Title How mammalian predation contributes to tropical tree community structure

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Abstract

The recruitment of seedlings from seeds is the key demographic transition for rain forest trees. Though tropical forest mammals are known to consume many seeds, their effects on tree community structure remain little known. To evaluate their effects, we monitored 8000 seeds of 24 tree species using exclosure cages that were selectively permeable to three size-classes of mammals for up to 4.4 years. Small and medium-bodied mammals removed many more seeds than did large mammals, and they alone generated beta diversity and negative density dependence, whereas all mammals reduced diversity and shaped local species composition. Thus, small and medium-bodied mammals more strongly contributed to community structure and promoted species coexistence than did large mammals. Given that seedling recruitment is seed-limited for most species, alterations to the composition of the community of mammalian seed predators is expected to have long-term consequences for tree community structure in tropical forests.

Keywords

Agouti, Beta diversity, Defaunation, Negative density dependence, Seed predation, Seed size, Species composition, Peru, Peccary

Introduction

The recruitment of seedlings from seeds is the key demographic transition for trees in tropical forests. Mortality rates are not only greater during this than any other ontogenetic stage, but they are also the most predictable and species-specific, often caused by host-specific natural enemies (Terborgh 2012). Mortality patterns become increasingly stochastic over ontogeny (Green et al. 2014). Thus, to understand the determinants of tropical tree community structure, one must study seedling recruitment. Though their relative importance continues to be debated, it is certain that terrestrial mammals, pathogenic fungi and herbivorous insects play strong roles in this transition, consuming and destroying many seeds and seedlings (Notman and Villegas 2005, Paine and Beck 2007, Alvarez-Loayza and Terborgh 2011, Bagchi et al. 2014). The objective of this study was to determine the extent to which mammalian predation contributes to the community structure of tropical forest trees.

Previous examinations of this topic have followed one of two approaches (Beck et al. 2013). The first compares seedling recruitment in intact and defaunated forests, from which anthropogenic hunting has extirpated large-bodied vertebrates (Asquith et al. 1997, Terborgh et al. 2008, Harrison et al. 2013). Because humans hunt both arboreal and terrestrial animals, however, such investigations can confound their potentially contrasting effects (Kurten et al. 2015). Arboreal vertebrates are largely frugivorous, consuming fruit pulp and dispersing seeds. Terrestrial vertebrates, on the other hand, mostly consume seeds and seedlings destructively, although scatter-hoarding rodents are also important vectors of secondary seed dispersal (Vander Wall et al. 2005, Hirsch et al. 2012). Moreover, abiotic factors may vary among sites, influencing recruitment patterns (Beck et al. 2013). In a second, more direct approach, the experimental use of selectively permeable cages (i.e., ‘exclosures’) allows investigators to manipulate the access of terrestrial vertebrates to seeds and seedlings in relatively homogeneous abiotic conditions (Daubenmire 1940). Exclosure technique is particularly powerful when coupled with the addition of seeds, through which investigators can generate artificial communities of known age and species composition (DeMattia et al. 2004, Paine and Beck 2007). Unfortunately, many studies of this type have been of very short duration, often less than two years (DeMattia et al. 2004, Hautier et al. 2010, Kuprewicz 2013). Moreover, the few long-duration studies have not included seeds of enough species to make strong inferences about the effects of mammals on tree community structure (Notman and Villegas 2005, Norghauer et al. 2006).

Paine and Beck (2007) provide the most-thorough analysis to date of the effects of mammalian predation on tropical tree community structure. Their study, however, suffered from a number of shortcomings, which we remedy in the current contribution. First, Paine and Beck (2007) analyzed diversity using species richness per individual. Though this metric is frequently assessed (Hubbell et al. 1999), it cannot be considered a diversity index as it does not account for the relative abundance of species (Magurran 2004). In fact, it is maximal when evenness is minimal. Secondly, their study was incomplete, as it did not examine important aspects of community structure such as functional traits, species composition or beta diversity. We expand upon Paine and Beck (2007) by studying 24 species for up to 4.4 years, compared with 14 species and 2.2 years in Paine and Beck (2007). Finally, we take advantage of new data on functional traits and tree demography to assess the effects of mammalian predation on all important aspects of tree community structure.

We sought to understand the relative effects of three size-classes of mammals on tree community structure. Though it is well known that terrestrial rain forest vertebrates consume many tree seeds (Paine and Beck 2007, Hautier et al. 2010, Beck et al. 2013, Kurten et al. 2015), their relative effects in generating tree community structure is less evident. We consider three size-classes. Small mammals, with adult body mass < 1 kg, include mice (Muridae) and spiny rats (Echimyidae). Medium-sized mammals (1–12 kg) are caviomorph rodents and include acouchis, agoutis and pacas (*Myoprocta pratti, Dasyprocta variegata* and *Cuniculus paca*, respectively). Large mammals (>20 kg) are predominantly peccaries (*Pecari tajacu* and *Tayassu pecari*, Tayassuidae), but also include deer (Cervidae) and tapirs (*Tapirus terrestris*, Tapiridae). Assessing the effects of each size-class separately is critical for predicting the effects of anthropogenic activities, such as hunting-induced defaunation, on the tree community. Large terrestrial mammals become locally scarce in lightly hunted forests, whereas even medium-sized mammals can be extirpated from intensively hunted forests (Endo et al. 2010). Small mammals are not typically hunted, but their populations frequently expand following hunting, presumably because of reduced competition from larger mammals (Asquith et al. 1997, Peres and Palacios 2007).

We posit five hypotheses linking predation by each size-class of mammal to tree community structure. First, mammals will shape tree community structure only if they generate inter-specific variation in seed survival. Only if this is the case can mammalian predation affect the relative abundance of tree species. Second, we hypothesize that predation will reduce evenness and thus species diversity (Paine and Beck 2007, Theimer et al. 2011, Beck et al. 2013). Third, because mammalian feeding preferences can vary spatially, we hypothesize that mammalian predation will affect local species composition and beta diversity, the change in species composition over space. Although distance-limited seed dispersal is understood to be the primary generator of beta diversity (Chave and Leigh 2002), environmental filtering, in the form of mammalian feeding preferences, may also play a role. Fourth, we hypothesize that mammals preferentially prey upon larger seeds, as nutritional rewards scale with seed mass, assuming that seeds do not vary in detectability or handling time (Paine and Beck 2007). If mammals disproportionately prey upon large-seeded species, they may also affect the distribution of wood density across the tree community, owing to a weakly positive association between seed mass and wood density in tropical forests worldwide (Wright et al. 2007). Thus, mammalian predation may affect the distribution of wood density among species recruiting as seedlings, with potential long-term effects on biomass and carbon sequestration (Peres et al. 2015). Finally, we hypothesized that mammalian predation generates a negative relationship between seedling recruitment and population density. Such negative density dependence is pervasive in seedling recruitment, and is essential for stable species coexistence (Harms et al. 2000, Chesson 2000). Therefore, we hypothesized that mammals may disproportionately prey upon species that are common as adults, because they may have stronger search images for such species.

Methods

This study was conducted in tropical moist forest in the vicinity of Cocha Cashu Biological Station (CCBS), Manu National Park, Peru (12° S, 71° W, ~350 m elevation; see site description in Gentry 1990). The forested floodplain of the Manu River is extremely diverse, with almost 350 species of trees that attain a diameter of 10 cm at breast height (dbh). Average annual precipitation is 2200 mm, falling mainly between October and April. The vastness and physical isolation of the 1.9 million ha Manu National Park, together with neighboring protected areas, have facilitated the preservation of the diverse vertebrate community of CCBS, making it one of few sites worldwide that remains intact and accessible for study (Endo et al. 2010). It is thus an ideal location to detail the effects of terrestrial mammals on seedling recruitment.

To determine the individual effects of small, medium and large mammals, we established exclosures that differed in their permeability to each size class. We built exclosures in eight randomly located blocks, separated by at least 250 m, within an area of 3 km^2. In each block, we located one 2 x 2 m exclosure cages of each of five types 20 m apart along a randomly oriented transect. There were 40 exclosures in total. NONE exclosures, which were impermeable to all terrestrial mammals, were 90-cm tall wire hardware cloth (mesh size 1 cm), reinforced with iron rebar at the corners and the middle of each side. SMALL exclosures were identical, but with 7 x 7 cm holes cut along the bottom edge of the walls, making them permeable to small mammals. MEDIUM–LARGE exclosures consisted of 20 cm tall sheet-metal barriers to small mammals (Supplemental Figure S1). Medium and large mammals could easily step over the walls to enter the exclosure. MEDIUM combined the sheet metal of MEDIUM–LARGE with a wrapping of barbed wire, which barred the entry of large mammals, making them permeable only to medium-sized mammals. Finally, ALL treatments were only marked with rebar at the four corners, permitting the entry of all terrestrial mammals.

Tree species were included in the study based upon three criteria. First, their fruit had to be single-seeded and their seeds had to be sufficiently large to be easily cleaned, sown and monitored. Second, fruiting adults had to be sufficiently common and fecund to provide enough seeds for placement in the exclosures. Third, as seeds were placed into the exclosures in four batches, fruit needed to be available at the beginning of one of the four experimental periods: November 1999-January 2000, June 2001, April–June 2004 or February 2005. These criteria yielded 24 species, representing 17 families, including 18 trees, five palms, and one liana

(*Sparattanthelium tarapotanum*). All species reach the canopy as adults and are primarily dispersed by mammals. Seed mass was measured for at least 30 seeds per species. Sapwood samples were obtained using an increment borer from up to three adults per species. Wood density was assessed with the water displacement method. Seed mass and wood density values were each missing for a single species, and were obtained from the Kew Seed Information Database (http://data.kew.org/sid) and Chave et al. (2009), respectively. Adult abundance (individuals ≥ 10 cm dbh), was determined in 38 permanent plots totaling 25 ha in the floodplain and uplands of the Manu river watershed (Manu Plant Network, J. Terborgh, unpublished data). Seed mass varied over two orders of magnitude, from 50 to 5400 mg (median 1800 mg), whereas wood density varied from 0.22 to 0.76 $g\cdot cm^{-3}$ (median 0.54 $g\cdot cm^{-3}$). Adult stem density of the focal species ranged from ~0.01 to 90 adults/ha (median 0.67 adults/ha), encompassing almost the entire range of densities observed among adult trees in this region. The distinguishing characteristics of species are presented in Table 1. We added seeds to exclosures and monitored their fates as in Paine and Beck (2007), except that seeds were placed in conspecific groups of six in experimental periods 1 and 2, and conspecific groups of 10 in experimental periods 3 and 4. We used seed removal as a proxy for seed mortality, given the uncertainty in the precise fate of missing seeds (Vander Wall et al. 2005). See Paine & Beck (2007) for further experimental details.

Data analysis

All analyses were performed on the sum of surviving seeds and germinated seedlings. We evaluated the effects of mammalian predation on seed and seedling survival using a parametric survival regression, in which survival was predicted from the interacting effects of species and treatment. As mortality risk is likely to decrease over time for seeds and seedlings, residuals were assumed to follow a Weibull distribution.

The effects of mammalian predation on species evenness, diversity, plot-mean seed mass, plot-mean wood density and plot-mean adult stem density were assessed using linear mixed-effect models. Evenness and diversity were expressed as Pielou's J and the effective number of species ($e^{H'}$, Magurran 2004), respectively. Plot-mean seed mass, wood density and adult stem density were calculated at each census time using species-mean trait values, weighted by the abundance of the species remaining in each exclosure. All five response variables were predicted on the basis of the interacting effects of treatment and observation day. To account for spatial variation in mammalian effects, blocks were included as random effect. Experimental periods entered the model with random slopes and intercepts, because species composition varied among them. All five response variables were log-transformed prior to analysis to control heteroscedasticity.

We assessed the degree to which predation by each size-class of vertebrates shaped species composition in two ways. First, to assess the effects of mammalian predation on local species composition, we calculated the Bray-Curtis dissimilarity in species composition caused by predation by each size-class of mammal *within* each of the eight geographical blocks at each time of observation. Separately, we assessed the degree to which mammalian predation generated beta diversity by calculating the Bray-Curtis dissimilarity in species composition within each exclosure type *among* all pairwise combinations of blocks. Because Bray-Curtis dissimilarity cannot exceed one (Magurran 2004) and because all exclosures began with identical species compositions, we modeled these compositional dissimilarities using asymptotic mixed-effect models that were forced through the origin (Pinheiro and Bates 2000). Asymptotes and rate constants were allowed to vary among mammal size-classes as fixed effects. We included experimental period as a random effect in the beta-diversity model, and both block and experimental period in the local species composition model.

For all aspects of tree community structure, our interest regarded the effects of each size-class of vertebrates, rather than of the treatments themselves. We used *a priori* orthogonal contrasts among treatments to test the separate effects of each mammal size-class on each aspect of tree community structure. The impact of each mammalian size-class was determined by contrasting the pair of 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. For species composition, dissimilarities between treatments were analyzed directly, obviating the need for orthogonal contrasts.

For all response variables, the effects of mammalian predation were compared at two points in time: 1.4 and 4.4 years, which were the durations of the shortest- and longest-duration experimental periods, respectively (Table 1). At each of these time points, each response variable was predicted using 1000 parametric bootstrap replicates. The effects of each size-class of mammals on the response variables was assessed as the base-10 logarithm of the ratio of the response variable in exclosures permeable to the given mammal size-class to its value in exclosures from which the mammal size-class was excluded. Log10-ratios of 1 or -1 indicate that a mammal size-class caused a 10-fold increase or decrease in the response variable, respectively. Mammalian effects were deemed significant if the 95% confidence intervals of the bootstrap replicates did not include zero. Analyses were performed in R 3.2.3 (R Core Team 2015). Survival and species composition models were fit using the ‘survival’ and ‘nlme’ libraries, respectively (Pinheiro and Bates 2000), whereas all other analyses were implemented using the ‘lme4’ library (Bates et al. 2014). All raw data and R code used in this study are available in a Github repository (doi: 10.5281/zenodo.154042).

Results

Over the eight-year duration of the study, 8000 seeds of 24 species were placed into the exclosures, yielding a total of 1917 seedlings, 515 of which survived to the end of the experimental period. Germination rate varied among species from 0 to 59%. Three species recruited no seedlings (Table 1). One of these, *Mauritia flexuosa*, is a swamp specialist, the seeds of which were rapidly consumed by terrestrial termites. *Virola calophylla* and *Matisia cordata* germinated weakly (7.5 and 14.6%, respectively), but all their seedlings perished, potentially as a result of host-specific natural enemies (Alvarez-Loayza and Terborgh 2011). In contrast, 45% of the seeds of *Calatola costaricensis*, a large-seeded tree that is rare as an adult, survived as seedlings to the end of the study (Supplemental Figure S2).

Our first hypothesis, that mammals generate interspecific variation in seed survival, was strongly supported by the data. Small, medium and large mammals reduced median survival time by up to 10.3, 15.1 and 2.0 months, respectively (Fig. 1). The strongest effects were generated by small and medium-sized mammals, which significantly reduced the survival of 17 and 14 species, respectively. Large mammals, on the other hand, significantly reduced the survival of only four species, all of which were also significantly impacted by small- or medium-bodied mammals. Survival of a few species was modestly increased by exposure to mammals; why this occurred is unclear.

Given their differential effects upon survival, mammalian predation also reduced evenness and species diversity, supporting our second hypothesis. All mammalian size-classes reduced species evenness (Pielou's J), with effects that strengthened over the duration of the experiment (Fig. 2A). All three size-classes of mammals also significantly reduced the effective number of species ($e^{H'}$), with effects that strengthened over time (Fig. 2B). For both evenness and diversity, the effects of large mammals were weaker than those of small and medium-bodied mammals (Fig. 2). Our third hypothesis found strong support, as predation by all three mammal size-classes caused rapid and significant changes in local species composition, which lasted through the end of the experiment (Fig. 3A). Beta diversity showed a strikingly different pattern. Small and medium-sized mammals rapidly generated significant beta diversity, which lasted throughout the experiment, whereas large mammals did not significantly contribute to beta diversity at any time (Fig. 3B).

There was strong support for the first part of our fourth hypothesis, that mammals preferentially preyed upon large-seeded species. Predation by all three size-classes of mammals lead to significant decreases in the plot-mean seed mass over time. Small mammals had the strongest effect, reducing plot-mean seed mass more than 10-fold ($\log_{10}$ ratio: -1.01), whereas the effects of medium-sized and large mammals were weaker (Fig. 4A). The evident preference of mammals for larger-seeded species generated only weak effects on plot-mean wood density, however, despite the significant negative relationship between seed mass and wood density (Supplemental Figure S3). After 1.4 years, wood density was significantly increased by small and large mammal predation, and significantly decreased by medium-sized mammals. Only the effects of large mammals persisted through the end of the experiment, and they only increased wood density by 4% ($\log_{10}$ ratio 0.039; Fig. 4B). Small and medium-sized mammals, on the other hand, strongly and significantly reduced plot-mean adult density by disproportionately removing seeds of species that are common as adults, thus generating negative density dependence (Fig. 4C). Both size-classes reduced plot-mean adult density by at least 100-fold by the end of the experiment ($\log_{10}$ ratios: -2.43 and -2.13 for small and medium mammals, respectively). Large mammals reduced plot-mean adult density initially, though this effect disappeared by the end of the study.

Discussion

By following the fates of seeds of 24 species for up to 4.4 years in a well-replicated experiment, we were able to assess aspects of community structure, such as beta diversity, that were beyond the scope of previous studies. Overall, mammalian predation on seeds and seedlings had strong and predictable effects on tree community structure. Small, medium and large-bodied species all reduced species evenness and diversity (Fig 2). This finding directly contradicts that of Paine and Beck (2007), who claimed that predation by small mammals increased diversity, measured as species richness per stem. Their error was that species richness per stem is not a diversity index, as it does not account for relative species abundance (Magurran 2004). In Paine and Beck (2007) and the current study, it would have been impossible for mammals to increase species diversity. They could not have increased species richness, as experimentally placed seeds were clearly distinguishable from naturally dispersed ones. Nor could they have increased evenness, as it was maximized at the beginning of each experimental period by the placement of equal numbers of seeds of each species in each exclosure.

Small and medium-bodied mammals more strongly affected tree community structure than did large mammals, in accordance with previous studies (Asquith et al. 1997, DeMattia et al. 2004, Norghauer et al. 2006, Paine and Beck 2007, Hautier et al. 2010). Not only did they remove more seeds than did large-bodied mammals, they also generated beta diversity and negative density dependence through their actions (Figs 1, 3B and 4C). The effects of large mammals were altogether weaker, although they alone favored the recruitment of species with dense wood by disproportionately preying upon species with low wood density (Fig. 4B). These findings broaden and generalize those of the few previous studies that have attempted to link the actions of mammalian seed predators to tree community structure (DeMattia et al. 2004, Paine and Beck 2007, Theimer et al. 2011, Kurten et al. 2015).

Notably, ours is the first study, to our knowledge, to demonstrate that mammalian predation can contribute to beta diversity, the change in species composition over space. Beta diversity is generally assumed to arise from distance-limited seed dispersal (Chave and Leigh 2002), though biogeographical history also makes an important contribution (Dexter et al. 2012). We suggest that spatial variation in canopy tree composition, together with the relatively small home ranges of small- and medium-bodied mammals, could lead to spatial variation in search images for preferred food items. This, in turn, would lead to spatial variation in species-specific rates of seedling recruitment. Such a process could amplify and contribute to the patterns of beta diversity observed in tropical tree communities.

Given the central role of negative density dependence for the maintenance of diversity and its pervasive nature (Harms et al. 2000, Chesson 2000), understanding its generative mechanisms is of great interest. Our findings add to the body of evidence that small-bodied mammals can generate negative density dependence (Paine and Beck 2007), thus contributing to stabilizing niche differences and thus species coexistence. Arthropods and pathogenic fungi can also do so (Notman and Villegas 2005, Alvarez-Loayza and Terborgh 2011, Bagchi et al. 2014). There remains a need for studies that evaluate the relative importance of the primary biotic sources of mortality on tropical tree seedlings: fungi, insects and mammals, so that we may better understand the mechanisms that generate tropical tree community structure.

Abundance versus biomass

The relative effects of small, medium and large-bodied mammals on tree community structure is not easy to predict *a priori*. At Cocha Cashu Biological Station, small mammalian seed predators outnumber medium- and large-bodied ones by an order of magnitude (419, 14 and 12 individuals·km^{-2}, respectively; Janson & Emmons 1990). The population-level biomass of large mammalian seed predators at this site, however, far exceeds that of medium or small ones (590, 10 and 12 kg·km^{-2}, respectively; Janson & Emmons 1990; Endo et al. 2010). Moreover, the large body size and rooting behavior of *Tayassu pecari* (White-lipped Peccary), the dominant large terrestrial mammal at CCBS and across the Neotropics, cause them to have very strong *per capita* effects (Beck 2005, Beck et al. 2013). The observation that small and medium-bodied mammals had consistently stronger effects on tree community structure indicates that ubiquity, imparted by very large population sizes, facilitates stronger trophic interactions than does great individual biomass. In other words, a seed predator's ability to locate seeds is a better predictor of its ecological impacts than is its jaw strength, at least for the 24 plant species used in this study. Notably, all mammal size-classes were able to consume seeds (or seedlings) of all studied species. Had this not been the case, for example, if some species had been chemically defended, other outcomes would have been observed (Kuprewicz 2013).

Why were large mammals observed to have such weak effects on tree community structure? The scale of the experimental exclosures may have played a role. Herds of *T. pecari*, containing up to 200 individuals, travel approximately 10 km per day as they 'bulldoze' through the understory (Wyatt and Silman 2004, Beck 2005). The 4-m^2 exclosure plots used in this study may have been too small to attract the attention of these wide-ranging mammals. Notably, *T. pecari* is the dominant seed predator of the palm *Astrocaryum murumuru* when it is found in high-density aggregations, whereas *Proechimys* spp. and other small rodents are the primary seed predators of isolated *A. murumuru* individuals (Beck and Terborgh 2002). Thus, *T. pecari* may have weak effects on the tree community as a whole, but strong effects on a few species (Silman et al. 2003, Wyatt and Silman 2004). It is likely that larger-scale exclosures would have more equitably assessed the effects of large mammals on tree community composition (Kurten et al. 2015), although it would have been logistically challenging to achieve sufficient replication with them.

In several regions, population sizes of *T. pecari* vary erratically, even repeatedly becoming undetectably scarce for years at a time (Vickers 1991, Reyna-Hurtado et al. 2009). Infectious disease, which could presumably spread rapidly in this highly social species, may cause these large-scale extirpations (summarized by Richard-Hansen et al. 2014). *T. pecari* were effectively absent from CCBS between 1978 and 1990, and disappeared again in 2012 (Silman et al. 2003). Nevertheless, they were present and abundant throughout the eight-year duration of the current study, meaning that population fluctuations should not have weakened their apparent effects on tree community structure.

Taken at face value, our results suggest that the consequences of hunting on tree community structure should be relatively minor, because small and medium-sized mammals, which are less-often hunted, more strongly contributed to tree community structure than did large-bodied mammals, which are the preferred prey of hunters (Peres and Palacios 2007, Endo et al. 2010). However, two considerations make this conclusion overly simplistic. First, in the absence of mammalian seed predation, many seeds are destroyed by fungal pathogens, bacteria, or arthropods, some of which can generate negative density dependence (Bagchi et al. 2014). This was observed in our study, as few seeds or seedlings survived to the end of the experiment, even in the CLOSED treatment (Supplemental Figure S2). Thus, the consequences for the tree community of the local extirpation of large mammalian seed predators could be, at least in part, compensated for by the actions of smaller-bodied organisms (Asquith et al. 1997). Second, hunting by humans extirpates large-bodied arboreal primates as well as terrestrial mammals, thus affecting both seed dispersal and seed predation. Across Amazonia, heavily hunted sites retain approximately 10% of the population density of ateline primates (*Ateles* and *Lagothrix*), compared to non-hunted sites of equivalent productivity (Peres and Palacios 2007). These genera of frugivorous primates provide the irreplaceable ecological service of seed dispersal to roughly 23% of genera of Neotropical trees (Peres et al. 2015). Thus, although the ecological consequences of human hunting on seed predation are likely to be relatively modest, the impacts on seed dispersal are substantial and detrimental (Kurten et al. 2015). Observational studies of hunted forests show strong directional change in tree species composition (Terborgh et al. 2008, Harrison et al. 2013). We suggest that these changes are more likely to be driven by reduced seed dispersal than by reduced seed predation.

Terborgh (2012) levelled three criticisms at studies such as the current one, which he referred to as ‘seed presentation trials’. First, *they are conducted with relatively large seeds*. Though seeds masses in the current study spanned two orders of magnitude, tree seeds in Neotropical forests vary over seven orders of magnitude (Wright et al. 2007). This could be seen as limiting our ability to make inferences on the effects of mammalian predation on small-seeded species. Most small-seeded species require high light to germinate, however, and our results suggest that very small-seeded species are likely to escape the notice of mammals (Fig. 4A). Thus, their recruitment dynamics are likely to be relatively independent of mammalian seed predators.

Second, *abundant seeds are displayed conspicuously.* In contrast, naturally dispersed seeds are often scattered as they fall from the canopy and are subsequently covered by leaf litter. In the current study, conspecific seeds were placed in groups in each 4 m^2 exclosure, a far greater density than the one viable seed per m^2 observed in a concurrent seed-trapping at CCBS (Swamy et al. 2010). By artificially elevating the natural density of seed rain, the exclosure cages could have become more attractive foraging sites for seed predators than they might otherwise have been. This increase in food abundance is likely to have influenced mammal behavior. Although this elevated abundance was unavoidable and necessary for efficient data collection, we partially addressed the concern about conspicuousness by replacing leaf litter that had fallen on the seeds after every census.

Third, *the seeds used are typically undispersed, and have been cleaned of pulp*. Such pre-treatment can alter the olfactory cues that attract both seed predators and secondary dispersers, and can thus affect the probabilities of being eaten or buried. Secondary dispersal and burial by rodents or dung beetles increase dispersal, reduce predation, and enhance survival to the seedling stage (Andresen and Levey 2004, Vander Wall et al. 2005, Hirsch et al. 2012). Cleaning seeds may have shaped the outcome of our experiment in two ways: our seeds may have been less likely to be found by mammalian seed predators than ones reeking of dung, and seeds buried by dung beetles or scatter-hoarding mammals were counted as dead. The former effect would lead us to underestimate the effects of mammalian predation, because more seeds would have been consumed, had they been covered in dung. The latter, on the other hand, would lead us to overestimate the effects of mammalian predation, because seeds that were removed or buried, and subsequently germinated, were considered by us to have died. The relative magnitude of these countervailing effects remains unclear. Nevertheless, we stand by our decision to clean seeds prior to their placement in the exclosures. To have done otherwise would have been impractical.

Conclusions

Mammals contribute strongly to tropical tree community structure through the consumption of seeds and seedlings. Multiple lines of evidence suggest that small- and medium-bodied mammals play a stronger role in the seed-to-seedling transition than do large mammals. They significantly reduce survival of many species, generate beta diversity and crucially, they contribute to the negatively density dependent nature of seedling recruitment by disproportionately preying upon tree species that are common as adults. In contrast, large mammalian seed predators had minimal effects on tree community structure. Predation, especially by rodents, plays an important role in maintaining tree diversity and shaping tree community dynamics in tropical forests.

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Table 1. Names and key attributes of the 24 woody plant species studied at Cocha Cashu Biological Station, Manu National Park, Peru. Adult density is based on observations on 38 permanent plots, totaling 25 ha, distributed across the floodplain and uplands of the Manu River watershed. Germination rate indicates the percentage of seeds that yielded observed seedlings, whereas Final survival indicates the percentage of seeds that yielded seedlings at the end of the experiment.

Species	**Experimental period**	**Number of censuses**	**Seed mass (mg)**	**Wood density ($g \cdot cm^{-3}$)**	**Adult density (ha^{-1})**	**Germination rate (%)**	**Final survival (%)**
Annonaceae *Duguetia quitarensis* Benth.	3	12	410	0.612	2.36	2.5	0.5
Arecaceae *Astrocaryum murumuru* Mart.	1	24	6000	0.508	37.44	6.3	3.3
Arecaceae *Attalea butyracea* (Mutis ex L.f.) Wess.Boer	2	11	54700	0.326	27.19	7.1	2.5
Arecaceae *Iriartea deltoidea* Ruiz & Pav.	3	13	3860	0.267	89.89	31.3	10.0
Arecaceae *Mauritia flexuosa* L.f.	1	18	13840	0.557	3.55	0.0	0.0
Arecaceae *Socratea exorrhiza* (Mart.) H.Wendl.	3	13	3440	0.226	0.12	34.8	4.3
Clusiaceae *Calophyllum brasiliense* Cambess.	1	23	2520	0.579	0.35	29.4	1.8
Combretaceae *Buchenavia grandis* Ducke	3	13	1930	0.755	0.12	15.8	0.5
Ebenaceae *Diospyros artanthifolia* Mart. ex Miq.	3	8	610	0.535	0.08	30.0	7.5

Ebenaceae *Diospyros subrotata* Heirn	3	13	790	0.498	0.95	22.8	9.0
Hernandiaceae *Sparattanthelium tarapotanum* Meisn.	4	7	550	0.432	0.03	25.3	17.5
Icacinaceae *Calatola microcarpa* Gentry ex Duno & Janovec	2	11	6000	0.472	1.10	37.1	15.0
Icacinaceae *Calatola costaricensis* Standl.	2	11	16000	0.545	4.02	52.1	45.4
Lecythidaceae *Bertholletia excelsa* Bonpl.	2	11	7500	0.624	0.39	7.5	3.8
Malvaceae *Matisia cordata* Bonpl.	1	24	5290	0.373	4.61	14.6	0.0
Meliaceae *Swietenia macrophylla* King	1	26	442	0.522	0.04	50.4	6.3
Moraceae *Clarisia racemosa* Ruiz & Pav.	4	7	1780	0.585	3.23	59.0	12.5
Myristicaceae *Otoba parvifolia* (Markgr.) Gentry	4	7	1800	0.426	27.39	13.5	9.0
Myristicaceae *Virola calophylla* (Spruce) Warb.	1	26	1310	0.329	0.16	7.5	0.0
Nyctaginaceae *Neea sp. nov.* ‘Foster 5005’	1	26	102	0.664	0.12	15.8	1.3
Olacaceae *Heisteria nitida* Engl.	3	13	220	0.602	1.10	15.3	0.8
Rubiaceae *Genipa americana* L.	4	7	50	0.643	0.35	39.8	1.3
Salicaceae *Casearia sp. nov.* ‘Huillca-Aedo 3561’	4	7	610	0.658	0.03	49.0	9.3
Verbenaceae *Vitex cymosa* Bertero ex Spreng.	4	7	490	0.570	0.32	0.3	0.3

Figure Legends

Figure 1 The effects of mammalian predation on the median survival time of seeds and seedlings of each species at Cocha Cashu Biological Station, Manu National Park, Peru. Solid points indicate significant effects of mammals ($p \leq 0.05$), whereas open points indicate non-significant effects. Lines indicate 95% confidence intervals around the estimated effect derived from a parametric survival regression. Small and medium-sized mammals reduced the survival of most species, whereas large mammals had far weaker effects. Species are sorted by magnitude of the effect of small mammals on survival.

Figure 2 Predation by mammals led to changes in A) Pielou's evenness (J) and B) Shannon's diversity index, expressed as the effective number of species ($e^{H'}$). The effects of mammals are represented as the $\log_{10}$ ratio of the response variable in exclosures to which the mammals had access, versus those from which they were excluded. Predicted effects and confidence intervals are derived from mixed-effect models.

Figure 3 Predation by all mammal size classes caused changes in A) tree species composition through time, whereas B) only small and medium-sized mammals generated significant beta diversity. The effects of mammals on beta diversity are represented as the $\log_{10}$ ratio of the Bray-Curtis dissimilarity among exclosures to which the mammals had access, versus that from which they were excluded. Predicted effects and confidence intervals are derived from nonlinear mixed-effect models.

Figure 4 Predation by mammals led to changes in plot-mean A) seed mass, B) wood density and C) adult density. The effects of mammals are represented as the $\log_{10}$ ratio of the response variable in exclosures to which the mammals had access, versus those from which they were excluded. Predicted effects and confidence intervals are derived from mixed-effect models. Note that the Y-axis scales vary among panels.

Supplemental Information

Supplemental Figure 1 Photographs of three of types of experimental exclosures.

Supplemental Figure 2 Change in the sum of seed and seedling abundance for each tree species in each of five types of exclosures over the study duration. For the 10 species used in experimental periods 1 and 2, six seeds were placed in each exclosure, whereas 10 seeds were used for the 14 species used in experimental periods 3 and 4. Open points indicate the date at which no seeds remained in a particular exclosure type. Ticks below the X-axis indicate the dates on which censuses were performed.

Supplemental Figure 3 Relationships among seed mass, wood density and adult density. Numbers above the diagonal represent pairwise Pearson correlation coefficients.