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Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest

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Summary

1 *Maximiliana maripa* is a large seeded palm that occurs in monodominant patches (clumps) in the Amazonian forest of Maracá Island, Roraima, Brazil.
2 Rodents, collared peccaries (*Tayassu tajacu*), deer (*Odocoileus virginianus* and *Mazama* spp.) and primates, all short-distance, small-to-medium bodied dispersers, ate the pulp of *Maximiliana* fruits and spat out intact seeds, from 97 to 100% of them within 5 m of parent plants (below the tree crown).
3 Tapirs (*Tapirus terrestris*) swallowed entire fruits and defecated intact seeds at latrines located up to 2 km from the nearest palm clump, creating a large-scale, punctuated seed shadow.
4 Bruchid beetle (*Pachymeris cardo*) larvae killed 77% of seeds remaining near parent trees, but only 0.7% of the 6140 seeds dispersed by tapirs to latrines.
5 Densities of zero-year seedlings to fifth-year saplings were significantly higher at tapir latrine sites than around parent trees located in conspecific aggregations; they were also significantly higher for the zero and one year classes at latrines than at randomly selected nonpalm, nonlatrine control trees.
6 Seeds dispersed by tapirs to latrines and secondarily dispersed by rodents gave rise to the seedlings and saplings located around the latrine sites, while seeds secondarily dispersed by rodents gave rise to the seedlings and saplings around control trees.
7 Collared (*Tayassu tajacu*) and white-lipped (*T. pecari*) peccaries accounted for high seedling and sapling mortality around parent trees.
8 Adult *Maximiliana* attained densities of 32 trees per 2500 m^2 within these patches.
9 Clump dispersal of seeds by tapirs, a meso-scale process, interacting with the small-scale process of seed dispersal by rodents, is sufficient to explain the creation of palm patches.

Keywords: bruchid beetles, forest structure, palms, seed shadows, tapirs

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Introduction

Patterns of seed and seedling mortality influence the diversity and dispersion patterns of individual trees and tree species (e.g. Janzen 1970; Connell 1971; Hubbell 1980; Howe & Smallwood 1982; Clark & Clark 1984; Forget 1992a; Portnoy & Willson 1993). In tropical rain forests, seed and seedling mortality due to predators is high immediately surrounding parent trees, but tends to decrease with distance from parent tree (e.g. Janzen 1970; Connell 1971; Hubbell 1980; Clark & Clark 1984; Hubbell & Foster 1987; Condit *et al.* 1992; Schupp 1992; Howe 1993; Leigh *et al.* 1993). This distance or density-dependent survival has been tested primarily at what I term the 'agouti scale' by comparisons between undispersed seeds located 0 m from the parent tree and rodent-dispersed seeds located 5–30 or 100 m from the parent tree (e.g. Janzen 1971; Wilson & Janzen 1972; Bradford & Smith 1977; Hallwachs 1986; Forget 1990, 1991, 1992a, 1992b). Such dispersal is a small-scale process occurring at the level of individual trees.

The assumption that the same process remains dominant at larger, forest-wide scales leads to the Janzen–Connell hypothesis of rain forest structure: same-species seedlings are less likely to be established

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near parent trees than different-species seedlings, resulting in an even spacing of species and high species diversity per unit area (e.g. Janzen 1970; Connell 1971; Clark & Clark 1984; Forget 1992b; Schupp 1992). There have been continuing field tests of this hypothesis, with varying outcomes (e.g. Hubbell 1979, 1980; Clark & Clark 1984; Hubbell & Foster 1987; Condit *et al.* 1992; Schupp 1992; Howe 1993; Leigh *et al.* 1993). However, much evidence now points to the fact that tropical rain forests have a patchy tree species distribution at the landscape scale (Lieberman & Lieberman 1994 and citations therein, Thorington *et al.* 1982). Can small-scale distance-dependent seed survival explain these large-scale patterns, or do larger-scale processes become dominant and entrain the smaller-scale processes (O'Neil *et al.* 1986; Holling 1992)?

Here I address these questions by simultaneously describing process and pattern at matching scales for the arborescent palm *Maximiliana maripa* ((Correa de Serra) Drude). Many species of arborescent palms occur in patches. While palms do respond to edaphic factors, with some species being resistant to waterlogged soil or high sunlight conditions (Kahn & de Granville 1992; Clark *et al.* 1995; Losos 1995), they also share another characteristic: large-seeded fruits with plentiful nutritious pulp highly attractive to large frugivorous mammals capable of extensive movements (Wallace 1853; Moore 1973; Pesce 1985; Uhl & Dransfield 1987; Kahn & de Granville 1992). Dispersal processes may thus also account for patchiness in palm species (Fragoso 1994; Losos 1995).

I document the process, from the seed through the sapling stages, by which seed dispersal by tapirs (*Tapirus terrestris* Linnaeus 1758) can create adult palm patches. I tested the hypotheses that:

1 seed dispersal by tapirs leads to higher survival of seeds than dispersal by rodents and other mammals;
2 seed dispersal by tapirs to sites distant from parent trees leads to higher densities of seedlings and saplings at these sites than near parent trees;
3 seed dispersal by tapirs, through enhanced seed and seedling survival, results in higher recruitment into older age classes.

The largest source of mortality for palm seeds in my study site, as well as elsewhere in the Neotropics, is infestation by bruchid beetle larvae (different beetle species at different sites; Bradford & Smith 1977; Fragoso 1994; Janzen 1971; Kiltie 1981; Smythe 1989; Terborgh 1983; Wilson & Janzen 1972). Since the area around the parent tree is the area of highest seed mortality (Janzen 1971; Kiltie 1981; Fragoso 1994), I tested the hypothesis of dispersal quality by describing the distances to which seeds were dispersed by different frugivore species and comparing the mortality of dispersed seeds and seeds remaining near parents and within conspecific aggregations to that of seeds dispersed far from parent trees and conspecific aggregations.

Materials and methods

STUDY SITE AND SPECIES

The study took place from July 1991 to December 1992 as part of a 2-year project (December 1990 to December 1992), on Maracá Island Ecological Reserve. Maracá Island lies at 3°25′N and 61°40′W, at the northern edge of the Amazon River basin in Roraima state, Brazil, near the boundary between savanna habitat and the Amazon rain forest. It is formed by the branching of the Uraricoera river, a tributary of the Rio Branco (Amazon drainage). All 110 000 ha of tropical rain forest and seasonal wetlands forming the reserve are protected by IBAMA (Instituto Brasileiro do Meio Ambiente; the Brazilian Secretariat for Wildlife, Ecological Reserves and Parks) as a site for research and forest protection. The dominant vegetation of the region is primary, tropical evergreen lowland rain forest (Moskovits 1985), contiguous with the Amazon rain forest to the west, south and north and the natural Rupunni–Roraima Savanna to the east (Milliken & Ratter 1989). Maracá supports substantial and unhunted populations of mammalian frugivores, including two peccary species (*Tayassu tajacu* Linnaeus 1758 and *T. pecari* Link 1795), three deer species (brocket deer, *Mazama americana* Erxleben 1777; *M. gouazoubira* G. Fischer 1814; and white-tailed deer, *Odocoileus virginianus* Zimmerman 1780), brazilian tapirs (*T. terrestris*), six primate species (*Cebus apella* Linnaeus 1758; *C. nigrivitatus* Schomburgk 1848; *Alouatta seniculus* Linnaeus 1766; *Ateles belzebuth* Geoffrey 1806; *Saimiri sciureus* Linnaeus 1758; *Aotus trivirgatus* Illiger 1811), and caviomorph rodents (*Dasyprocta leporina* Linnaeus 1758; *Agouti paca* Linnaeus 1766, *Myoprocta* sp. Thomas 1903) (Nunes *et al.* 1988; Nunes 1993). Only the eastern half of the island currently has a trail system (of about 60 km) allowing access to a variety of habitat types; this constituted the primary study area.

Rainfall varies between 1750 and 2250 mm per year. The dry season, with less than 100 mm monthly on average, occurs between October and April, and the wet season, with greater than 350 mm monthly, occurs between May and September. There are two forest-wide fruiting peaks, a marked one during the middle of the rainy season and a weaker one at the end of the dry season (Moskovits 1985).

Maximiliana maripa is a large subcanopy to canopy palm common throughout the Amazon basin, Maranhão, Mato Grosso, Ceará, and the Guianas (Pesce 1985; Kahn & de Granville 1992). *Maximiliana*'s large yellow fruits (and seeds) are easily located on the forest floor. Adult trees reach heights of 35 m (Pesce 1985; Kahn & de Granville 1992) and produce from one to four infructescences, each bearing from several hundred to over two thousand fruits. Counts of two mature fruit bunches on Maracá revealed 2405 fruits in one and 1108 in the other (Kirsten Silvius, unpublished data). Fresh fruits (pericarp and seed) weighed 14–26 g and measured 5–6.5 cm in length ($n = 30$), while fresh seeds weighed 7–17 g. The hard woody endocarp ranged from 1.5 to 6.5 mm in thickness ($n = 1034$) and contained one, two or three endosperms ($n = 305$). On Maracá, *Maximiliana* frequently occurs in large patches, commonly adjacent to *Mauritia* swamps. It also occurs as solitary individuals in the upland forest and in high density patches beneath the forest canopy (personal observation; Milliken & Ratter 1989). During two study years (December 1990 – December 1992), the *Maximiliana* population flowered synchronously at the end of the dry season (March–April) and then produced fruit synchronously during the middle of the wet season (May–August). Seeds are parasitized on the ground by the bruchid beetle species *Pachymeris cardo*; beetle larvae feed on the endosperm for two to six or more months after fruit fall (Kirsten Silvius, unpublished data).

Methods

ADULT *MAXIMILIANA* DISPERSION PATTERN

To ascertain adult dispersion patterns I searched the 60 km of trails (laid out over an area of 999 ha) for areas with and without adult *Maximiliana* palms and noted the number of high density aggregations encountered. The clump ended with the last tree when no conspecifics were encountered in a clump formation for a minimum distance of ≈ 200 m. I verified the clumps identified from the ground (boundaries and extent) during 280 h of slow flight in a Challenger ultralight airplane over the 999 ha, a subunit of a larger 10 000 ha 'flight only' study area. During these flights I took over a hundred aerial photographs of forest areas with and without *Maximiliana* to confirm and illustrate the pattern noted from the ground. To describe adult densities within clumps I randomly selected five aggregations and counted all the *Maximiliana* in a 10-m × 250-m quadrat placed through the centre of the patch.

SEED DISPERSAL NEAR PARENT PLANTS

I opportunistically selected six fruiting *Maximiliana* palms, located in forest dominated by *Maximiliana* (conspecific patches) but including other tree species. Palm patches were identified visually both from the air and on the ground and were defined as aggregations with a density of 13 or more trees per 0.25 ha. All the study plants had ripe fruit beneath them, but only one had completed fruit fall. Seeds in intact fruits were considered undispersed, as were those in rotted fruit; seeds whose pulp had been consumed by frugivores were considered dispersed even if they remained beneath or near the parent crown. Opportunistic but intensive searches (carried out daily from July 1991 to January 1992 during daily forest census transects for large vertebrates) for the seeds at each location revealed that only tapirs were dispersing seeds beyond 30 m from parents at the time of peak fruit fall (July). To determine the dispersal distance of non-tapir-dispersed seeds, I demarcated a circular area of 30 m radius around each tree, then subdivided this area with rope into four equal-size wedge-shaped quadrats. These units were further subdivided by concentric rings spaced at 5 m intervals from the tree out to the 30 m line. A 30 m radius was chosen based on research indicating that up to 90% of rodent-dispersed seeds remain within 10 m of parents (Hallwachs 1986 for *Hymenea courbaril*, Forget 1990, 1991, 1992a for *Gustavia superba* and *Euperua grandiflora*), and work indicating that a 20 m radius is sufficient to intersect the majority of vertebrate-generated seed shadows (see de Steven 1994 and papers cited therein). On 31 July, two people walking abreast of one another searched each ring for seeds and fruits. All *Maximiliana* fruit and seeds observed were counted and categorized as (1) intact fresh ripe fruit, (2) intact rotted fruit, (3) bare seeds with no exocarp or mesocarp attached, (4) rodent-attacked fruit (seeds with small teeth marks gnawed in a circular pattern around bits of remaining mesocarp), and (5) fruits attacked by other vertebrates. The number and percentage of fruits in each category were calculated.

I was able to distinguish between fruits handled by different vertebrates by examining fruits handled by captive animals (peccaries) or fruits handled by animals observed feeding in the wild (peccaries and all other consumers). Rodents characteristically left a small amount of pulp and fibre attached to the endocarp relative to the other frugivores discussed here. Collared peccaries (*Tayassu tajacu*) left more pulp than rodents, and their larger, more pointed teeth left deeper and v-shaped gashes in the remaining pulp. White-lipped peccaries (*Tayassuu pecari*) were not foraging in the *Maximiliana* patches in July. Monkeys (*C. apella*, *C. nigrivitatus*, *A. belzebuth* and *S. sciureus*) left finer and flatter gashes in the fruit-pulp than did the peccaries. Tapirs and deer used their molars to scrape off the fruit pulp. Deer spat out much of the fruit and left a pattern of pulp chunks seemingly removed by plier-like tools (the molars). Because of the difficulty of separating deer- and tapir-spat fruits, these were grouped together in the analysis. In cases where I could not identify the frugivore responsible for fruit consumption, the fruits were categorized as 'unknown.' Note the distinction in this paper between the terms 'seeds' and 'fruits;' even though a free seed is produced as a result of fruit-eating, it is the fruit rather than the seed that is the focus of attention of the consumer. Thus, rodents may initially feed on fruit pulp without moving the seed away from the parent tree, and later return to feed on or hoard the seed.

SEED DISPERSAL TO TAPIR LATRINES

Although tapirs are frequently reported to defecate in wet areas such as rivers and ponds (Fragoso 1987; Janzen 1981), I found that on Maracá tapirs also defecated in terra firme 'latrines' (Fragoso 1994). These were sites, usually next to an emergent buttressed tree, where at least one animal defecated repeatedly throughout the study period (Fragoso 1994). I initially searched for tapir latrines at all large emergent trees in terra firme forest along 60 km of trails and in the forest between trails. Later searches focused on *Couratari multiflora* (Eyma) trees (tauri trees), virtually the only species used as latrine sites (henceforth 'tauri tapir-latrines'). Piles of tapir faeces were easily recognized; they consisted of aggregations of poorly digested plant matter, similar in appearance to horse dung. One faeces consists of all boluses defecated at one time. I searched for *Maximiliana* seeds in all intact tapir faeces encountered from October to December 1991 (the last months of the *Maximiliana* fruit-fall period) within the study area.

SEED SURVIVORSHIP

Because they remained at similar distances from the parent tree (within 10 m), for this analysis I combined non-tapir-dispersed and undispersed seeds together, thus ignoring for this study the impact of seed handling by frugivores on survivorship. I compared the survivorship of these seeds to those dispersed by tapirs 100–1000 m distance from *Maximiliana* aggregations in late October, several months after peak fruit fall. I randomly selected 10 seeds ($N = 440$ seeds) from 44 faeces (those with at least 30 seeds) distributed over eight tapir latrines. I also randomly selected (by choosing the seed nearest the marked end of a stick thrown under the tree) 10 seeds from underneath each of 20 randomly selected (coordinates and distances from the trail chosen from a random number table) parent trees ($N = 200$ seeds), from six conspecific patches. Each seed was categorized as (1) whole, (2) killed by bruchid beetles, either with larvae or with an exit hole, (3) killed by fungus, (4) aborted with an undeveloped endosperm, and (5) germinated. No seeds were found cracked by white-lips or opened by rodents at this time. Seeds that appeared whole were opened to confirm their viability.

SEEDLINGS AND SEEDLING PATTERNS

I classified juvenile palms into six size classes (0–5), the first four of which correspond to yearly age classes, as estimated from individual seedlings that were tracked over time. Class zero *Maximiliana* seedlings were those that had recently germinated and had a cotyledon still attached to the hypocotyl. The hypocotyl and cotyledon remained below ground, the seedling consisted of one or two unsplit (no pinnae) leaves without obvious petioles, and all were less than 20 cm long. Class one seedlings had two to three unsplit leaves, which attained 20–35 cm lengths. The number of leaves on class two saplings ranged from two to four, some of which may be in the process of splitting, and some of which may have short petioles. Class three saplings had well-formed petioles, three to four split and splitting leaves and attained heights of about 130 cm. Class four saplings were similar in appearance to class three, but their stems were thicker, they ranged from 140 to 160 cm heights, and all leaves had well developed pinnae. Class five saplings had four or more exceptionally thick petioles. The leaves had well-developed pinnae, and the plant attained 170–210 cm heights but had yet to develop a trunk.

I compared seedling abundance in the six age classes around three tree categories: under 25 randomly selected *Maximiliana* adults that produced fruit in 1991 (chosen from random coordinates and distances along a trail, within conspecific clumps randomly chosen from all known clumps in the study area); at 25 tauri tapir-latrines, most located more than 500 m from *Maximiliana* clumps; and around 25 randomly selected nonlatrine, nonpalm (henceforth 'controls'), emergent trees located more than 60 m from tauri-latrines and most more than 500 m from *Maximiliana* clumps. The second and third types had few to no individual adult *Maximiliana* trees in the vicinity. All seedlings in the six age classes were counted within concentric circles to a distance of 20 m from the tree trunk (four 5 m radial increments). To ensure accuracy in counting, I roped off the 20 m diameter area into 12 equal parts. Each part was then searched by two or three people walking abreast. These data were gathered from October to December 1992, with three to five trees sampled per day.

I used a two-factor ANOVA to compare seedling densities between the three tree types and the six age classes. I followed the two-factor ANOVA with single-factor ANOVAs for amongst site comparisons and subsequently applied Fisher's Protected LSD adjustment to control for type I error resulting from multiple pair-wise comparisons. I chose the Fisher's Protected LSD technique because it produced smaller MSD values (MSD = minimum significant difference = (critical difference) × (SE); Sokal & Rolf 1981) than the Bonferroni–Dunn test. When selecting a statistical test that adjusts *P*-values to control for type I errors one should use the procedure that yields the smallest MSD (Sokal & Rolf 1981).

Results

VERTEBRATE DISPERSERS OTHER THAN TAPIRS

The number of fruits under each tree ranged from 181 to 1788 (mean ± SD = 778.17 ± 537.54). A total of 4468 fruits and seeds were found on the ground under

Table 1. The number of *Maximiliana* fruit and seeds eaten by different frugivores beneath six fruiting trees. Samples from one day at the peak of the fruiting season. Within-category percentages given in parentheses. Percentages in total column represent percentage of total seeds

	Distance from parent (m)													
Fruit category	0–5		5–10		10–15		15–20		20–25		25–30		Total	
Ripe	694	(97.9)	15	(2.1)	0	(0)	0	(0)	0	(0)	0	(0)	709	(15.9)
Rotted	1659	(99.2)	14	(0.84)	0	(0)	0	(0)	0	(0)	0	(0)	1670	(37.4)
Seeds only, no pulp	0	(0)	1	(100)	0	(0)	0	(0)	0	(0)	0	(0)	1	(0.02)
Rodent left	1381	(97.3)	33	(2.3)	4	(0.28)	1	(0.07)	0	(0)	0	(0)	1419	(31.8)
Collared peccary left	121	(99.2)	1	(0.82)	0	(0)	0	(0)	0	(0)	0	(0)	122	(2.7)
Primate left	160	(99.4)	0	(0)	1	(0.62)	0	(0)	0	(0)	0	(0)	161	(3.6)
Deer/tapir left	25	(100)	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)	25	(0.56)
Unknown	336	(93.7)	21	(5.82)	1	(0.28)	0	(0)	0	(0)	3	(0.86)	361	(8.1)
Total	4373	(97.9)	85	(1.9)	6	(0.13)	1	(0.02)	0	(0)	3	(0.07)	4468	

all six trees combined. The pulp of 47% of this total had been at least partially consumed by frugivores, but an almost equal amount, 37%, rotted (Table 1). Rodents were the primary fruit-pulp consumers, accounting for 32% of the attacked fruits found within 30 m of parent trees (Table 1). Collared peccaries ate 3% of the fruit, primates 4%, and deer and tapirs only 0.6%. The unknown category contained 8% of the attacked fruits. There was no evidence that rodents or other vertebrates fed on the *seeds themselves* at this point in the fruiting period, although they did so after the fruit-fall period. There was high variation among individual trees in the number of fruits in each category (Table 2).

Rodents left 1381 intact seeds (97% of the fruits they handled) within 5 m of the parent tree's trunk (Table 1), the approximate diameter of parent tree crowns. Only 2% were moved from 5 to 10 m ($n = 33$), 1% from 10 to 20 m ($n = 5$) and none were found between 20 and 30 m beyond the parent tree (Table 1). Ninety-eight per cent of all seeds found within 30 m remained within 5 m of the tree trunk (Table 1). Only three seeds were carried more than 15 m from palm trunks. While I sampled distances beyond 30 m from the parent tree more informally than those within 30 m, I am confident that there were few seeds in that area because, in my study site, seeds dispersed or buried by large rodents (e.g. agoutis, *Dasyprocta leporina*) were easily found, even if buried, due to conspicuous sign of digging left on the soil surface. This sign became obvious to me after I watched agoutis burying objects throughout the forest.

Table 2. Mean and standard deviations of fruits in each category under six *Maximiliana* palm trees sampled once at the peak fruiting period

Fruit category	Mean	SD	Range
Ripe	118.17	65.80	30–188
Rotted	278.33	491.62	0–1249
Seeds only, no pulp	0.17	0.41	0–1
Rodents	236.50	109.82	39–344
Collared peccaries	20.33	27.51	0–61
Primates	26.83	38.14	0–98
Deer/tapir	4.17	10.21	0–25
Unknown	60.17	70.79	0–191
Total	778.17	537.54	181–1788

DISPERSAL BY TAPIRS

Tapirs defecated thousands of seeds from 38 tree species into both seasonally flooded wetlands and terra firme forest (Fragoso 1994, Jose M. V. Fragoso and Jean M. Huffman, unpublished data). Over 2 years, I found tapir latrines in eight seasonally flooded wetlands, one dry stream bed and 25 terra firme forest sites. In the latter habitat they defecated almost exclusively around the base of tauri trees (96% of tapir latrines). One latrine was located by an emergent *Ficus* sp. tree, and two other emergent trees, a *Peltogyne gracilipes* (Ducke) and a *Ficus* sp. had one defecation each. These were not considered latrines because there was no accumulation of older faeces indicating long-term repeated use. Four tapirs were known to use the study area, three adults and one infant (the animals were individually recognizable from scars and other markings, making a census possible during mammal density transects).

Six seasonally flooded latrines (Forest Lake, Savanna Lake, Bactris Swamp, Trail 4 Buritizal, Tapir Pool and New Buritizal, all dry during the study period) found from October to December 1991 were used in this analysis. Seeds were counted and their fate monitored at wetland latrines as part of another study; when I found the terra firme latrines, I confirmed the presence of *Maximiliana* seeds in faeces there and assumed a similar fate for those seeds as for seeds at wetland latrines. At the wetland latrines, tapirs passed 6140 *Maximiliana* seeds in 78 faeces, and two additional faeces contained no *Maximiliana* seeds (mean of 78.71 seeds per faeces containing *Maximiliana* seeds, range 11–210) (Table 3). Tapirs defecated a mean of 994.67 ($n = 5{,}968$, sd $= 742$, range 51–1790) seeds per latrine. Seeds were not germinated

Table 3. The sum of *Maximiliana* seeds for all faeces at eight wetland tapir latrines sampled from October to December 1991. Only data from the first six sites were used in the analysis

Area	No. faeces with seeds	Total no. of seeds	Mean ± SD no. seeds per faeces
Forest Lake	24	1790	74.58 ± 8.80
Savanna Lake	16	1197	74.81 ± 12.31
Bactris Swamp	14	1024	73.41 ± 17.68
Trail 4 Buritizal	3	182	60.67 ± 29.21
Tapir Pool	1	51	51.00 ± 0.00
New Buritizal	18	1724	95.78 ± 27.86
Western End of Island	1	80	80.00 ± 0.00
Station Savanna	1	92	92.00 ± 0.00
Total	78	6140	70.82 ± 8.03

in the laboratory, but were opened to test viability, and also observed germinating into seedlings in the dung piles and latrines in September 1992, indicating that passage through the tapirs gut did not harm seeds (personal observation). Seeds at both types of latrines are subject to secondary dispersal by rodents (Fragoso 1994).

There was no significant difference between the number of seeds found at the six parent trees and the six latrines (Mann–Whitney $U = 14$, $P = 0.5218$). However, only one tree had completed fruit fall at the time of sampling. It dropped at least 1788 fruits, a number almost equal to that found at the latrine with the greatest number of tapir defecated seeds ($n = 1790$). Thus, the differences in seed survivorship are probably not attributable to differences in seed abundance between the two site types.

SEED SURVIVAL

Ninety-eight per cent of the randomly sampled, tapir-dispersed seeds were viable, compared to only 17% of the randomly sampled seeds beneath parent trees (Table 4). Beetle larvae infested 63% of the latter seeds, and adult beetles had already emerged from and killed an additional 14%. A few seeds were killed by fungus, and a few had never developed endosperm and presumably had been aborted. In total, 81% of the seeds were already dead or would soon die (Table 4). Seeds classified as intact were the most recently fallen. I did not find any *Maximiliana* seed fragments in tapir faeces.

Table 4. Condition of *Maximiliana* seeds beneath parent trees, and at tapir latrines. Sampling dates as in previous tables

Seed category	Tapir faeces *N*	Tapir faeces (%)	Parent tree *N*	Parent tree (%)
Viable	433	(98.4)	34	(17)
With beetle larvae	1	(0.1)	126	(63)
With beetle exit hole	2	(0.45)	28	(14)
With fungus	2	(0.45)	7	(3.5)
Undeveloped	2	(0.45)	5	(2.5)
Total	440		200	

ADULT TREE PATTERNS

Adult *Maximiliana* occurred as solitaires and as high density adult clumps. I located 23 adult *Maximiliana* clumps by walking throughout the trail system. I confirmed their presence through visual observation and aerial photographs from the airplane. Adult *Maximiliana* attained a mean density of 20.2 trees per 2500 m^2 area (SD = 8.17; 12, 23, 32, 13, and 21 palms per quad) within the five randomly selected clumps. In contrast, there was an average of one or less adult trees per 1257-m^2 area within 20 m of tauri-latrine ($n = 25$) and randomly selected control trees ($n = 25$) (Table 5). The same method yielded an average of 8 adults within 20 m of 25 parent trees (Table 5). Fourteen tauri latrines and 18 control trees had no adult *Maximiliana* within 20 m of their trunk.

SEEDLING PATTERNS

Latrine and control trees had no or few *Maximiliana* adults within 20 m (Table 5), and most were located 500 m or more from adult clumps, indicating that most seeds had been carried in by animals from distant parent trees. The number of seedlings and saplings ranged from 240 to 686 per 20-m radius area (1257 m^2) at latrine sites, from 46 to 533 at parent sites, and from 52 to 545 at control trees, respectively. A two-factor ANOVA showed significant differences in seedling densities among sites ($F_2 = 30.23$,

Table 5. The number of *Maximiliana* adults within 20 m of study sites in the three site types

	Number of sites with given no.of adults		
No. of *Maximiliana* adults	Tauri	Nonlatrine tree	Parent tree
0	14	18	0
1	3	2	1
2	3	1	1
3	0	2	2
4	1	2	2
5	3	0	1
6–20	0	0	15
Unknown	1	0	0
Summary statistics			
Total adults per site type	28	18	201
Mean no. per site type	1.12	0.72	8.04
SE	0.35	0.27	0.91

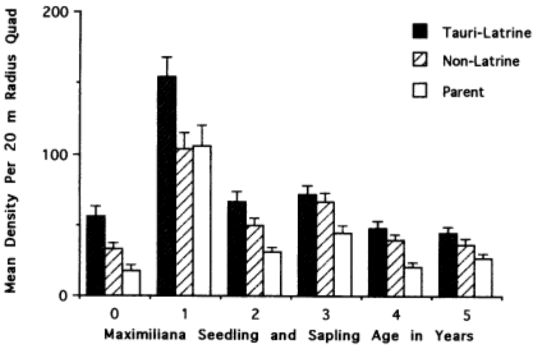

Fig. 1. The mean density (+SE) of *Maximiliana* seedlings and saplings per 1257 m^2 quad (20-m radius) at tauri-latrine ($n = 25$), randomly selected nonlatrine ($n = 25$) and *Maximiliana* parent trees ($n = 25$).

$P = 0.0001$), and among size classes ($F_5 = 64.38$, $P = 0.0001$), but the interaction among site type and age class was not significant. However, there was a trend for seedling densities to decrease from tauri to control to parent trees (Fig. 1); subsequent single-factor ANOVAs confirmed significant differences between the age classes amongst sites (Table 6). Pairwise comparisons (Fisher's Protected LSD test) showed that densities were significantly higher at tauri tapir latrines than at the parent trees for all size classes; and at tauri-latrines than at nonlatrine control trees for age classes zero and one (Table 6). The control trees had significantly higher seedling and sapling densities than parent trees for all but 1- and 5-year-old plants (Table 6).

Discussion

Long-distance seed dispersal by tapirs influenced the recruitment patterns of seedlings, with significantly higher densities of seedlings of all age classes occurring in tapir latrines than under parent trees and for some age classes under latrine trees than randomly selected control trees. This occurred even though the number of undispersed seeds, and seeds dispersed by rodents and other nontapir frugivores near parent trees was equal to or greater than that dispersed by tapirs to latrines at Maracá. Several processes, acting sequentially or in concert were responsible for these differences: (1) class zero seedling densities were highest at latrine trees because tapirs dispersed thousands of viable *Maximiliana* seeds into latrines; (2) they were low at parent trees because most seeds that remained there were killed by bruchid beetles and white-lipped peccaries (although peccaries did not root at the focal plants during this study, during other study years they caused extensive damage to both seeds and seedlings; previous generations of seedlings would thus have been affected; Fragoso 1994); (3) the density of class zero seedlings starts out high within a metre of parent trees, but by the end of the year seedling predators (white-lipped and collared peccaries and rodents) have lowered densities to levels lower than at sites > 5 m from adults (personal observation); (4) white-lipped peccaries incidentally uproot and kill older seedlings when searching for buried seeds and invertebrates around the parent plant (personal observation); (5) control trees generally supported higher densities of seedlings and saplings than parent trees because the seeds that gave rise to these seedlings were most likely secondarily dispersed by rodents from latrine trees, the nearest source of seeds; (6) latrine trees held higher densities of zero and 1-year-old seedlings than control trees, but not the older age classes, because as plant size increases intraspecific competition thins densities to levels similar to those at control trees; and (7) latrine and control trees had similar numbers of older age saplings because the latter locations were extensions of the latrines; they were all located between 60 and 150 m from tauri-latrine trees, well within the short-term movement range of large rodents such as agoutis (K. Silvius, personal communication).

Maximiliana individuals and clumps occur in different forest and soil types on Maracá, with the exclusion of swamp habitats. Like tapir latrines, *Maximiliana* clumps occur both in highland forest and around wetland areas. *Maximiliana* is a colonizing species of abandoned pastures and forest clearings in northern Roraima (personal observation), indicating that it can establish populations under both hot, sunny conditions and shaded understorey conditions. In previously agricultural fields, the high density of *Maximiliana* seems to be due in part to dispersal by

Table 6. Adjusted probability values (derived from Fisher's protected LSD) for *Maximiliana* seedling density comparisons among tauri-latrine, nonlatrine and *Maximiliana* parent trees. Nonsignificant comparisons are in bold numbers, all others are significant at $P < 0.05$

	Seedling age					
	0	1	2	3	4	5
P-value one factor ANOVA for three sites	0.0001	0.0146	0.0002	0.0101	0.0001	0.0045
Fisher's protected LSD adjusted *P* values for among-site comparisons						
Tauri vs. *Maximiliana*	0.0001	0.0139	0.0001	0.0043	0.0001	0.0010
Tauri vs. nonlatrine	0.0033	0.0096	**0.0514**	**0.5718**	**0.1149**	**0.1006**
Nonlatrine vs. *Maximiliana*	0.0487	**0.8884**	0.0175	0.0199	0.0023	**0. 0839**

domestic animals (pigs and cattle). These observations support the conclusions of this study that seed dispersal rather than edaphic factors is responsible for the clumped distribution of *Maximiliana*. Since Maracá has an intact fauna, similar to that of other undisturbed Amazonian sites, the interaction occurring today between palm fruits and tapirs has probably existed for many generations of trees, and the adult clumps visible today would have been created by past tapir dispersal.

SEED SURVIVAL

Rodents, generally considered good seed dispersers, initially discarded most attacked fruits within 5 m of parent trees. These results are similar to those of Hallwachs (1986), for *Hymenea courbaril*, and Forget (1990, 1991, 1992a), for *Gustavia superba* and *Euperua grandiflora*), who found that 90% of seeds were dispersed no further than 10 m from parent trees. The timing of fruit removal is key to the survival of *Maximiliana* seeds, because it determines the amount of time that the seeds are exposed to bruchid beetles and other predators. As fruit availability declines, rodents begin to both feed on and scatterhoard the seeds of *Maximiliana maripa* (Fragoso 1994), but by this time all seeds have been subject to infestation by bruchid beetles. Tapirs, on the other hand, although they do spit out the larger seeds of other palm species (Bodmer 1990), removed large numbers of *Maximiliana* seeds away from the parent plant and clump immediately after fruit fall. At times when they do feed on the seeds, rodents may contribute to seed dispersal through scatter hoarding (although most seeds originating below parent trees may already be infected by beetle larvae; Kirsten Silvius, unpublished data for *Maximiliana* from Maracá, Wright 1983). Rodents are also important secondary dispersers for *Maximiliana* and other seeds first dispersed by tapirs (Fragoso 1994) and domestic horses (*Equus caballus*; Janzen 1982b).

Predispersal seed destruction by beetle larvae is also high for other palm species. Kiltie (1981) found that 98% of undispersed *Astrocaryum macrocalyx* fruits beneath parent trees were attacked by bruchid beetles. Smythe (1989) recorded a similar pattern for *Astrocaryum standleyanum* on Barro Colourado Island, Panama, with 100% mortality of seeds. Janzen (1971) examined bruchid beetle destruction of predispersal seeds of *Scheelea rostrata* palms that appeared whole and found that mortality, while initially low in the newly dropped fruit, in time reached 90–98%. Mortality in that study would have been higher had Janzen included seeds already killed by beetles (with adult exit holes) or other agents.

Tapirs appear to be moving seeds beyond the range of bruchid infestation and removing eggs and/or any larvae already on the fruits/seeds. While fruit-eating rodents also may remove larvae and eggs from fruits when they scrape pulp from seeds with their teeth, the mechanical nature of rodent pulp removal leaves much of it (and perhaps larvae) on the seed, and the seed remains available for reinfestation. *Maximiliana* pulp is fibrous and well attached to the seed, and much of it remains attached when peeled by the teeth of rodents, peccaries, deer, and monkeys. Tapirs, in contrast, remove the pulp by chemical means and defecate seeds with no attached pulp. Thus, any eggs or larvae on the fruit would be chemically removed along with the pulp. In addition, the digestive fluids in a tapir's stomach or perhaps its body temperature could kill larvae already in the endosperm. Similar patterns of larvae removal have been documented for other plant species. Howe (1989) found that passage of fruit through the digestive tract of domestic cattle and horses killed beetle larvae already in *Guazuma. ulmifolia* (Sterculiaceae) fruit.

SEEDLING SURVIVAL

The fact that there was lower seedling mortality at latrine sites, in spite of their high density of class zero and class one seedlings, indicates that distance (white-lipped peccaries) and density-responsive predators are focusing on the more common parent trees rather than on the rarer latrine trees: it is high-density adult *Maximiliana* clumps and their associated fruit rather than seed or seedling density that white-lipped peccaries and beetles use as an indicator of food availability. Tauri trees occur as solitaires and thus may be more difficult for foraging white-lipped peccary herds to locate.

For all age classes, densities were much higher at latrines than at parent trees. They were also higher for four age classes at control sites than by parent trees. These results indicate that recruitment levels into older age classes were higher at tapir latrines than at the other sites. Recruitment rates into age classes older than those studied here should remain high because by 5 years of age *Maximiliana* saplings are large enough that they no longer attract vertebrate predators. Eventually, these aggregations should become high-density clumps of adults.

MESO- AND MICRO-SCALE PROCESSES AND RAIN FOREST PATCHINESS

Adult *Maximiliana* tree aggregations are meso-scale or medium-range phenomena (*sensu* Holling 1992). They are created by tapirs, through a seed dispersal process unique to large mammals, and through interaction with seed, seedling and seedling destruction dynamics generated by white-lipped peccaries, another large mammal with a unique socio-ecology (Sowls 1984; Fragoso 1994). Tapir and white-lipped peccary socio-ecology induces meso-scale processes because individuals of both species range over tens to hundreds of km^2 (peccaries, Fragoso 1994; tapirs, personal observation; Williams 1984), and their ecological consequences interact over this large range. Due to this scale of movement, individuals influence (forage in, create, or inhibit the formation of) many *Maximiliana* clumps. In fact, white-lipped peccaries appear to search out conspecific tree clumps rather than individual palms (Fragoso 1994).

Rodent seed dispersal and predation are small-scale processes (Holling 1992). Due to their small body size, short distance movements and small home ranges (2 ha or less for agoutis, Smythe 1978; 0.25–1 ha for squirrels and less than 1 ha for most other rodents, Eisenberg 1981, 1989), individual rodents search out individual seeds and trees. These life-history traits suggest that their ecological/energetic requirements can be met within one or two *Maximiliana* clumps. Like rodents, seed predation by individual bruchid beetles is a small-scale process, since their ecological/energetic needs can probably be met by one or a few seeds around one or a few trees (personal observation, Wright 1983).

Although my results support the Janzen–Connell model in the sense that seedling mortality is highest near parent trees due to the activities of density- and seedling-specific predators, they also show that recruitment patterns are more complex than those described by the model. Increased recruitment is occurring near nonconspecifics, as predicted by the Janzen–Connell hypothesis, due in part to high predation at parent sites. But rather than being evenly dispersed, survival and mortality are concentrated in certain areas, resulting in a clumped pattern. The clump site is directly related to the behaviour of a single animal – a large bodied mammal repeatedly defecating large amounts of seeds at sites throughout the forest. Secondary dispersal by rodents – a small-scale phenomenon – is then entrained by the larger-scale pattern set by the tapir: most seeds are originally scattered to latrine sites and only thence to nonlatrine nonparent trees. In this small-scale scenario, individual seeds and trees are the units upon which bruchids and rodents impose pattern (a bruchid–rodent–tree complex). However, pattern resulting from the interactions within this complex is overshadowed at a larger forest scale by tapirs (they affect the bruchid–rodent–tree complex as one unit), which impose pattern on large numbers/sections of these units. Thus, entire areas of the forest, which before were viewed as individual trees with different predation rates by bruchids and rodents, now become one patch/complex with a similar treatment by one tapir. Bruchids and rodents are still killing and dispersing seeds, but tapirs are affecting where they do and where they don't.

Although palm tree clumping is visible from the ground, during this study it was made far more conspicuous to me by two factors:

1. I was regularly flying at 300–600 m over 10 000 ha of forest while radio-tracking peccaries, so that pattern in the canopy was readily apparent; few studies of forest structure have the advantage of an aerial view of such a large study area.

2. Once I discovered the occurrence of terra firme tapir latrines, the aggregations of seedlings around a definite focus became apparent. I was thus presented with both the process and the pattern simultaneously in my study area. Since tapirs and white-lipped peccaries are either rare or extinct at the Central American sites where forest structure has been studied in most detail, such a connection could not be apparent to researchers (John Eisenberg, personal communication; Glanz 1990; Timm 1994). Tapir latrines have not been reported thus far for Barro Colorado Island, Panama, La Selva and Guanacaste Park, Costa Rica or any other of the well-studied Central American sites. They have not been reported in publications from other Amazonian sites, although native American and other informants have reported to me the occurrence of such latrines in Acre and Mato Grosso, Brazil.

Several other large-seeded species used by tapirs and peccaries appear to be clumped at large scales within the Maracá study site, although this needs to be confirmed by mapping and density estimates. For those concerned with preservation of forests and the maintenance of ecological/evolutionary mechanisms and processes, a scale-sensitive approach may be the best method for studying forest structure. Such an approach will indicate which factors must be maintained, controlled or imitated (in the case of restoration ecology); if such meso-scale processes are indeed key processes in tropical forests, then the trend of extinction of large mammals and their ecological replacement by rodents is cause for concern.

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