SEED PREDATION BY NEOTROPICAL RAIN FOREST MAMMALS INCREASES DIVERSITY IN SEEDLING RECRUITMENT

C. E. TIMOTHY PAINE1,3 AND HARALD BECK2

1Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA
2Department of Biological Sciences, Towson University, Towson, Maryland 21252 USA

Abstract. Seed dispersal and seedling recruitment (the transition of seeds to seedlings) set the spatiotemporal distribution of new individuals in plant communities. Many terrestrial rain forest mammals consume post-dispersal seeds and seedlings, often inflicting density-dependent mortality. In part because of density-dependent mortality, diversity often increases during seedling recruitment, making it a critical stage for species coexistence. We determined how mammalian predators, adult tree abundance, and seed mass interact to affect seedling recruitment in a western Amazonian rain forest. We used exclosures that were selectively permeable to three size classes of mammals: mice and spiny rats (weighing <1 kg), medium-sized rodents (1–12 kg), and large mammals (20–200 kg). Into each exclosure, we placed seeds of 13 tree species and one canopy liana, which varied by an order of magnitude in adult abundance and seed mass. We followed the fates of the seeds and resulting seedlings for at least 17 months. We assessed the effect of each mammalian size class on seed survival, seedling survival and growth, and the density and diversity of the seedlings that survived to the end of the experiment. Surprisingly, large mammals had no detectable effect at any stage of seedling recruitment. In contrast, small- and medium-sized mammals significantly reduced seed survival, seedling survival, and seedling density. Furthermore, predation by small mammals increased species richness on a per-stem basis. This increase in diversity resulted from their disproportionately intense predation on common species and large-seeded species. Small mammals thereby generated a rare-species advantage in seedling recruitment, the critical ingredient for frequency dependence. Predation by small (and to a lesser extent, medium-sized) mammals on seeds and seedlings significantly increases tree species diversity in tropical forests. This is the first long-term study to dissect the effects of various mammalian predators on the recruitment of a diverse set of tree species.

Key words: density dependence; maintenance of biodiversity; Manu National Park, Peru; seed dispersal; seed predation; seedling recruitment; Tayassu peccari; tropical rain forest.

INTRODUCTION

The vast majority of seeds that fall in forest understories fail to recruit as seedlings. Mortality rates during seedling recruitment (the seed to seedling transition) are greater than at any other life stage (Muller-Landau et al. 2004). This mortality tends to be negatively frequency dependent, which increases the diversity of the seedling layer (Webb and Peart 1999, Harms et al. 2000, Hille Ris Lambers et al. 2002). The filters that limit seedling recruitment thus contribute to species coexistence. It is therefore essential to study the causes of seed and seedling mortality to understand the processes that maintain forest diversity. However, the agents of mortality are rarely identified because the death of an individual seed or seedling is unlikely to be observed through sampling. For these reasons, our understanding of the mechanisms that contribute to seed and seedling mortality in forests remains incomplete.

Terrestrial mammals affect all stages of seedling recruitment. Many terrestrial mammals are predators of seeds and seedlings, and predation can dramatically affect patterns of seedling recruitment (Terborgh et al. 1993, Ostfeld et al. 1997, Notman and Gorchov 2001, Silman et al. 2003, DeMattia et al. 2004). Terrestrial mammals also disperse seeds (e.g., Brewer 2001) and trample seedlings (Clark and Clark 1989). Nevertheless, following Beckage and Clark (2005), we refer to terrestrial mammals as predators of seeds and seedlings, understanding that their effects on seedling recruitment encompass various processes. Mammals consume more seeds than do invertebrates (Holl and Lulow 1997, Notman and Gorchov 2001), and small mammals may consume more seeds than large mammals (DeMattia et al. 2004). Excluding terrestrial mammals can increase seedling recruitment and survival (Ostfeld et al. 1997, Connell et al. 2005), change seedling community composition (DeMattia et al. 2006), and increase seedling growth rates (Wahungu et al. 2002). Nevertheless, many studies of mammalian predation on seeds and seedlings have been of short duration (<6 months; Holl and Lulow 1997, Notman and Gorchov 2001, Wahungu...
et al. 2002), or focused on few species (≤3 species; Asquith et al. 1997, Connell et al. 2005, Norghauer et al. 2006), limiting their scope for inference.

Among trees, two axes of variation that may interact with mammalian predation to affect seedling recruitment are population density and seed mass. An inverse relationship between population density and the recruitment, survival, or growth of conspecifics constitutes negative frequency dependence, which is common in tropical and temperate forests (Webb and Peart 1999, Harms et al. 2000, Hille Ris Lambers et al. 2002, Peters 2003, Uriarte et al. 2005). Recruitment rates that are greater for rare species than for common species would indicate a rare-species advantage, the critical factor to generate frequency dependence (Connell 1978). We use “frequency dependent” to indicate a relationship with the abundance of conspecific adult trees, rather than with seed or seedling density. Studies focused on one or a few species indicate that predator aggregation, rather than resource competition, is likely to be the primary mechanism causing frequency dependence (Augspurger 1984, Blundell and Peart 1998). However, the processes that generate frequency dependence have rarely been elucidated at the community level.

The per capita likelihood of seedling recruitment increases with increasing seed size (Moles and Westoby 2004), but with their greater fecundity, seeds of small-seeded species may arrive at a more diverse set of microsites than those of large-seeded species. Large-seededness reduces susceptibility to biotic and abiotic hazards like deep shade or leaf litter (Molofsky and Augspurger 1992, Saverimuttu and Westoby 1996). However, large-seeded species may be more susceptible to predation because, all else being equal, foragers can maximize their energetic return by preferentially consuming large food items (Schoener 1971, Brewer 2001, Augspurger 1992, Saverimuttu and Westoby 1996). The advantages that accrue to large-seeded species during seedling recruitment are strong, but may dissipate rapidly if predation is intense (Moles and Westoby 2004).

**Objectives**

Our primary objective was to determine how terrestrial mammalian predation, adult abundance, seed mass, and their interactions affect seedling recruitment and contribute to species coexistence. We tested their effects on all stages of seedling recruitment: the survival of seeds, the survival and growth of seedlings, and the density and diversity of recruited seedlings.

First, we determined whether groups of terrestrial mammals differ in their predation rates. In particular, we asked whether the biomass or abundance of each of three size classes of mammals better explains the variance in each stage of seedling recruitment. Second, we determined the effects of adult abundance and seed mass on each stage of seedling recruitment. Third, we determined the strength of the interactions between mammalian predation and seed mass, and between predation and adult abundance, during each stage of seedling recruitment. Our overall goal was to understand how predation during seedling recruitment affects the diversity of the seedling layer.

**Methods**

**Study site and species**

This study was conducted at Estación Biológica Cocha Cashu (EBCC) in Peru’s two million hectare Manu National Park (~1°S, 71°W, ~350 m elevation; see site descriptions in Terborgh [1983, 1990]). The forest-covered floodplain of the Manu River is extremely diverse, with almost 350 species of trees that attain a diameter of 10 cm at breast height (Foster 1990). The site is characterized as Tropical Moist Forest (Holdridge 1947). Average annual precipitation is 2200 mm, falling mainly between October and April.

EBCC is one of few sites worldwide where diverse communities of terrestrial mammals remain intact and accessible for study. The vastness and physical isolation of Manu National Park has facilitated the preservation of EBCC’s mammal community (Terborgh 1999). It is thus an ideal location to detail the varied effects of terrestrial mammals on seeds and seedlings. We divide the terrestrial mammal community into three size classes. Small mammals, with body mass < 1 kg, include mice (Muridae) and spiny rats (Echimyidae). Medium-sized mammals (1–12 kg) are caviomorph rodents and include green acouchis, pacas, and agoutis (Myoprocta spp., Agouti paca, and Dasyprocta variegata, respectively). Large mammals (>20 kg) are predominantly peccaries (Pecari tajacu and Tayassu pecari, Tayassuidae; see Plate 1), but also include deer (mostly Mazama spp, Cervidae) and tapirs (Tapirus terrestris, Tapiridae). Tapirs and both species of peccaries that occur at EBCC are threatened with extinction, listed in CITES Appendix II. Seeds and fruit form an important component of the diet of all three size classes (Beck-King et al. 1999, Vieira et al. 2003, Beck 2005).

Seeds were included in the exclosure experiment based upon three criteria. First, fruit had to be single-seeded and the seeds had to be sufficiently large to be easily cleaned, sown, and monitored in the field. Second, fruit needed to be available during the two periods of placement of seeds into the exclosures, I (April–June 2004) and II (February 2005). Third, fruiting adults had to be sufficiently common and fecund to provide 400 seeds for placement in the exclosures. These criteria yielded 14 species, representing 12 families, all of which are primarily dispersed by mammals (Foster and Janson 1985) including 11 trees, two palms, and one liana (Sparattanthelium tarapotanum Hernandiaceae), which remains free-standing until reaching at least 3 m in height (C. E. T. Paine, personal observation). All species reach the canopy as adults. Adult abundance was determined in three permanent plots totaling 10.25 ha in the EBCC trail system (J. Terborgh, unpublished data). These plots were representative of mature
Table 1. Details of species sown in mammal exclosures, sorted by family.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Period</th>
<th>Adult density (no./ha)</th>
<th>Seed mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annonaceae</td>
<td>Duguetia quitarensis Benth.</td>
<td>I</td>
<td>3.60</td>
<td>0.4 ± 0.07 (9)</td>
</tr>
<tr>
<td>Areaceae</td>
<td>Iriartea deltoidea Ruiz &amp; Pav.</td>
<td>I</td>
<td>32.30</td>
<td>3.9 ± 0.4 (10)</td>
</tr>
<tr>
<td>Socratea exorrhiza (Mart.) H. Wendl.</td>
<td></td>
<td>I</td>
<td>0.08</td>
<td>3.4 ± 0.6 (10)</td>
</tr>
<tr>
<td>Clusiaceae</td>
<td>Calophyllum brasiliense Cambess.</td>
<td></td>
<td>I</td>
<td>0.38</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>Buchenavia grandis Ducl.</td>
<td>I</td>
<td>0.17</td>
<td>1.9 ± 0.5 (20)</td>
</tr>
<tr>
<td>Ebenaceae</td>
<td>Diospyros parviflora (A. DC.) J.F. Macbr.</td>
<td>I</td>
<td>0.17</td>
<td>0.6 ± 0.1 (84)</td>
</tr>
<tr>
<td>Ebenaceae</td>
<td>Diospyros subtorta Hier.</td>
<td>I</td>
<td>2.33</td>
<td>0.8 ± 0.1 (37)</td>
</tr>
<tr>
<td>Flacourtiaceae</td>
<td>Casearia sp. nov.</td>
<td>II</td>
<td>0.17</td>
<td>0.6 ± 0.1 (25)</td>
</tr>
<tr>
<td>Hernandiaceae</td>
<td>Sparattanthelium tarapotanum Mein.</td>
<td>II</td>
<td>−0.03</td>
<td>0.5 ± 0.1 (26)</td>
</tr>
<tr>
<td>Moraceae</td>
<td>Clarisia racemosa Ruiz &amp; Pav.</td>
<td>II</td>
<td>3.80</td>
<td>1.8 ± 0.9 (25)</td>
</tr>
<tr>
<td>Myristicaceae</td>
<td>Otoba parvifolia (Markgr.) A.H. Gentry</td>
<td>II</td>
<td>37.30</td>
<td>1.8 ± 0.2 (25)</td>
</tr>
<tr>
<td>Olacaceae</td>
<td>Heisteria nitida Engl.</td>
<td>I</td>
<td>0.25</td>
<td>0.2 ± 0.04 (5)</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Genipa americana L.</td>
<td>II</td>
<td>0.94</td>
<td>0.05 ± 0.004 (25)</td>
</tr>
<tr>
<td>Verbenaceae</td>
<td>Vitex cymosa Bertero ex Spreng.</td>
<td>II</td>
<td>0.40</td>
<td>0.5 ± 0.2 (25)</td>
</tr>
</tbody>
</table>

Notes: All species are canopy trees, except Sparattanthelium tarapotanum, a canopy liana, which is not censused in the EBCC (Estación Biológica Cocha Cashu, Peru) tree plots. Extensive cruising has shown it to be very rare (C. E. T. Paine, personal observation). Seeds were sown in two periods (I, II), in 2004 and 2005. Seed masses are given as mean ± SD, with sample size in parentheses.

floodplain forest, and were interspersed with the locations of exclosures. Adult abundance of the 14 focal species ranged from 0.08 to 37 adults/ha (median = 0.94 adults/ha), encompassing the entire range of adult abundances observed among canopy trees in this forest. Our use of the descriptors “common” and “rare” refers only to local conspecific abundance of adults, rather than to seed or seedling density. Seed mass of the 14 species ranged from 0.05 to 3.9 g (median = 1.8 g). Adult abundance and seed mass were not significantly correlated among the 14 species used in this experiment ($R^2 = 0.09$, $P = 0.31$). Species names and distinguishing characteristics are presented in Table 1.

Experimental design

To determine the individual effects of small, medium, and large mammals, we used exclosures, differing only in their permeability to each size class, that were designed and built by H. Beck and J. Terborgh (unpublished manuscript) for an earlier study. One year after that study was completed, we reinforced the existing enclosures for the current study. The 40 exclosures were established in eight randomly located blocks in an area of 3 km$^2$ of mature lowland rain forest at EBCC. The mean distance between blocks was 1.1 km (minimum distance between blocks = 250 m). Within each block, we located five 2 × 2 m exclosure cages, one of each of five types, 20 m apart along a randomly oriented transect.

The five types of exclosures were designed to preclude or permit the entry of small, medium, or large mammals (Fig. 1). The name of each enclosure indicates the size class of mammals that was permitted access. NONE exclosures were 90 cm tall wire hardware cloth (mesh size 1 cm), reinforced with 8 mm diameter rebar at the corners and the middle of each side. No terrestrial mammals could enter NONE exclosures. SMALL exclosures were identical to NONE, with the exception that 7 × 7 cm holes were cut in the bottom edge of the walls. SMALL exclosures permitted the entry of small mammals, while precluding the entry of medium and large mammals. MEDIUM–LARGE exclosures consisted of 20 cm tall walls of sheet metal meshing that small mammals were unable to climb over. Medium and large mammals could, in contrast, step over the meshing to enter the enclosure. MEDIUM combined the sheet metal of MEDIUM–LARGE with a wrapping of barbed wire between 45 and 90 cm high. The sheet metal barred the entry of small mammals, and the barbed wire barred the entry of large mammals. Only medium-sized mammals had access to MEDIUM exclosures. Finally, ALL treatments were marked with rebar at the four corners, permitting the entry of mammals of all three size classes. The walls of all exclosures (except ALL) were dug 5 cm into the soil to prevent the entry of burrowing mammals. No evidence of burrowing mammals was detected for the duration of the experiment. All exclosures had open tops, which facilitated monitoring and allowed the entry of granivorous birds, such as wood-quail (Odontophorus spp.) and cracids (Cracidae), and arboreal mammalian granivores, such as squirrels (Sciuridae). All exclosures were likewise accessible to invertebrates and microbial pathogens.

We prepared seeds for placement as fruit matured. We collected freshly fallen fruit from at least five adult trees located throughout the 12-km$^2$ area of the EBCC trail system, thereby controlling for genetic and environmental factors. Fruit pulp was removed manually by methods that varied among species. As necessary, seeds were washed or scrubbed to remove pulp and then air-dried. Seeds that bore any sign of insect or fungal damage, such as exit holes or visible hyphae, were discarded. Seeds of non-floating species were subjected to a flotation test: any floating seed was discarded. Seeds were stored in cotton bags in ambient humidity for fewer than seven days prior to placement.
We placed seeds in exclosures as follows. Conspecific seeds were laid in groups of 10 on top of the leaf litter in each exclosure (400 seeds/species, in total). The density and clumping of seeds that we placed into exclosures thus mimicked those naturally dispersed by frugivorous monkeys (Russo 2005), although our seed groups were placed without feces. Groups were placed in the corners and the middle of each side of each exclosure at least 25 cm from the exclosure walls, so that mammals outside the exclosure could not disturb the seeds. The conspecific groupings were unlikely to affect seed removal rates (Notman et al. 1996), and facilitated repeated monitoring. The locations of conspecific seed groupings were marked with colored plastic toothpicks, but the seeds themselves were not individually marked.

Seeds, and as they germinated, seedlings, were monitored repeatedly. Eight species were monitored for 790 days (12 censuses; Period I), whereas the remaining six species were monitored for 509 days (six censuses; Period II). Intervals between censuses lengthened over the course of the experiment from an initial interval of two weeks to a final interval of six months. At each census, all remaining seeds were scored as alive, germinated, or missing. We use seed removal as a proxy for mortality, given the uncertainty in the precise fate of missing seeds (Vander Wall et al. 2005). We thus scored missing seeds as dead, whereas intact or slightly damaged seeds were scored as alive. Seeds that were gravely damaged, e.g., engulfed by fungal hyphae, were scored as dead. At each census, we searched for missing seeds and maintained the exclosures to ensure their ongoing effectiveness. Leaf litter disturbed during a census was replaced. Because seeds were placed in small groups, it was easy to distinguish and exclude naturally dispersed seeds. Finally, at each census, we marked seedlings individually as they germinated, and measured the height of their apical meristems.

Data analysis

Seed survival was estimated in two ways: the total number of seedlings observed to germinate per 10-seed grouping, and the median time to seed removal. The total number of seedlings observed provides a minimal estimate of the fraction of placed seeds that survived to germination. Because seeds were placed in exclosures in groups of 10, the time to median seed removal can be interpreted as an estimate of the survival time of an average seed. For most 10-seed groups (557 of 560), no seeds remained viable at the end of the experiment, and the time to median seed removal could be calculated empirically (nonparametrically). In each of the remaining three groups, one seed remained alive at the termination of the experiment. In these cases, Weibull survival functions were used to estimate median survival times (Klein and Moeschberger 1997).

We evaluated seedling performance with two response variables: survival and relative growth rate. Post-germination seedling survival was calculated as the density of recruited seedlings divided by the total number of seedlings observed to germinate. We defined a seedling to have recruited if it lived 509 days after sowing (the maximum time observed on both Period I and Period II species). Mean height relative growth rate (RGR<sub>ht</sub>) was calculated for each individual seedling observed alive more than once over the course of the experiment, excluding those (n = 3 individuals) crushed under falling debris. RGR<sub>ht</sub> was calculated as <sup>\[
\frac{\ln(h_{t+1}) - \ln(h_t)}{T}
\]
where h is the individual’s height in centimeters at times t and t + 1, and T is time in days (Hoffmann and Poorter 2002). Individual RGR<sub>ht</sub> was
averaged over each conspecific seed group. Seedling performance data were unbalanced because of the differences in seedling germination across species and treatments, but the statistical models used were robust to unbalanced data (Littell et al. 2002).

Finally, we evaluated seedling density and species richness, which we report as the number of seedlings and species alive in each exclosure at 509 days. Exclosures in which many seedlings recruited were speciose, resulting in a significant positive relationship between seedling density and species richness (\( r = 0.93, F_{1,38} = 274.2, P < 0.0001 \)). We therefore use species richness per stem as a metric of diversity because it controls for differences in stem density among exclosures (Hubbell et al. 1999).

Our true interests in this analysis regarded the effects of each size class of mammals as predators, rather than overall treatment effects. We used a priori orthogonal contrasts (\( df = 1 \)) to test the separate effects of small, medium, and large mammals on each stage of seedling recruitment. The impact of each mammal size class was determined by contrasting each response variable between exclosure treatments that differed only in their permeability to that size class. Accordingly, we contrasted NONE vs. SMALL exclosures to estimate the effect of small mammals, NONE vs. MEDIUM for medium mammals, and MEDIUM vs. MEDIUM–LARGE for large mammals. Finally, we used linear mixed models to determine the effects of adult abundance and seed mass, and their interactions with each mammal size class, on each stage of seedling recruitment.

We evaluated the relationships between each aspect of seedling recruitment and treatments, species, and blocks in a split-plot design. Within blocks, treatment was the main-plot effect and species was the subplot effect. An examination of residual plots revealed heteroscedasticity in time to median seed removal and species richness per stem, which was adequately resolved with a log transformation. Other variables conformed to the assumption of homogeneous variance. Transformed variables were back-transformed for plotting. Analyses were performed in SAS 9.1 (SAS Institute 2005).

**RESULTS**

Mammalian predators strongly reduced seed and seedling survival. The number of seeds surviving plus seedlings germinated was consistently greater in exclosures from which all terrestrial mammals were excluded (NONE) than in exclosures open to all mammals (ALL; Fig. 2). Survival rates in each treatment were rank-concordant between periods, indicating that the pattern of seed survival among exclosures was robust to changes in species composition. As an example using Period I species, as of November 2004, 200 days after sowing, the number of seeds plus seedlings in NONE exclosures was 18 times greater than in ALL exclosures. Mortality was substantial, even in NONE exclosures (45% through 200 days), indicating that many seeds succumb to the combined attacks of pathogens, invertebrates, arboreal mammals, and granivorous birds. Nevertheless, survival differed widely among exclosure treatments, indicating that mammalian predation explained a substantial fraction of seed and seedling mortality.

Exclosure treatment, seed species, and their interaction had significant effects on time to median seed removal, seed survival, and recruited seedling density (Table 2). Seedling survival differed significantly among treatments and species, whereas \( RGR_{ht} \) differed only among species. Data on seedling growth and survival
were unbalanced enough to preclude estimation of treatment \times species interactions. On a per-stem basis, i.e., after normalizing for stem density, treatments differed significantly in the species richness of recruited seedlings.

Size classes of mammals differed in the strength of their effects on seed survival and seedling performance (Fig. 3). Large mammals had no significant effect on any stage of seedling recruitment. In contrast, the exclusion of small- and medium-sized mammals significantly increased the time to median seed removal, seed survival, and post-germination seedling survival. On average, excluding small and medium mammals doubled the time to median seed removal, tripled seed survival, and doubled seedling survival. The joint effect of excluding small and medium mammals was to triple seedling recruitment. Seedling RGR, on the other hand, was unaffected by mammals of any size class. Furthermore, predation by small mammals significantly increased seedling per-stem species richness. Overall, the effects of small and medium mammals were greater than those of large mammals on all aspects of seedling recruitment.

We then determined the relationship between adult abundance and each stage of seedling recruitment. Seeds of species that are rare as adults germinated significantly

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Exclosure treatment</th>
<th>Species</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to median seed removal (d)</td>
<td>4, 28</td>
<td>15.2</td>
<td>0.0001</td>
</tr>
<tr>
<td>Seed survival (%)</td>
<td>4, 28</td>
<td>20.6</td>
<td>0.0001</td>
</tr>
<tr>
<td>Seedling survival (%)</td>
<td>4, 28</td>
<td>8.6</td>
<td>0.0001</td>
</tr>
<tr>
<td>Seedling RGR (cm(^{-2}) cm(^{-1}) d(^{-1}))</td>
<td>4, 128</td>
<td>1.1</td>
<td>0.0001</td>
</tr>
<tr>
<td>Seedling recruitment (no. individuals)</td>
<td>4, 28</td>
<td>17.3</td>
<td>0.0001</td>
</tr>
<tr>
<td>Species richness per stem</td>
<td>4, 23</td>
<td>7.5</td>
<td>0.0005</td>
</tr>
</tbody>
</table>

**Notes:** Data for seedling survival and relative growth rate were so unbalanced as to preclude estimation of treatment \times species interactions. Blank cells indicate interactions that were not tested. Abbreviations: RGR, relative growth rate; NS, not significant.

**Table 2.** Overall treatment effects of mammal exclosures, seed species, and their interactions.

**Fig. 3.** (a) Time to median seed removal, (b) mean seed survival, (c) mean seedling survival, (d) height relative growth rate (RGR\(_{ht}\)), (e) abundance of recruited seedlings, and (f) species richness of recruited seedlings in exclosures that excluded or allowed mammals of the specified size classes. Each bar represents the mean of 112 values. Error bars indicate 95\% confidence intervals.
more seedlings than did relatively common species ($F_{1,558} = 4.78, P = 0.029$), but no other stage of recruitment differed between rare and common species ($F_{1,558} = 4.90, P = 0.029$; data not shown). On the other hand, species differing in adult abundance fared very differently when interacting with mammalian predators (Fig. 4). Small mammals rapidly removed seeds of common species and strongly reduced the relative abundance of their seedlings. Although they did not disproportionately affect seed removal rates or survival, medium-sized mammals similarly reduced the relative abundance of recruited seedlings of common species. A 10-fold increase in adult abundance predicted a 17% increase in seedling recruitment in the absence of small or medium mammals. Large mammals, having had no effect on any stage of seedling recruitment, did not interact significantly with adult abundance ($F_{1,220} = 1.15, P = 0.29$). Together, these results suggest that small- and medium-sized mammals may impose frequency-dependent mortality by disproportionately preying upon the seeds of common species, generating a rare-species advantage.

Seed mass had limited direct effects on seedling recruitment, as it was correlated only with seed removal rates. Small-seeded species were removed more rapidly than large-seeded species ($F_{1,558} = 28.12, P < 0.0001$; data not shown). Large- and small-seeded species did not differ in any other stage of seedling recruitment ($F_{1,558} = 2.05, P = 0.15$). When interacting with mammalian predators, on the other hand, any advan-

**Fig. 4.** Interacting effects of adult abundance and access by small and medium-sized mammals on seed survival and seedling recruitment. Predation by small and medium-sized mammals interacts significantly with adult abundance. Where mammals are excluded, survival and recruitment increase with adult abundance (crosses and dashed lines). However, in enclosures to which they had access, small and medium mammals disproportionately consumed common species, significantly reducing their recruitment (circles and solid lines). Statistics indicate the significance of the interaction of adult abundance and mammal access. Large mammals had no overall or interaction effects on any response variable and are not plotted.
tage accruing to large-seeded species disappeared (Fig. 5). Small and medium mammals disproportionately reduced the survival of large-seeded species, and reduced the relative abundance of their seedlings. A 1-g increase in seed mass predicted a 10% increase in seedling recruitment in the absence of small mammals. Large mammals, having had no effects on any stage of seedling recruitment, did not interact significantly with seed mass ($F_{1,220} = 0.49, P > 0.49$). Although small and medium-sized mammals reduced the overall recruitment of seedlings, they increased the relative abundance of seedlings germinated from small seeds.

**Summary**

Surprisingly, large mammals had no effect on any aspect of seedling recruitment. Rather, smaller mammals affected all stages of seedling recruitment more strongly than did large mammals. Small and medium mammals significantly reduced the survival of seeds and seedlings, which jointly reduced seedling density. Small mammals increased the per-stem species richness of recruited seedlings by disproportionately preying upon seeds of common species and large-seeded species, which increased the relative abundance of seedlings of rare and small-seeded species. Altogether, predation by small mammals significantly increased the diversity of the seedling layer.

**Discussion**

**Mammal effects**

Both large and small mammals may be expected to have substantial effects on seedling recruitment. In
intact Neotropical forests, the biomass of large terrestrial mammals exceeds that of medium or small mammals (400, 57, and 14 kg/km², respectively; Janson and Emmons 1990). On the other hand, small mammals are by far the most abundant size class of mammals in Neotropical forests. At EBCC, large, medium, and small mammals occur at average densities of 12, 14, and 410 individuals/km², respectively (Janson and Emmons 1990).

Previous experimental and comparative studies have suggested that small mammals are more important predators of seeds and seedlings than are large mammals (DeMattia et al. 2004, Asquith and Mejia-Chang 2005). A study conducted at EBCC from 1988 to 1990 indicated that small mammals were more important seed predators than large mammals (Terborgh et al. 1993). However, the abundance of peccaries at EBCC was greatly depressed at that time, perhaps by an epidemic disease (Silman et al. 2003). We expected that large mammals would play a stronger role in our study because their density, especially that of peccaries, was greater at EBCC at the time of our study than at any site where exclosure studies have previously been conducted. Instead, small mammals were the dominant predators of seeds and seedlings, confirming the results of previous investigations.

Why did small mammals affect seedling recruitment more than large mammals did? Small mammals are ubiquitous in the forest understory, with small, sometimes nonoverlapping territories (Emmons 1982, Beck et al. 2004). Conversely, large mammals are scarce and occupy large home ranges, as exemplified by white-lipped peccaries (Tayassu pecari). White-lipped peccaries range through the understory of intact rain forests in "nomadic" herds of 50–200 individuals. As they "bulldoze" through the understory of Neotropical forests, their effects are intense but tightly localized (Beck 2006). Therefore, the interval between successive visits of a peccary herd to any point in the understory is likely to be on the order of months to years. For small rodents, on the other hand, the recurrence interval is on the order of hours to days. Any single seed in the understory is thus more likely to be located by a rat than by a peccary. The difference in effects between small and large mammals is essentially a sampling issue: in both space and time, small mammals sample the forest understory more thoroughly than do large mammals. Moreover, small mammals can consume even hard palm seeds (Brewer 2001, Beck and Terborgh 2002). None of our study species had such strong mechanical defenses as to be invulnerable to small-mammal attack (cf. Terborgh et al. 1993). Small mammals thus more strongly affected seedling recruitment than did large mammals.

In addition to their intense predation on seeds, small and medium mammals imposed stronger herbivory on seedlings than did large mammals. We found that only smaller mammals, and not large mammals, reduced seedling survival significantly. The only other study (DeMattia et al. 2006) to partition seedling herbivory between size classes of tropical mammals gave largely inconclusive results. Generally, deer and tapirs are
considered the most important terrestrial mammalian herbivores in Neotropical forests (Bodmer and Ward 2006). However, they are relatively scarce near EBCC, possibly because of the abundance and diversity of large carnivores at the site. Generalist phytophagous insects, such as leaf-cutter ants (Atta spp.), can be very important herbivores in tropical forests (Terborgh et al. 2001). Because they had free access to all exclosures, however, their effects were not evaluated in this study. Ours is thus the only study to have identified rodents as the dominant mammalian herbivores of seedlings in a tropical forest.

Herbivory by small mammals reduced seedling survival, but no size class of mammals significantly affected relative height growth rates. Mammals evidently killed seedlings outright, rather than merely browsing them, just as Beckage and Clark (2005) found in North Carolina. In contrast, two Australian studies found that seedlings in exclosures grew more rapidly than unprotected seedlings do (Osunkoya et al. 1993, Wahungu et al. 2002). This is an important result because it indicates that, as herbivores, small mammals may remove seedlings from the rain forest understory. They thus generate open space that is subsequently available for colonization, rather than simply slowing seedling growth rates. Should this open space be colonized by previously absent species, small-scale species richness would increase.

Predation increases species diversity

Small mammals increased species diversity, measured as species per-stem richness. Although they reduced the species richness of recruited seedlings, small mammals reduced seedling density even more sharply. They therefore increased species richness on a per-stem basis. Moreover, this effect was nonrandom with respect to the 14 species that we added as seeds. Specifically, small mammals disproportionately preyed upon common and large-seeded species. Thus, the increase in per-stem species richness was generated by increases in the relative abundance of rare and small-seeded species.

Adult abundance and seed mass were weak predictors of success in seedling recruitment overall. Rare species and large-seeded species fared better than common and small-seeded species only initially, in terms of the time until median seed removal. Thereafter, neither adult abundance nor seed mass predicted seedling performance or recruit density. The result for seed size is consistent with the analysis of Moles and Westoby (2004) that the advantages of large seed size dissipate rapidly.

Nevertheless, adult abundance and seed mass each interacted strongly with mammalian predation because small and medium mammals preferentially consumed both common and large-seeded species. In exclosures to which they had access, small- and medium-sized mammals reduced the recruitment of large-seeded species to levels comparable with those of small-seeded species. Predation thus increased the relative abundance of small-seeded species in the seedling layer. Insofar as seed size may correlate with competitive ability of young seedlings (Saverimuttu and Westoby 1996), predation by small and medium mammals increased the relative abundance of competitively inferior species. Similarly, small and medium mammals disproportionately consumed seeds of common species, increasing the relative abundance of rare species. Why rodents may preferentially prey upon seeds of common species is unknown, although they may develop stronger search images for relatively common species, which may be more consistently rewarding than rare species.

Adult abundance and seed mass captured some of the variation among species in this experiment, but a substantial portion remained unexplained. Species showed idiosyncratic recruitment patterns, shaped by details of their morphology and physiology. For example, large-seeded Buchenavia grandis germinated many seedlings, but few survived to the end of the experiment. Sparattanthelium tarapotanum and Casearia sp. nov., on the other hand, recruited at unexpectedly high densities, despite germinating from relatively small seeds.

This is the first experimental evidence that mammalian predation contributes positively to the maintenance of tree species diversity. By preferentially consuming seeds of common and large-seeded species, rodents increased diversity and generated some of the negative frequency dependence observed in the recruitment of tropical trees (Harms et al. 2000). To evaluate whether abundance-biased predation also occurs in the seedling stage as well as in the seed stage, it would be necessary to conduct experimental transplantations of seedlings into exclosures (cf. DeMattia et al. 2006). Beckage and Clark (2005), in the only previous study to relate mammalian predation to seedling diversity, found that predation uniformly reduced the recruitment of temperate trees that varied in competitive ability. Because they studied only three species, they were unable to test the effect of predation on species richness or relative abundance.

Contributions to recruitment limitation

Does the variation in seedling recruitment generated by predation arise primarily in the seed stage or in the seedling stage? In this study, mammals had stronger and more variable effects on seed survival than on seedling survival. The pattern of recruited seedling density thus mirrored that of seed survival, with only minor modifications occurring during seedling survival. Although our data on seedling growth were unbalanced (due to variation in seed survival), growth rates were not affected by exclosure treatment, adult abundance, or seed mass. This may be explained by the scarcity of mammalian herbivores, relative to that of seed predators, at EBCC. The present data suggest that patterns of seedling recruitment are primarily driven by differences in seed survival, which persist through the seedling stage.
Conclusions

Mammalian predation on seeds and seedlings strongly affects the recruitment of tree seedlings in tropical forests. Small and medium mammals significantly reduce the density of recruiting seedlings, while increasing recruit diversity. They increase per-stem species richness by increasing the relative abundance of rare and small-seeded species. Large mammals have minimal effects on the recruitment of tree seedlings. Predation, especially by rodents, plays an important role in maintaining tree diversity in tropical forests.

Acknowledgments

The Peruvian National Institute of Natural Resources (INRENA) granted us permission to conduct research in Manu National Park. We thank Pamela Weisenhorn, Kristen Schmitt, Patricia Alvarez, Cecilia Carrasco, Beth Pringle, and Karim Ledesma for field assistance. Luis Escobar and Qingfang Wu helped develop the data analysis. Mac Alford determined the *Crasea* sp. nov. Comments from Jane Carlson, Jonathan Myers, Adriana Bravo, John Orrock, and one anonymous reviewer strengthened the manuscript. Discussions and suggestions from Kyle Harms guided this manuscript through its gestation. A LASPAU fellowship from the Organization of American States and a Grant-in-Aid-of-Research from Sigma Xi supported this research. This contribution is dedicated to the memory of E. Barry Moser, who we miss as a mentor and a friend.

Literature Cited


