

Size-Related Differential Seed Predation in a Heavily Defaunated Neotropical Rain Forest

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ABSTRACT

Hunting and habitat loss represent an increasingly common anthropogenic impact. Available evidence suggests that defaunation is typically differential: medium/large mammals are most affected while small rodents are less affected, or even favored. In heavily impacted areas, such as Los Tuxtlas, the residual mammalian fauna is dominated by small rodents. We tested the expectation that if small rodents will preferentially attack small-seeded species, large-seeded species may escape predation in the absence of medium/large seed predators and that this may affect germination and, possibly, recruitment. Experiments with caged rodents (*Heteromys desmarestianus*) under laboratory conditions showed a preference for smaller seeds. A field experiment involving seeds of contrasting size showed that small, unprotected seeds experienced a predation risk 30-times larger than protected seeds, while the effect of protection was not significant for large seeds. These patterns of predation led to significant differences in germination: protected small-seeded species had a fourfold greater germination than unprotected small-seeded species, while germination was not significantly different between exposed and protected large seeds. The observed contrasts in germination suggest that under heavy defaunation, small-seeded species are likely to be penalized by the overabundance of small rodents, while large-seeded species escape predation. Our results are consistent with the observation of dense seedling carpets dominated by large-seeded species in the understory of Los Tuxtlas. We speculate that the patterns we uncovered may explain, at least partly, the impoverished diversity of the understory vegetation that characterizes heavily defaunated understories and that this has the potential to affect forest regeneration.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: differential defaunation; Los Tuxtlas; Mexico; recruitment; seed germination; seed predation; seed-size.

GLOBAL MAMMALIAN BIODIVERSITY IS CURRENTLY THREATENED due to anthropogenic impact (Robinson *et al.* 1999, Dirzo 2002, Milner-Guilland *et al.* 2002, Ceballos *et al.* 2005). Defaunation, the contemporary pulse of mammalian loss (see Dirzo & Miranda 1991a) is driven by the direct effects of hunting and illegal trading, by the indirect effects of habitat loss (deforestation and fragmentation), and by interactions among these factors (Peres 2001, Dirzo 2001, Wright 2003). The magnitude of this anthropogenic impact is reflected, for example, in the number and percentage of species of the Class Mammalia currently listed by IUCN as endangered (in different categories). A total of 1372 species of nonvolant terrestrial mammals, equivalent to about 30 percent of the total number of species in the Class, is included in IUCN's 2003 Red List (see Mendoza 2005). Recent studies show that, in addition to the risk of species extinction, there is a substantial loss of populations through local extirpations. For example, an analysis of 173 species of mammals showed they had lost more than 50 percent of the area of their historic ranges (Ceballos & Ehrlich 2002). The alarming rates of tropical defaunation have been recognized for some time and popularized since the publication of Redford's classic "Empty Forest" (Redford 1992) and more recent and detailed studies (*e.g.*, Peres 2000) confirm that tropical defaunation is an anthropogenic impact

of considerable magnitude in numerous localities throughout the tropics.

Overall, populations of large terrestrial mammals are much more at risk of extinction than those of small mammals (Cardillo *et al.* 2005), and rain forests are no exception to this trend. Differential defaunation in the Neotropics is now widely recognized in a variety of studies at local scales (Bodmer 1995, Peres 2000, 2001, Dirzo 2001). In general, larger animals are preferred by hunters due to both their value and ease of hunting. In addition, larger animals have a series of intrinsic traits that make them particularly vulnerable to human impact. These include demographic and life history features such as longevity, length of generation time, time for gestation, area required to maintain viable population size, and intrinsic population growth rate, all of which are significantly correlated with body size (Bodmer *et al.* 1997; see reviews in Dirzo 2001 and Wright 2003). These relationships are epitomized by a specific study in Amazonia (Peres 2000), which showed that both body size and population density of animals were negatively correlated with intensity of hunting in those species larger than 5 kg, while the relationship was positive for species of 1 kg or less. In Neotropical forests, the former would be represented by the large- and medium-sized ungulates, large primates and large rodents, while the latter would be represented by the small rodents. The first group also includes the medium and large carnivores. The differential defaunation pattern in terms of animal size is a central argument for our

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analysis, given our working hypothesis that mammals of different size interact with plants in different ways, including in their role as postdispersal seed predators.

THE CONCEPTUAL FRAMEWORK.—The conceptual framework underlying our analysis is based on the existence of a defaunation gradient, ranging from situations of absence or undetectable impact of humans on the mammalian community, to situations in which human impact is of such magnitude that only the mammals of no interest or value to hunters, and tolerant to habitat loss and degradation, will remain. This implies that a situation of, strictly speaking, “empty forest” (Redford 1992) or total defaunation does not occur. Such a gradient determines a predictable response of the mammalian community in terms of the size and functional role of animals that (1) will be lost from the community and (2) will remain, that is, the residual fauna left to interact with plants (seeds in this case).

We develop our argument relying on a graphical model (Fig. 1) derived from that produced by Wright (2003) in his analysis of hunter selectivity and the compensatory potential of the remaining fauna. Under conditions of no human impact, seed predators represent a considerable proportion of the total mammalian biomass. Such mammalian biomass is predominantly represented by the medium (*e.g.*, agouties, pacas, brocket deer) and large (*e.g.*, tapirs, peccaries, white-tail deer) seed predators (Janson & Emmons 1990). Small seed predators (mass ≤ 1 kg), in particular small rodents, represent a relatively small fraction of the mammalian biomass (Fig. 1A). As human impact (in terms of subsistence and commercial hunting and habitat alteration) moves toward a moderate level, the most vulnerable or preferred game, represented by the large-bodied herbivores (*e.g.*, tapirs), abruptly declines. In contrast, less preferred or vulnerable seed predators will increase due to the absence of some of their competitors (Wright 2003). This would come about, evidently, as a synergistic effect with the anthropogenically driven absence of the top predators (see Terborgh 1992 for a conceptual framework). As human impact on the habitat progresses, hunting targets on the medium herbivores and their abundance steadily declines until, in conditions of extreme defaunation, all of these predators disappear. Small rodents, instead, free of the hunters' interest and resistant to habitat loss, may remain unaffected or may even increase in their abundance. At the extreme of the defaunation gradient, mammalian biomass may be represented only by the small rodents (Fig. 1A).

We used this model to investigate the second-order effect that defaunation might have on predation patterns in the forest understory in relation to seed size. To evaluate the consequences of differential defaunation on predation we focus on plant species with contrasting seed size because of the following reasons: (1) interspecific seed size variation in tropical plants is considerable, of 5–6 orders of magnitude (Coomes & Grub 2003); (2) seed size is recognized to be positively associated with seedling performance (Foster 1986, Guzmán-Grajales & Walker 1991, Dalling *et al.* 1997), and (3) predation by large mammals (most able to deal with large seeds) has been proposed as a mechanism potentially responsible of preventing large-seeded seedlings from outperforming

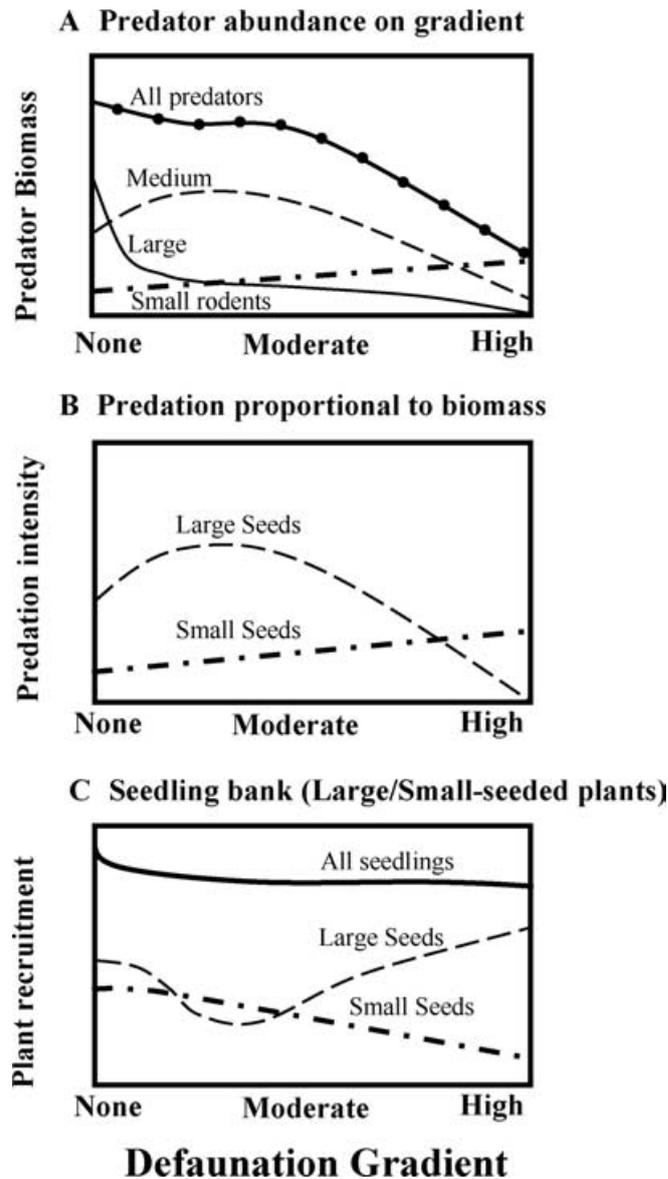


FIGURE 1. A model of the relationship between human impact and (A) abundance of mammalian seed predators of different size; (B) predation intensity assuming it is proportional to predator abundance; and (C) patterns of plant recruitment, depending on seed size. In (C) the dashed lines represent two cases of overall recruitment, reduced or increased, with respect to the intact forest situation (Modified from Wright 2003).

small-seeded seedlings in the forest floor (Grubb 1998, Mendoza 2005). While optimal foraging theory predicts that predators should consistently prefer seeds with the greatest net reward, which, other things being equal, should be the largest seeds (Harper 1977), this is likely to vary with the species of animal and, in particular with animal body size. Thus, we predict that large seed predators are more likely to (1) find and handle larger seeds (as compared to small seeds) per unit of search or foraging time; and (2) overcome defensive barriers (proximally or ultimately determined) associated

with large seed size. Small predators, in contrast, are at least equally likely to find large seeds per unit of search or foraging time, but should be more capable of finding and handling comparatively smaller seeds (with less defensive attributes). Based on the previous rationale we assume that seed predation patterns should closely follow the changes in size-related faunal composition (Fig. 1A). Thus, as anthropogenic pressure increases, predation of large seeds should first increase and then, after reaching a peak, should steadily decrease (Fig. 1B). In comparison, predation of smaller-seeded species should undergo a monotonic increase as anthropogenic pressure favoring small rodents increases (Fig. 1B). If this relationship holds, we further predict that germination and plant recruitment should be differential also: large-seeded seedlings may experience a reduction in abundance as human impact moves from the intact situation toward a situation of moderate defaunation. As human impact progresses, recruitment of large-seeded seedlings is predicted to steadily increase while recruitment of small-seeded seedlings will steadily decrease in association with the continuous increase of their rodent predators (Fig. 1C). As part of a larger study comparing forests located along contrasting positions in the defaunation gradient, in this paper we specifically focus on examining size-related seed predation patterns in a site located toward the extreme of the defaunation gradient. Specifically, we tested the expectation that differential defaunation in a heavily defaunated site will correlate with a greater predation pressure on small-seeded species, in comparison with large-seeded species. The latter should escape predation in the absence of medium and large seed predators. Furthermore, we speculate that this may lead to contrasting patterns of seed-size related germination and possibly recruitment: greater germination and recruitment of large-seeded species and lower germination and recruitment of small-seeded species. Given that seed length and weight at our study site are strongly correlated, we use the term size to refer to either weight or length.

METHODS

STUDY SITE AND A FIRST-ORDER EFFECT: DEFAUNATION.—We carried out this study in the lowland rain forest in the Los Tuxtlas Tropical Biology Field Station (LTBFS), Veracruz, in southeastern Mexico. This forest constitutes the northernmost remnant of the biome in the Americas (Dirzo & Miranda 1991b). In spite of its extreme geographical location, Los Tuxtlas originally had a rich mammalian fauna, with some 39 species of nonvolant mammals (Coates-Estrada & Estrada 1986). Beginning in the 1950s, Los Tuxtlas suffered an intense process of deforestation that significantly reduced its original area and led to the fragmentation of the remaining vegetation (Dirzo & García 1992, Mendoza *et al.* 2005). This process of deforestation has been particularly well documented for an area of 83,644 ha of land that includes the northernmost portion of the Sierra de Los Tuxtlas, as well as the LTBFS (Dirzo & García 1992, Mendoza *et al.* 2005). From the early 19th century to 2000, the forest in this area lost approximately 86 percent of its original extent (E. Mendoza, pers. obs.). The LTBFS harbors the largest remnant of lowland rain forest and, with its westerly connection to the San Martin vol-

cano, constitutes the largest forest tract (9365 ha) among the more than 1000 fragments existing within the area of study (Mendoza *et al.* 2005). The intense deforestation and fragmentation of the remaining forest has considerably increased the level of exposure of mammals to hunting. Shelters and platforms for hunting are commonly found in the area (mean 0.53 per km and 0.47 per km in 1995 and 1997, respectively). Encounters with poachers, likewise, are not uncommon (mean 0.40 per km and 0.27 per km in 1995 and 1997, respectively) (R. Dirzo, pers. obs.). As a consequence of such a level of anthropogenic perturbation, the mammalian fauna in Los Tuxtlas shows a contemporary impoverishment, particularly evident in the case of the largest mammals (Table 1). Of the 19 species of medium and large terrestrial herbivorous (of all types) mammals historically known to have occurred at Los Tuxtlas, only eight were detected in 1999 and 2001 and only five of these weighed more than 1.1 kg (Mendoza 2005). Furthermore, no sightings of the top predators have been reported in about three decades of continuous work in the LTBFS, including the jaguar and puma among the terrestrial mammals, and the harpy eagle, among the large birds. Even if not totally extinct from the area, we can hypothesize that most of the medium and large mammals are functionally extinct at the local level (Dirzo & Miranda 1991a, Mendoza 2005). In contrast,

TABLE 1. Comparison of the historic and contemporary presence of herbivore, frugivore, and granivore mammals in Los Tuxtlas. Historic occurrence is based on Coates-Estrada and Coates (1986), contemporary presence is based on Mendoza (2005). Species names follow Reid (1997).

Taxon	Weight (kg) ^a	Feeding guild ^b	Presence	
			Historic	2005
<i>Tapirus bairdii</i>	240	F, H	×	-
<i>Odocoileus virginianus</i>	34	H, G	×	-
<i>Dicotyles pecari</i>	33.5	F, H	×	-
<i>Mazama americana</i>	22	H, G	×	-
<i>Tayassu tajacu</i>	19	F, H	×	-
<i>Agouti paca</i>	8.5	F, GN	×	-
<i>Ateles geoffroyi</i>	7	F, H	×	-
<i>Alouatta palliata</i>	6.8	F, H	×	×
<i>Nasua narica</i>	4.8	F, O	×	×
<i>Procyon lotor</i>	4.5	F, O	×	×
<i>Potos flavus</i>	3.3	F, O	×	×
<i>Dasyprocta mexicana</i>	3	F, H	×	×
<i>Conepatus semistriatus</i>	2.4	F, O	×	×
<i>Didelphis</i> sp.	1.1	F, O	×	×
<i>Bassariscus sumichrasti</i>	1.1	F, O	×	-
<i>Sylvilagus</i> sp.	1	H, G	×	-
<i>Philander opossum</i>	0.8	F, O	×	-
<i>Sciurus</i> sp.	0.4	GN	×	×
<i>Caluromys derbianus</i>	0.3	F, O	×	-

^aWeights correspond to the middle point of ranges provided by (Reid 1997).

^bGuild classification follows Medellín (1994). F = frugivore, H = herbivore, G = grazer, GN = granivore, O = omnivore.

native small rodent seed predators, particularly *Heteromys desmarestianus* and *Peromyscus mexicanus* remain very common in the forest understory (Sánchez-Cordero 1993, Mendoza 2005). All available evidence regarding the residual nonvolant mammalian community in Los Tuxtlas indicates that the location of this site along the defaunation gradient depicted in Figure 1A should be toward the extreme right.

CONSEQUENCES ON SEED PREDATION.—To analyze the consequences of differential defaunation we first tested the hypothesis that small rodents will prefer small seeds under controlled conditions using the most important granivorous rodent at Los Tuxtlas, the spiny pocket mice *H. desmarestianus* (Mendoza 2005). For this experiment we collected mice from the field 1 d prior to the experiments using Sherman traps. Rodents were individually placed in laboratory cages (20 × 23 × 44 cm) and maintained on a diet of sunflower seed and water *ad libitum* until 4 h before starting the trails. For these experiments we used freshly collected seeds of 21 common woody plant species from Los Tuxtlas, ranging in size from 0.085 g (*Poulsenia armata*) to 31.5 g (*Entada gigas*) (Table 2). Mice were presented with a known mass of seeds of each of the species for a period of one night. The number of seeds presented per cage varied with species and size. Each species was presented separately using 10 independent trials (*i.e.*, one mouse in a cage representing a replicate). Experiments were carried out throughout a year, according to seed availability, which was in turn determined by natural plant phenology. This determined that, for most seed species we assayed, we used a different set of mice. On the few occasions in which more than one seed species was available, the same group of mice was used. In these cases, mice were allowed to have a 1-d rest in which they were fed with sunflower seed *ad libitum* and then starved for a standardized period as described above. Thus, we considered that in all cases mice can be treated as independent samples.

The fresh weight of each mouse and seeds offered were measured immediately prior to each trial. The seed mass remaining after each trial was measured to calculate seed mass eaten. The ratio of seed mass consumed per mice weight was calculated to account for individual variation in animal body size. Data were analyzed using a regression analysis with seed size as the independent variable and seed mass eaten per mass of mice as the dependent variable. Both variables were log transformed for the analysis. Since these experiments were designed to assess preference (rather than the consequences of predation on seed germination and recruitment) as a function of seed weight, amount of mass consumed was considered the appropriate variable to analyze. The log transformed data met the requirements of normality for the statistical analysis.

In a second experiment we tested the prediction of escape to predation of large seeds under conditions of extreme defaunation in the field, using a set of 11 species. Seeds were classified as large or small (Table 2) based on a cut-off limit of 25 mm width (5 small- and 6 large-seeded species) (see DeMattia *et al.* 2005). The smallest-seeded species among the “large” category was *Omphalea oleifera* (30 mm), and the largest among the “small” category was *Chamaedorea alternans* (15 mm). Seeds of each species were placed

TABLE 2. Species used to evaluate small rodent preferences in laboratory cages (experiment 1) and predation patterns in the field (experiment 2). Fresh weights are from Ibarra-Manríquez and Oyama (1992), with the exception of those marked with a star (*pers. obs.*). Plant nomenclature follows Ibarra-Manríquez and Sinaca (1987).

Species	Code	Weight (g)	Exp. 1	Exp. 2
<i>Entada gigas</i> * (Fabaceae)	ENGI	31.5	×	×
<i>Pouteria sapota</i> (Sapotaceae)	POSA	22.5		×
<i>Calatola laevigata</i> (Icacinaceae)	CALA	9.7		×
<i>Omphalea oleifera</i> (Euphorbiaceae)	OMOL	5.15	×	×
<i>Astrocaryum mexicanum</i> (Arecaceae)	ASME	5.05	×	
<i>Rheedia edulis</i> (Guttiferae)	RHED	3.3	×	×
<i>Salacia megistophylla</i> * (Hippocrateaceae)	SAME	2.51	×	×
<i>Couepia polyandra</i> (Chrysobalanaceae)	COPO	2.1	×	
<i>Spondias radlkoferi</i> (Anacardiaceae)	SPRA	1.93	×	
<i>Nectandra ambigens</i> (Lauraceae)	NEAM	1.8	×	
<i>Diospyros digyna</i> (Ebenaceae)	DIDI	1.1	×	
<i>Quararibea funebris</i> (Bombacaceae)	QUFU	0.92	×	
<i>Brosimum alicastrum</i> (Moraceae)	BRAL	0.91	×	
<i>Pseudolmedia oxyphyllaria</i> * (Moraceae)	PSOX	0.86	×	
<i>Clarisia biflora</i> (Moraceae)	CLBI	0.69	×	
<i>Ampelocera hottlei</i> (Ulmaceae)	AMHO	0.67	×	
<i>Dipholis minutiflora</i> (Sapotaceae)	DIMI	0.56	×	
<i>Reinhardtia gracilis</i> (Arecaceae)	REGR	0.23	×	
<i>Chamaedorea alternans</i> * (Arecaceae)	CHAL	0.2	×	×
<i>Sp 1</i> (Sapindaceae)*	SASP	0.15	×	
<i>Hampea nutricia</i> (Malvaceae)	HANU	0.11	×	×
<i>Chamaedorea pinatifrons</i> * (Arecaceae)	CHPI	0.1	×	×
<i>Poulsenia armata</i> (Moraceae)	POAR	0.085	×	×
<i>Eugenia mexicana</i> (Myrtaceae)	EUME	NA		×

on the forest floor in two treatments: (1) free access to mammals and (2) mammal enclosure (chicken wire cages 40 × 40 × 40 cm); the enclosures had the four sides buried into the ground (*ca* 5 cm) and featured a roof as well. There were 15 replicates of each treatment per species, with 20 seeds for the small size category and 10 for the large size category. Seed clusters of each of the two treatments (caged, control) were randomly assigned to points within a 5 × 5 m grid encompassing an area of 600 m². The experiments were run at different times, determined by the natural phenology of the species. Experimental set-ups were visited daily for those species with rapid germination (*e.g.*, *O. oleifera*, *Poulsenia armata*) or weekly for species with slow germination (*e.g.*, *Pouteria sapota*) and monthly in the case of species that took several months to germinate (*e.g.*, *Calatola laevigata*). The experiments were terminated when all seeds germinated, were removed, or died *in situ*. We analyzed the effect of treatment on the proportion of seeds removed (using average removal per species per treatment as replicates) with a two-way ANOVA (factor 1 = caged treatment, factor 2 = seed size). The proportion of seeds removed was transformed using Box–Cox’s best

transformation (Sokal & Rohlf 2003) to improve agreement with the assumptions of ANOVA. The percentage of germinated seeds was analyzed in the same way. As indicated, seed length and weight are strongly correlated (E. Mendoza and R. Dirzo, pers. obs.), and we use the term size to refer to either weight or length.

RESULTS

SEED PREDATION IN LABORATORY CAGES.—There was a significant negative relationship between seed consumption and seed weight ($F = 12.83$; $P = 0.002$). The results (Fig. 2) show a clear trend of seed consumption as a function of seed weight: the lightest seeds were increasingly preferred relative to the heaviest seeds. However, the proportion of explained variance in seed consumption was moderate ($R^2 = 0.40$). We observed that the attack of mice on the seeds varied depending on the species. In general, light and palatable seeds were consumed entirely while intermediate or heavy and unpalatable seeds were eaten only partly. This result lends support to the expectation that, in the field, given the absence of medium and large seed predators, and the abundance of small rodents, seed predation would be greater on the lighter (smaller) seeds.

SEED REMOVAL IN THE FOREST FLOOR.—A significant effect of treatment ($F = 160.72$, $P < 0.001$), size ($F = 142.52$, $P < 0.001$), and the interaction term ($F = 111.87$, $P < 0.001$) were found for the seed removal experiment (Fig. 3). In the case of the small seeds (Fig. 3A), those protected by cages showed low levels (2%) of predation. In contrast, unprotected small seeds experienced a dramatic risk of predation, with cumulative levels that ranged from 50 (*Eugenia mexicana*) to 80 percent (*Chamaedorea pinnatifrons*). On average, in comparison with protected small seeds, exposing those same seeds to natural predation brought about a risk of predation that was ca. 30 times greater (Fig. 3C). In the case of the large-seeded species (Fig. 3B), overall levels of predation were very low, 2.3 percent on

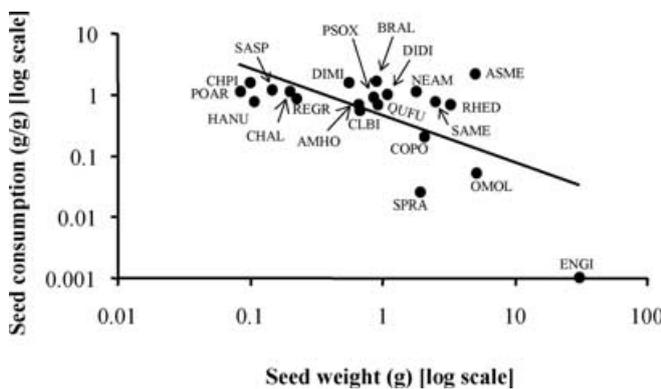


FIGURE 2. The relationship between seed size and small rodent (*H. desmarestianus*) consumption under laboratory conditions in Los Tuxtlas ($R^2 = 0.40$, $P = 0.002$). Seed consumption was measured as mass of seed per mass of mice. Code names for all the species are given in Table 2.

average. The single largest proportion of predation observed was only 9.5 percent and corresponded to the exposed seeds of *Salacia megistophylla*. This was followed by the exposed seeds of *Rheedia edulis*, which had a value of 5 percent. The rest of the seeds experienced consistently lower levels of predation ($< 1.5\%$). Although protection of the large seeds meant some degree of reduction of the level of predation in all species, the overall contrast between treatments (3.5 vs. 1.5%) was only 2.3-fold (Fig. 3C), considerably lower than that observed in the case of the small-seeded species, as reflected by the high significance of the interaction term.

For the set of species common to the two experiments (see Table 2) we calculated a Spearman rank correlation coefficient for the relationship between acceptability (consumption rank in the laboratory cages) and predation in the field (rank of percentage removal in control plots). This yielded a positive and significant

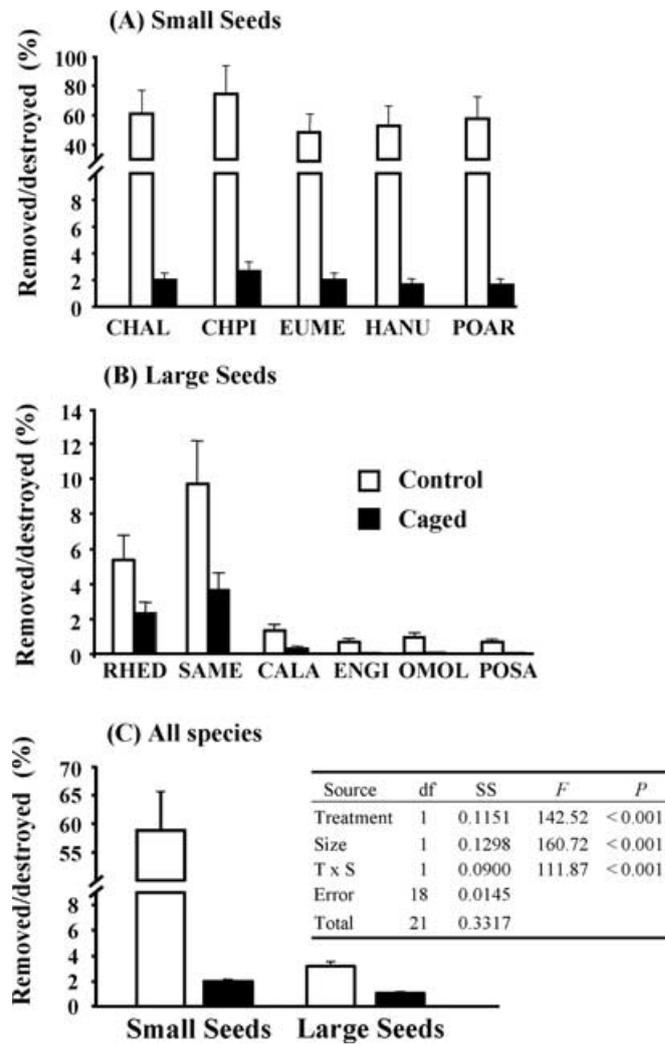


FIGURE 3. Seed predation of a sample of species of contrasting size (Large, Small) from Los Tuxtlas, under two treatments of exposure to predators (Caged, Control) in the field. Data represent means \pm SE. Code names for all the species are in Table 2.

relationship ($r_s = 0.93$, $P = 0.0009$, $N = 8$ species). This suggests that the *Heteromys* rodents used in the laboratory choice experiments are likely to be relevant seed predators under field conditions.

SEED GERMINATION.— The seed predation experiment was extended to observe germination of the surviving seeds. We found a significant effect of treatment ($F = 17.64$, $P < 0.001$). The interaction term was also highly significant ($F = 16.42$, $P < 0.001$), but size was not ($F = 3.72$, $P = 0.07$). In the small-seeded species (Fig. 4A) germination was consistently low in the exposed seeds, largely as a result of the intense predation in this treatment. The protected seeds had germination values that ranged between 15 and 35 percent. Overall (Fig. 4C), the protected seeds had a relatively high germination value, of 21 percent, which was four times greater than that of the exposed seeds. It appears that recruitment of these species is strongly constrained by predation.

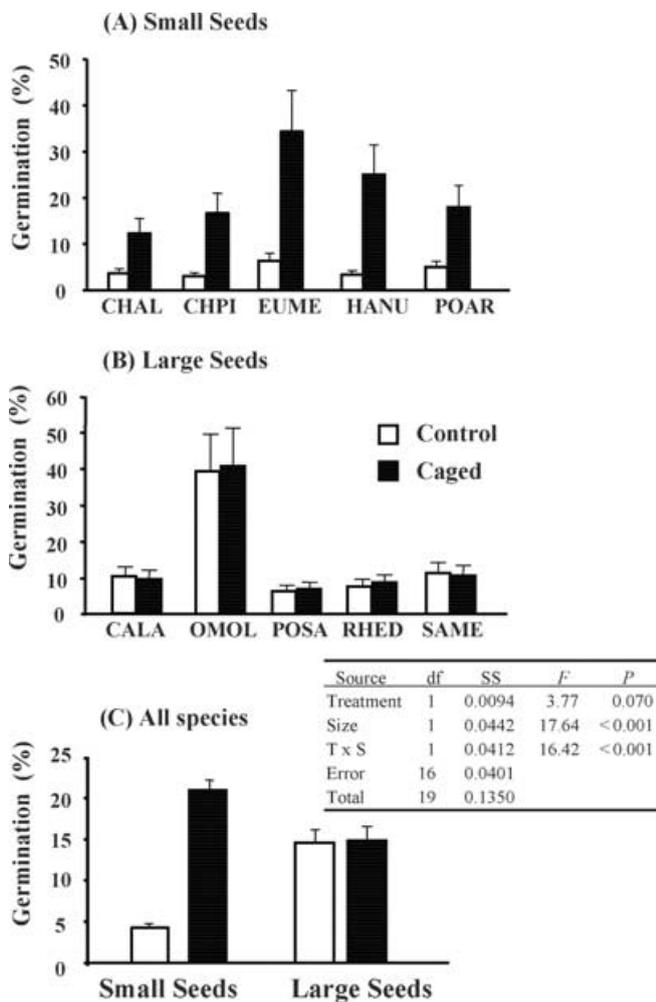


FIGURE 4. Germination of a sample of species of contrasting size (Large, Small) from Los Tuxtlas, under two treatments of exposure to predators (Caged, Control) in the field. Data represent means \pm SE. Code names for all the species are in Table 2.

Germination of the large-seeded species (Fig. 4B) was consistent among species, except in the case of *O. oleifera*, which exhibited a considerably higher germination, around 40 percent, regardless of treatment. In great contrast to the small-seeded species, overall germination of the large-seeded species was indistinguishable among treatments (Fig. 4C), with a mean value of 15 percent, as reflected by the highly significant effect of the interaction term. The high germination observed in the small protected seeds compensates for the low germination of the exposed seeds, reaching an overall mean that is statistically indistinguishable from the germination of the large seeds.

DISCUSSION

The current pace of human disturbance in tropical ecosystems has brought about a significant negative impact on the mammalian communities of these forests. Los Tuxtlas is no exception to this phenomenon and represents a site located toward the extreme of the gradient of defaunation depicted in the graphical model underlying the present study. Consistent with the expectations derived from the documented differential defaunation of Los Tuxtlas (Dirzo & Miranda 1991a, Mendoza 2005), we found associated patterns of seed predation in relation to seed size, which in turn led to contrasting germination as a function of seed size. These relationships were consistent with the predictions derived from our model. It is interesting to note that the great contrast observed in overall seed predation of small versus large seeds (*ca* 10 times) is greater than that observed in germination (*ca* 3 times). A host of environmental variables might be responsible for such a “dilution” of the predation contrast, including pathogen attack (Bell *et al.* 2006), physical impact of materials falling from the canopy (Clark & Clark 1989), herbivory (Coley & Barone 1996), etc. Therefore, we speculate that the patterns we uncovered in this study may explain, at least in part, the impoverished diversity of the understory vegetation that characterizes Los Tuxtlas (Dirzo & Miranda 1991a).

Our experimental results with caged animals are consistent with other studies showing a preference of relatively small seeds by small rodents in rain forest sites. The selectivity we observed with *H. desmarestianus* is similar to that observed using similar trials with small rodents from an Indonesian rain forest: caged spiny rats preferred smaller-sized seeds over large seeds (Blate *et al.* 1998). In a more controlled series of experiments, pairs of phylogenetically controlled species (same family or genus) with contrasting seed size (large vs. small), were offered to individual mice of *H. desmarestianus* (Mendoza 2005). In both these studies the selectivity observed under controlled conditions was also reflected in the intensity of predation under natural conditions in the field: in both cases predation rates in the field were negatively associated with seed size.

The results of the Mexican and the Indonesian forests are not consistent with Optimal Foraging Theory (Charnov 1976). This inconsistency may be explained by the fact that optimal foraging can be obscured by attributes such as handling time (which in turn

may expose small predators to their own predators) and theoretical expectations may be applicable only within a given animal size-range, even within the group of small rodents. For example, Adler (1995) found a significant rodent preference for large seeds, but this may be explained by the fact that his study involved the much larger spiny rat (*Proechymis semispinosus*). Therefore, we speculate that the identity of the remaining small rodent fauna in heavily defaunated forests will determine the patterns of seed predation: the smaller the residual rodents, the greater the intensity of predation on smaller seeds.

Despite the fact that we did not implement a protocol to document the identity of animals visiting our experimental seeds in the field, we believe the strong correlation between consumption in laboratory cages and the patterns of seed removal in the understory make it reasonable to assume that the main predators were small rodents. During the routine recordings of our experimental seeds bird predation was not readily evident, but studies in other sites have found seed predation by birds to be important (see Pizo & Vieira 2004). This is an aspect that warrants further investigation at Los Tuxtlas. In addition, the range of seed sizes we used is beyond that typically observed in the case of removal by granivorous ants. On the other hand, it is possible that some of the removal we recorded might have been secondary dispersal of the small seeds by the abundant, cheek-pouched, *H. desmarestianus*, but we have observed that many of the seeds scattered by this mouse do not successfully germinate (R. Dirzo, pers. obs.). Again, this is an aspect that warrants further clarification.

Our results suggest that small rodents in heavily defaunated sites may not necessarily compensate for the lack of the medium and large seed predators. The possibility of compensatory seed predation by insects needs to be investigated, but available information suggests that in the absence of mammalian seed predators, insect seed predation cannot fully compensate for predation by mammals (Wright & Duber 2001). The importance of studying rodent–plant interactions and their interplay with predation by invertebrates in understories can hardly be overemphasized, given the expected prevalence these interactions will have in the increasingly fragmented, hunted and otherwise disturbed tropical forests.

Beyond changes in seed predation and germination in defaunated understories, we can speculate about the possible consequences on the recruitment and eventual composition of the understory seedling banks along the gradient of human impact (see Fig. 1C). As human impact progresses, recruitment of large-seeded seedlings is predicted to steadily increase while recruitment of small-seeded seedlings will steadily decrease in association to the continuous increase of their rodent predators. Eventually, the contrasting trajectories of recruitment of the small-seeded and the large-seeded plants, may lead, under conditions of extreme human impact, to seedling communities dominated by large-seeded plants, with an underrepresentation of the small-seeded plants, as compared to the intact forest understory. The overall seedling bank is predicted to take a variety of responses depending on a host of complex interactions, both among plants and with the residual fauna, including the phytophagous insects present in the defaunated understory (see Dirzo 2001). Conceivably, the overall seedling bank can experience

responses that range from a net reduction to a net increase (as depicted in Fig. 1C), but this remains largely unexplored. Evidence from previous work shows some consistent tendencies with these speculations (Dirzo & Miranda 1991a). For example, in contrast to an intact forest at Montes Azules, Chiapas (see Mendoza 2005), the understory of the defaunated understory at LT is characterized by seedling banks with overall lower seedling diversity and in which one or a few species dominate. At Los Tuxtlas such dominance is typically achieved by large-seeded species such as *Astrocaryum mexicanum*, *O. oleifera*, *Nectandra ambigens*, and *S. megistophylla*. In addition, seedling density is significantly higher in the heavily defaunated site, as compared to the intact forest. A similar pattern of increased representation of large-seeded seedlings in other defaunated understories is reported by Wright *et al.* (2007). The fact that *A. mexicanum* was one of the most palatable seed species and yet is one of the species that dominates the understory as seedlings and saplings may be related to the absence of herbivores such as peccaries, tapirs, and deer that might otherwise reduce its abundance. Peccaries are known to be an important seed predator of *A. murumuru* (Beck & Terborgh 2002) and peccaries, together with tapirs and deer, may have an important impact on seedlings and saplings due to herbivory and trampling. This apparent paradox however, requires further investigation.

To what extent can we extrapolate from the sort of results reported here? We suggest that the position of a given site along the defaunation gradient is a critical determinant of how plant–mammal interactions will play out. The identity of the residual fauna is likely to determine the potential for compensatory response (see Wright 2003) and may be a driver of the variance in the outcomes from the few available studies in different sites (Terborgh & Wright 1994, Adler 1995, Asquith *et al.* 1997). All of the above underscores the need for longer-term studies, in a variety of sites, preferably located in different positions along the defaunation gradient, and the need for adoption of comparable methodologies among sites and research groups. We suggest that undertaking such a comprehensive research agenda would be extremely valuable to our understanding of the ecology of plant–mammal interactions and to gain insights about the importance of mammalian defaunation for conservation, management and restoration of tropical forests.

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