The large seeds (on average 21 ± 3 mm $\times$ 47 ± 6 mm in size, n = 100) are encased within a large (11–15 cm in diameter), extremely hard, globose, woody capsule weighing 816 ± 246 g (n = 10), which eventually drops to the ground after a maturation period of *c.* 15 mo (Figure 1a). This capsular fruit (hereafter, pyxidium) is unique in the Lecythidaceae in being functionally indehiscent (Mori & Prance 1990b). Mature pyxidia do not break open upon fruitfall, and on average retain 17.1 seeds per fruit (range = 7–29, n = 361) because the opercular lid drops inwards (rather than outwards) and the operculum diameter is too narrow (*c.* 1 cm) to allow effective seed release. Mature seeds are, therefore, doomed to remain trapped inside the thick pericarps of fruits laying on the ground, unless these are gnawed open or fractured near the operculum by vertebrate seed predators. The seeds consist of a lignified seed testa (shell) protecting a
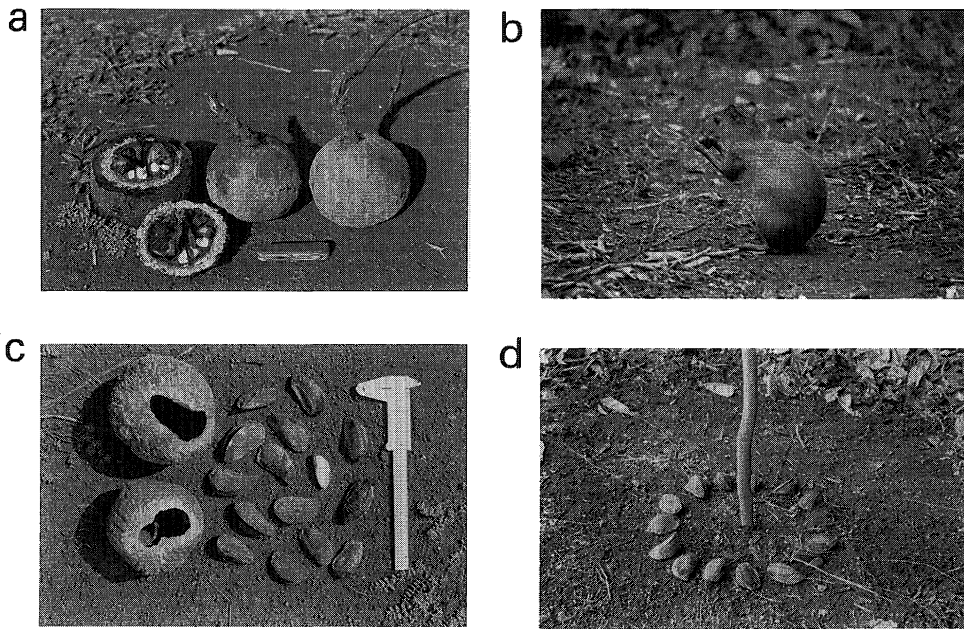
Figure 1. The extremely hard, globose fruits of *Bertholletia* (a) are largely opened by agoutis (b), in this case *Dasyprocta leporina*, which laboriously gnaw through the hard pyxidium wall (c) in order to remove the large seeds. Seed stations exposed during dispersal trials (d) consisted of a circle of 15 marked seeds (see text).

massive embryo weighing 5.8 ± 0.9 g (n = 53; Figure 1). The highly palatable endosperm is packed with 17–25% protein and 70–72% lipids (Peres 1991a, Pesce 1985) and is highly attractive to seed predators.

Like many large-seeded plant species in the neotropics, effective dispersal and predation of *Bertholletia* seeds is primarily mediated by agoutis, *Dasyprocta* sp. (Huber 1910), a large-bodied diurnal caviomorph rodent which occurs throughout the geographic range of *Bertholletia* (Figure 1c). Agoutis and a few other seed predators – including brown capuchin monkeys (*Cebus apella*) and giant Amazonian squirrels (*Sciurus spadiceus*) – are known to be capable of overcoming the protection afforded by the hard pyxidium wall and removing mature seeds (Batión Kayapó, *pers. comm.*; S. Almeida, *pers. comm.*; C. Baider & C. Peres, unpubl. data). Other arboreal predators, such as bearded saki monkeys (*Chiropotes satanas*), scarlet and blue-and-yellow macaws (*Ara macao* and *Ara ararauna*), red-necked woodpecker (*Campephilus rubricollis*), and smaller macaws (e.g. *Ara severa*), appear to be only capable of cracking immature (and less lignified) pyxidia still hanging from the trees. Seed dispersal services which may be occasionally provided by these agents, however, are either unconfirmed or far more infrequent than those of *Dasyprocta* spp.

Agoutis and acouchis (*Myoprocta* spp.) are the only rodents known to habitually bury large seeds intact (rather than simply caching underneath the leaf litter) in neotropical forests (Dubost 1988; Forget 1990, 1991; Smythe 1978).

The interactions between these dasyproctids and the seeds of other similarly rodent-scatterhoarded tree species have been examined in Panama (Forget & Milleron 1991, Forget *et al.* 1994, Smythe 1978), Costa Rica (Hallwachs 1986), and French Guiana (Forget 1990, 1991). By gnawing through the extremely hard pericarp, and removing the tightly packed seeds (Figure 1c), agoutis can seasonally store hundreds of scatterhoards (here defined as diffuse surface caches of single seeds covered with 1–3 cm of soil) for later retrieval. For whatever reasons, agoutis may then fail to recover a small fraction of the scatterhoards, which may eventually germinate should they remain buried long enough to overcome the prolonged seed dormancy period of 12–18 mo (Müller 1981). Alternatively, seeds left intact trapped inside closed pyxidia, once exposed to the more humid conditions on the ground, are rapidly attacked by fungal pathogens such as those of the genus *Aspergillus* (Souza 1984), succumbing to almost 100% mortality. Kayapó reports indicate that on very rare occasions, a single seed per fruit may be able to germinate inside a decayed pyxidium, resulting in one surviving seedling underneath the parental crown, but this is yet to be confirmed. Natural regeneration of *Bertholletia* thus relies heavily on dispersal by large terrestrial rodents such as agoutis, especially if seeds are to be released from the nearly inviolate mechanical protection provided by their hard pericarp and enjoy some probability of survival and subsequent germination.

STUDY SITE

This study was carried out near a second-order tributary of the upper Xingú river, within the Kayapó Indian Area of southeastern Pará, eastern Brazilian Amazonia (7°46′S; 51°57′W). The study area of Pinkaití – named after the only *perennial stream that intersects the study area – is located on the southern* bank of the Riozinho river, 14 km upriver of the Kayapó village of A'Ukre (Figure 2). Because several rapids and waterfalls downriver of A'Ukre have prevented motorboat traffic, access to Pinkaití is restricted to small aircraft. Harvest of Brazil-nuts at Pinkaití has therefore never been undertaken on a commercial basis, although Kayapó Indians (currently some 4,000 occupying over 10 million ha) have a long tradition of small-scale subsistence collection of this resource.

Unlike much of the forest at more accessible Kayapó areas closer to the frontier, anthropogenic disturbance at the territory controlled by A'Ukre villagers has been negligible to non-existent. Natural forest structure at Pinkaití is nevertheless highly heterogeneous and includes mixed palm forests dominated by *Attalea* maripa palms, liana forests (*sensu* Balée & Campbell 1990), high unflooded (terra firme) forests where *Bertholletia* is a common emergent, and small savanna enclaves ('cerrado') where the surface bedrock fails to sustain arborescent vegetation. The study area ranges from 230 to over 400 m above sea level, and is thus atypical of lowland Amazonia. Each of two 1-ha floristic
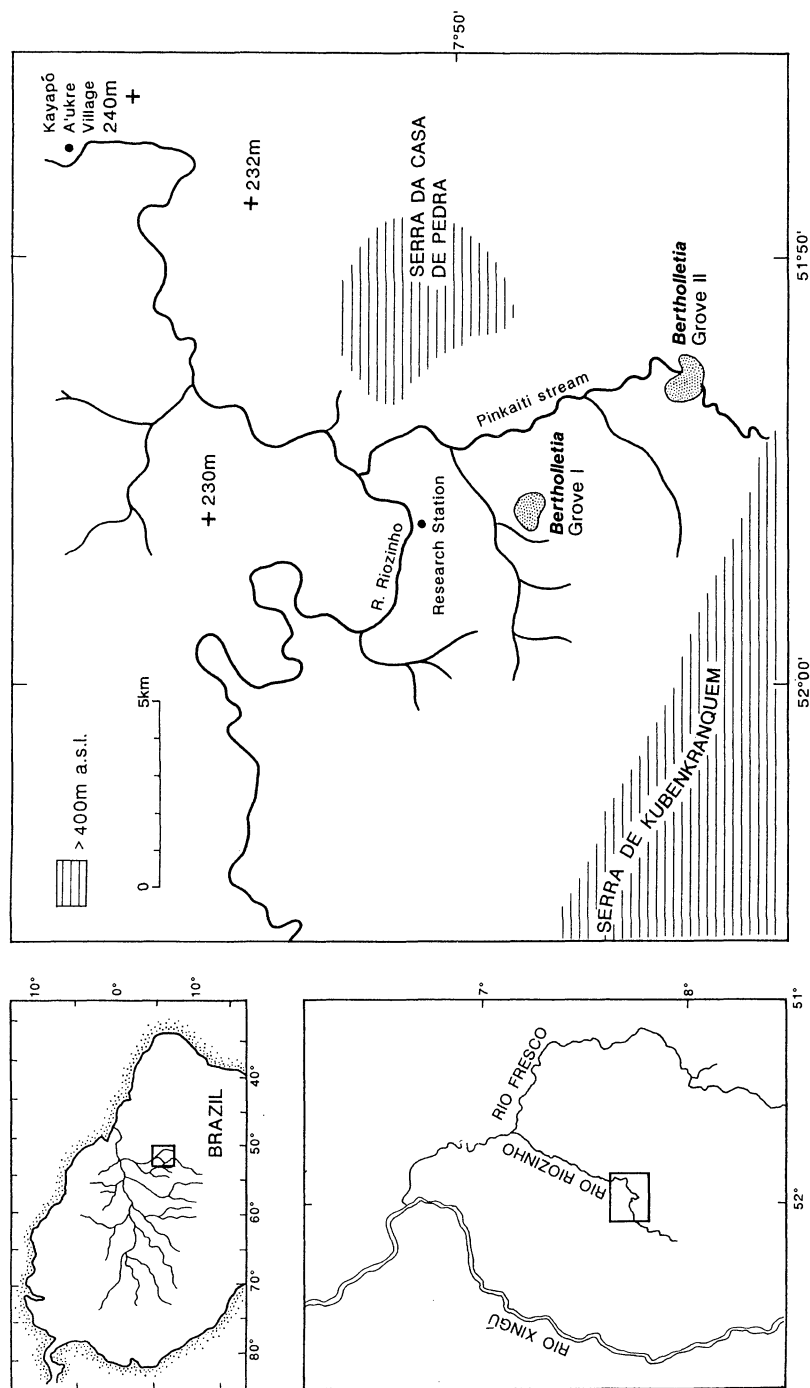
Figure 2. Location of the Pinkaití forest within the Kayapó Indian Area, southeastern Pará, Brazil. Small shaded areas represent the approximate boundaries of the two major Bertholletia tree groves found within the study area.

plots surveyed at Pinkaití contained a total of 573 and 652 trees ⩾10 cm dbh per hectare, accounting for a total basal area of 18.3 and 27.1 m^2 ha^{-1} respectively (C. Peres, unpubl. data). These values are considerably lower than those of typical terra firme forests in central Amazonia (e.g. Peres 1991b) and well within the range for 'open terra firme forests' (Pires & Prance 1985), which has been corroborated by a comprehensive airborne radar survey of Amazonia (Radam 1974) that classifies the vegetation at our study area as an 'open canopy forest'. The study site is nevertheless highly representative of the dry-belt archway of transitional forest mosaics of southern Amazonia, where structural heterogeneity and cerrado enclaves are common. Rainfall is unusually low for Amazonia as a whole, averaging 1640 mm y^{-1} (n = 5 y, 1985–1989) with a single clearly demarcated dry season (June–September) during which continuous dry spells of over 90 d are common.

METHODS

Density and spatial distribution of Bertholletia

We estimated the density of Brazilnut trees using both a line-transect census and a plot-based technique. Line-transect censuses were conducted along two trails of 3300 and 2300 m cut on the south and north bank of the Riozinho river, respectively. All trees detectable from the transect, but at most 40 m from it, were counted and marked, and their perpendicular distance to, and along, the transect recorded. Density estimates were analysed using the hazard-rate model with cosine function adjustments (Buckley *et al.* 1993). We also examined the distribution of trees along these transects using the number of trees detected along each transect segment of 100 m.

In addition, we exhaustively censused, number-tagged, measured (dbh and height), and spot-mapped all Brazilnut trees ⩾10 cm dbh within a 28.5 ha plot of terra firme forest, located 2.5 km south of the Riozinho river. This plot roughly overlapped the boundaries of a natural *Bertholletia* cluster (Grove I), and consisted of a 27.5 ha plot (550 m × 500 m) plus four adjacent 0.25-ha quadrats (Figure 3). Intensive searches of all *Bertholletia* trees within this plot were conducted by four people (the authors plus two Kayapó assistants), and aided by the clearly distinctive longitudinally fissured, light-colored bark of basal tree boles of *Bertholletia*. Plotting the position of each tree was conducted using a Suunto compass, a 50 m tape, and an extensive trail grid (100 m × 100 m) covering the entire plot, which had been cut and marked every 25 m. Given the relative accuracy of our mapping procedure, we estimate a plotting error of at most ± 5 m.

Morisita's index of dispersion (I$_\delta$) was used to measure the extent to which *Bertholletia* trees were spatially clumped within the study plot, given a specified quadrat size (Poole 1974). An *F*-statistic can be computed to test for significant departure of the index from unity (randomness). Values greater than 1 indicate clumping, whereas those between 0 and 1 indicate spatial uniformity. Because
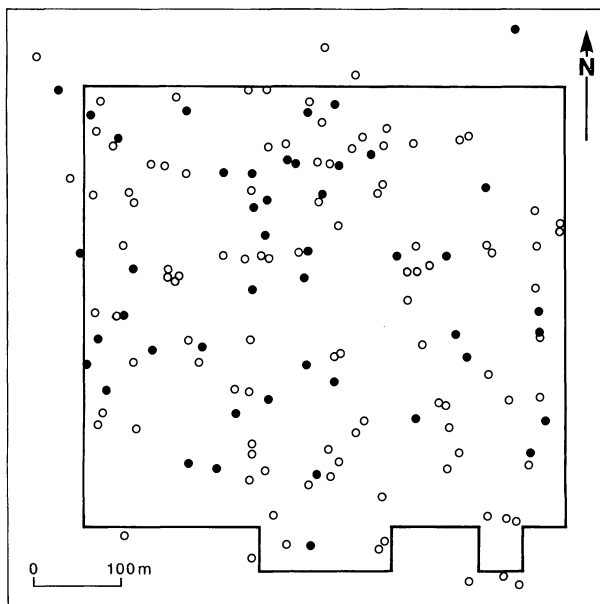
Figure 3. Spatial distribution of all *Bertholletia* trees ≥10 cm dbh mapped within an area of 28.5 ha overlapping Grove I, Pinkaití, Pará, Brazil. Trees outside the plot boundaries are also considered as part of the grove but these areas have not been exhaustively sampled. Open circles indicate trees 10 cm < dbh < 100 cm; Solid circles indicate trees ≥100 cm dbh.

this index may be sensitive to quadrat size, we used quadrats of 1/16, 1/4, and 1 ha, respectively with 25, 50 and 100 m on the side. We also tested observed nearest neighbour distances (d) of Brazilnut trees, obtained from a 1:2500 map of Grove I, against those expected based on $d = 1/(2 \sqrt{\rho})$, where ρ is the mean density of trees in number of individuals ≥10 cm dbh per square metre (Clark & Evans 1954).

At a second cluster of Brazilnut trees (Grove II), located 7.6 km from the research station, we restricted our survey to tagging and measuring all trees ≥10 cm dbh encountered.

Finally, we carried out a community-wide inventory of all trees ≥10 cm dbh contained within two randomly placed 1-ha plots (10 m × 1000 m) on opposite banks of the Riozinho river. Tree species within these plots were identified and their dbh, height and indigenous names were recorded.

Observations on seed dispersal

In September–October 1994, systematic observations were conducted on a family group of red-rumped agoutis (*Dasyprocta leporina*) making daily visits to artificial piles of Brazil-nuts consisting of five unshelled seeds (embryo + woody seed testa), which were laid out prior to each trial at the forest edge next to the field station. This group of three agoutis (one adult female, one adult male, and one juvenile) clearly became habituated to observers and could be

approached to within 5 m without disturbance. Observations were carried out using a pair of 10×40 binoculars during 1-h intervals of daylight early in the morning (0600–0700 h) and at dusk (1730–1830 h), which overlapped the peak foraging periods of agoutis. The duration of seed shelling, proportions of seeds eaten or scatterhoarded, and the distance between seed piles and the point at which seeds were buried was recorded.

Seed dispersal experiments

Dispersal trials with marked seeds were conducted during the late dry and early wet season (October–November 1995), at the onset of the 6-mo long *Bertholletia* fruitfall season. These were based on a set of 709 unshelled seeds which had been cleaned and sun dried in order to allow firm surface adherence of an inconspicuous piece of epoxy used to cement the end of a 60-cm long copper filament (0.2 mm caliber). A small piece (5 cm) of bright-orange Vinyl flag numbered with permanent ink was then tied to the opposite end of the filament. This marking technique is similar to that successfully used by Schupp (1988) and Forget (1990; *pers. comm.*) for other large seeds in Panama and French Guiana. Seed removal rates were comparable to those of unmarked seeds used in a previous set of experiments (Peres *et al.* 1997), which suggests that markers introduced little bias to this study. Seeds used in dispersal trials were collected from early crops of fresh pyxidia found underneath several adult Brazilnut trees. Embryo viability was tested using a water immersion technique commonly used in the Brazil-nut shelling industry: all seeds failing to sink to the bottom of a plastic bucket were discarded.

Marked seeds were placed at 36 seed stations sited near 12 large Brazilnut trees (≥ 100 cm dbh). Groups of three stations were positioned at 10 m from the base of each tree, forming an equilateral triangle centred at the base of each tree. Seed stations consisted of a flagged 1.5-m pole standing upright at the centre of a circular patch of soil of 1 m in diameter, from which the leaf-litter had been partially removed. At each station, a batch of 15 marked seeds was arranged in a circular manner with their copper filament markers stretched outwards (Figure 1d). This seed batch size roughly corresponds to the average number of seeds counted from 361 Brazilnut fruits (mean = 17.1, range = 7–29) collected during two consecutive fruiting seasons (1994–95 and 1995–96), and thus mimics the number of seeds found by an agouti upon opening a typical pyxidium. Other trials were conducted at 12 of the 36 stations over a 2-wk period, but three of those contained only 10, 11 and 13 seeds (hence the overall tally of 709 seeds exposed in all trials). Once seeds had been laid out, stations were monitored every other day until all seeds had either been removed or eaten.

Seed stations were monitored by four observers undertaking simultaneous searches within concentric areas radiating outwards from each station at increasing distances of up to 40 m from station poles. However, searches were often called off by any observer at shorter radial distances if all 15 numbered

seed flags from a given station had been recovered. Upon finding a given seed, seed fragment, or seed flag, we determined the seed status and position (e.g. intact at station, eaten at station, buried intact elsewhere, or eaten elsewhere), and measured the displacement angle and distance between each seed and its seed station using a compass and a Sonin® electronic distance measurer (accurate to 1 cm).

Finally, at one control station placed near the research base, we used an infra-red triggered Trailmaster® camara-trap and Tomahawk live-traps baited with *Bertholletia* seeds to monitor seed removal activity by diurnal and nocturnal visitors over a 1-mo period. It was thus possible to infer, with a certain degree of confidence, on the identity of mammal species visiting other seed stations on the basis of associated patterns of seed removal and seed predation.

<div align="center">RESULTS AND DISCUSSION</div>

Density and spatial distribution of Bertholletia

On the basis of our line-transect censuses, the density of *Bertholletia* trees ⩾10 cm dbh for the entire study area was estimated to be 1.3 trees ha⁻¹ (95% CI = 0.9–1.8 trees ha⁻¹). However, there were obvious differences in the local abundance of Brazilnut trees in the Pinkaití forest. For instance, the tree density along the transect on the south bank (2.1 trees ha⁻¹, 95% CI = 1.5–2.9 trees ha⁻¹), where the study groves are located, was approximately six-fold greater than that estimated for the north-bank transects (0.35 tree ha⁻¹, 95% CI = 0.05–0.8 tree ha⁻¹).

The spatial distribution of *Bertholletia* at Pinkaití was strongly clumped. Only 13 (23%) of the 100-m transect segments censused (n = 56) contained 100% individuals detected, whereas all others contained none. Moreover, not a single *Bertholletia* tree ⩾10 cm dbh was found within the two randomly placed 1-ha plots on each bank of the Riozinho river. Indeed *Bertholletia* was clearly missing in most of our study area encompassing approximately 950 ha, and at that was largely restricted to well-drained soils occupied by high terra firme forest (Figure 2).

The two study groves of at least 75 and 149 trees ⩾10 cm dbh comprised the only major clusters of *Bertholletia* trees known to occur at Pinkaití by Kayapó Indians thoroughly familiar with the study area. In both of these groves, the *Bertholletia* density gradually decreased into diffuse clouds of more isolated individuals as one moved away from their centres. Sparse groups of *Bertholletia* also occurred along a 2-km section of a trail bordering the Pinkaití stream. Other groves of variable tree density and size do occur outside the boundaries of our study area, but these are located several kilometres apart and with few Brazilnut trees in between.

Considering the forest plot overlapping Grove I, the overall density of *Bertholletia* trees ⩾10 cm dbh was 4.8 trees ha⁻¹ (137 trees in 28.5 ha; Figure 3). Grove II had a similar density of approximately 5.1 trees ha⁻¹. Within Grove I, the

number of *Bertholletia* trees contained within different-sized quadrats varied from 0 to at most 2, 4 and 13 neighbouring trees in the case of quadrats of 1/16, 1/4, and 1 ha, respectively. The mean observed nearest neighbour distance for Brazilnut trees at this grove was 20.8 ± 10.6 m (range $= 7.5$–63.4 m, n = 137). This was similar to the nearest neighbour distance expected for a randomly dispersed population with the same density of trees (22.8 m), indicating virtually no tendency towards clumping within the grove. This is confirmed by comparisons with a Poisson distribution which yielded χ^2-values well below significance ($P>0.05$) for different sized quadrats. Moreover, nearest neighbours were skewed towards even shorter distances, with 50% of all trees being within 20 m of another (Figure 4). Distances to first nearest neighbours were thus surprisingly short for a large-crowned emergent such as *Bertholletia* (mean crown radius $= 12.1 \pm 3.4$ m, range $= 5$–18 m, n = 39 adults of any size).

Morisita's index of dispersion (I_δ) for *Bertholletia* trees at Grove I was calculated to be 1.48, 1.20, and 1.09 for quadrats of 1/16, 1/4, and 1 ha, respectively. These values did not depart significantly from unity (F-tests, P>0.05), again showing no tendency towards clumping. However, trees with a dbh $\geqslant 100$ cm, which accounted for 31% of the trees in the plot, were regularly dispersed across 1/16-ha quadrats ($I_\delta = 0.51$ for quadrats of 1/16 ha), but randomly dispersed across 1/4 ha and 1-ha quadrats ($I_\delta = 0.76$ and 1.07, respectively). This pattern suggests some repulsion among the largest Brazilnut trees because of purely physical reasons (i.e. two large adults could not be easily accommodated within a quadrat of 25 m dimension). The spatial distribution of *Bertholletia* is thus best described as random at the level of tree groves, but noticeably clumped at the level of the wider landscape.

Fate of seeds

Early wet season observations on habituated agoutis visiting artificial piles of seed placed near the research station indicated that agoutis buried between 3 and 7 *Bertholletia* seeds for each seed they ate. Agoutis clearly displayed considerable dexterity in shelling and burying *Bertholletia* seeds. These were either shelled prior to consumption over an interval of 48 ± 12 s (n = 15) and eaten next to the seed pile, or carried away and buried using a rapid, stereotyped maneouver which lasted 7–18 s (n = 20). Of the few cases in which scatterhoarding could be observed, seeds had been buried at distances of 10.7 ± 5.6 m (range $= 3$–25 m, n = 21) from the seed piles, often at the base of a dead log at the edge of the clearing. As many as six soil pits could be dug up before a seed was finally buried into pits of 1–3 cm below ground which never contained more than one seed.

Brazil-nuts exposed to seed dispersal trials were rapidly removed intact or eaten at the seed stations, usually within 4 d of exposure (Table 1). These trials were largely successful in that markers were recovered from 97.3% of all 709 seeds placed for removal. However, the fate of seeds could not be accurately determined for over a third of the samples because 37.5% of these seeds
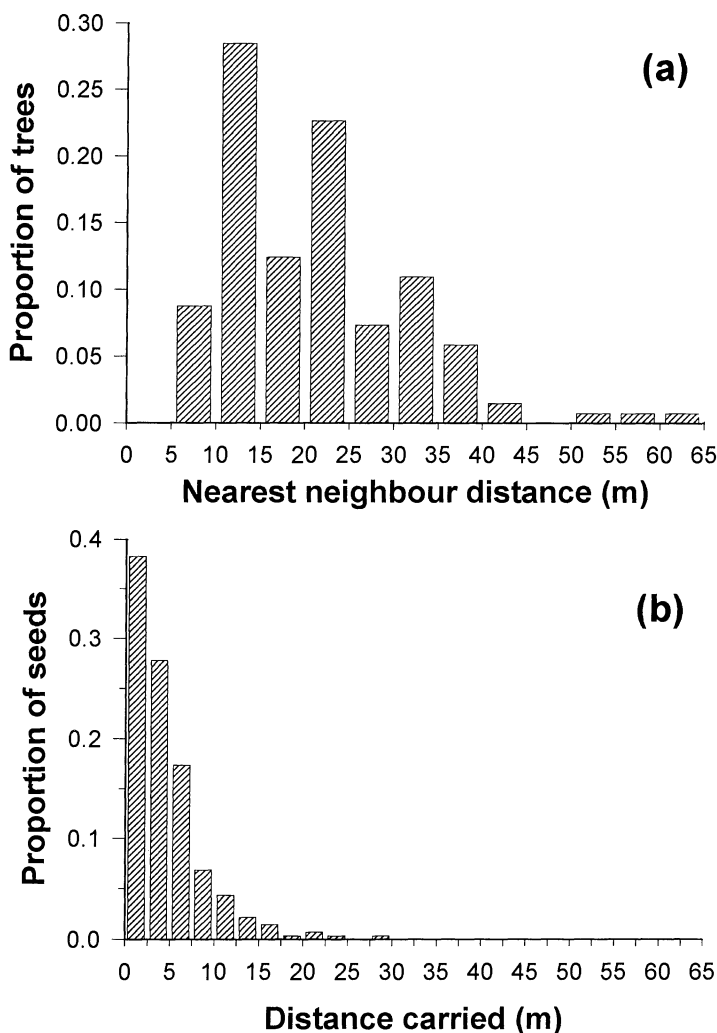
Figure 4.   Relative proportions of (a) distances to first nearest neighbours for *Bertholletia* trees ≥10 cm dbh (n = 137), and (b) intact seeds recovered at increasing distances from experimental seed stations (n = 217) in Grove I, Pinkaití, Pará, Brazil.

had their flagged wires cut off by one or more unknown rodent species, either at the stations or in their immediate vicinities. Therefore, only 424 (59.8%) of the seeds (or fragments of the seed testa) were actually retrieved. Experimental control trials near the research station indicated that copper wires were invariably severed between 1800 and 0600 h, by nocturnal rather than diurnal rodents. Camara-trap photographs and successful captures of live animals showed that this seed handling pattern was primarily attributed to an unidentified species of spiny rat (*Proechimys* sp.) rather than agoutis. Other visitors to seed stations placed underneath *Bertholletia* trees also included arboreal seed predators. At one station, over half of the seed markers were found hanging

Table 1. Fate of marked *Bertholletia* exposed in dispersal trials at Pinkaití, Pará, Brazil, as shown by the distance to which seeds, seed fragments or markers were recovered, and the time required for seed removal.

Fate of seeds	Number (and %) of seeds	Distance carried (m) Mean ± SD (range)	Removal time (d) Mean ± SD (range)
Seeds removed from stations			
Buried intact	217 (30.6)	5.0 ± 4.2 (0.5–28.4)	4.2 ± 2.1 (2–10)
Eaten elsewhere	14 (2.0)	4.7 ± 5.0 (0.3–16.7)	3.2 ± 1.5 (2–6)
Intact but left unburied	10 (1.4)	1.3 ± 0.5 (0.9–2.3)	4.1 ± 2.7 (1–11)
Markers cut off and recovered elsewhere	36 (5.1)	4.1 ± 3.8 (1.0–18.7)	5.4 ± 3.0 (2–13)
Markers cut off and recovered at station	230 (32.4)	—	4.5 ± 3.3 (2–13)
Markers unrecovered	19 (2.7)	—	4.9 ± 2.3 (2–9)
Seeds remaining at stations			
Buried	95 (13.4)	0 (0)	5.0 ± 2.6 (2–10)
Intact	88 (12.4)	0 (0)	—
All seeds exposed	709 (100.0)	4.7 ± 4.2 (0.3–28.4)	4.5 ± 2.7 (1–13)

on branches at heights of 0.5–2.0 m from the ground, presumably left by brown capuchin monkeys (*Cebus apella*), which were common at the *Bertholletia* groves.

Of 424 seeds recovered with markers, one quarter (26%) had been eaten at the stations or within 17–m from them (Table 1). Over half (51%) of the seeds recovered were buried intact near seed stations, in a manner typical of that exhibited by habituated agoutis. Successfully retrieved buried seeds were on average at 5.0 ± 4.2 m from their stations of origin (range = 0.5–28.4 m, n = 217), but highly skewed towards even shorter distances (skew = 2.2) of less than 3 m of the stations (44% of the seeds; Figure 4). Indeed angular measurements of the direction towards which buried seeds were dispersed showed that 38% (n = 173) of the seeds were carried from stations towards the base of the focal Brazilnut trees, rather than away from them. To put this in perspective, the farthest dispersal distance recorded from either direct observations or dispersal trials was approximately only one average Brazilnut crown diameter away from the seed point of origin. While agouti scatterhoarding could result in greater dispersal distances, these must be relatively rare events not detected even by these relatively robust removal trials.

Distribution and abundance of Bertholletia

This study confirms that *Bertholletia* trees in Amazonian forests are often clustered into fairly discrete natural groves, which results in a highly clumped spatial distribution at the landscape level. This contagious distribution has long been recognized by Amazonian tribal and non-tribal folks who refer to discernible aggregates of 50 to several hundred Brazilnut trees as 'castanhais' in Brazil (Dias 1959) or 'manchales' in Peru (Sánchez 1973). Within these natural groves, however, the spatial distribution of adults clearly failed to depart from a random pattern.

Bertholletia densities are highly variable throughout Amazonia. The density

at the entire Pinkaití study area (1.3 trees ha^{-1}) is comparable to that reported for O Deserto, lower Xingú river (c. 1 tree ha^{-1}: Campbell *et al.* 1986), the Tambopata Reserve, Peru (mean of 6 ha sampled = 1.3 trees ha^{-1}: Gentry 1988), and Manu National Park, Peru (<1 adult ha^{-1}: Terborgh *et al.* 1993). Only three adults were recorded in a 500-ha area of terra firme forest of central-western Amazonia (upper Urucu river: Peres 1991b), whereas a mean estimate of 2.4 trees ha^{-1} is reported for several hundred hectares in Madre de Dios, Peru (E. Ortiz, unpubl. data). In a survey of 51 ha at two extractive reserves in Xapurí, Acre, Brazil, the *Bertholletia* density was estimated at 5.9 plants ⩾1 mm in height per hectare (Viana *et al.* in press). On the higher end of the scale, densities of 0.2–20 trees ha^{-1} have been reported for several sites in eastern Peru and northern Bolivia (Clement 1993, Sánchez 1973, DHV Consultants 1993). Ten 1-ha plots overlapping Brazilnut groves in southern Amapá and eastern Pará contained between 6 and 26 'trees' of an unspecified minimum size (Miller 1990). This is as much as twice the highest density of 13 trees ⩾10 cm dbh recorded in a hectare within Grove I. Although the details of some of these estimates remain unclear, it is difficult to conceive how a giant emergent such as *Bertholletia* could attain some of the highest reported tree densities within or outside a grove. Moreover, there is often a misleading tendency to extrapolate within-grove tree densities to much larger study areas. A simple geometric model considering a single-species grove of Brazilnut trees with neighbouring but non-overlapping crowns would predict an average crown radius of only 11.2 m so that a density of 20 trees ha^{-1} could be attained. For the largest-crowned *Bertholletia* at Pinkaití (crown radius = 18 m), this model would predict at most 7.7 trees ha^{-1}, which is only marginally higher than that of our study groves. Because tree density decreases exponentially with increasing crown diameters, the unrealistically high *Bertholletia* densities reported for some sites would only be possible in contexts of monodominant stands where most Brazilnut trees were relatively small. We therefore surmise that the highest within-grove densities of *Bertholletia* at Pinkaití could not be much lower than that found in most other natural stands.

Seed dispersal in Bertholletia

Our dispersal trials can be considered largely successful in that we were able to find 97% of the seed markers, a rate considerably higher than that of other studies (e.g. Forget *et al.* 1994). The overall seed removal of 87.6% over a 2-wk period was similar to that reported for *Gustavia superba* over 28 d (85.5%; Forget 1992) and somewhat higher than that of *Vouacapoua americana* (78%) over a 1-wk period (Forget 1994). Seeds hoarded intact represented 65% of seeds handled by rodents and subsequently recovered, a proportion which was likely to be higher than that outside the late dry to early wet season (Smythe *et al.* 1982). In any case, burial minimizes the probability of seeds succumbing to other invertebrate and vertebrate seed predators (Forget 1990, Smythe 1989),

and is likely to enhance germination (Sork 1985) thus promoting seedling recruitment.

Because acouchis do not occur at Pinkaití (Peres *et al.* 1997) and much of eastern Amazonia (Emmons & Feer 1990), seeds exposed to dispersal trials were almost certainly buried by agoutis. In the course of their foraging activities, agoutis appeared to visit almost all of the focal trees at least once every other day, preying upon or scatterhoarding seeds at relatively short distances, which is consistent with their small home range sizes and narrow ranging patterns (Smythe 1978). This spatially restricted seed shadow confirms those documented for other rodent-dispersed tree species in neotropical forests (e.g. *Hymenaea courbaril*, Hallwachs 1986; *Vouacapoua americana*, Forget 1990; *Scheelea zonensis*, Forget *et al.* 1994) which often also have a large-scale patchy distribution and form relatively isolated groves (Condit *et al.* 1992, Forget 1994). This supports the general association between limited dispersal distances and clumped distributions for other tree species in neotropical forests (Howe & Smallwood 1982, Hubbell 1979).

Although seed disappearances (seed markers cut off) could not be readily equated to mortality, our experiments were unlikely to be significantly biased against longer dispersal distances. This is because almost all detached seed markers were recovered at seed stations or in their immediate vicinities. Moreover, control seed stations monitored by either camara-traps or live-traps indicated that most, if not all, markers were severed by spiny rats (*Proechimys* sp.), which appear to mainly prey upon, rather than disperse, *Bertholletia* seeds. The agouti-generated seed shadow could, however, be expanded subsequently if some of the seeds cached are subsequently relocated by secondary dispersers (Price & Jenkins 1987). Trials conducted at other times of the year, or with a greater sampling effort, could yield larger seed shadows. For instance, an exceptionally long dispersal distance of 100 m was reported from a study of *Bertholletia* in Madre de Dios, Peru, but most seeds were deposited at much shorter distances (E. Ortiz, *pers. comm.*). Even so it is difficult to imagine how *Bertholletia* seeds could be carried by rodents well beyond the limits of a grove, thus functioning as an effective mechanism of grove formation.

The overall seed shadow imparted by *Dasyprocta* largely accounts for the spatial distribution of adult *Bertholletia*. The apparently poor congruence between the distribution curves of seed dispersal and nearest neighbour distances (Figure 4) can be understood given that (i) most fruits are dropped towards the periphery of the crown zone (some 12 m away from the base of the tree), (ii) whole fruits may often be rolled on the ground by agoutis away from the tree prior to opening, and (iii) the compensatory mortality of seedlings established too close to parents may operate (Janzen 1970, Connell 1971). These factors often add 10–15 m to the distance at which seeds are buried, which is what is required to almost match the two distributions. So considering the seed shadow imparted by agoutis, one would expect distances between nearest

neighbours to be even shorter than those at the main grove. Seedling recruitment over short distances from parents would not necessarily be prevented by seed predators because there were no short-term benefits of escape distance accrued to seed survival at this stand (Peres *et al.* 1997). Seeds placed at 10 m from large Brazilnut trees were no more likely to be removed by seed predators than those at 35 m. In practice, however, it would be physically impossible to compress the density of adults much further because of the sheer size of *Bertholletia* crowns.

Size structure of Bertholletia *stands*

Brazilnut trees ⩾10 cm dbh at the Pinkaití area were on average 82.1 ± 58.8 cm and at most 323 cm dbh (n = 224). This upper size limit is not so impressive considering that *Bertholletia* holds the distinction of largest recorded tree girth in Brazilian Amazonia. Giant Brazilnut trees with girths of 14–16 m (446–509 cm dbh), and an estimated lifespan of >1600 y (Pires 1984), have been recorded in different parts of eastern Amazonia (N. T. Silva, *pers. comm.* to Pires 1984; C. H. Müller, *pers. comm.* to Clay 1995; J. F. Ramos, *pers. comm.*). Trees at our site, albeit apparently smaller than those of other Amazonian stands, may nevertheless enjoy a long reproductive life in that they can reach maturity at relatively small size classes. The smallest fertile individual observed flowering at the main grove was only 21 cm dbh and 23 m in height, which given the number of trees examined is probably close to the minimum plant size at first flowering.

Small Brazilnut trees at Pinkaití were not necessarily more common than those in larger size classes (Figure 5). For instance, although the modal size class was 10–20 cm dbh, trees 90–100 cm dbh were more common than those in some smaller size classes. Similar patterns showing a predominance of large *Bertholletia* trees have also been observed in other Amazonian stands. Large trees of 35–40 m in height and 110 cm dbh were the most common size class in a harvested area near the Jarí river, Amapá, Brazil (Pires 1984). Nepstad *et al.* (1992) found no *Bertholletia* trees smaller than 100 cm dbh in an exploited 0.5-ha area at Seringal Porongaba, Acre, Brazil, where local extractors confirmed that it was virtually impossible to find seedlings and saplings.

The predominance of large trees in these stands and at Pinkaití is at odds with the classic reversed-J curve of frequently recruiting canopy tree populations (Foster & Brokaw 1982) fueling concerns about their future demographic viability. Three alternative hypotheses could be advanced to explain this pattern. First, this size structure could result from a severe scarcity of seeds caused by exceedingly high levels of seed extraction over the time scale of several decades (the 'seed bottleneck hypothesis'). Indeed it could be argued that a dwindling number of increasingly older trees will result in reduced seed crop yields and senescent stands, unless enforced seed quotas are introduced. This is supported by the fact that Brazil-nut production in eastern Amazonia (state
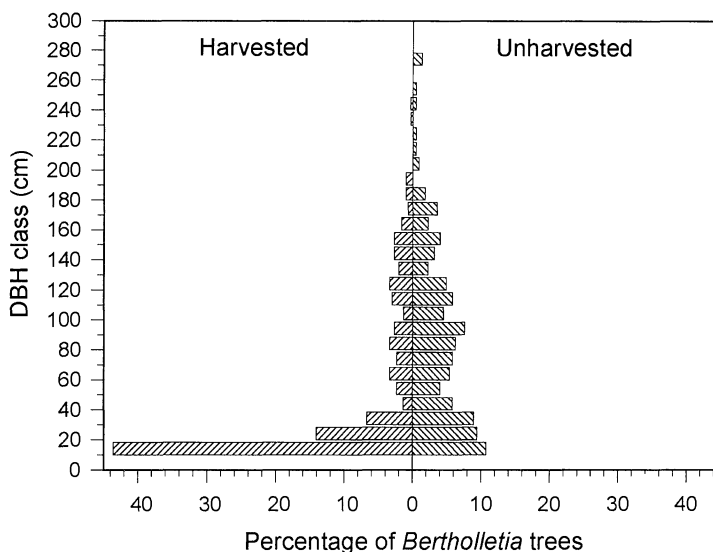
Figure 5. Comparison of the size structure for *Bertholletia* trees ≥10 cm dbh found at an intensively harvested (Xapurí Extractive Reserve, Acre, western Brazilian Amazonia; n = 299 trees; Viana *et al.* in press) and an unharvested stand (Pinkaití, Kayapó Indian Area, Pará, eastern Brazilian Amazonia, n = 224 trees; this study).

of Pará) has declined from 37,000 MT (metric tons) in 1973 to 18,000 MT in 1987 (Clay 1995) despite an apparent increase in harvest effort.

Alternatively, a 'mutualist bottleneck hypothesis' would state that seedling demography could be affected by insufficient levels of effective seed and pollen dispersal services, which could take place where agoutis are heavily hunted, and where atmospheric smoke caused by an excessive number of slash and burn fires interferes with bee activity (Kitamura & Müller 1984). Finally, effective seedling recruitment and regeneration of *Bertholletia* in mature forests may depend on the availability of appropriate gap-phase sites created by patchy treefalls or less frequent storm-induced events of large-scale canopy disturbance (Pires 1984, Müller 1981), which are more common in Amazonia than previously realized (Nelson *et al.* 1994). According to this 'suitable regeneration site bottleneck hypothesis', peaks of seedling recruitment following such events would correspond to the prevalent large size classes now observed many decades thereafter.

A comparison of the *Bertholletia* size distribution at the unharvested Pinkaití stand with that at two extractive reserves in Xapurí, State of Acre, western Brazilian Amazonia, which have been harvested on a long-term basis (Viana *et al.* in press), tentatively rejects the first two hypotheses. Exploitation of *Bertholletia* seeds at the Xapurí stands goes back at least 100 y, and has become particularly heavy in recent decades. Contrary to expectations from a 'seed bottleneck hypothesis', Brazilnut trees in Xapurí (mean = 52.8, skewness = 4.1, n = 299) were far more biased towards smaller size classes than those at

Pinkaití (mean = 82.1, skewness = 0.96, n = 224; Kolmogorov-Smirnov test, z = 6.5, two-tailed P<0.001) despite the almost complete absence of seed extraction in our study area (Figure 5). The size structure of the Xapurí stands is, therefore, far closer to the negative exponential distribution characteristic of a more continuous recruitment pattern. The 'mutualist bottleneck hypothesis' is also rejected because agouti populations at Xapurí are expected to be under far greater hunting pressure than those at Pinkaití, which have never been hunted. On the basis of intensive line-transect censuses, the density of agoutis at Pinkaití was estimated at 44 individuals km^{-2} (Peres *et al.* 1997), which is higher than the agouti densities estimated for 23 other Amazonian forests censused in the same manner (C. Peres in press, and unpubl. data). This density would be equivalent to an average non-overlapping but contiguous home range size of 2.3 ha, each of which would contain an average of 11 adult Brazilnut trees given their density at Grove I.

We are thus left with the hypothesis addressed at suitable regeneration sites which predicts that *Bertholletia* is unable to develop in the shaded understorey because of its light-demanding seedlings (Müller & Calzavara 1989, Pires 1984, Pires & Prance 1985). Evidence for this hypothesis comes from the Xapurí study where 84% of the trees <40 cm dbh were found in small canopy gaps (Viana *et al.* in press). That would place *Bertholletia* in the same regeneration niche as other 'gap opportunist' (Whitmore 1975) or 'long-lived pioneer' species (Whitmore 1989) which typically exhibit a conspicuous absence of saplings and juveniles (Richards 1952, Sarukhan 1980) unless in areas experiencing some form of disturbance. It may, however, be misleading to use size structure data to infer on population dynamics, so that a more detailed study on the regeneration and breeding biology of *Bertholletia* should be undertaken. In particular, further data on the size structure and population dynamics are necessary to understand the long-term effects of forest structure and persistently depleted seed crops on *Bertholletia* demography at harvested and unharvested stands.

Formation of Bertholletia *groves*

The highly clumped distribution of Brazilnut trees throughout Amazonia has been attributed to direct human intervention through deliberate seed dispersal, since the idea was first proposed by Ducke (1946). Areas in which *Bertholletia* groves are common have thus been considered to be relics of pre-Colombian plantations established by native Amazonians (Müller *et al.* 1980). These areas have been suggested as present indicators of the so-called 'anthropogenic forests', which are said to have resulted from large-scale manipulation of the forest structure and composition by Paleoindians and post-contact indigenous groups (Balée 1989, Balée & Campbell 1990, Hecht & Posey 1989, Posey 1985). In contrast, data presented here suggest an alternative mechanism for *Bertholletia* grove formation, which predates the 11,000 y history of humans in Amazonia (Roosevelt *et al.* 1991). Once a few adults of *Bertholletia* become estab-

lished in a given area via any means of long-distance dispersal, agoutis are perfectly capable of facilitating the formation of a natural grove by consistently generating a highly restricted seed shadow through scatterhoarding activities within a limited dispersal radius. Because the flower morphology of *B. excelsa* largely promotes self-incompatibility (Mori & Prance 1990a, b), efficient seed set in newly established trees would have to rely on relatively specialized pollination services provided by several genera of large-bodied euglossine bees, which can nevertheless travel over long distances (Janzen 1971). Long-range seed dispersal to suitable colonization sites can be provided on very rare occasions by highly mobile volant seed predators that can cover several kilometres in a few minutes. This is the case of red-and-green macaws (*Ara chloroptera*), which can open large *Bertholletia* pyxidia in southern Amapá (S. Almeida, *pers. comm.*), and are known to occasionally drop large seeds of other plant species in mid-flight (C. A. Peres, *pers. obs.*). Such rare dispersal events would benefit from the substantially lower post-dispersal predation rates accrued to seeds moved well beyond the limits of a grove (Peres *et al.* 1997). Grove initiation and expansion are, however, likely to be constrained by abiotic factors such as soil types and microclimate of regeneration sites, and regional climate which largely restricts high-density *Bertholletia* stands to areas of highly seasonal rainfall of eastern, southern, and southwestern Amazonia (Clement 1993, Diniz & Bastos 1974, Müller 1981). This hypothetical scenario is consistent with (i) the rarity at which incidental dispersal of founder propagules takes place over long distances, (ii) the subsequent agouti-mediated dispersal of descendant individuals over short distances, and (iii) the relatively even-sized distribution of adjacent cohorts in many areas of mature forest. It also explains the presence of *Bertholletia* groves in vast expanses of terra firme forests uninhabited by indigenous groups, presumably because of low availability of animal protein (C. A. Peres, unpubl. data), as well as their conspicuous absence from large areas known to have been densely populated by Amerindians (lower Rio Negro: Nelson *et al.* 1985). Admittedly, the occurrence of *Bertholletia* does appear to be associated with areas subjected to natural or man-made disturbance, gap-phase sites within a closed-canopy forest matrix, or even previously burned areas (Müller & Calzavara 1989, Pires & Prance 1985, Viana *et al.* in press), which is precisely why this species has been considered to be a disturbance indicator (Balée 1989, Balée & Campbell 1990, Miller 1990). But previous changes in vegetation structure do not necessarily equate to anthropogenic disturbance nor deliberate human intervention. It can be merely seen as providing favourable seedling establishment and growth conditions for a light-dependent gap specialist tree.

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