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Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities

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Abstract Animals aid population growth and fitness in tropical forest communities through dispersal and negatively impact populations through seed predation. The interaction between dispersal and seed predation can produce distance- or density-dependence; powerful mechanisms for maintaining species diversity incorporated in the Janzen–Connell model. Large mammals, the highest biomass seed predators of intact Amazonian communities and at risk due to human disturbance, are potentially central to these interactions. This study tests the Janzen–Connell model and investigates the impact of mammalian seed predators on seedling recruitment and maintenance of tree diversity. Patterns of both vertebrate and invertebrate seed predation and seedling recruitment were studied in the two most abundant canopy tree species in western Amazonia (Arecaceae: *Astrocaryum murumuru* and *Iriarteia deltoidea*). We specifically examined effects of both spatial and temporal variation of the highest biomass seed predator in southwest Amazonian forests, the white-lipped peccary (*Tayassu pecari*), on recruitment through disturbed and undisturbed sites and through a fortuitous 12 year natural extinction and recolonization event of *T. pecari*. Distance-dependent seedling recruitment was found in *Astrocaryum* and *Iriarteia* at both sites. However, the median distance of seedlings was $\sim 1.5\times$ farther from reproductive adults in both palms at the undisturbed site. The number of *Iriarteia* seeds escaping predation increased 6,000% in both space and time due to the decline of *T. pecari* abundance. The results demonstrate that Janzen–Connell effects are stronger in intact ecosystems and tie these mechanistically to changes in seed predator abundance. This study shows that anthropogenic changes in mammal communities decrease the magnitude of Janzen–Connell effects in Amazonian forests and may result in decreases in tree diversity.

Keywords Diversity · Janzen–Connell hypothesis · Seedling recruitment · *Tayassu pecari*

Introduction

The life history of tropical trees is inextricably connected to vertebrates through seed dispersal, which positively affects recruitment—more than 80% of tree and shrub species in tropical rain forests require vertebrate dispersal agents (Levey et al. 1994)—and seed predation, which negatively influences recruitment. Seed predation rates are heavily influenced by life history characteristics of the tree (Foster 1986; Silman 1996; Blate et al. 1998; DeSteven and Putz 1984), and species with vertebrate dispersed seeds can have similar seed shadows but drastically different seed predation rates (Silman 1996). The dual role of vertebrates suggests that changes in vertebrate communities can alter tree community composition.

An essential process in maintaining tree diversity is preventing individual species from dominating space. This is true whether species are viewed as ecological equivalents (neutral theory; e.g., Hubbell 2001) or highly structured competitive hierarchies (Tilman 1994). Variabilities in species life history traits can be powerful mechanisms for maintaining diversity and factor into the proposed theories of diversity maintenance (Silman 1996; Hubbell 2001; Nakashizuka 2001; Condit et al. 2002). The combination of plant–animal interactions and life history characteristics are essential components for maintaining tropical tree diversity in the Janzen–Connell model (Janzen 1970; Connell 1971). The Janzen–Connell model predicts that seed predators will exert greater predation pressures where dispersed seeds are densest or closest to a reproductive conspecific. Distance- or density-dependent mortality during recruitment leads to a decreased probability that a species will replace itself at a site and promotes maintenance of diversity (Janzen 1970; Augspurger 1984; Clark and Clark 1984; Howe 1989; Forget et al. 2000). The Janzen–Connell predictions have been studied intensively, but most studies have been

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conducted in areas without a full complement of large mammals (Wright 2002).

The Janzen–Connell hypothesis has been repeatedly tested with mixed results. Many studies report seedling recruitment increasing with distance from conspecifics (Clark and Clark 1984; DeSteven and Putz 1984; Wills et al. 1997; Barot et al. 1999; Barone 2000; Grau 2000; Packer and Clay 2000). Both small- and large-scale trends show seedling survival decreasing as adult tree abundance increases, providing evidence of density-dependent or compensatory processes contributing to species coexistence (Connell et al. 1984; Webb and Peart 1999). Contrary to the Janzen–Connell model, seed survival was not enhanced at greater distances from reproductive conspecifics or recruitment probability was increased close to adults (Condit et al. 1992; Forget 1993; Howe 1993; Wenny 2000, though with an interesting exception). Review studies by Hammond and Brown (1996) and Wright (2002) concluded that invertebrate seed and seedling predation provide support for the Janzen–Connell model while vertebrate predation does not. However, Hyatt et al. (2003) concluded through meta-analysis that Janzen–Connell effects are not important at the community level.

Mammalian seed predators

Historically, the highest biomass seed predator throughout the Neotropics was the white-lipped peccary (*Tayassu pecari*, Kiltie 1982), which has a large impact on palm seed survival (Silman et al. 2003). Collared peccaries (*T. tajacu*) are also present, but have less of an impact because of their smaller herds, localized ranges, and diets of less resistant seeds (Kiltie 1982). White-lipped peccaries also account for high seedling and sapling mortality near parent trees, which are indicators of food availability (Fragoso 1997). Due to their biomass in the ecosystem and dietary preferences, *T. pecari* are likely to have an essential, although poorly understood, role in altering the seed shadow of large seeded tree species. *T. pecari* are quickly eliminated in the presence of human inhabitants (Peres 1996) and most Amazonian seed predation studies have been conducted in areas with reduced *T. pecari* populations (Burkey 1994; Notman et al. 1996; Forget et al. 2000).

The present study examines changes in seed shadows for two Neotropical dominant trees and tests (1) for distance-dependence recruitment and (2) whether changes in the mammal seed predator community (focusing on large, mobile vertebrate seed predators) translate into changes in recruitment and distance-dependence in these tree species. We took advantage of spatial variation in *T. pecari* and *T. tajacu* abundance between disturbed and undisturbed study sites, as well as 20 years of temporal variation in *T. pecari* abundance at an undisturbed study site to specifically test for their effects on seedling recruitment in two Amazonian dominant trees.

Materials and methods

Study species

The palms *Astrocaryum murumuru* and *Iriartea deltoidea* are the two most abundant trees within western Amazonia (Pitman et al. 2001), and palms are the numerical dominants of Amazonian and Guianan forests (Terborgh and Andresen 1998). Both species are keystone resources for Amazonian frugivore and seed predator communities (Terborgh 1986).

Astrocaryum murumuru is the second most abundant tree species in the Rio Manu floodplain, with ~30 *Astrocaryum* adults ha⁻¹ and is widespread throughout the Amazon basin (Kiltie 1981b; Terborgh et al. 1996). Reproduction is via one to five inflorescences enclosed in a spiny bract, each about 80–150 cm long with 300–800 fruits (*A. standleyanum*, Smythe 1989). Fruits are obovoid containing a single seed (3.5–9 cm long and 2.5–4.5 cm diameter; 10 g) and mature between late May and early August (Terborgh 1993). *Astrocaryum* seeds have a maximum crushing resistance of 200±50 kg (Kiltie 1981a). Seed predators include bruchid beetle larva (*Speciomerus* spp. and *Pachymerus* spp.), spiny pocket mice (*Heteromys* spp.), squirrels (*Sciurus granatensis*), spiny rats (*Proechimys* spp.), agoutis (*Dasyprocta* spp.) and both *T. pecari* and *T. tajacu* (Kiltie 1981b; Smythe 1989; Martinez-Gallardo and Sanchez-Cordero 1993).

Iriartea deltoidea is the most common tree in upper Amazonian forests with ~45 *Iriartea* adults ha⁻¹ in the Manu floodplain forest (Pitman 2000; Pitman et al. 2001). At the study site, reproductive *Iriartea* produce ~300–1,000, 2–2.8 cm in diameter fruits containing exceptionally hard 5 g seeds (crushing resistance 350±70 kg; Kiltie 1981a). Primary seed predators include *T. pecari* and rodents (Kiltie 1981b). *Iriartea* seeds are too hard for collared peccary, *T. tajacu*, to consume (Kiltie 1981b).

Spatial variation

Spatial variation in *T. pecari* abundance was examined by recruitment patterns in *A. murumuru* and *I. deltoidea* at undisturbed (Cocha Cashu) and disturbed (Boca Manu) study sites.

Undisturbed site

Cocha Cashu Biological Station is located in the Manu National Park (Department of Madre de Dios in southeastern Peru) at 11°54'S and 71°22'W. It is an unlogged, un hunted, moist tropical forest that is protected within the 20,000 km² Manu National Park. The study area lies in primary floodplain forest along the Rio Manu. The annual rainfall is 2,400 mm, distributed seasonally, with the majority occurring between November and May (Terborgh 1990). There are less than 1,000 people living within the boundaries of the park (S.R. Silman, personal observation), all indigenous with no firearms. Manu harbors a complete Amazonian fauna including large herds of the palm specialist, *T. pecari* (Emmons 1984). Herds of white-lipped peccaries average over 100 individuals each weighing from 25 to 40 kg (Kiltie 1981b; Kiltie 1982). Herds move in a patchy, course-grained style covering about 10 km a day (Kiltie and Terborgh 1983). *T. pecari* crush hard seeds and nuts with their interlocking canines and forage by turning over the leaf litter especially around cover objects (Kiltie 1981b).

Disturbed site

Boca Manu is a town of ~100 families that borders Manu National Park, 60 km downstream of Cocha Cashu on the Manu River. The main economy of Boca Manu is tourism and boat-building from old-growth logs washed out of Manu National Park during floods. Vertebrate seed predator fauna in Boca Manu differs from Cocha

Cashu because of anthropogenic disturbance—namely the defaunation of game species. At Boca Manu, peccaries are absent due to hunting pressure, providing comparative spatial variation in peccary abundance. Boca Manu and Cocha Cashu are both within mature floodplain forest of similar composition and topographical position. Species composition, phenology, and physiognomy are similar (Terborgh et al. 1996; Pitman et al. 1999, 2001). The two surveyed palm species are abundant over a wide geographical area, with similar densities throughout their range (Clark et al. 1995; Pitman et al. 2001). Reproductive effort in these palms is also relatively constant over a wide range of environments and ages (Pinero et al. 1982; DeSteven et al. 1987).

Seedling census

Ten reproductive individuals of each palm species were surveyed at both Cocha Cashu and Boca Manu from June to July of 2001. For each tree a 30° wide transect 30 m long was established (following Wright and Duber 2001) in order to compensate for changing density effects with distance (Clark and Clark 1984). No adult conspecifics of the focal tree were within the 30° wedge or 5 m of its boundary. Within the transect, conspecific, simple-leaved seedlings were measured for height and distance to focal tree.

Seed census

Seed surveys were conducted within the focal tree transects with 0.25 m² seed plots spaced ~1 m apart beginning 2 m from the focal tree and every 3 m following (see Wright and Duber 2001). Seeds of the focal species were recovered from the leaf litter and top 3 cm of soil. The cause of seed mortality was determined by the characteristic damage seed predators caused to the endocarp: drilled holes (bruchids), long gnaw marks (rodents), and broken *Astrocaryum* endocarps with jagged edges (*T. pecari* and *T. tajacu*). White-lipped peccaries consume entire *Iriartea* seeds and leave no evidence while collared peccaries do not eat *Iriartea* (Kiltie 1981b). Fates of seeds with multiple predators were assigned to the final predator (beetle–rodent predation: assumed rodents final predators; peccary predation assumed to occur after both rodent and beetle predation; Silviu 2002).

Temporal variation

In 1978 *T. pecari* vanished from the Manu National Park and surrounding area of at least 71,000 km² and returned to the study site in 1990 (Silman et al. 2003). Losos (1995) recovered intact seeds beneath the bases of nine *Astrocaryum* and 25 *Iriartea* in 1988, 10 years after the disappearance of *T. pecari*. The number of uneaten *Astrocaryum* and *Iriartea* seeds recovered at Cocha Cashu during 2001, 11 years after *T. pecari* returned to the area, was compared to the number collected at the same time of the year (dry season) in 1988. Using the data from 1988 and 2001, we estimated

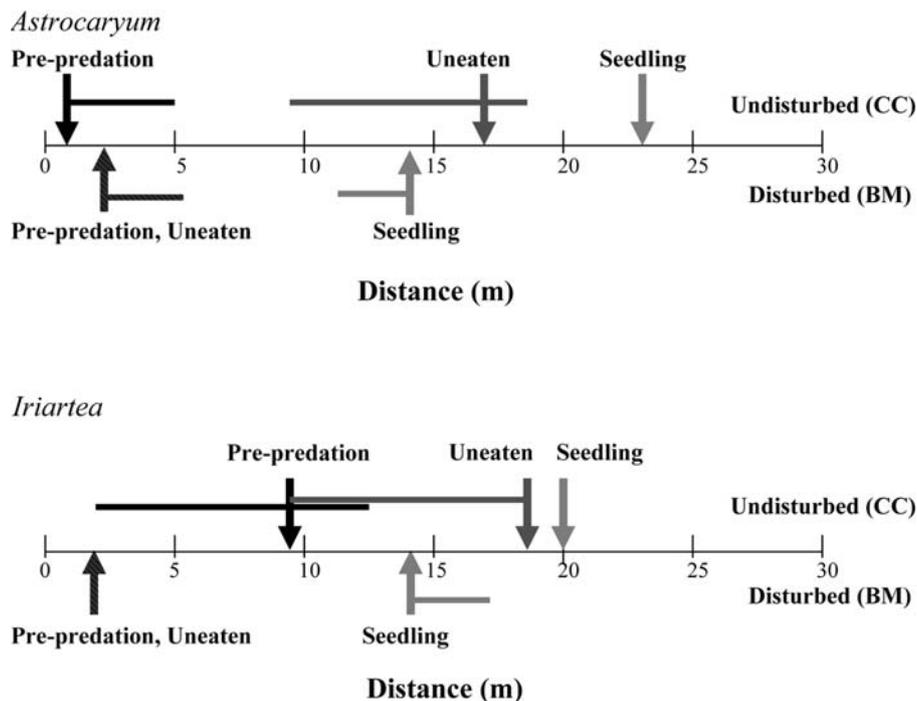


Fig. 1 Median recruitment distances for *Astrocaryum* and *Iriartea* at the undisturbed site (Cocha Cashu) and the disturbed site (Boca Manu). *Pre-predation*, *Uneaten* and *Seedling* represent the median distance of these stages from the reproductive adult. The arrows on top of the line for each species represent the undisturbed site (Cocha Cashu) and the arrows beneath the line are the distances for the disturbed site (Boca Manu). Error bars are empirical interquartile (IQ) ranges of bootstrapped medians and may be asymmetrical about the medians. For *Astrocaryum* at CC median distance of pre-predation ($n=246$): 2 m, IQ range 2–5 m; uneaten ($n=10$): 17 m, IQ range 9.5–18.5 m; seedlings ($n=112$): 23 m, IQ range 23–26 m; at BM median distance of uneaten ($n=20$) and pre-predation ($n=127$)

were identical: 2 m; IQ range 2–5 m; seedlings ($n=127$): 14 m, IQ range 11–14 m. Total number of pre-predation *Astrocaryum* seeds, uneaten seeds, and seedlings did not differ between sites (pre-predation: $\delta=0.01$, $df=1$; $P=0.21$; uneaten: $\delta=-0.34$, $df=1$; $P=0.17$; seedlings: $\delta=-0.06$, $df=1$, $P=0.59$). For *Iriartea* at CC median distance of pre-predation seeds ($n=22$): 9.5 m, IQ range 4.25–17 m; uneaten ($n=6$): 18.5 m, IQ range 11–20 m; seedlings ($n=126$): 20 m, IQ range 20 m; at BM median distance of pre-predation ($n=465$) and uneaten ($n=283$) were identical: 2 m; IQ range 2 m; seedlings ($n=153$): 14 m, IQ range 14–17 m. The disturbed site had more pre-predation seeds ($\delta=-1.47$, $df=1$, $P<0.001$), although number of seedlings did not differ between sites ($\delta=-0.10$, $df=1$, $P=0.36$).

uneaten seed density in 5 and 30 m annuli of both species to compare over the temporal variation in *T. pecari* abundance.

Data analysis

In the Janzen–Connell hypothesis, survival probability is related to distance with the median distance of any cohort from the reproductive adult increasing over time (Clark and Clark 1984). The median distance, along with quartiles obtained from bootstrapping, was determined for the pre-predation seed shadow, uneaten seeds, and seedlings for *Astrocaryum* and *Iriartea* at both sites (Efron and Tibshirani 1993; S-Plus 2002). The pre-predation seed shadow includes both uneaten seeds and all seeds with evidence of predation. Uneaten seeds are intact seeds with no evidence of predation. Differences among the median distances of each life stage were tested using randomization tests (RT) for both within and between site comparisons (Crowley 1992; Davison and Hinkley 1997; S-Plus 2002).

We tested whether the probability of the pre-predation seed shadow, survival (uneaten seeds), and seedling establishment depended on distance using a negative binomial generalized linear model [negative binomial regression (NBR)] based on count data (Venables and Ripley 1997; S-Plus 2002). These models were also used to test for an interaction between distance and site for the two species by comparing the frequency distribution of counts with distance between sites. This approach compares groups based on frequency distribution of counts and is used for skewed data where the mean and variance are not equal (White and Bennetts 1996).

Results

Evaluation of Janzen–Connell predictions

Astrocaryum

Median distance of pre-predation seed shadow, uneaten seeds and seedlings was compared for *Astrocaryum* at both sites (Fig. 1). At Cocha Cashu (undisturbed) seeds escaping predation (uneaten) were significantly farther from the reproductive adult than the shadow of pre-predation seeds (RT: $P=0.008$). Seedlings were significantly farther from the focal tree than the pre-predation shadow (RT: $P<0.001$). The difference between the median distance of uneaten seeds and seedlings was not significantly different (RT: $P=0.209$; Fig. 1).

At Boca Manu (disturbed) the median distance and range of seeds escaping predation was no different from the original seed shadow (RT: $P=0.437$) and 15 m closer to the focal tree than at the undisturbed site (Fig. 1). Median distance of both pre-predation seed shadow and seeds escaping predation was significantly closer to the adult than seedlings (RT: $P<0.001$; Fig. 1). Between sites, the median distance of the pre-predation seed shadow did not differ (RT: $P=0.329$). The median distance of *Astrocaryum* seeds that escaped predation was 8.5× farther from the reproductive tree at the undisturbed compared to disturbed site (RT: $P=0.04$). Seedling recruitment in *Astrocaryum* was 1.6× farther from the reproductive tree at the undisturbed site (RT: $P<0.001$; Fig. 1).

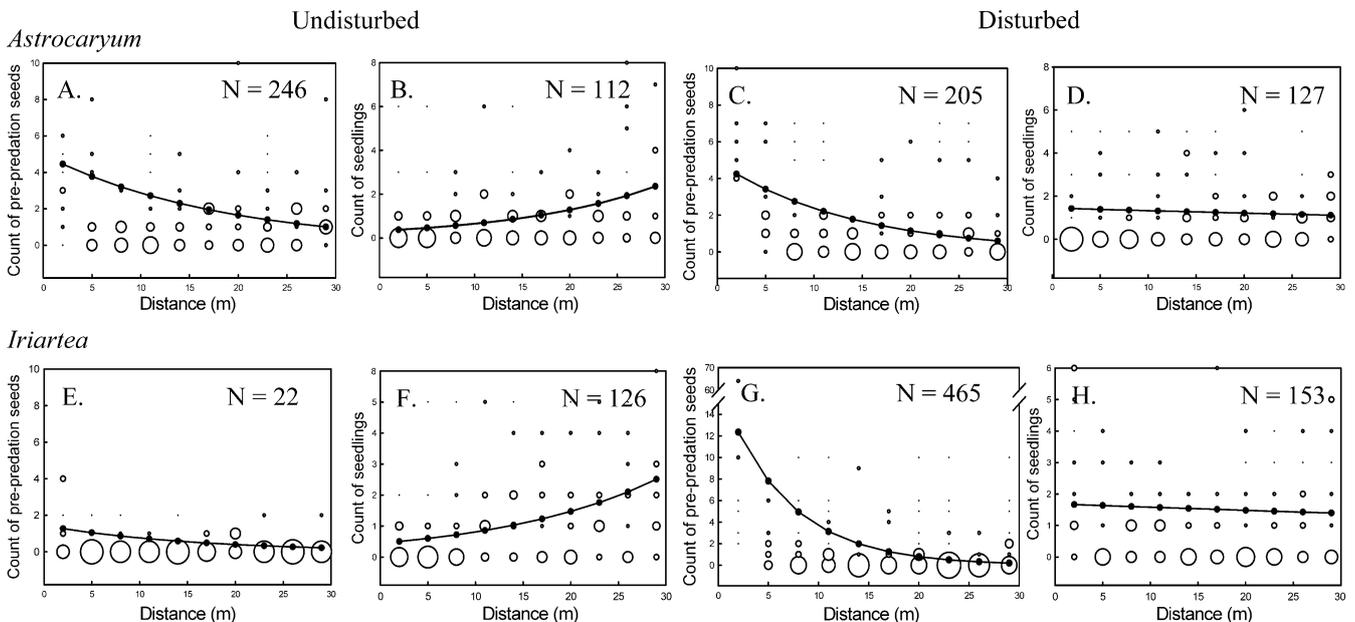


Fig. 2a–h Count data fit with a negative binomial model for seeds and seedlings of *Astrocaryum* and *Iriartea* at both Cocha Cashu (undisturbed) and Boca Manu (disturbed) versus distance from the reproductive tree. Size of circles represents the number of trees with that count of seeds at each distance. *Astrocaryum* at the undisturbed site: **a** count of pre-predation seeds decreases with distance ($\delta=-0.05$, $df=98$, $P<0.001$), **b** seedling counts increase with distance ($\delta=0.07$; $df=98$; $P<0.001$); at the disturbed site: **c** pre-predation

seeds decrease with distance ($\delta=-0.07$, $df=98$, $P<0.001$), **d** no relationship between seedling counts and distance ($\delta=-0.01$; $df=98$; $P=0.66$). *Iriartea* at the undisturbed site: **e** pre-predation seeds decrease with distance ($\delta=-0.04$, $df=88$, $P=0.16$), **f** seedling counts increase with distance ($\delta=0.06$, $df=98$, $P<0.001$); at the disturbed site: **g** pre-predation seeds skewed near adult, **h** seedlings have no distance relationship ($\delta=-0.33$, $df=98$, $P=0.72$)

The pre-predation seed shadow for *Astrocaryum* shows a decreasing probability of encountering a seed with increasing distance from the parent tree at both sites (Fig. 2a,c). Seedling counts increased with distance from the reproductive tree at the undisturbed site (Fig. 2b). There was no relationship between count of seedlings and distance from the reproductive tree at the disturbed site (Fig. 2d). Total number of pre-predation *Astrocaryum* seeds, seeds escaping predation, and seedlings did not differ between undisturbed and disturbed sites (Fig. 1).

Iriartea

Median recruitment distance of *Iriartea* at the undisturbed site increased over life stages (Fig. 1). Median distance of seeds escaping predation was 9 m farther than the pre-predation seed shadow (RT: $P=0.019$) and seedlings were 10.5 m farther than the pre-predation seed shadow (RT: $P<0.001$).

At the disturbed site, the median distance of the pre-predation seed shadow and seeds escaping predation were both 2 m (RT: $P=1.00$) while seedling recruitment was 14 m (RT: $P<0.001$; Fig. 1). At the undisturbed site the median distance of seeds escaping predation is 4.8× farther than at the disturbed site. Seeds escaping predation were 9.3× farther from the nearest reproductive tree at the undisturbed site compared to the altered site (RT pre-predation: $P<0.001$; uneaten: $P<0.001$). Recruitment of *Iriartea* seedlings at undisturbed site was 1.4× farther from

the reproductive adult than at the disturbed site (RT: $P<0.001$).

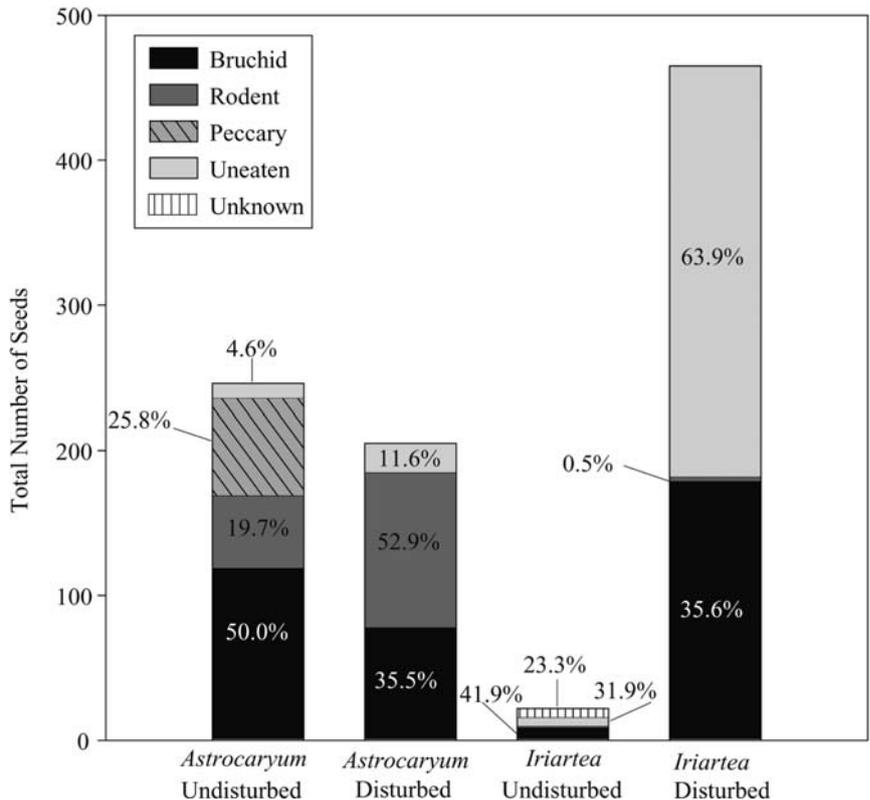
Twenty-one times more *Iriartea* seeds were recovered at the disturbed site, although number of seedlings did not differ between sites (Fig. 2). Pre-predation seed shadows differed between sites, with seed distributions heavily skewed towards the reproductive adult at the disturbed site (Fig. 2g), and *Iriartea* seeds decreasing with distance from the adult at the undisturbed site (Fig. 2e). At the seedling stage, the undisturbed site has a significant positive relationship with seedlings increasing with distance (Fig. 2f), while at the disturbed site seedlings show no distance relationship (Fig. 2h).

Components of seed mortality

Astrocaryum

The majority of *Astrocaryum* seeds at both sites were eaten with no significant differences in total seed predation between sites ($\delta=0.04$, $df=1$, $P=0.38$; Fig. 3). However, seed predation type differed between sites. At the undisturbed site, bruchids were the primary seed predators (50.0±5.3%) followed by peccaries (25.8±5.1%) and rodents (19.7±2.0%; Fig. 3). At the disturbed site, rodents were the dominant seed predators (52.9±6.0%) followed by bruchids (35.5±5.3%). There was no evidence of peccary predation at the disturbed site (Fig. 3). The cause of *Astrocaryum* seed mortality was not independent of site ($\chi^2=169.8$, $df=3$, $P<0.001$), with more rodent eaten, fewer

Fig. 3 The number of seeds recovered for each seed fate category compared for the undisturbed (Cocha Cashu) and the disturbed (Boca Manu) sites for *Astrocaryum* and *Iriartea*



bruchid eaten, and no peccary-eaten seeds at the disturbed site (Fig. 3).

Iriartea

Significantly more seeds were eaten at the undisturbed site ($44.8 \pm 15.6\%$) than the disturbed site ($36.1 \pm 5.0\%$; $\delta = 1.25$, $df = 1$, $P < 0.001$; Fig. 3). Bruchids were the primary seed predators at both sites (undisturbed: $41.9 \pm 16.0\%$; disturbed: $35.6 \pm 5.0\%$). Rodent predation was rare at both sites (undisturbed: $0.3 \pm 0.1\%$; disturbed: $0.5 \pm 0.3\%$). *Iriartea* seeds are completely consumed by peccaries so peccary predation was determined only via comparisons with areas or times when peccaries are absent. There were significantly more uneaten *Iriartea* seeds in the absence of peccaries (disturbed site) than at the intact site ($47\times$ more;

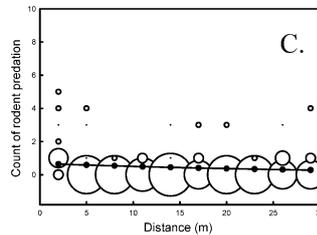
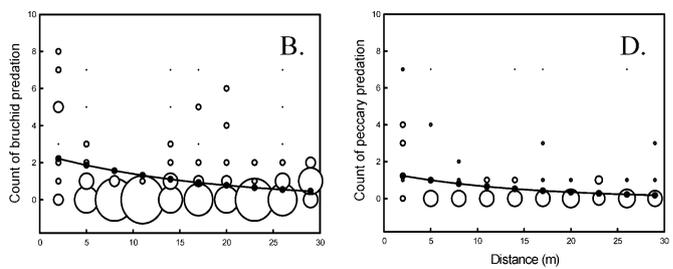
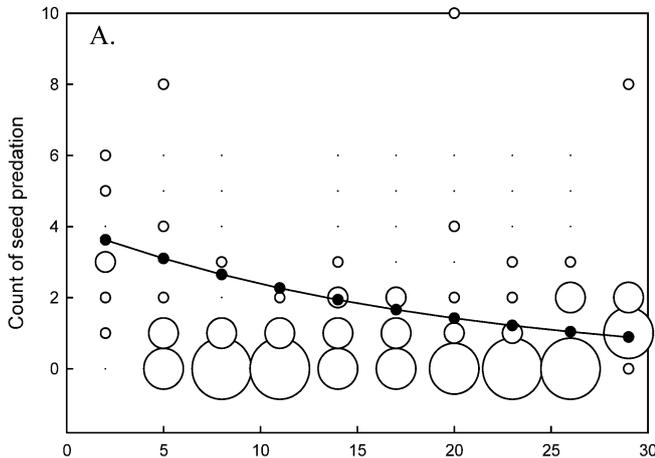
$\delta = -1.93$, $df = 1$, $P < 0.001$). The cause of seed mortality in *Iriartea* was independent of site ($\chi^2 = 3.24$, $df = 3$, $P = 0.07$), though this was due to the scarcity of rodent predation at either site and because peccary predation could not be explicitly included due to absence of a hard endocarp (Fig. 3).

Components of the Janzen–Connell effect

Astrocaryum

The probability of escaping predation significantly increased with distance from adult at both sites (Fig. 4a, e). At the undisturbed site, both bruchid and peccary seed predation was negatively distance dependent with greater predation close to reproductive adults (Fig. 4b, d). Rodent

Undisturbed Site



Disturbed Site

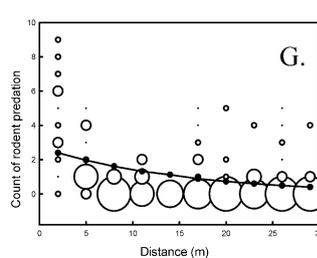
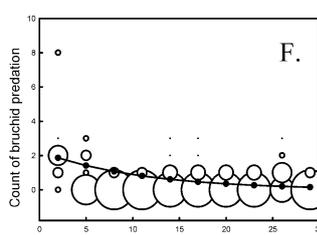
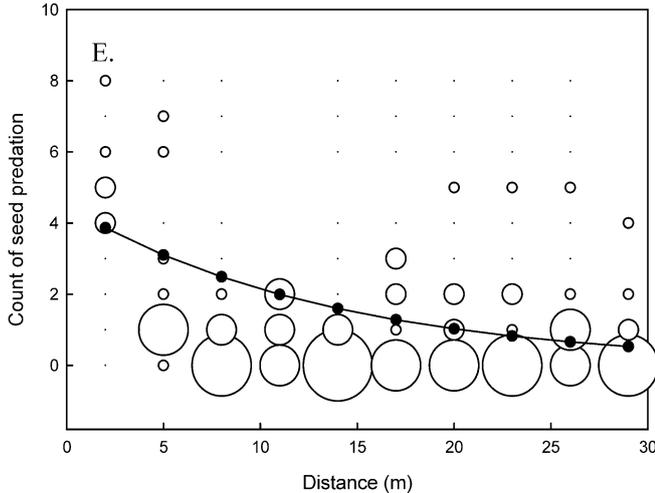


Fig. 4a–g Count data fit with negative binomial models for all seed predation in *Astrocaryum* and the different seed predators (bruchids, rodents, and peccaries) at both the undisturbed and disturbed sites versus distance from the reproductive tree. Size of circles represents the number of trees with that count of seeds at each distance. At the undisturbed site: **a** all seed predation ($\delta = -0.05$; $df = 98$; $P = 0.001$) and **b** bruchid predation ($\delta = -0.06$; $df = 98$; $P = 0.001$) decrease with

distance, **c** rodent predation has no distance relationship ($\delta = -0.03$; $df = 88$; $P = 0.20$), **d** peccary predation decrease with distance ($\delta = -0.07$; $df = 78$; $P = 0.002$); at the disturbed site: **e** all seed predation ($\delta = -0.07$; $df = 98$; $P < 0.001$), **f** bruchid predation ($\delta = -0.09$; $df = 98$; $P < 0.001$), and **g** rodent predation ($\delta = -0.07$; $df = 88$; $P < 0.001$) decrease with distance from reproductive tree

predation was not distance dependent at the undisturbed site (Fig. 4c). At the disturbed site both bruchid and rodent seed predation were highest near the parent and decreased with distance, showing negative distance-dependence (Fig. 4f, g).

Iriartea

Seed predation in *Iriartea* showed negative distance-dependence at both sites (undisturbed: $\delta=-0.06$; $df=58$; $P=0.07$; disturbed: $\delta=-0.14$; $df=98$; $P<0.001$) although the low number of seeds recovered at the undisturbed site led to marginal significance. Bruchid predation showed no relationship with distance at the undisturbed site ($\delta=-0.02$; $df=48$; $P=0.61$), but was significantly associated with distance at the disturbed site ($\delta=-0.14$; $df=98$; $P<0.001$). Rodent predation exhibited a negative distance dependent pattern at the disturbed site (rodent: $\delta=-0.15$; $df=28$; $P=0.07$) but too few rodent-eaten seeds were found at the undisturbed site to analyse.

Temporal comparison in *T. pecari* abundance: undisturbed site

In 1988, Losos (1995) recovered 267 *Astrocaryum* seeds and 120 *Iriartea* seeds within a 5-m radius of each adult. In 2001 there were only 12 *Astrocaryum* and 6.6 *Iriartea* seeds per tree in the entire 30-m annulus: an area three times greater (Fig. 5a). Adjusted for an equal (5 m) radius, only five *Astrocaryum* seeds per tree escaped predation in the presence of *T. pecari*, while 267 per tree escaped predation in their absence, a 5,340% increase (Fig. 5b). For *Iriartea*, in a 5-m annulus there were two uneaten seeds per tree when *T. pecari* are present compared to 120 uneaten seeds per tree in their absence, a 6,000% increase (Fig. 5b).

Discussion

Janzen–Connell predictions

Janzen–Connell effects of distance-dependent seed predation were found at both the undisturbed (Cocha Cashu) and disturbed (Boca Manu) sites, with median distance of both *Astrocaryum* and *Iriartea* seedlings significantly greater than the median distance of the pre-predation seed shadow (Fig. 1). However, seedling recruitment patterns are qualitatively different between sites, with seedlings 1.6× farther for *Astrocaryum* and 1.4× farther for *Iriartea* at the undisturbed site (Cocha Cashu) than the disturbed site (Boca Manu) (Fig. 2b, d, f, h). The impact of seed predators is evident with the location of uneaten seeds 8.5× farther from the focal tree for *Astrocaryum* and 9.3× farther for *Iriartea* at the undisturbed site than at the disturbed site (Fig. 1). The Janzen–Connell spacing effects

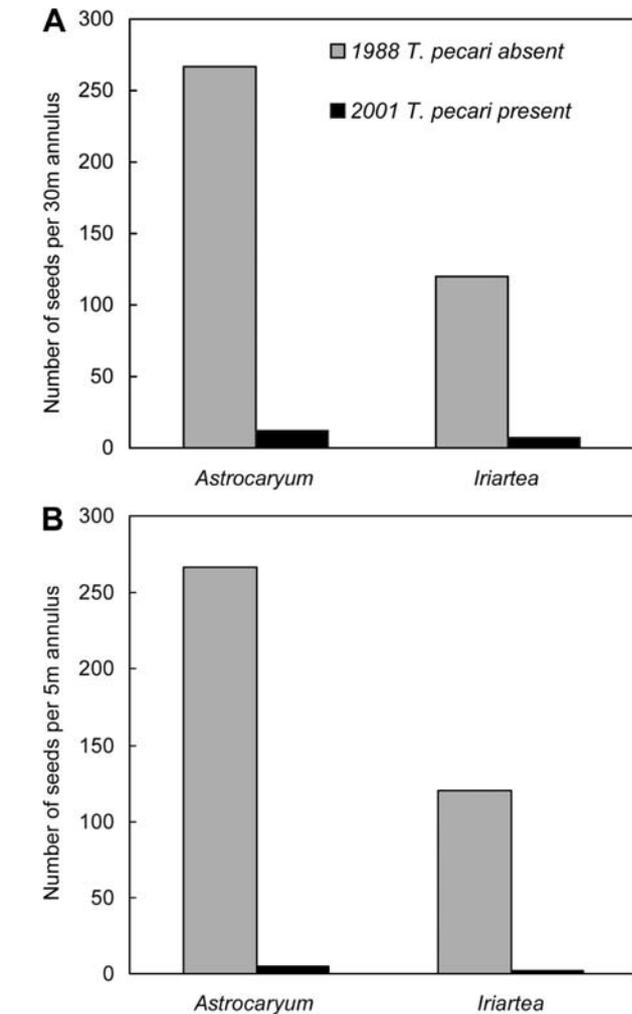


Fig. 5a, b Comparisons between the number seeds at the undisturbed site (Cocha Cashu) during 1988 (when *T. pecari* were absent) with 2001 (when *T. pecari* present) for *Astrocaryum* and *Iriartea*. **a** Number of seeds recovered around crowns in 1988 ($N_{Astrocaryum} = 9$; $N_{Iriartea} = 25$) compared to a 30-m annulus in 2001 ($N_{Astrocaryum} = 10$; $N_{Iriartea} = 10$). **b** Number of seeds recovered around crowns in 1988 ($N_{Astrocaryum} = 9$; $N_{Iriartea} = 25$) compared to an estimated 5-m annulus in 2001 ($N_{Astrocaryum} = 10$; $N_{Iriartea} = 10$)

are greater in the intact ecosystem compared to disturbed site where large mammalian seed predators are lacking.

Temporal variation in *T. pecari* abundance

The temporal absence of *T. pecari* at Cocha Cashu (undisturbed) resulted in abundant uneaten seeds beneath the crowns of *Astrocaryum* and *Iriartea*. In 1978, minimum counts of *T. pecari* individuals in a herd ranged from 90 to 138, comprising 21% of the aggregate biomass of terrestrial granivorous mammals at Cocha Cashu (Terborgh 1993). However, in 1978 *T. pecari* disappeared from a minimum of 71,000 km² in southeastern Peru and were not documented again until 1990 (Silman et al. 2003); they now comprise ~50% of the terrestrial granivorous mammal biomass (M.R. Silman and J.W. Terborgh, unpub-

lished data). During their absence, there was a 5,340% increase in the number of uneaten *Iriartea* seeds and a 6,000% increase in uneaten *Astrocaryum* seeds (Fig. 5). As surveys of the proportion of reproductive adults and infructescence size for *Iriartea* revealed no difference between Cocha Cahsu (undisturbed) and Boca Manu (disturbed), and because fruiting time is predictable and synchronous year to year and reproductive effort is relatively constant for these palm species (Pinero et al. 1982; Terborgh 1986; DeSteven et al. 1987), the dramatic differences in seed survival can be ascribed to the loss of the highest biomass seed predator in the ecosystem. The high abundance of *T. pecari* also explains the lack of *Iriartea* seeds recovered at the undisturbed site during the 2001 census: the radical difference in seed number between the undisturbed and disturbed sites in *Iriartea* ($n_{\text{undisturbed}} = 22$ vs $n_{\text{disturbed}} = 465$) is due to absence of *T. pecari* at the disturbed site (Peres 1996; Peres 2001), not reproductive failure.

The temporal absence of *T. pecari* at Cocha Cashu (undisturbed) also resulted in an increase of *Astrocaryum* seeds, which was not found with spatial variation in *T. pecari* abundance. This may be due to human hunting pressures at the disturbed site that did not accompany the temporal change of *T. pecari* at the undisturbed site. At Boca Manu (disturbed) there has been a reduction of all large mammals through hunting, which has allowed rodent populations to increase (Terborgh et al. 2001). Evidence of increased rodent abundance and compensatory predation at the disturbed site is shown by increased rodent predation ($52.9 \pm 6.0\%$) in the absence of peccaries in comparison to the undisturbed site ($19.7 \pm 2.0\%$; Fig. 3). Rodent predation is low in *Iriartea* at both sites with the majority of seeds uneaten (60.9%) in the absence of peccaries (Fig. 3). The large increase in viable *Iriartea* seeds is the same ($\sim 50\times$) when white-lipped peccaries are absent either in time or in space.

Bruchid predation did not compensate for the loss of vertebrate seed predators at the disturbed site. The rate of bruchid predation was not significantly different between sites or among species for *Astrocaryum* and *Iriartea* (Fig. 3). Current rates of bruchid infestation at Cocha Cashu (undisturbed; $50.0 \pm 5.3\%$) are equivalent to rates during the temporal absence of *T. pecari* (54% in 1989; Terborgh and Wright 1994; Wyatt 2002; Silman et al. 2003).

Components of the Janzen–Connell effect

The differences in the strength of Janzen–Connell effects between disturbed and undisturbed sites can be directly tied to differences in the distance–dependent action of seed predators (Fig. 4). *T. pecari* are important distance dependent seed predators, limiting seedling recruitment near adult *Astrocaryum* and *Iriartea*. Both bruchids and *T. pecari* contribute to distance-dependent seed mortality in both species at the undisturbed site (Fig. 4b, d). In the absence of *T. pecari*, beetle predation remains a distance-

dependent mortality agent in both species and rodents compensate with negative distance dependent seed predation in *Astrocaryum* at the disturbed site (Fig. 4f, g). However, bruchids did not exert predation pressure strong enough to alter *Iriartea* seedling recruitment because seedlings were not distance dependent at the disturbed site (Fig. 2h). Despite the increased amount of rodent predation in *Astrocaryum* at the disturbed site, seedling recruitment is independent of distance, and the median distance between adults and recruits decreased compared to the undisturbed site (Fig. 1). As a result, Janzen–Connell effects in *Astrocaryum* and *Iriartea* seedlings are weakened at the disturbed site.

Mammals and distance-dependence

Our study demonstrates that *T. pecari* seed predation results in distance-dependent seedling recruitment in *Astrocaryum* and *Iriartea*, which is contrary to previous studies where only invertebrates were found to be responsible for distance-dependence (Hammond and Brown 1996; Janzen et al. 1976; Wright 1983; Howe et al. 1985; Traveset 1990; Terborgh et al. 1993; Hart 1995). Results for *Astrocaryum* and *Iriartea* demonstrate that distance-dependent seedling recruitment is due to *T. pecari*, not invertebrate (bruchid) seed predation alone (Figs. 3, 5). Adult trees are indicators of food availability for *T. pecari* (Fragoso 1997). Possible mechanisms for distance-dependent seed predation by *T. pecari* may be their specialization on palm seeds and their use of scent or visual cues on distinctive palm trunks.

The results of this study agree with several community-level studies, which support Janzen–Connell predictions and the role of distance- or density-dependent mortality agents (Clark and Clark 1984; Wright 2002). Other explanations for a negative distance-dependence have been proposed, including allelopathy, intraspecific competition and abiotic resources (Wright 2002). However, these alternative explanations do not explain differences in seedling recruitment for species in the same ecosystem with constant abiotic resources over space and time. In the present study only the mammal seed predator community changed in any systematic way. The clear differences in seed predation and seedling recruitment between sites are due to hunting pressures on large mammals, specifically *T. pecari* (Bodmer et al. 1994).

Conservation implications

With the degradation of tropical rain forests worldwide, understanding how diversity is maintained in an intact ecosystem is becoming increasingly important. The idea of an “empty forest” in which the animals are absent but the structure remains (Redford 1992) describes much of the Neotropics. The importance of now ecologically extinct animals in shaping forest structure, however, is unknown. Terborgh et al. (2001) provided strong evidence of top-

down regulation where loss of predators increased consumer abundance and decreased recruitment of canopy trees. *T. pecari* are among the species that are quickly eliminated from areas under even moderate hunting pressures (Peres 1996). We found that the largest biomass seed predators, *T. pecari*, exert heavy and distance-dependent predation on seeds of two of the most abundant tree species in western Amazonia. In the absence of peccaries, seeds of *Astrocaryum* and *Iriartea* increased 6,000% and, important for diversity, seedling recruitment was shifted closer to the reproductive adult. Both factors suggest that trees will be replaced by conspecifics. With the loss of *T. pecari* from the Neotropics, we predict that the structure and composition of Neotropical forests will undergo extensive alterations if saplings and adults exhibit the same patterns found in seedlings. The results of this and other studies suggest that without large vertebrates, the basic mechanism controlling community structure and diversity—dispersal and seed predation—will be substantially altered.

Conclusions

Distance-dependent seedling recruitment was supported in *Astrocaryum* and *Iriartea* at both sites, however Janzen–Connell effects were weaker when *T. pecari* were absent. Without *T. pecari*, recruitment of seedlings was significantly closer to reproductive adults in these two abundant palm species. The number of *Iriartea* seeds escaping predation increased dramatically with both spatial and temporal declines in *T. pecari* abundance. In the absence of *T. pecari* these abundant tree species are released from distance-dependent mortality allowing seedlings to recruit closer to the parent tree. Evidence of distance-dependent seed predation by *T. pecari* does not conform to assertions that only fungal and invertebrate predation exhibit this pattern (Hammond and Brown 1996; Wright 2002) and to conclusions of Janzen–Connell effects being unimportant at the community level (Hyatt et al. 2003). We demonstrated that large mammalian seed predators do induce distance-dependent seedling recruitment. Implications are centered on the abundance of these tree species in the community. *Iriartea* is the dominant tree in western Amazonia (Pitman et al. 2001) and *T. pecari* are quickly eliminated when human inhabitants come into an area (Peres 1996). By eliminating *T. pecari* from the ecosystem, two abundant tree species are released from distance-dependent control and these palms may proliferate and exclude the rarer tree species that make tropical rain forests so diverse.

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