



Seed-size variation determines interspecific differential predation by mammals in a neotropical rain forest

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It has been suggested that the anthropogenically driven loss of herbivorous mammals might lead to changes in the recruitment patterns of tropical rain forest plants, but few studies have examined the explicit mechanisms that might account for this effect. Here we propose a conceptual model linking differential mammalian defaunation and differential plant recruitment. We posit that in the absence of medium/large herbivores but with small rodent granivores still present (i.e. differential defaunation), predation pressure will be greater on small-seeded species than on large-seeded species. We tested such differential predation hypothesis (DPH) by means of a series of experiments directed to assess: 1) seed consumption by small rodents in laboratory cages; 2) seed-removal rates in small rodent enclosures in the field and 3) removal of seeds placed on the forest floor and exposed to either the full complement of mammals or only small rodents. Seeds used in the experiments were arranged in pairs consisting of species from the same taxonomic family but with a contrasting size (large, small). We found: 1) a significantly greater consumption of smaller seeds (a 2.3- to 20.5-fold difference) in cages and 2) a significantly greater removal of small-seeded species (a 3.7- to 65-fold difference) in field enclosures. Results of seed removal experiments in free-access plots and selective enclosures were more complex, with a general absence of significant differences among treatments but we found that predation was in general concentrated on small-seeded species and small rodents were the predominant visitors to the plots. This, together with the overall short distance of dispersal among large seeds suggest that in differentially defaunated forests large-seeded species are more likely to escape predation. We posit that such size related differential predation may lead to the floristic impoverishment observed in some defaunated forests.

Mammals dwelling in the rain forest understory have complex interactions with plants, including seed predation (Terborgh et al. 1993, Asquith et al. 1997, Wright and Duber 2001), seed dispersal (Forget 1990, Forget and Milleron 1991, Fragoso et al. 2003), herbivory (Howe 1990, Dirzo and Miranda 1991), use of plant materials for nest building (Ickes et al. 2005) and trampling (Clark and Clark 1989). Yet, mammal populations are undergoing a major global decimation and local extinctions as a consequence of hunting, habitat loss, and combinations thereof (Robinson et al. 1999, Peres 2001). Ultimately, one indirect effect of mammalian defaunation might be the impoverishment of floristic diversity (Dirzo and Miranda 1991, Terborgh 1992, Leigh et al. 1993). For instance, Dirzo and Miranda (1991) found that

defaunated understories had higher plant density and were less diverse than intact understories in southeast Mexico. Such differences were greater than expected from differences in the canopy composition of these forests (Dirzo and Miranda 1991). Ickes et al. (2001) and Terborgh and Wright (1994) found that the experimental exclusion of understory mammals has a significant positive impact on the survival of rain forest seedlings; Ickes et al. (2001) also found a negative impact on the diversity of the understory plant community. Despite the practical and theoretical implications these findings may have for the study and conservation of tropical diversity, few attempts have been undertaken to explore the mechanisms involved in this phenomenon (Dirzo 2001, Terborgh et al. 2002, Wright 2002).

A possible explanation of the relationship defaunation–diversity reduction in the rain forest understory is that, as a consequence of defaunation, a subset of the available pool of plant species outperforms other potential recruits. This may occur if and when plant species that have the potential to outperform their neighbors are kept in control by herbivorous mammals. There is evidence showing the existence of this type of top-down control in deserts (Brown and Heske 1990) and grasslands (Olf and Ritchie 1998), but evidence from rain forests is scant (Terborgh et al. 2001, Wright et al. 2007).

Here we examine the existence of interspecific size-related differential seed predation by neotropical understory mammals of contrasting body-size as a plausible mechanism contributing to post-defaunation floristic impoverishment. We focus on seed-size contrast because size is positively related with the capacity to withstand several of the hazards seeds/seedlings face in the forest understory, including: 1) greater tolerance to physical damage and higher capacity to re-sprout (Dalling et al. 1997), 2) better ability to emerge through thick layers of litter (Molofsky and Augspurger 1992), and 3) greater capacity to survive under light stress (Foster 1986). All this suggests that, other things being equal, large-seeded seedlings might have some advantages over small-seeded seedlings in the understory. On the other hand, rain forest ground-based mammals are avid seed predators (Terborgh et al. 1993, Asquith et al. 1997, Silman et al. 2003) and some studies indicate that they discriminate among seed species based on size (Bodmer 1991, Blate et al.

1998, Jansen et al. 2002, DeMattia et al. 2004). Finally, some relatively large-seeded species have been found particularly well represented in heavily defaunated neotropical forests (Dirzo and Miranda 1991, Leigh et al. 1993, Wright et al. 2007).

This study focuses on testing what we will refer to as the differential predation hypothesis (DPH), which also provides the conceptual framework that guides this study (Fig. 1). Our hypothesis posits that small rodents concentrate predation upon seed species of relatively small size, while larger seed species are depredated preferentially by larger mammals. Our rationale is that large seed predators are more likely to find and handle larger seeds per unit of search or foraging time. Such predators are also more likely to overcome defensive barriers associated with large seed size. In contrast, we expect small predators to be capable of finding small and large seeds, but to be more capable of handling comparatively smaller seeds. Therefore, the proposed mechanism distinguishes between two body size-related guilds of seed predators in an intact forest: small rodents (<200 g) and medium/large mammals (Fig. 1, upper pair of boxes). These two groups have the potential to negatively (and asymmetrically) interact in the forest floor (e.g. via competitive interactions), with larger mammals having a greater effect on small rodents (effects represented by the width of horizontal arrows). Seeds that escape predation have the potential to germinate and become established, but seedlings emerged from large seeds are likely to outperform seedlings emerged from small seeds (Leishman and Westoby 1994) (Fig. 1, horizontal arrows between the third pair of boxes). The

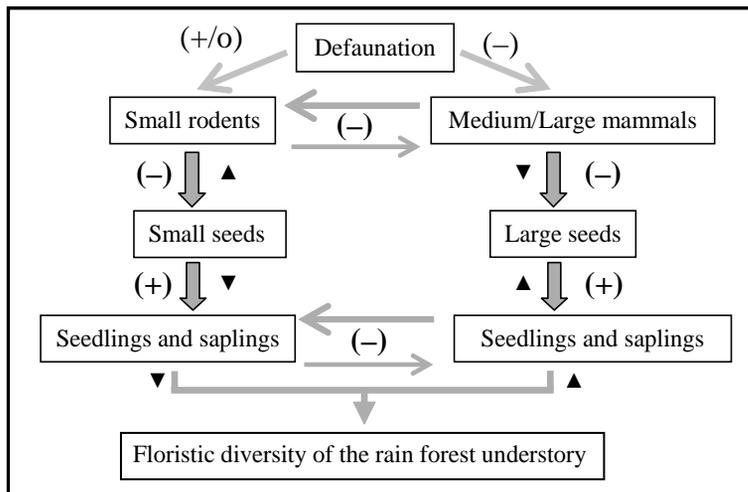


Fig. 1. Network of interactions between mammals, seeds and seedlings/saplings in the rain forest understory. Horizontal arrows depict interspecific interference and vertical arrows depict seed predation or seedling recruitment. The size of horizontal arrows indicates their relative weight in the interaction. Signs indicate the nature (+, positive; -, negative; neutral, o) of the effects. The \blacktriangle , \blacktriangledown symbols indicate increases or decreases, respectively, in the intensity of seed predation and seedling recruitment brought about by defaunation.

balance in the recruitment between seedlings emerging from small or large seeds determines, at least in part, the understory diversity observed in intact forests (bottom-level box, Fig. 1).

In forests impacted by human activity, large-bodied species are the first affected due to the combination of their lower densities, lower population growth rates and higher value for hunters. In contrast, small-bodied species, with higher densities, higher population growth rates and lower value for hunters, are less susceptible (Peres 2000, 2001, Wright 2003, Cardillo et al. 2005) (see uppermost level in Fig. 1). The predominance of small rodents may be further favored by the cancellation of negative interactions with larger mammals (Fig. 1, first pair of boxes). As a direct consequence of such differential defaunation large seeds escape depredation while depredation upon smaller seeds remains high. The escape of large seeds from predation in a defaunated forest may exacerbate the relative advantages in performance that large seeds and their seedlings have over smaller seeds/seedlings (Fig. 1, horizontal arrows between third pair of boxes). Ultimately, an increase in the recruitment of seedlings emerged from large seeds at the expense of the recruitment of seedlings emerged from smaller seeds may lead to a floristically impoverished understory (Dirzo and Miranda 1991). A complementary conceptual framework emphasizing the importance of the spatio-temporal variation in determining trophic interactions has been developed by Fragoso (2005).

To test the HDP we designed a series of experimental manipulations to specifically address the following questions: a) do small rodents preferentially consume small seeds over large seeds? b) do small rodents remove smaller seeds more than larger seeds? and c) does exclusion of medium and large mammalian seed predators favor large seeds more than small seeds? Previous studies have assessed size-related seed or fruit preferences by tropical rodents (Adler 1995, Blate et al. 1998), but not in the context of the consequences of anthropogenic defaunation. Furthermore, no phylogenetic control was attempted in those comparative studies. Several plant traits tend to be more conserved among related species than among unrelated species because of phylogenetic inertia (Jordano 1995). Therefore, phylogenetic control provides more straightforward comparisons of focal traits in a more homogeneous template. We performed four interspecific comparisons with seeds of contrasting size but belonging to the same taxonomic family in order to try to control for other seed traits that might affect predation. Our sample includes some representative species of three prominent taxonomic groups in the Neotropics: four legumes, two Sapotaceae and two Arecaceae.

Our conceptual model (Fig. 1) involves a multiplicity of interactions and variables that call for extensive study. To our knowledge, no comprehensive analysis of all the variables depicted in the model has been undertaken in any given system. In order to begin to analyze this network of interactions in this paper we specifically concentrate on testing the DPH.

Methods

Study site

This study was conducted in the Chajul Field Station, located in the southernmost extreme of the Montes Azules Biosphere Reserve (MABR), state of Chiapas, Mexico (Fig. 2). This 331, 200 ha preserve is naturally connected to the forests of the Guatemalan Petén, collectively constituting one of the largest tracts of tropical rain forest in Meso America (Mendoza and Dirzo 1999). Temperature averages 25°C and annual rainfall is 2500–3500 mm, with the greatest concentration from June to September, and the lowest from March to April (Mendoza and Dirzo 1999). Given its extent and relative inaccessibility, this forest maintains a well conserved fauna that includes the 48 historically known species of non-volant mammals naturally occurring in the area, ranging from small rodents (e.g. spiny pocket mice) to large herbivores and granivores (e.g. tapirs, deer and peccaries), as well as the top predators (e.g. jaguars and pumas) (Dirzo and Miranda 1991, Mendoza 2005).

Study species

Based on availability, size contrast, and phenological coincidence, we selected four pairs of seed (fruits, in the case of palms) species. A summarized description of the “seeds” of the study species is given in Table 1.

Pair 1. *Attalea cohune* and *Reinhardtia simplex* (Arecaceae: Arecoideae tribes Cocoeae and Areceae, respectively, Uhl and Dransfield 1987). The palms of *A. cohune* reach a height of 20 m and a diameter at breast height (dbh) of 30 cm (Pennington and Sarukhán 1998). *R. simplex* occurs in the understory; its average height is 1 m and average stem basal diameter is 0.5 cm (Henderson 2002). Fruits of both species are ellipsoid nuts.

Pair 2. *Pouteria sapota* and *Manilkara zapota* (Sapotaceae). Trees of *P. sapota* reach a height of 40 m and a dbh of 80 cm (Pennington and Sarukhán 1998). Its seeds are ovoid, shiny brown, with a conspicuous hilum scar on the side. Trees of *M. zapota* reach 30 m of height and a dbh of 30 cm (Pennington and Sarukhán 1998); seeds are black, ellipsoid and laterally flattened, with a white hilum scar on the side.

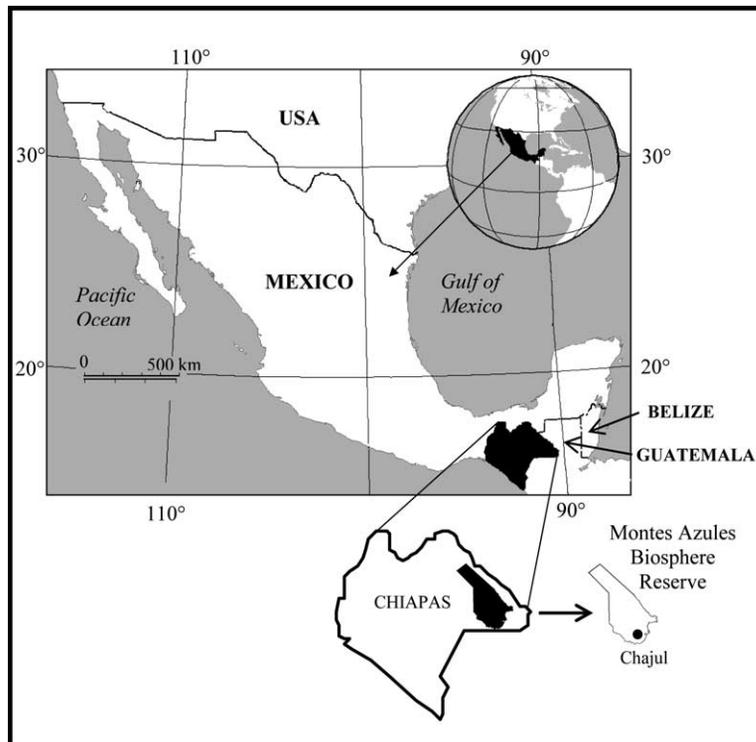


Fig. 2. Location of the Chajul Field Station in the southern limit of the Montes Azules Biosphere Reserve (MABR), in the state of Chiapas, Mexico.

Pair 3. *Mucuna argyrophylla* and *Canavalia oxyphylla* (Fabaceae). The seeds of these two lianas are contained in pods. Seeds of *M. argyrophylla* are black, circular, and laterally flattened. Seeds of *Canavalia oxyphylla* are brown, ellipsoid, and laterally flattened.

Pair 4. *Mucuna sloanei* and *Schizolobium parahybum* (Fabaceae). Seeds of the liana *M. sloanei* are brown, ellipsoids, with dark spots. Trees of *S. parahybum* reach a height of 35 m and dbh of 1 m (Pennington and

Sarukhán 1998); the dark brown seeds are ellipsoid and laterally flattened.

There are no studies on the seed dispersal ecology of the study species in our study site. However, studies in other tropical forests with these, or related species, indicate that seeds of *A. cohune*, *P. sapote* and *M. zapota* are dispersed by mammals, ranging from bats to primates (Heithaus et al. 1975, Marsh and Loisille 2003, Wright et al. 2007). In addition, it is known that

Table 1. Characteristics of the seeds of the four pairs of species used in the experiments. LS = large seed, SS = small seed. Lengths and weights (average \pm SE) were obtained from a sample of 30 seeds of each species.

Pair	Growth form	Length (mm)	Weight (g)	Weight contrast (LS/SS)
1. Arecaceae				
<i>Attalea cohune</i> (LS)	palm	88 \pm 0.8	92.8 \pm 1.34	154
<i>Reinhardtia simplex</i> (SS)	palm	11 \pm 0.1	0.6 \pm 0.16	
2. Sapotaceae				
<i>Pouteria sapota</i> (LS)	tree	79 \pm 1.5	28.6 \pm 1.35	41
<i>Manilkara zapota</i> (SS)	tree	20 \pm 0.4	0.5 \pm 0.03	
3. Fabaceae				
<i>Mucuna argyrophylla</i> (LS)	liana	35 \pm 0.6	6.8 \pm 0.27	34
<i>Canavalia oxyphylla</i> (SS)	liana	13 \pm 0.3	0.2 \pm 0.01	
4. Fabaceae				
<i>Mucuna sloanei</i> (LS)	liana	30 \pm 0.2	7.3 \pm 0.12	9
<i>Schizolobium parahybum</i> (SS)	tree	22 \pm 0.1	0.8 \pm 0.01	

some species of *Attalea* and *Pouteria* are secondarily dispersed by scatterhoarding rodents (Adler and Kestell 1998, Wenny 2005). In contrast, seeds of *M. argyrophylla*, *M. sloanei*, *C. oxyphylla* and *S. parahybum* seem to be dispersed by abiotic means (Wright et al. 2007). There is no information regarding dispersal of *R. simplex*, however, fruit characteristics such as color and fleshy mesocarp, suggest the potential for dispersal by birds.

It has been shown that rodents can discriminate among seeds depending on whether they are infested (Silvius 2002). To avoid this possible confounding effect we used only non-infested seed by directly gathering ripe fruits from source trees/lianas with no visible evidence of damage by invertebrates or pathogens. In addition, seeds were placed in containers filled with water and those that floated were discarded. We dissected a subset of the discarded and non-discarded seeds to confirm the assumption that contrasts in floatability were related to seed viability. In the case of palms, the procedure described was applied to fruits.

We used *Heteromys desmarestianus* gray mice (46 to 87 g) to test seed selection and removal capacity by small seed predators in our study site. Specialization of this rodent on seeds is reflected by its cheek pouches, used to transport seeds to their burrows for later consumption (Fleming 1983). Because of its abundance and feeding specialization *H. desmarestianus* is the predominant granivore within the small rodent community present in our study site (Mendoza 2005).

The experiments described below were repeated for each pair of species based on seed availability. Therefore, during each experimental session only one pair of species (large vs small; Table 1) was evaluated. Seeds of the four legumes were taken out of their pods for all the experiments.

Experiment 1. Seed selection in laboratory cages

We captured *H. desmarestianus* rodents in the vicinity of the Chajul Field Station during the previous four days prior to each experimental session. Rodents were placed individually in laboratory cages (20 depth \times 23 width \times 44 length cm) with wood chips to provide shelter. The number of rodents (independent replicates) used in each experimental session ranged between nine and twelve. All rodents were supplied with sunflower seeds, *Helianthus annuus*, and water ad libitum. Before the start of the experiment sunflower seeds were removed from the cages for a four-hour period. These procedures were aimed at standardizing feeding potential of all the animals. After this period we simultaneously presented, to each individually caged animal, a standardized mass of seeds (both large and small) of the particular pair of species to be evaluated. Masses offered

(mean \pm SD) were: 73.6 \pm 7.1 g (*A. cohune*/*R. simplex*); 21.2 \pm 1.3 (*M. sloanei*/*S. parahybum*); 64.6 \pm 14.8 g (*P. sapota*/*M. zapota*) and 14.8 \pm 6.3 g (*M. argyrophylla*/*C. oxyphylla*). These masses corresponded to the following amounts of large and small seeds per cage: 1 (*A. cohune*)/123 (*R. simplex*); 2 (*P. sapota*)/141 (*M. zapota*); 2 (*M. argyrophylla*)/170 (*C. oxyphylla*). Each of the four experimental trials lasted two days.

With the help of a screen sieve we collected and weighed all the remaining seed material in each cage (including seed coats, partially consumed seeds and entire seeds) after each night of the experiment. Seed material collected after the first night was returned to the corresponding cage. In addition, we counted the number of seeds left intact after each night. Measurements after each of the two nights were intended to evaluate if there were switches in seed preferences. The only exception to this protocol was the pair *M. argyrophylla*–*C. oxyphylla*, where mass consumption was measured only at the end of the experiment. We estimated seed consumption based on the difference between initial and final seed weight. Since we weighed all the seed material (edible+inedible) left over by rodents we can safely assume that differences in weight correspond to seed consumption. In addition, to correct for possible changes in seed weight due to changes in water content we measured a subset of seeds under the same experimental conditions, but not included in the experiment, before and after the two days of the experiment.

For each replicate we used the difference in weight of the consumed mass from large-small seeds to perform paired t-tests (Sokal and Rohlf 1995). When data (absolute difference in seed weight from each pair) significantly deviated from normal distribution we used the equivalent non-parametric Wilcoxon signed-ranks test for matched pairs. In the latter case we report the sum of the signed ranks (*W*), the sample size, and the corresponding *P* values.

Experiment 2. Seed removal in field experimental enclosures

To complement Experiment 1 we evaluated the capacity of small rodents not just to consume seeds but also to remove them in the field. This additional variable is of particular interest since *H. desmarestianus*, uses its cheek pouches to carry seeds to its burrow for later consumption. We built 3 \times 3 m enclosures which were placed on the forest floor to maintain captive *H. desmarestianus* rodents (one per enclosure) during two-day periods (12 replicates per experimental session). The walls (sides) of the enclosures were made of 1.20 m height metallic foil, and buried 20 cm into the ground to prevent the escape of rodents. Each enclosure

was covered with chicken-wire to avoid escape of and predation on rodents. A similar quantity of stones and pieces of bark were placed at the center of each enclosure to provide shelter.

On each experimental session we placed three clusters of large seeds and three of small seeds in randomly selected points (defined from a grid of 25 0.5×0.5 m quadrats) within each enclosure. The numbers of seeds per cluster within each enclosure were: 5 (*A. cohune*)/20 (*R. simplex*), 3 (*P. sapota*)/9 (*M. zapota*), 9 (*M. argyrophylla*)/15 (*C. oxyphylla*) and 6 (*M. sloanei*)/12 (*S. parahybum*). In the experiments described in this and the following section we did not attempt to match the weight of seeds (small and large) we offered. This was due in part to the limitation in our small-seed stock and partially because that would have led to unusually high densities of the small-seeded species in the experimental plots. We quantified the number of seeds removed after one and two nights in each enclosure. Arbitrarily we defined seeds moved at least 50 cm from their original location as removed. We replaced removed seeds with new seeds after the first night of the experiment. When the experiment ended rodents were released at their site of capture.

For each pair of species and replicate (enclosure) we used the difference of the proportion of large seeds removed from the proportion of small seeds removed to perform paired t-tests (Sokal and Rohlf 1995).

Experiment 3. Seed removal under contrasting conditions of access to mammalian fauna

In the vicinity of the Chajul Field Station, we selected five independent sites of mature forest (separated by at least 100 m). In each of the five sites we placed six pairs of experimental plots at randomly selected points (with reference to a 60 m line transect) thus totaling 60 experimental plots. Paired plots were separated by 3 m. We randomly assigned each of the plots in a pair to one of two treatments: partial enclosure or free access. In free-access treatments, 1 m² plots were marked with small PVC stakes at the corners. In partial-enclosure treatments 1 m² plots were completely covered with galvanized wire cloth (25 mm mesh; 1.10 m tall), supported by 1m stakes at the corners. The wire cloth was firmly attached to the ground with stakes to prevent access to larger mammals. These enclosures had three 10×10 cm openings at the base of each of the walls to allow access to small rodents. This design was aimed at mimicking differential defaunation (i.e. loss of medium and large mammals, presence of small rodents). In our study site this situation would represent the loss of animals ranging from agouties, *Dasyprocta punctata*, and pacas, *Agouti paca*, to peccaries (*Pecari tajacu*, *Tayassu pecari*), deer (*Odocoileus virginianus*, *Mazama*

americana) and tapir, *Tapirus bairdii*. Pairs of experimental plots were provided with either large or small seeds (three pairs with large seeds and three pairs with small seeds in each of the five sites). Seed type (large or small) was randomly assigned to paired plots at the beginning of each experimental session. We consistently stocked plots with a larger number of small seeds than large seeds. Numbers of seeds per plot in each experimental session were: 6 (*A. cohune*)/20 (*R. simplex*), 6 (*P. sapota*)/ 9 (*M. zapota*), 9 (*M. argyrophylla*)/ 20 (*C. oxyphylla*) and 10 (*M. sloanei*)/20 (*S. parahybum*). Seed monitoring lasted 11 days in the case of *A. cohune*/*R. simplex* and *M. sloanei*/*S. parahybum*, 33 days in *P. sapota*/*M. zapota* and 45 days in *M. argyrophylla*/*C. oxyphylla*. In all cases seeds were initially checked every one or two days; later, as the experiment progressed and less seed were left to be removed, this was done at larger intervals.

To determine the fate of large seeds (depredated or dispersed) we tied a line of fishing monofilament (1.5 m length with a 30-cm piece of flagging tape attached at the end), to a set of the large seeds in each plot. Flagging tape was labeled to identify the plot where the seed originated. Similar techniques of marking seeds have been previously employed in studies of seed dispersal in the tropics with no apparent effect on seed fate (reviewed by Forget and Wenny 2005). Marked seeds that were removed were searched for in concentric circles from the plot up to a distance of 25 m. At the beginning of each experimental session we placed sand quadrats around each plot to record tracks of visiting fauna. These quadrats were replaced one or two times during the corresponding experiment. Tracks recorded in the sand quadrats were erased after their detection to avoid double counting.

We compared the curves of removal of large and small seeds over time in excluded and free-access plots using survival analysis with the Kaplan-Meier method (Kaplan and Meier 1958). We carried out this analysis considering both all the sites pooled and on a site by site basis. Seeds remaining intact at the end of each experimental session were considered "censored" for the survival analysis. Heterogeneity among curves was examined using log-rank tests (Cox 1972). For each curve we calculated the average time of seed permanence in the plots. Analyses were performed with JMP4 from SAS 2001.

Given that seeds moved out from the semi-enclosure plots become exposed to the full complement of mammal seed predators (thus ending the effect of treatment), we only recorded seed fate after their first detected displacement. For consistency, we applied the same criteria in seeds removed from free-access plots. Large seeds partially consumed, located inside burrows or treetops, and those with only the monofilament remaining, were classified as preyed. Intact seeds found

lying around the experimental plots were classified as dispersed. All small seeds removed were classified as having been preyed upon.

Results

Experiment 1

We found that seed consumption was greater in small-seeded species than in large-seeded species in all four pair of species (Fig. 3). This contrast was consistent between nights in each experimental session ($p \leq 0.034$, t or Wilcoxon tests). Therefore, we show results of statistical analyses for the total mass consumed after two days: *A. cohune*/*R. simplex* ($W = -83$, $p = 0.004$, $n = 13$); *P. sapota*/*M. zapota* ($t = 8.79$, $p < 0.001$, $DF = 9$); *M. argyrophylla*/*C. oxyphylla* ($t = 6.30$, $p < 0.001$, $DF = 11$); *M. sloanei*/*S. parahybum* ($W = -76$, $p = 0.001$, $n = 12$). Within pairs of large and small seeds the lowest average difference in mass consumption after two nights corresponded to *M. zapota* and *P. sapota* (2.94 ± 0.34 g), while the highest difference was in the pair *A. cohune*/*R. simplex* (16.84 ± 5.07 g). Differential mass consumption resulted in a marked reduction in the number of small seeds. Therefore, among small-seeded species, the average proportion of seeds that remained intact after the experiment was 63% for *R. simplex*, 55% for *S. parahybum* and 11.4% for *M. zapota*. In contrast, no large seed was completely consumed and, in some instances, such as in *A. cohune*, damage affected only the seed coat.

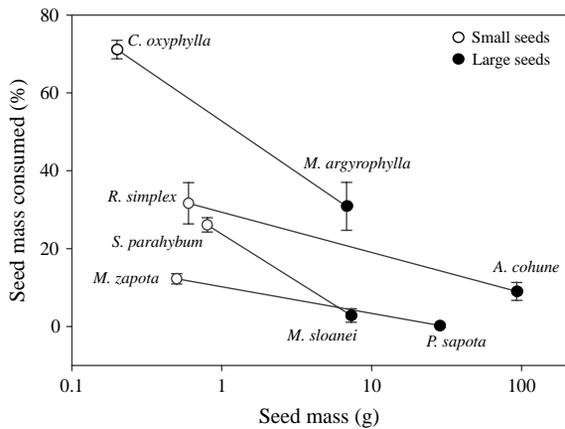


Fig. 3. Relationship between species seed weight and consumption in laboratory cages. Each point corresponds to the percentage (average \pm SE) of seed mass eaten by *H. desmarestianus* after two days. Lines connect pairs of species (large vs small) assessed on the same trial. In all cases differences within pairs are statistically significant. See text for p-values and sample sizes.

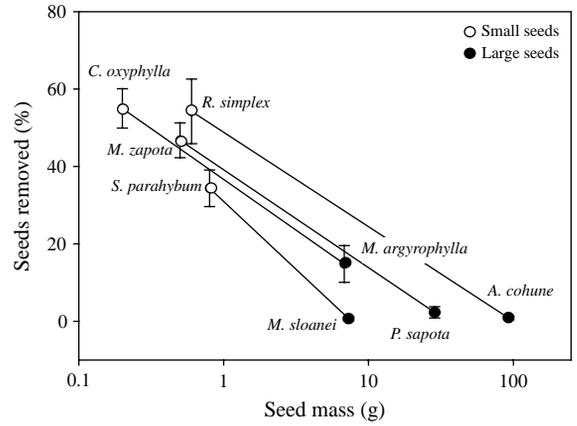


Fig. 4. Relationship between species seed weight and removal within enclosures. Each point corresponds to the percentage of seeds removed by *H. desmarestianus* (averaged over two nights \pm SE). Lines connect pairs of species (large vs small) assessed on the same trial. In all cases differences within pairs are statistically significant. See text for p-values and sample sizes.

Experiment 2

Removal in the field enclosures was consistently higher in small-seeded species than in large-seeded species (Fig. 4). As in experiment 1, differences in predation were consistent between nights for all species ($p \leq 0.0035$, t or Wilcoxon tests). Therefore we show results of statistical analyses for the proportion of seeds removed, averaged for the two nights of each experiment: *A. cohune*/*R. simplex* ($t = 6.51$, $p < 0.001$, $DF = 11$); *P. sapota*/*M. zapota* ($t = 10.16$, $p < 0.001$, $DF = 11$); *M. argyrophylla*/*C. oxyphylla* ($t = 6.44$, $p < 0.001$, $DF = 11$); *M. sloanei*/*S. parahybum* ($t = 6.93$, $p < 0.001$, $DF = 11$).

The largest contrast in seed removal within paired species corresponded to *M. sloanei* and *S. parahybum* where the percentage of small seeds removed per night was almost 70-times higher than for large seeds (Fig. 4). On the other hand, the smallest contrast corresponded to the pair *M. argyrophylla*/*C. oxyphylla*, where percent removal per night was 4 times higher for small seeds than for large seeds (Fig. 4). Among large-seeded species the lowest percentage of seeds removed in one night was that of *A. cohune* (0%) and the highest that of *M. argyrophylla* ($17.9 \pm 6.1\%$). Among small-seeded species the lowest average removal in one night was in *S. parahybum* ($32.2 \pm 6.9\%$) and the highest was in *C. oxyphylla* ($63.3 \pm 8.0\%$).

Experiment 3

Overall, we found small differences between seed survival curves of semi-excluded and free-access plots.

Only in the case of the small-seeded *S. parahybum* were differences statistically significant ($\chi^2 = 9.9$, $p = 0.0016$, $DF = 1$), while in the case of another small-seeded species, *R. simplex*, the same trend was marginally non-significant ($\chi^2 = 3.4$, $p = 0.066$, $DF = 1$). Seeds of *S. parahybum* lasted longer in free access plots (6.7 ± 0.22 days, average \pm SE) than in partially excluded plots (5.6 ± 0.19 days). The same analysis applied individually to each of the five sites and four pairs of species was, in general, consistent with the overall analysis. Yet, among the small-seeded species, *C. oxyphylla*, in which we did not detect differences in the overall analyses, showed a significant contrast in two sites. However, in one site removal was higher in semi-excluded plots ($\chi^2 \geq 16.6$, $p < 0.001$, $DF = 1$) and in the other removal was higher in free-access plots ($\chi^2 \geq 37.0$, $p < 0.001$, $DF = 1$). Among large seeded-species we found significant differences in one site with seeds of *A. cohune* and two sites with seeds of *M. argirophylla*. In these three sites removal was higher in free-access plots than in semi-excluded plots ($\chi^2 \geq 6.8$, $p \leq 0.009$, $DF = 1$).

Time of permanence of seeds in experimental plots was, in general, greater among large seeded species than among small seeded species although the magnitude of contrast varied among species pairs: *A. cohune*/*R. simplex* ($\chi^2 = 3.6$, $p = 0.056$, $DF = 1$); *P. sapota* and *M. zapota* ($\chi^2 = 428.4$, $p < 0.001$, $DF = 1$); *M. argirophylla* and *C. oxyphylla* ($\chi^2 = 33.5$, $p < 0.001$, $DF = 1$) and *M. sloanei* and *S. parahybum* ($\chi^2 = 41.5$, $p < 0.001$, $DF = 1$) (Fig. 5 A).

Comparisons between large marked seeds and small seeds (treatments pooled) showed that seed predation (angular transformation of predation proportion) was consistently greater among small-seeded species than among large-seeded species: *A. cohune*/*R. simplex* ($t = 10.9$, $p < 0.001$, $DF = 8$); *P. sapota*/*M. zapota* ($t = 33.7$, $p < 0.001$, $DF = 8$); *M. argirophylla*/*C. oxyphylla* ($t = 4.3$, $p = 0.003$, $DF = 8$); *M. sloanei*/*S. parahybum* ($t = 4.7$, $p = 0.002$, $DF = 8$) (Fig. 5 B, Table 2). A remarkable finding was that 38.8% ($n = 14$) of the preyed seeds of *A. cohune* were detected, because of their attached flagging tape, on tree crowns, indicating squirrel predation. The proportion of seeds dispersed among marked large seeds decreased in the following order: *A. cohune*, *P. sapota*, *M. argirophylla*, and *M. sloanei* (Table 2).

In the experiment with *P. sapota* and *M. zapota* we found 34 cases of tracks in the sand quadrats. The most common tracks corresponded to small rodents and squirrels (*Sciurus* sp.), each one with 24.4% of the total number of tracks. The second most common tracks corresponded to opossums (*Didelphis* sp.) with 18.2%, followed by raccoons, *Procyon lotor*, with 9.1%, and the (carnivorous) felid jaguarundi, *Herpailurus yaguarondi*. The remaining tracks included deer, *Mazama americana*,

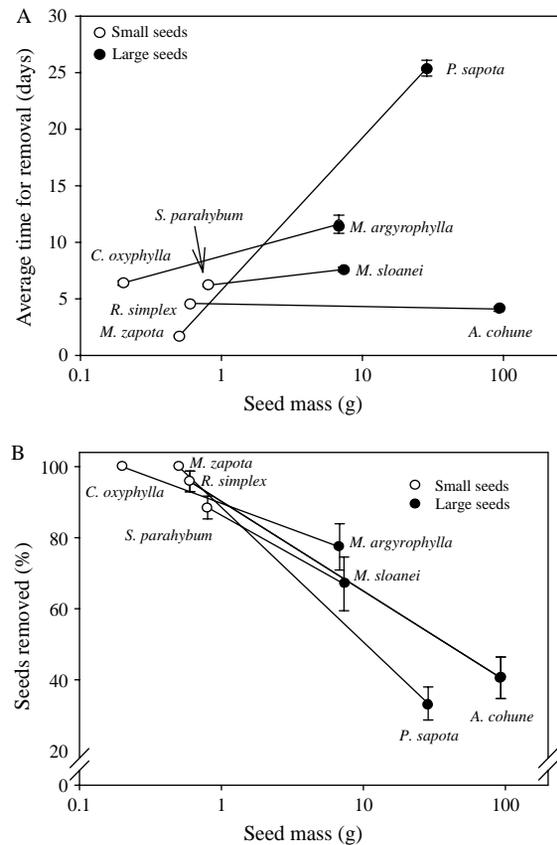


Fig. 5. Seed removal in partially excluded and free-access plots in the field. (A) Relationship between species seed weight and time of permanence of seeds in the plots. Each point corresponds to the number of days seeds lasted in the plots (average \pm SE). Lines connect pairs of species (large vs small) assessed on the same trial. See text for p-values and sample sizes. (B) Relationship between species seed weight and predation. Each point corresponds to the percentage of seeds predated in experimental plots (average \pm SE). Lines connect pairs of species (large vs small) assessed on the same trial. See text for p-values and sample sizes. In both cases treatments and sites were pooled.

collared peccaries, *Tayassu tajacu*, and tapirs, *Tapirus bairdii*. In the experiment with *A. cohune* and *R. simplex* we found 30 records of tracks among which the most common corresponded to squirrels (63.3%), followed by raccoons (16.7%). The remaining tracks included opossums, deer, collared peccaries, ocelots, *Leopardus pardalis*, and small rodents. Finally, in the experiment with *M. argirophylla* and *C. oxyphylla* we had 13 records of tracks, of which 54% corresponded to small rodents, 38% to squirrels and 8% to collared peccaries. Therefore, small rodents were the most common visitors to plots in both treatments in the three pairs of species were visitor's identity was recorded.

Table 2. Fate of seeds used in experiment 3, enclosure and free access plots pooled. Values for large seeded species correspond only to tagged seeds, values for small seeded species correspond to the total of seeds used (L = large, S = small).

Species	n	Intact (%)	Depredated (%)	Dispersed (%)	Dispersal distance (avg. \pm SS m)
<i>A. cohune</i> (L)	90	3.7	40.6	55.7	4.50 \pm 0.40
<i>R. simplex</i> (S)	600	5.5	94.5	0	–
<i>P. sapota</i> (L)	90	10.5	33.3	56.2	2.78 \pm 0.23
<i>M. zapota</i> (S)	270	0	100.0	0	–
<i>M. argyrophylla</i> (L)	120	16.3	77.4	6.3	2.18 \pm 0.66
<i>C. oxyphylla</i> (S)	600	0	100	0	–
<i>M. sloanei</i> (L)	120	29.7	67.0	3.3	0.95 \pm 0.32
<i>S. parahybum</i> (S)	600	11.5	88.5	0	–

Discussion

Size-related differences in predation

Our experiments represent an increasing gradient of realism (and decreasing experimental control) to test predictions derived from the DPH. Following such gradient, we found that rodents attacked a greater proportion of smaller seeds than of large seeds in laboratory cages (experiment 1). In addition, rodents removed a greater proportion of the small seeds than of the large seeds in controlled conditions in the field (experiment 2). Yet, seed removal on the forest floor, contrasting seed exposure to small rodents or the full mammalian community (experiment 3), did not reflect such a clear preference. However, if seed fate and records of the fauna visiting the experimental plots are taken into account, results of seed removal experiments in the field seem more congruent with those of experiments carried out in the two more controlled conditions. First, both free-access and enclosure plots were mainly visited by small rodents, as asserted from the foot prints detected in the sand quadrats. The low visitation by larger mammals might have hindered the chances to observe contrasts between treatments. This finding underscores the need of documenting the fauna responsible for seed removal in this type of studies, as stressed by Jansen and Den Ouden (2005). Second, we found that, among the small rodents, squirrels were able to move the large seeds of *A. cohune*, even when this implied taking seeds several meters away and onto the forest canopy. Similarly, Pimentel and Tabarelli (2004) and Silvius (2002) found that squirrels were important consumers of the large seeded palm *Attalea* in the Amazon. The role of squirrels as post-dispersal seed predators in rain forest floors has received little attention, but our results suggest they deserve more detailed studies. In addition, a methodological aspect has some bearings on the apparent discrepancy between experiments 1 and 2 vs experiment 3. For the purposes of our seed survival analyses we only distinguished between seeds remaining intact within the plots

(“survivors”) and seeds taken off the plots (“lost”). Yet, our survey of seeds attached to a flagging tape revealed that displacement was a common fate among largest seeds. Thus, although large seed displacement outside the plot by small rodents led to our classifying of them as “lost” in the survival analyses, such movement did not necessarily implied predation. In contrast to removal of large-seeded species, removal of small-seeded ones meant predation. This is because: 1) the chances of being scatterhoarded (i.e. dispersed) decreases with seed size (Hallwachs 1994, Xiao et al. 2004), 2) storage of small seeds in rat burrows most probably results in death, given the impossibility of these seeds to emerge from such depths; and 3) rats typically remove seed coat from small seeds prior to being transported (Mendoza unpubl.). If abandoned, such coatless seeds are more exposed to desiccation or pathogen attack.

Our suite of experiments shows how seed exposure to the full community of small rodents (mice and squirrels) reveals a more complex interaction than would be predicted from the experiments involving cages and enclosures. Nevertheless, the results of all three experiments are consistent with the expectation of greater predation on relatively smaller seeds in defaunated settings, in concordance with the DPH. In addition, these results are consistent with those of a parallel study carried out in a defaunated forest, but still retaining small rodents, in southeast Mexico, in which experimental protection of seeds from small rodents led to an increase in seed survival and germination in small-seeded but not in large-seeded species (Dirzo et al. 2007).

Interplay between the effects of the loss of seed predators and dispersers

Our results indicate that relatively larger seeds may increase their potential to escape from mammal predation in differentially defaunated forest, and we argue that the disruption of this interaction might ultimately lead to differential recruitment in the understory.

However, defaunation might bring about other consequences in addition to those related to seed predation. For example, several large-seeded species strongly rely, for their dispersal, on medium and large mammals, including tapirs (Fragoso et al. 2003), caviomorph rodents such as agouties and acouchies (Forget and Milleron 1991, Jansen et al. 2002), and large primates (Peres and Roosmalen 2002). Therefore, the loss of medium and large mammals might reduce recruitment of some large-seeded species. This situation might seem contradictory to our proposed mechanism of floristic impoverishment via the loss of medium and large seed predators. Several aspects need to be taken into consideration in reconciling this apparent contradiction. For example, although dispersal might increase seed survival, several species are able to recruit in the parent tree's vicinity (Hubbell 1980). In these species dispersal limitation brought about by defaunation would exacerbate seed accumulation near parent trees. This and a reduction of seed predation may enhance large-seeded plant recruitment (Wright and Duber 2001). It has been shown that in the palms *Attalea butyracea* and *Astrocaryum standleyanum*, the simultaneous anthropogenic loss of their mammal seed predators and dispersers result in an increase in seedling recruitment near reproductive individuals (Wright et al. 2000, Wright and Duber 2001).

Differential seed predation and understory floristic diversity

Changes in the seed bank might set the stage for subsequent changes in seedling recruitment and understory structure and diversity. However, seedlings face a myriad of complex challenges on their way to the forest canopy, including vertebrate and invertebrate herbivores (Howe 1990, Dirzo 2001), pathogens (Bell et al. 2006) and mammal trampling and physical damage by falling debris (Clark and Clark 1989). All these have the potential to arrest, reinforce, or compensate for the effects of missing mammalian seed predators and herbivores (Fragoso 2005). Although there is evidence that natural enemies such as invertebrates and pathogens might be strong density-dependent controls for rain forest seed and seedling populations (Fragoso 2005, Bell et al. 2006), some results show that such natural enemies fail to compensate for the anthropogenically driven absence of mammals. For example, invertebrate seed predators did not compensate for the absence of mammalian seed predators of a neotropical palm (Wright and Duber 2001) and specialist invertebrate folivores (caterpillars) failed to override the seedling patches dominated by large seeded species in a defaunated understory (Dirzo 2001). In agreement with our results, Wright et al.

(2007) recently found, in Panama, that large-seeded tree species are over-represented in the seedling bank of defaunated forests, when compared with forests that still retain their mammalian fauna.

Conclusions

With increasing defaunation, even in seemingly pristine forests, only the omnipresent and more resilient small rodents may be left to perform processes such as seed predation. Apart from those cases in which the residual rodent fauna includes large-bodied species such as *Proechymis*, small rodents do not seem to be able to accomplish the roles played by larger mammalian seed predators. Under these circumstances large-seeded species (less palatable or inaccessible to small rodents) may increase their chances to become established. This might set the stage for future changes on the forest structure contributing to the unleashing of an understory defaunation syndrome: seedling banks of low diversity, with an over-representation of large seeded and wind-, bat-, and small-bird dispersed plants (Dirzo and Miranda 1990, Wright et al. 2007). Studies directed to unravel the possible subsequent trajectories of tropical forest vegetation impacted by defaunation require, in addition to modeling exercises (Muller-Landau 2007), long-term, comparative studies involving a variety of sites. These studies are a priority in view of the increasing pantropical defaunation.

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