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LONG-DISTANCE SEED DISPERSAL BY TAPIRS INCREASES SEED SURVIVAL AND AGGREGATES TROPICAL TREES

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Abstract. The dominant models explaining tree species diversity and distribution patterns in tropical forests are the Janzen-Connell and Recruitment Limitation models, neither of which considers the effect of long-distance seed dispersal on seed survival, seedling establishment, or the aggregated distributions of trees empirically observed at mesoscales in tropical forests. At a neotropical forest site (Maracá Island Ecological Reserve, Roraima, Brazil), we experimentally reproduced long-distance clumped seed dispersal by tapirs for the palm *Maximiliana maripa*. Such dispersal protects seeds from attack by species-specific bruchid beetles by (1) covering them in protective fecal material and (2) placing them in sites distant from conspecific adult tree aggregations, where beetles are less active. Endocarps distant from parent patches survived bruchid attack at a significantly higher rate than those in parent patches, as did in-feces endocarps compared to clean endocarps. A significant interaction effect between distance from patches and feces treatment showed that feces conferred protection to seeds within a parent patch but did not appear to confer additional protection to seeds already protected by distance from the parent patch. A mesoscale map compiled from aerial photography, satellite imagery, and air- and ground-truthing revealed an aggregated pattern of *M. maripa* palms associated with tapir latrine sites, supporting the view that long-distance seed dispersal by tapirs is responsible for the generation of palm patches and potentially important in forest–savanna boundary dynamics. We conclude that seed shadows and survival rates can justifiably be studied at the scale of tree aggregations rather than at the scale of individual trees, and that long-distance seed dispersal is neither rare nor unpredictable once we understand the movements and behavior of large, mobile animals.

Key words: aggregated distribution; Attalea; *bruchid beetles; Janzen-Connell; long-distance dispersal;* Maximiliana maripa; *mesoscale; palm; patchiness; seed dispersal, tapir; tropical forest.*

INTRODUCTION

Tropical forest trees are aggregated at small scales (a few meters to hundreds of meters; Thorington et al. 1982, Lieberman and Lieberman 1994, Wills and Condit 1999), mesoscales (hundreds to thousands of meters; ter Steege 1993, Fragoso 1994, 1997) and landscape scales (tens of kilometers; Tuomisto et al. 1995). Aggregations at landscape scales and small (microhabitat) scales are often explainable by edaphic factors such as soil type, topography, and drainage (Tuomisto and Rukolainen 1993, Clark et al. 1998, 1999, Svenning 2001), whereas aggregations at mesoscales are less often correlated with edaphic factors (ter Steege 1993, Milliken and Ratter 1998). Here, we argue that long-distance endozoochorous seed dispersal is responsible for the establishment of such aggregations for one palm species in a Neotropical forest, and document the mechanism that leads to higher survival of seeds dispersed long distances compared to those dispersed within the parent aggregation.

Models and hypotheses that address the maintenance of high tree-species diversity in the tropics also address the dispersion pattern of tropical trees, based on the basic assumption that a relatively even dispersion of tree species leads to a higher number of species per unit area. The most enduring and frequently tested explanation to date was conceived by Janzen (1970) and Connell (1971). The Janzen-Connell model proposes that density- and distance-dependent seed and seedling mortality caused by species-specific predators reduces conspecific recruitment near the parent trees, making that area available for colonization by heterospecific seedlings. The maintenance of high community-level diversity is thus postulated to result from small-scale, intraspecific population dynamics driven by the proximity of parent trees. Intuitively, this would prevent the establishment of monospecific or monodominant tree patches. The Janzen-Connell model thus does not

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account for empirically observed tree aggregations, nor does it incorporate the high degree of spatial and temporal variability empirically observed in recruitment processes (Hubbell 1979, Clark and Clark 1984, Schupp 1992, Fragoso 1997).

We suggest that the mismatch between the pattern observed in adult tropical tree dispersion and the pattern predicted by the Janzen-Connell model exists because predictions derived from the Janzen-Connell hypothesis were based on mechanisms and processes operating at small scales, while conspecific clumping is a consequence of large-scale processes. Specifically, we suggest that long-distance, contagious seed dispersal can account for the aggregation of conspecific tropical trees at mesoscales. The behavior of vertebrate fruit eaters frequently results in contagious seed dispersal, in which seeds are deposited in single-species or multispecies aggregations at sleeping trees, roost sites, latrines, or other repeatedly used sites (Schupp et al. 2002). Here we examine the specific case of such dispersal occurring over distances of more than 1 km.

Recently, several researchers have emphasized the role of dispersal and/or recruitment limitation (Hurt and Pacala 1995) in tropical forests as an explanation for species aggregations at the scale of several hundred meters (Dalling et al. 1998, Svenning 2001). In this scenario, seeds of competitively dominant species fail to arrive at suitable sites, allowing seedlings of competitively inferior species to establish and persist in such areas. Dominance by a few species is reduced, and diversity is increased. While recruitment limitation addresses the existence of conspecific tree aggregation at the scale of a few hundred meters, it does not address the origin of new aggregations at the landscape or mesoscale, at large distances from another conspecific aggregation. Like Janzen-Connell dynamics, it emphasizes processes occurring at small spatial scales, and does not incorporate the effect of long-distance seed dispersal by large, mobile animals (but see Schupp et al. 2002 for a broader interpretation of recruitment limitation).

Mechanisms responsible for large-scale pattern will only be apparent if measured at the appropriate scale, which for tropical trees would be a distance that places seeds beyond the influence of mechanisms and dynamics that dominate at the scale of the conspecific tree aggregation. In this paper, we document (1) the mesoscale aggregation pattern of one neotropical forest area using aerial mapping techniques, and (2) a mechanism, endozoochory by an ubiquitous, large, and mobile neotropical mammal, the lowland tapir (*Tapirus terrestris*), that leads to fundamentally distinct survival dynamics for seeds far from the parent aggregation relative to seeds within the parent aggregation.

STUDY SITE

Maracá Island Ecological reserve is a 110 000-ha area of mainly old growth tropical rain forest, with a few small areas of *Mauritia flexuosa* palm swamps and shrub-dominated wetlands. It is located between 3°15′ and 3°35′ N, 61°22′ and 61°58′ W in Roraima State, Brazil. The island is formed by the bifurcation of the Uraricoera River, a third-order tributary of the Amazon River. The forests surrounding Maracá extend unbroken for from hundreds of kilometers to up to 1500 km to the north, west, and south. To the east, the naturally occurring Rupununni Savanna bounds the island. There is little or no deforestation near Maracá. The island supports unhunted populations of vertebrate species considered sensitive to human disturbance (Milliken and Ratter 1998). Rainfall over the last 15 years has ranged from 1750 to 2300 mm per year. The island is far from human population centers, and low densities of indigenous and other rural peoples inhabit the natural savanna regions northeast and southeast of the island.

STUDY SYSTEM

On and around Maracá, the palm *Maximiliana maripa* (revised by Henderson 1995 as *Attalea maripa*; the same revision also places *Orbignya* and *Scheelea* palms in the genus *Attalea*) occurs in riverine forest, forest islands in the savanna, and in terra firme forest. It can occur in high-density aggregations or as scattered individuals. Each tree can produce one to three fruit bunches per year, containing from a few hundred to several thousand, 5–8 cm long fruits. Each fruit consists of a fibrous resistant husk, thick yellow pulp, and a hard woody endocarp up to 7 mm in thickness enclosing from one to three seeds (Fragoso 1994). *M. maripa* seeds are parasitized by bruchid beetles in the genera *Pachymerus* and *Speciomerus*, as are the seeds of all palms currently placed in the genus *Attalea* (Johnson et al. 1995). The most common beetle species at the study site is *P. cardo* (Silvius and Fragoso 2002). Females oviposit on the endocarp or pulp of fallen fruits, but never on the intact husk (Silvius and Fragoso 2002), and one week after oviposition first instar larvae hatch and make their way through the endocarp into the seed. After two to three months, larvae are full grown and have consumed most of the endosperm, but they may not pupate or emerge as adults until one year later (Silvius 2002). Endocarps remaining near the parent tree show 73–100% beetle infestation rates (Fragoso 1997, Silvius 2002).

Oviposition occurs on the first night the endocarp is exposed on the ground; that is, on the first night after a vertebrate consumer has removed the husk and part or all of the pulp (Silvius and Fragoso 2002). Primates, agoutis (*Dasyprocta leporina*), pacas (*Agouti paca*), deer, and other pulp consumers leave fruits within a few meters of the parent tree after removing the pulp. Agoutis rarely if ever scatterhoard endocarps during the palm's fruiting season (Fragoso 1997, Silvius 2002). Therefore, almost all fruits that (1) fall to the ground after having been handled by primates or other arboreal consumers, or (2) are handled by terrestrial consumers after falling intact from the tree, are beetle-infested. Only those few fruits buried by trampling or falling litter, by scarabid beetles, agoutis, or squirrels (*Sciurus igniventris*) escape infestation near the parent tree. Although rodents and white-lipped peccaries (*Tayassu pecari*) feed heavily on the endocarps lying by the parent tree during the season of fruit scarcity, they are feeding on larvae, not seeds (Silvius 2002). With the exception of endocarps used by squirrels early in the fruiting season, most endocarps opened by vertebrates have been killed by beetles, making beetles the primary cause of mortality at the study site.

Brazilian or lowland tapirs weigh up to 250 kg, move over home ranges of several thousand hectares (P. Medici, *personal communication*), and are capable of straight-line movements of over 20 km (J. Fragoso, *personal observation*). Along with two other species of neotropical tapirs, they are known to be important seed dispersers for both large- and small-seeded plants (Williams 1984, Naranjo 1995, Salas and Fuller 1996, Fragoso and Huffman 2000, Downer 2001). When feeding on *M. maripa* on Maracá, they ingest large numbers of ripe, intact-husk, beetle-free fruits from beneath the parent tree. The pulp is digested in the animal's gut, and endocarps with no pulp and with some fragments of husk are defecated intact in tapir feces. On Maracá, tapirs defecate in both upland and wetland latrines, and large aggregations of endocarps are created away from the parent clump (Fragoso 1997). At these sites, endocarps show much higher survival rates than those remaining near parent trees (98% vs. 17%), and juvenile palm densities in all age classes from seedlings to five-year-old ''saplings'' are higher around tapir latrines than around parent trees (Fragoso 1997). The mechanism responsible for this higher survival is the focus of the current study. We hypothesize that high seed survival rates in tapir latrines may be due to one or more effects unique to dispersal by tapirs: (1) burial of seeds under large amounts of fecal matter where bruchid beetles cannot access them; and/or (2) transportation of seeds away from palm-rich areas supporting large numbers of bruchid beetles.

METHODS

Vegetation mapping

We mapped gross vegetation features of the eastern end of the island from a black and white aerial photograph of Maracá taken in the dry season in the early 1980s. This photo allowed us to delineate boundary lines between open vegetation and forest, and to distinguish deciduous forest from evergreen forest (Fragoso 1999). Three hundred and fifty flight hours in an ultralight airplane piloted by J. Fragoso from May 1991 to November 1992 at altitudes of 200 to 300 m above the ground at slow speeds (55 to 80 km/h) allowed J. M. Huffman and J. Fragoso to confirm the delineations and to identify the vegetation association and/or species generating the pattern (e.g., leafless *Peltogyne*-dominated forest, where *Peltogyne gracilipes* forms up to 70% of all stems (Nascimento et al. 1997), *Mauritia flexuosa* palm swamps, and vegetation with distinctive structural-morphological features such as low stature riverine forest). This ''air truthing'' also allowed us to subdivide low stature vegetation into shrub-dominated wetlands, savanna wetlands, and *Mauritia*-savanna wetlands. We compared our results to a satellite image of the area produced by C. Place (Milliken and Ratter 1989), and confirmed or corrected their delineations while expanding the coverage of our map by matching their pattern delineations with our aerial identifications. Finally, from June 1995 to May 1997 we added detail and more species distributions to the map during an additional 400 h of flight by Fragoso over the study region. F. Bonnato, a Brazilian botanist trained in forest engineering and cartography, flew as a passenger in the plane for 150 of these hours, added patches of *M. maripa* palms, tauri (*Couratari multiflora*) emergents, and other species onto the base map, and drew the final version of the map. Pattern matches between base map delineations and aerial truthing were confirmed by ground truthing using rivers and forest trails.

Seed survival experiment

To determine the mechanism by which long-distance dispersal by tapirs protects *M. maripa* seeds from bruchid beetles, unprotected (clean) endocarps and endocarps in feces were placed in palm patches and at sites distant from conspecifics. Locations for experiments were chosen using the map described above. To procure clean endocarps, entire ripe *M. maripa* fruits without bruchid beetle eggs, larvae, or adults were collected from the ground around several trees, and their husk and pulp removed. Endocarps from all trees were combined and mixed before selection for subsequent experiments. To procure uninfested, in-feces endocarps, freshly defecated tapir feces (≤ 3 d old) were collected in the forest and all *M. maripa* endocarps removed. All endocarps were inspected for bruchid eggs and entry holes three separate times. Endocarps from all latrines were combined and mixed before selection for subsequent experiments.

Five meters from the trunk of each of 13 fruiting adult *M. maripa* trees located within four different dense palm aggregations, 30 ''clean endocarps'' were placed in a chicken-wire cage (mesh size 1.5 × 1.5 cm) to exclude seed-eating/dispersing vertebrates. Ten meters from this treatment, on the opposite side of the tree, a second cage contained 30 ''in-feces'' endocarps. These were embedded in a mass of fecal material, derived from the combined feces from which the endocarps were originally extracted. All fecal masses were of equal size and similar in mass to normal tapir fecal piles (Fragoso and Huffman 2000). The number of endocarps per pile was within the range commonly found in tapir defecations dropped at the peak *M. maripa* fruiting period (Fragoso and Huffman 2000).

The same two endocarp treatments—clean and in-feces—were placed 5 m from the trunk of 13 emergent forest trees (simulated tapir latrines; Fragoso 1997), all located from 4 to 7 km from conspecific tree aggregations (henceforth ''palm patches'') and reproductive age conspecific individuals. Exclosures were loosely grouped in four different areas to balance the four palm patches used in the within-patch exclosures. By excluding vertebrates, our experiment focused on the role of the dominant seed predator, the bruchid beetle. This is justified by the fact that, by the time vertebrate predators begin to intensively use *Attalea* endocarps, most of these are already infested by beetles (Silvius 2002).

All exclosures were left in the forest for 7 mo, from August 1996 to February 1997. This period included the last 3 mo of the *M. maripa* fruiting season (Silvius 2002) and a 4-mo period beyond the end of the peak season, when low frequencies of individuals produce fruits. Endocarps were collected at the end of the 7-mo period and checked for bruchid beetle exit holes. Endocarps with exit holes were always dead. Endocarps without exit holes were opened carefully with a machete to determine if adult, pupae, or larval beetles were present. Endocarps containing any beetle life stage, or parasitoids of beetles, no longer contained endosperm and were classed as dead. We also noted the number of endocarps with viable seeds remaining in each treatment.

Statistical analysis

A two-way ANOVA was performed with two factors: location, with two levels (within and distant from palm patches), and status, with two levels (in-feces and clean). An interaction effect between the two factors was also included in the model. The dependent variable was the number of live endocarps at the end of the 7-mo period. Two replicates of distant, clean endocarps were excluded from the analysis (one replicate could not be relocated, and 23 of the endocarps disappeared from the other, presumably removed by rodents). ANOVA residuals had a normal distribution, and only three residuals were outside the -2 to 2 range (6% of the total sample) and none outside the -3 to 3 range. A multiple comparison of means by combinations of categories was also completed, using a Bonferroni adjustment for the data. SAS 8.1 (SAS Institute 1999) was used for all analyses.

RESULTS

Mapping

Vegetation mapping revealed a highly aggregated distribution for adult *M. maripa* palms, and the co-occurrence of these patches with individual emergent *Couratari multiflora* (Lecythidaceae) trees, the sites preferred by tapirs for the establishment of upland latrines (Fig. 1). *Peltogyne gracilipes* exhibited clumping at a landscape scale, and the patchiness of vegetation types suggests that species associated specifically with these vegetation types will also be distributed in an aggregated fashion (Fig. 1).

Seed survival

Endocarp status and location significantly affected seed survivorship (overall model $F_{3,46} = 66.84$, $P < 0.0001$). Endocarps were significantly more likely to survive if they were distant from *M. maripa* patches ($F_{1,46} = 130.63$, $P < 0.0001$). They were also significantly more likely to survive if they were in feces ($F_{1,46} = 51.48$, $P < 0.0001$) than if they were clean. There was a significant interaction effect between distance and feces treatments ($F_{1,46} = 18.34$, $P < 0.0001$). A more detailed analysis of the data using Bonferroni adjustments revealed (a) no difference in survivorship for distant, in-feces relative to distant, clean endocarps ($P = 0.3069$; Fig. 2); (b) significantly higher survivorship for distant, clean relative to within-patch, clean endocarps ($P < 0.0001$); (c) significantly higher survival for distant, in-feces relative to within-patch, in-feces endocarps ($P < 0.0001$); (d) significantly higher survival for distant, in-feces relative to within-patch, clean endocarps ($P < 0.0001$); and (e) significantly higher survival for distant, clean seeds relative to within-patch, in-feces endocarps ($P = 0.0303$).

DISCUSSION

Large scale tree distribution

Mesoscale tree aggregations (i.e., aggregations of single species, forming a monodominant forest patch) in the tropics cannot be mapped with traditional plot methods, which involve the identification of all trees and saplings within a delimited area, because the labor involved is prohibitive. The largest plots sampled in this way are 50 ha in extent (Condit 1995), and may at best sample one to a few mesoscale aggregations of trees. While they are excellent at describing microscale aggregations and long-term tree turnover dynamics, they cannot address mesoscale or ecotone dynamics. In this study, we classified plant aggregations according to the dominant tree species, and plant communities according to the dominant structure. While it was relatively easy to identify palm aggregations and aggregations of leafless deciduous species, at this stage it was not possible to identify aggregations of other species, although canopy emergents could certainly be identified.

Mapping the vegetation of Maracá Island Ecological Reserve revealed conspecific clumping for *M. maripa*, *Peltogyne gracilipes* and a few other tree species that could be easily identified from an airplane (Fig. 1). The map allowed the detection of palm-free areas essential for the establishment of the seed dispersal manipulations, revealed the co-occurrence of tauari trees (possibly former tapir latrine sites) and palm patches (see Fragoso 1997), and showed a decrease in the density of palm aggregations from the river toward the forest interior. Tapirs routinely move across such vegetation boundaries and are able to transport seeds between single species aggregations or plant associations. This landscape scale is the scale at which processes responsible for aggregation dynamics may occur, suggesting that one could study tree distribution patterns from the perspective of aggregation dynamics rather than from the perspective of individual trees, by monitoring the appearance and disappearance of tree aggregations over large temporal scales. Because it would be prohibitive to work at the time scales required, it may be possible to look at the age structure of the aggregations and reconstruct the history of their establishment. This should especially be feasible for palm trees, which can be aged using leaf scars.

The high density of *M. maripa* palms and palm patches at the forest/savanna and forest/river boundary (Fig. 1) suggests that environmental factors play a role in allowing the competitive dominance of the palm in relatively open areas that are subject to occasional flooding or occasional fires. The occurrence of palm patches over a band of terra firme forest at least 10 km from the river, however, indicates that the palm can grow in a variety of soil, drainage, slope, and disturbance conditions. The occurrence of terra firme palms in a clumped rather than even or random distribution (whether it be at high or at low densities) suggests a role of contagious seed dispersal in setting these distributions.

At this study site, tapirs appear to be the only effective agent of persistent, high-volume, long-distance, seed dispersal for palms. Spider monkeys (*Ateles belzebuth*) are common on Maracá and may also contribute to long-distance seed dispersal, because they ingest entire ripe fruits and defecate intact endocarps over a large (300 ha) home range (Nunes 1992). At one site in southern Venezuela, *M. maripa* seeds do aggregate under spider monkey sleeping trees, making them potential foci for new palm aggregations (H. Castellano, *personal communication*). However, at our study site the home range of a single troop does not include several major habitat types, nor do they use the riverine or other edge forests, as tapirs do. Furthermore, they only use *M. maripa* during one month of the year, when it makes up ~10% of feeding observations (1.2% of observations over one year; Nunes 1992). They deposit endocarps in low-density clumps (1–10 endocarps) and, because fecal volume is low relative to endocarp size, defecated endocarps are not covered by fecal matter and therefore remain exposed to bruchid beetle oviposition (K. Silvius, *personal observation*). Feces per se (smell, chemical staining) do not deter oviposition by beetles (K. Silvius, *unpublished data*). To our knowledge, no other animal at Maracá ingests intact *M. maripa* fruits and carries them long distances from the parent tree (Fragoso 1997; Silvius and Fragoso 2002).

Seed dispersal by tapirs

Fragoso (1997) found higher densities of recently germinated *M. maripa* seeds around tapir latrine sites than around parent trees. For older seedling classes, densities were always higher around latrine sites in the forest than around parent trees, and greater than or equal to densities at randomly located trees. Previous work thus showed that (1) tapirs create high-density aggregations of seeds around latrine trees, rivaling densities around parent plants; (2) seed mortality by bruchid beetles is lower at latrine trees than at parent trees, leading to the higher densities of very young seedlings, and (3) secondary dispersal by rodents around latrine sites is responsible for the higher numbers of older seedlings and saplings around latrine sites and randomly located trees. But why is mortality by bruchid beetles lower at tapir latrines, even those that are located within a parent palm aggregation?

The present study shows that tapirs reduce mortality by bruchids at latrine sites by (1) placing endocarps in a medium that is relatively impenetrable by bruchid beetles, and (2) moving endocarps at the landscape scale into nonconspecific tree aggregations, sites where beetles are absent, rare, or inactive (currently, no information is available on the population dynamics of any species of palm bruchid beetle). Because seeds at conspecific aggregations were being infested while those in nonconspecific clumps were not, it appears that beetle populations are concentrated in the area of conspecific *M. maripa* clumps. This is supported by the lack of statistical difference in survivorship for clean and in-feces seeds located distant from parent clumps. In contrast, both seed treatments were attacked by beetles when in aggregations, with clean seeds suffering extremely high mortality by beetles.

The study trees were distributed equally among four palm patches, all located in the same type of forest at the eastern end of the study site. Endocarps in exclosures at all trees had similar mortality levels, indicating that there was no difference among palm patches in infestation rates. This is corroborated by a large scale field experiment carried out during the same fruiting season in the same palm patches (Silvius and Fragoso 2002) that showed no differences in seed survival rates among endocarps placed in 112 exclosures at 28 different trees in June, July, and September. Although there was some variation among trees in oviposition rates (Silvius and Fragoso 2002), the difference did not translate to differences in infestation rates.

Thus, clumped, long-distance, seed dispersal by tapirs can result in almost complete escape from bruchids. In nonexperimental situations, when seeds are not protected by exclosures, some tapir feces are disturbed by vertebrate seed predators and dispersers (rodents and peccaries). Endocarps that are not eaten may

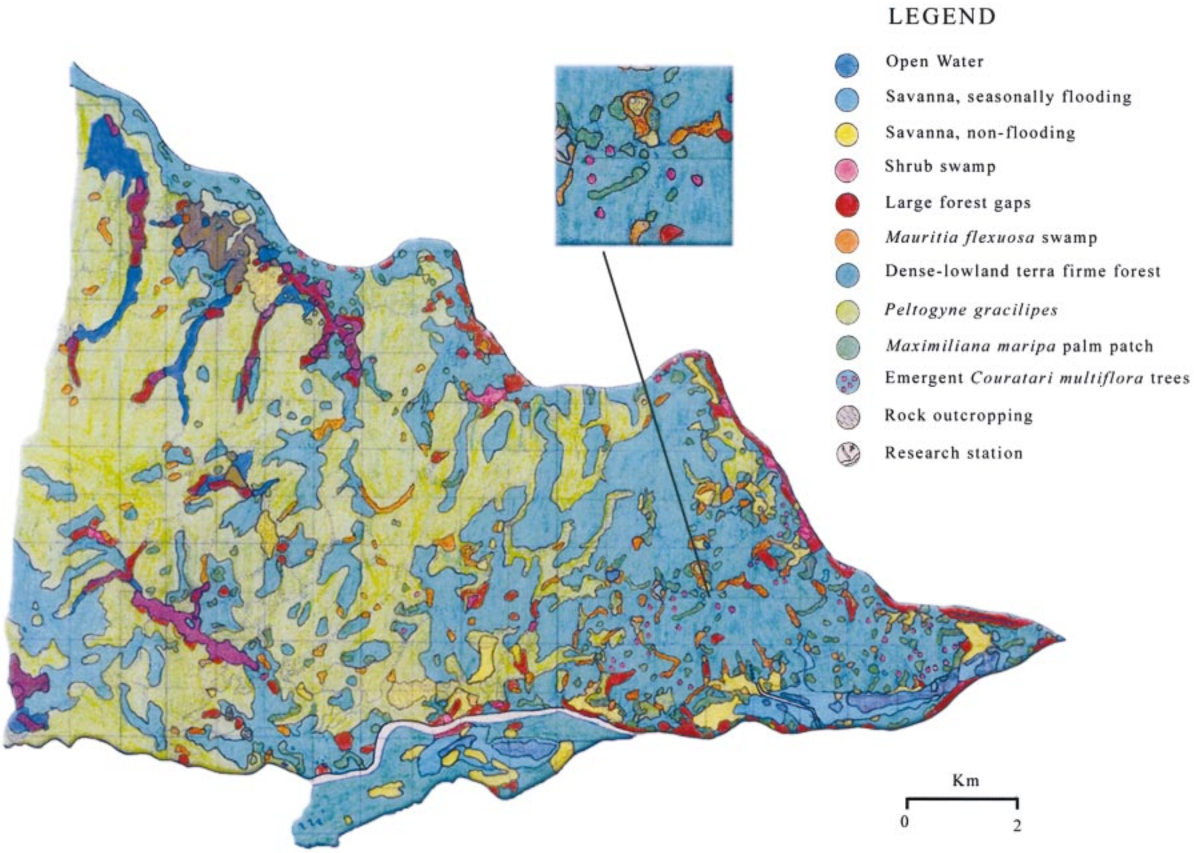

FIG. 1. Meso-scale map of plant associations and some plant species on the eastern third of Maracá Island Ecological Reserve, Roraima, Brazil. Nonflooding savanna supports a mixed vegetation of grasses and shrubs (*Curatella americana* and *Byrsonima* sp.). Forest gaps include open areas near the river dominated by *Triplaris* sp. and *Cecropia* sp. trees. *Peltogyne gracilipes* forest is dominated by this leguminous species but also supports palms and species in the Sapotaceae at low densities. The inset shows a close-up of a section of forest with intermingled *Couratari multiflora* emergents (pink) and *M. maripa* palm patches (dark green); the two species co-occur throughout the eastern end of the study site.

be uncovered and exposed to bruchid attack, if they are located within or near a palm patch (Fragoso 1994). Enough survive and are secondarily dispersed by rodents, however, to give rise to high seed and seedling densities around latrines (Fragoso 1997).

Animals that move at large spatial scales relative to conspecific tree-clumping patterns thus appear to play a crucial role in plant population dynamics, biodiversity pattern generation, and ecological matrix maintenance because they operate at high hierarchical levels relative to the tree-dispersion patterns. Animals operating at smaller scales, including the tapir when it does not move seeds beyond conspecific aggregations, do not generate the same survival patterns. They generate patterns at the within-aggregation (small scale) levels of <1 km, or, more importantly, within the spatial zone under the influence of bruchid beetle populations, which this study suggests is restricted to adult palm clumps and their border regions. Any seed moved away from a parent plant within or near a palm aggregation will have mortality probabilities equal to those of seeds remaining directly under the parent plant. Endocarps placed 100 m from fruiting palms, at the fringes of palm aggregations, received the same number of bruchid eggs as endocarps placed under the canopy of fruiting palms and nonfruiting palms (K. Silvius, *personal observation*). Long distance dispersal beyond this mortality sphere ensured the survival of nearly all seeds, suggesting that a qualitative difference in survivorship pattern occurs when seeds are moved by long-distance dispersal into what amounts to a different ecological context. In the case of *M. maripa* and other rainforest trees, the occurrence of parent trees in aggregations creates these different ecological contexts.

When the agent of mortality (in this case the bruchid beetle) has a threshold limit on its radius of infection, the potential exists for a scale break in the occurrence of mortality and survivorship rates, which will lead to different demographies for the same plant species at increasing distances from a parent aggregation. For plants with a different scale of aggregation, and mortality agents with different mobilities, the dispersal distance required for this shift may be smaller. However, for many rainforest trees, the scale of aggregation will

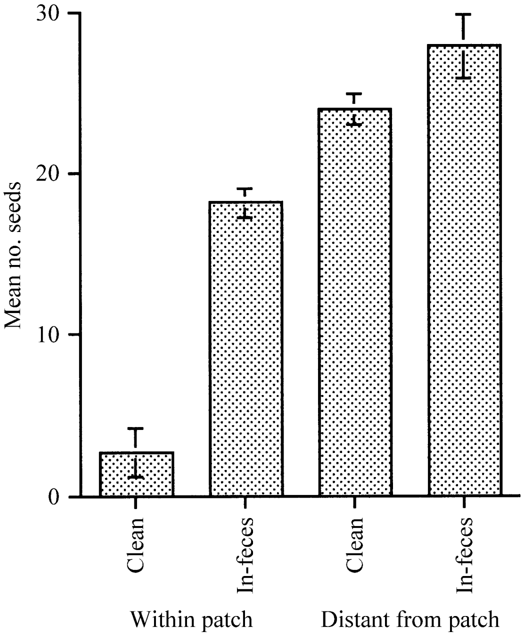

FIG. 2. The mean number (±1 SE) of *M. maripa* seeds alive within and distant from conspecific aggregations (''patch'') and in-feces or clean after 7 mo exposure in the field. Seed survivorship was significantly different in all pairwise comparisons, using the Bonferroni adjustment, except for distant clean vs. distant in-feces, which had similar survivorship rates.

be similar to that found for *M. maripa* (Fig. 1). Thus, seed survival may not increase monotonically with distance from the parent tree as suggested by the Janzen-Connell model. At large scales, interactions between aggregations of different species of trees begin to drive mortality and survivorship patterns. These patterns are more similar to those common to invasive and colonizing species than to those surrounding parent trees.

The dispersal distance of adult palm bruchids is not known. They do not fly to ultraviolet traps, and are rarely captured in any form of standard insect trap (H. Barrios, *personal communication*). Some species of the smaller and more speciose bruchids that specialize on legume seeds are known to disperse long distances after emergence, e.g., up to 4.8 km for *Bruchis pisorum*, and dispersing legume bruchids have been captured as high as 1520 m up in the air column (Johnson 1969). The cowpea weevil *Callosobruchus maculatus* produces two forms of adults, the smaller and lighter ones of which are more active and flight prone (Johnson 1969). Based on our observations of emerging adults, individuals of *Pachymerus cardo* immediately head for the leaf litter and avoid flying after emergence, suggesting that they tend to remain near their emergence site and therefore may be less mobile than the legume bruchids. However, the potential exists for colonization of newly created palm patches by bruchids, who may use individual trees or palm patches as ''stepping stones'' to reach distant patches, or who may occasionally reach far patches through their own long-distance dispersal events. Once beetles reach a patch, the parasitoids that attack their eggs and larvae (Silvius 1999) may follow, so that gradually the entire community of organisms that is associated with a palm patch is reconstituted. Because there may be lag time between the establishment of different organisms, and the discovery of the reproductive palm patches by vertebrate frugivores and seed predators, the community may have very different dynamics at different times since its initial establishment, resulting in a wave-like pattern of community establishment, development, and perhaps eventual disintegration through time. Because new patches are created ahead of or around the source patches, over very long periods of time the palm aggregations, or aggregations of other species, could move in a slow wave or concentric pattern through the forest matrix.

Implications for long-term forest dynamics

As indicated by the mesoscale map, Maracá Island Ecological Reserve includes a forest–savanna edge within its boundaries and along its eastern border. Tapirs move into and across these savannas for distances up to 20 km (Fragoso 1997), and defecate *M. maripa* seeds out in the savanna (Fragoso 1997). There are many forest islands distributed throughout the savanna around Maracá, many of them dominated by *M. maripa* palms. Tapirs commonly shelter in forest patches when traveling in savanna and savanna like vegetation (P. Medici, *unpublished data*). Fragoso and Huffman (2000) found that, at Maracá, tapirs defecated viable seeds of 39 species over a 14-mo period, most of which consisted of terra firme forest trees. Tapirs defecating seeds of forests species into savannas or forest islands in savannas may influence the extent and floristic composition of these patches. At a minimum, they will move large seeds out of the forest and increase tree diversity in tree islands in savannas. Hovestadt et al. (1999) documented a much higher frequency of animal-dispersed than wind-dispersed species in forest islands along an old-world forest–savanna boundary, supporting the important role of endozoochory in determining forest island species composition.

The pattern of forest islands in a savanna matrix is typical of tropical forest–savanna boundaries (Hemming 1994, Hovestadt et al. 1999), and the expansion and contraction of forests and savannas in response to climate change may be a frequent event over geological time scales in tropical zones (Haffer 1969, Prance 1982). Mayle et al. (2000) have recently documented the expansion of the southern boundary of the Amazon forest over millennial scales in response to shifts in the southernmost extent of the Intertropical Convergence Zone. The rapidity with which a forest advances into a savanna should be affected by the characteristics of its forest islands, if these act as the nuclei of forest expansion and advance. Long-distance contagious dispersal by tapirs and other animals that move long distances to cross ecotones can thus affect the advance and retreat of a forest–savanna ecotone in natural and anthropogenic savannas. The continued local and total extinction of these large bodied species throughout the tropics may thus significantly alter the way in which tropical forests respond to climate change in the future.

Conclusions

In the study of long-distance dispersal of seeds away from parent aggregations, we suggest that each aggregation, rather than each parent plant, be viewed as a source of seeds. This focuses attention on the ''tail end'' of the seed shadow, made up of what have been considered rare, long-distance, seed-dispersal events (Clark et al. 1999, Higgins and Richardson 1999, Cain et al. 2000). It eliminates the need for a single model to incorporate both extremes of the seed shadow, which, as shown in this paper, may have fundamentally different dynamics. This study and others on Maracá (Fragoso 1997, Fragoso and Huffman 2000) indicate that long-distance seed dispersal is neither rare nor unpredictable once we understand the movements and behavior of large mobile animals. Furthermore, creation of entire tree aggregations at significant distances from a parent aggregation may better explain potentially rapid migration rates of tree populations during periods of rapid climate change. Although such migration rates are rarely documented in the tropical paleorecord (but see Mayle et al. 2000, they are documented in the temperate record (Clark 1998).

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