

This is the peer reviewed version of the following article: Paine CET, Beck H & Terborgh J

How mammalian predation contributes to tropical tree community structure

(Forthcoming/Available Online), *Ecology*, which will be published in final form at

<http://onlinelibrary.wiley.com/wol1/doi/10.1002/ecy.1586/abstract>. This article may be used

for non-commercial purposes in accordance with Wiley Terms and Conditions for self-archiving.

1 **Title** How mammalian predation contributes to tropical tree community structure

2 **Authors**

3 C. E. Timothy Paine¹, Harald Beck², John Terborgh^{3,4}

4 1. Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA UK

5 2. Department of Biological Sciences, Towson University, 8000 York Road, MD, 21252,
6 USA

7 3. Duke University Center for Tropical Conservation, Nicholas School of the Environment
8 and Earth Sciences, P. O. Box 90318, Durham, NC, 27708 USA

9 4. University of Florida, Gainesville, FL 32611, USA

10 **Email addresses**

11 C. E. Timothy Paine c.e.t.paine@stir.ac.uk

12 Harald Beck hbeck@towson.edu

13 John Terborgh manu@duke.edu

14 **Corresponding Author**

15 C. E. Timothy Paine

16 Biological and Environmental Sciences

17 University of Stirling

18 Stirling FK9 4LA

19 United Kingdom

20 Phone: +44 (0) 1786 467785

21 Fax: +44 (0) 1786 467843

22

23 **Abstract**

24 The recruitment of seedlings from seeds is the key demographic transition for rain forest trees.

25 Though tropical forest mammals are known to consume many seeds, their effects on tree
26 community structure remain little known. To evaluate their effects, we monitored 8000 seeds of
27 24 tree species using exclosure cages that were selectively permeable to three size-classes of
28 mammals for up to 4.4 years. Small and medium-bodied mammals removed many more seeds
29 than did large mammals, and they alone generated beta diversity and negative density
30 dependence, whereas all mammals reduced diversity and shaped local species composition.

31 Thus, small and medium-bodied mammals more strongly contributed to community structure and
32 promoted species coexistence than did large mammals. Given that seedling recruitment is seed-
33 limited for most species, alterations to the composition of the community of mammalian seed
34 predators is expected to have long-term consequences for tree community structure in tropical
35 forests.

36

37 **Keywords**

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

40

41 Introduction

42 The recruitment of seedlings from seeds is the key demographic transition for trees in tropical
43 forests. Mortality rates are not only greater during this than any other ontogenetic stage, but they
44 are also the most predictable and species-specific, often caused by host-specific natural enemies
45 (Terborgh 2012). Mortality patterns become increasingly stochastic over ontogeny (Green *et al.*
46 2014). Thus, to understand the determinants of tropical tree community structure, one must study
47 seedling recruitment. Though their relative importance continues to be debated, it is certain that
48 terrestrial mammals, pathogenic fungi and herbivorous insects play strong roles in this transition,
49 consuming and destroying many seeds and seedlings (Notman and Villegas 2005, Paine and
50 Beck 2007, Alvarez-Loayza and Terborgh 2011, Bagchi *et al.* 2014). The objective of this study
51 was to determine the extent to which mammalian predation contributes to the community
52 structure of tropical forest trees.

53 Previous examinations of this topic have followed one of two approaches (Beck *et al.*
54 2013). The first compares seedling recruitment in intact and defaunated forests, from which
55 anthropogenic hunting has extirpated large-bodied vertebrates (Asquith *et al.* 1997, Terborgh *et*
56 *al.* 2008, Harrison *et al.* 2013). Because humans hunt both arboreal and terrestrial animals,
57 however, such investigations can confound their potentially contrasting effects (Kurten *et al.*
58 2015). Arboreal vertebrates are largely frugivorous, consuming fruit pulp and dispersing seeds.
59 Terrestrial vertebrates, on the other hand, mostly consume seeds and seedlings destructively,
60 although scatter-hoarding rodents are also important vectors of secondary seed dispersal (Vander
61 Wall *et al.* 2005, Hirsch *et al.* 2012). Moreover, abiotic factors may vary among sites,
62 influencing recruitment patterns (Beck *et al.* 2013). In a second, more direct approach, the
63 experimental use of selectively permeable cages (*i.e.*, ‘exclosures’) allows investigators to

64 manipulate the access of terrestrial vertebrates to seeds and seedlings in relatively homogeneous
65 abiotic conditions (Daubenmire 1940). Exclosure technique is particularly powerful when
66 coupled with the addition of seeds, through which investigators can generate artificial
67 communities of known age and species composition (DeMattia *et al.* 2004, Paine and Beck
68 2007). Unfortunately, many studies of this type have been of very short duration, often less than
69 two years (DeMattia *et al.* 2004, Hautier *et al.* 2010, Kuprewicz 2013). Moreover, the few long-
70 duration studies have not included seeds of enough species to make strong inferences about the
71 effects of mammals on tree community structure (Notman and Villegas 2005, Norghauer *et al.*
72 2006).

73 Paine and Beck (2007) provide the most-thorough analysis to date of the effects of
74 mammalian predation on tropical tree community structure. Their study, however, suffered from
75 a number of shortcomings, which we remedy in the current contribution. First, Paine and Beck
76 (2007) analyzed diversity using species richness per individual. Though this metric is frequently
77 assessed (Hubbell *et al.* 1999), it cannot be considered a diversity index as it does not account for
78 the relative abundance of species (Magurran 2004). In fact, it is maximal when evenness is
79 minimal. Secondly, their study was incomplete, as it did not examine important aspects of
80 community structure such as functional traits, species composition or beta diversity. We expand
81 upon Paine and Beck (2007) by studying 24 species for up to 4.4 years, compared with 14
82 species and 2.2 years in Paine and Beck (2007). Finally, we take advantage of new data on
83 functional traits and tree demography to assess the effects of mammalian predation on all
84 important aspects of tree community structure.

85 We sought to understand the relative effects of three size-classes of mammals on tree
86 community structure. Though it is well known that terrestrial rain forest vertebrates consume

87 many tree seeds (Paine and Beck 2007, Hautier et al. 2010, Beck et al. 2013, Kurten et al. 2015),
88 their relative effects in generating tree community structure is less evident. We consider three
89 size-classes. Small mammals, with adult body mass < 1 kg, include mice (Muridae) and spiny
90 rats (Echimyidae). Medium-sized mammals (1–12 kg) are caviomorph rodents and include
91 acouchis, agoutis and pacas (*Myoprocta pratti*, *Dasyprocta variegata* and *Cuniculus paca*,
92 respectively). Large mammals (>20 kg) are predominantly peccaries (*Pecari tajacu* and *Tayassu*
93 *pecari*, Tayassuidae), but also include deer (Cervidae) and tapirs (*Tapirus terrestris*, Tapiridae).
94 Assessing the effects of each size-class separately is critical for predicting the effects of
95 anthropogenic activities, such as hunting-induced defaunation, on the tree community. Large
96 terrestrial mammals become locally scarce in lightly hunted forests, whereas even medium-sized
97 mammals can be extirpated from intensively hunted forests (Endo et al. 2010). Small mammals
98 are not typically hunted, but their populations frequently expand following hunting, presumably
99 because of reduced competition from larger mammals (Asquith et al. 1997, Peres and Palacios
100 2007).

101 We posit five hypotheses linking predation by each size-class of mammal to tree
102 community structure. First, mammals will shape tree community structure only if they generate
103 inter-specific variation in seed survival. Only if this is the case can mammalian predation affect
104 the relative abundance of tree species. Second, we hypothesize that predation will reduce
105 evenness and thus species diversity (Paine and Beck 2007, Theimer et al. 2011, Beck et al.
106 2013). Third, because mammalian feeding preferences can vary spatially, we hypothesize that
107 mammalian predation will affect local species composition and beta diversity, the change in
108 species composition over space. Although distance-limited seed dispersal is understood to be the
109 primary generator of beta diversity (Chave and Leigh 2002), environmental filtering, in the form

110 of mammalian feeding preferences, may also play a role. Fourth, we hypothesize that mammals
111 preferentially prey upon larger seeds, as nutritional rewards scale with seed mass, assuming that
112 seeds do not vary in detectability or handling time (Paine and Beck 2007). If mammals
113 disproportionately prey upon large-seeded species, they may also affect the distribution of wood
114 density across the tree community, owing to a weakly positive association between seed mass
115 and wood density in tropical forests worldwide (Wright *et al.* 2007). Thus, mammalian
116 predation may affect the distribution of wood density among species recruiting as seedlings, with
117 potential long-term effects on biomass and carbon sequestration (Peres *et al.* 2015). Finally, we
118 hypothesized that mammalian predation generates a negative relationship between seedling
119 recruitment and population density. Such negative density dependence is pervasive in seedling
120 recruitment, and is essential for stable species coexistence (Harms *et al.* 2000, Chesson 2000).
121 Therefore, we hypothesized that mammals may disproportionately prey upon species that are
122 common as adults, because they may have stronger search images for such species.

123

124 **Methods**

125 This study was conducted in tropical moist forest in the vicinity of Cocha Cashu Biological
126 Station (CCBS), Manu National Park, Peru (12° S, 71° W, ~350 m elevation; see site description
127 in Gentry 1990). The forested floodplain of the Manu River is extremely diverse, with almost
128 350 species of trees that attain a diameter of 10 cm at breast height (dbh). Average annual
129 precipitation is 2200 mm, falling mainly between October and April. The vastness and physical
130 isolation of the 1.9 million ha Manu National Park, together with neighboring protected areas,
131 have facilitated the preservation of the diverse vertebrate community of CCBS, making it one of

132 few sites worldwide that remains intact and accessible for study (Endo et al. 2010). It is thus an
133 ideal location to detail the effects of terrestrial mammals on seedling recruitment.

134 To determine the individual effects of small, medium and large mammals, we established
135 exclosures that differed in their permeability to each size class. We built exclosures in eight
136 randomly located blocks, separated by at least 250 m, within an area of 3 km². In each block, we
137 located one 2 x 2 m exclosure cages of each of five types 20 m apart along a randomly oriented
138 transect. There were 40 exclosures in total. NONE exclosures, which were impermeable to all
139 terrestrial mammals, were 90-cm tall wire hardware cloth (mesh size 1 cm), reinforced with iron
140 rebar at the corners and the middle of each side. SMALL exclosures were identical, but with 7 x
141 7 cm holes cut along the bottom edge of the walls, making them permeable to small mammals.
142 MEDIUM–LARGE exclosures consisted of 20 cm tall sheet-metal barriers to small mammals
143 (Supplemental Figure S1). Medium and large mammals could easily step over the walls to enter
144 the exclosure. MEDIUM combined the sheet metal of MEDIUM–LARGE with a wrapping of
145 barbed wire, which barred the entry of large mammals, making them permeable only to medium-
146 sized mammals. Finally, ALL treatments were only marked with rebar at the four corners,
147 permitting the entry of all terrestrial mammals.

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

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

173

174 *Data analysis*

175 All analyses were performed on the sum of surviving seeds and germinated seedlings. We
176 evaluated the effects of mammalian predation on seed and seedling survival using a parametric
177 survival regression, in which survival was predicted from the interacting effects of species and

178 treatment. As mortality risk is likely to decrease over time for seeds and seedlings, residuals
179 were assumed to follow a Weibull distribution.

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

191 We assessed the degree to which predation by each size-class of vertebrates shaped
192 species composition in two ways. First, to assess the effects of mammalian predation on local
193 species composition, we calculated the Bray-Curtis dissimilarity in species composition caused
194 by predation by each size-class of mammal *within* each of the eight geographical blocks at each
195 time of observation. Separately, we assessed the degree to which mammalian predation
196 generated beta diversity by calculating the Bray-Curtis dissimilarity in species composition
197 within each exclosure type *among* all pairwise combinations of blocks. Because Bray-Curtis
198 dissimilarity cannot exceed one (Magurran 2004) and because all exclosures began with identical
199 species compositions, we modeled these compositional dissimilarities using asymptotic mixed-
200 effect models that were forced through the origin (Pinheiro and Bates 2000). Asymptotes and

201 rate constants were allowed to vary among mammal size-classes as fixed effects. We included
202 experimental period as a random effect in the beta-diversity model, and both block and
203 experimental period in the local species composition model.

204 For all aspects of tree community structure, our interest regarded the effects of each size-
205 class of vertebrates, rather than of the treatments themselves. We used *a priori* orthogonal
206 contrasts among treatments to test the separate effects of each mammal size-class on each aspect
207 of tree community structure. The impact of each mammalian size-class was determined by
208 contrasting the pair of enclosure treatments that differed only in their permeability to that size
209 class. Accordingly, we contrasted NONE vs. SMALL enclosures to estimate the effect of small
210 mammals, NONE vs. MEDIUM for medium mammals, and MEDIUM vs. MEDIUM–LARGE
211 for large mammals. For species composition, dissimilarities between treatments were analyzed
212 directly, obviating the need for orthogonal contrasts.

213 For all response variables, the effects of mammalian predation were compared at two
214 points in time: 1.4 and 4.4 years, which were the durations of the shortest- and longest-duration
215 experimental periods, respectively (Table 1). At each of these time points, each response variable
216 was predicted using 1000 parametric bootstrap replicates. The effects of each size-class of
217 mammals on the response variables was assessed as the base-10 logarithm of the ratio of the
218 response variable in enclosures permeable to the given mammal size-class to its value in
219 enclosures from which the mammal size-class was excluded. Log₁₀-ratios of 1 or -1 indicate that
220 a mammal size-class caused a 10-fold increase or decrease in the response variable, respectively.
221 Mammalian effects were deemed significant if the 95% confidence intervals of the bootstrap
222 replicates did not include zero. Analyses were performed in R 3.2.3 (R Core Team 2015).
223 Survival and species composition models were fit using the ‘survival’ and ‘nlme’ libraries,

224 respectively (Pinheiro and Bates 2000), whereas all other analyses were implemented using the
225 ‘lme4’ library (Bates et al. 2014). All raw data and R code used in this study are available in a
226 Github repository (doi: 10.5281/zenodo.154042).

227

228 **Results**

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

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

246 Given their differential effects upon survival, mammalian predation also reduced

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

258 There was strong support for the first part of our fourth hypothesis, that mammals
259 preferentially preyed upon large-seeded species. Predation by all three size-classes of mammals
260 lead to significant decreases in the plot-mean seed mass over time. Small mammals had the
261 strongest effect, reducing plot-mean seed mass more than 10-fold (\log_{10} ratio: -1.01), whereas the
262 effects of medium-sized and large mammals were weaker (Fig. 4A). The evident preference of
263 mammals for larger-seeded species generated only weak effects on plot-mean wood density,
264 however, despite the significant negative relationship between seed mass and wood density
265 (Supplemental Figure S3). After 1.4 years, wood density was significantly increased by small
266 and large mammal predation, and significantly decreased by medium-sized mammals. Only the
267 effects of large mammals persisted through the end of the experiment, and they only increased
268 wood density by 4% (\log_{10} ratio 0.039; Fig. 4B). Small and medium-sized mammals, on the
269 other hand, strongly and significantly reduced plot-mean adult density by disproportionately

270 removing seeds of species that are common as adults, thus generating negative density
271 dependence (Fig. 4C). Both size-classes reduced plot-mean adult density by at least 100-fold by
272 the end of the experiment (\log_{10} ratios: -2.43 and -2.13 for small and medium mammals,
273 respectively). Large mammals reduced plot-mean adult density initially, though this effect
274 disappeared by the end of the study.

275

276 **Discussion**

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

290 Small and medium-bodied mammals more strongly affected tree community structure
291 than did large mammals, in accordance with previous studies (Asquith *et al.* 1997, DeMattia *et*
292 *al.* 2004, Norghauer *et al.* 2006, Paine and Beck 2007, Hautier *et al.* 2010). Not only did they

293 remove more seeds than did large-bodied mammals, they also generated beta diversity and
294 negative density dependence through their actions (Figs 1, 3B and 4C). The effects of large
295 mammals were altogether weaker, although they alone favored the recruitment of species with
296 dense wood by disproportionately preying upon species with low wood density (Fig. 4B). These
297 findings broaden and generalize those of the few previous studies that have attempted to link the
298 actions of mammalian seed predators to tree community structure (DeMattia *et al.* 2004, Paine
299 and Beck 2007, Theimer *et al.* 2011, Kurten *et al.* 2015).

300 Notably, ours is the first study, to our knowledge, to demonstrate that mammalian
301 predation can contribute to beta diversity, the change in species composition over space. Beta
302 diversity is generally assumed to arise from distance-limited seed dispersal (Chave and Leigh
303 2002), though biogeographical history also makes an important contribution (Dexter *et al.* 2012).
304 We suggest that spatial variation in canopy tree composition, together with the relatively small
305 home ranges of small- and medium-bodied mammals, could lead to spatial variation in search
306 images for preferred food items. This, in turn, would lead to spatial variation in species-specific
307 rates of seedling recruitment. Such a process could amplify and contribute to the patterns of beta
308 diversity observed in tropical tree communities.

309 Given the central role of negative density dependence for the maintenance of diversity
310 and its pervasive nature (Harms *et al.* 2000, Chesson 2000), understanding its generative
311 mechanisms is of great interest. Our findings add to the body of evidence that small-bodied
312 mammals can generate negative density dependence (Paine and Beck 2007), thus contributing to
313 stabilizing niche differences and thus species coexistence. Arthropods and pathogenic fungi can
314 also do so (Notman and Villegas 2005, Alvarez-Loayza and Terborgh 2011, Bagchi *et al.* 2014).
315 There remains a need for studies that evaluate the relative importance of the primary biotic

316 sources of mortality on tropical tree seedlings: fungi, insects and mammals, so that we may
317 better understand the mechanisms that generate tropical tree community structure.

318

319 *Abundance versus biomass*

320 The relative effects of small, medium and large-bodied mammals on tree community structure is
321 not easy to predict *a priori*. At Cocha Cashu Biological Station, small mammalian seed predators
322 outnumber medium- and large-bodied ones by an order of magnitude (419, 14 and 12
323 individuals·km⁻², respectively; Janson & Emmons 1990). The population-level biomass of large
324 mammalian seed predators at this site, however, far exceeds that of medium or small ones (590,
325 10 and 12 kg·km⁻², respectively; Janson & Emmons 1990; Endo et al. 2010). Moreover, the large
326 body size and rooting behavior of *Tayassu pecari* (White-lipped Peccary), the dominant large
327 terrestrial mammal at CCBS and across the Neotropics, cause them to have very strong *per*
328 *capita* effects (Beck 2005, Beck et al. 2013). The observation that small and medium-bodied
329 mammals had consistently stronger effects on tree community structure indicates that ubiquity,
330 imparted by very large population sizes, facilitates stronger trophic interactions than does great
331 individual biomass. In other words, a seed predator's ability to locate seeds is a better predictor
332 of its ecological impacts than is its jaw strength, at least for the 24 plant species used in this
333 study. Notably, all mammal size-classes were able to consume seeds (or seedlings) of all studied
334 species. Had this not been the case, for example, if some species had been chemically defended,
335 other outcomes would have been observed (Kuprewicz 2013).

336 Why were large mammals observed to have such weak effects on tree community
337 structure? The scale of the experimental exclosures may have played a role. Herds of *T. pecari*,
338 containing up to 200 individuals, travel approximately 10 km per day as they 'bulldoze' through

339 the understory (Wyatt and Silman 2004, Beck 2005). The 4-m² enclosure plots used in this study
340 may have been too small to attract the attention of these wide-ranging mammals. Notably, *T.*
341 *pecari* is the dominant seed predator of the palm *Astrocaryum murumuru* when it is found in
342 high-density aggregations, whereas *Proechimys* spp. and other small rodents are the primary seed
343 predators of isolated *A. murumuru* individuals (Beck and Terborgh 2002). Thus, *T. pecari* may
344 have weak effects on the tree community as a whole, but strong effects on a few species (Silman
345 *et al.* 2003, Wyatt and Silman 2004). It is likely that larger-scale enclosures would have more
346 equitably assessed the effects of large mammals on tree community composition (Kurten *et al.*
347 2015), although it would have been logistically challenging to achieve sufficient replication with
348 them.

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

357 Taken at face value, our results suggest that the consequences of hunting on tree
358 community structure should be relatively minor, because small and medium-sized mammals,
359 which are less-often hunted, more strongly contributed to tree community structure than did
360 large-bodied mammals, which are the preferred prey of hunters (Peres and Palacios 2007, Endo
361 *et al.* 2010). However, two considerations make this conclusion overly simplistic. First, in the

362 absence of mammalian seed predation, many seeds are destroyed by fungal pathogens, bacteria,
363 or arthropods, some of which can generate negative density dependence (Bagchi et al. 2014).
364 This was observed in our study, as few seeds or seedlings survived to the end of the experiment,
365 even in the CLOSED treatment (Supplemental Figure S2). Thus, the consequences for the tree
366 community of the local extirpation of large mammalian seed predators could be, at least in part,
367 compensated for by the actions of smaller-bodied organisms (Asquith et al. 1997). Second,
368 hunting by humans extirpates large-bodied arboreal primates as well as terrestrial mammals, thus
369 affecting both seed dispersal and seed predation. Across Amazonia, heavily hunted sites retain
370 approximately 10% of the population density of ateline primates (*Ateles* and *Lagothrix*),
371 compared to non-hunted sites of equivalent productivity (Peres and Palacios 2007). These genera
372 of frugivorous primates provide the irreplaceable ecological service of seed dispersal to roughly
373 23% of genera of Neotropical trees (Peres et al. 2015). Thus, although the ecological
374 consequences of human hunting on seed predation are likely to be relatively modest, the impacts
375 on seed dispersal are substantial and detrimental (Kurten et al. 2015). Observational studies of
376 hunted forests show strong directional change in tree species composition (Terborgh et al. 2008,
377 Harrison et al. 2013). We suggest that these changes are more likely to be driven by reduced seed
378 dispersal than by reduced seed predation.

379 Terborgh (2012) levelled three criticisms at studies such as the current one, which he
380 referred to as ‘seed presentation trials’. First, *they are conducted with relatively large seeds*.
381 Though seeds masses in the current study spanned two orders of magnitude, tree seeds in
382 Neotropical forests vary over seven orders of magnitude (Wright et al. 2007). This could be seen
383 as limiting our ability to make inferences on the effects of mammalian predation on small-seeded
384 species. Most small-seeded species require high light to germinate, however, and our results

385 suggest that very small-seeded species are likely to escape the notice of mammals (Fig. 4A).
386 Thus, their recruitment dynamics are likely to be relatively independent of mammalian seed
387 predators.

388 Second, *abundant seeds are displayed conspicuously*. In contrast, naturally dispersed
389 seeds are often scattered as they fall from the canopy and are subsequently covered by leaf litter.
390 In the current study, conspecific seeds were placed in groups in each 4 m² enclosure, a far greater
391 density than the one viable seed per m² observed in a concurrent seed-trapping at CCBS (Swamy
392 et al. 2010). By artificially elevating the natural density of seed rain, the enclosure cages could
393 have become more attractive foraging sites for seed predators than they might otherwise have
394 been. This increase in food abundance is likely to have influenced mammal behavior. Although
395 this elevated abundance was unavoidable and necessary for efficient data collection, we partially
396 addressed the concern about conspicuousness by replacing leaf litter that had fallen on the seeds
397 after every census.

398 Third, *the seeds used are typically undispersed, and have been cleaned of pulp*. Such pre-
399 treatment can alter the olfactory cues that attract both seed predators and secondary dispersers,
400 and can thus affect the probabilities of being eaten or buried. Secondary dispersal and burial by
401 rodents or dung beetles increase dispersal, reduce predation, and enhance survival to the seedling
402 stage (Andresen and Levey 2004, Vander Wall et al. 2005, Hirsch et al. 2012). Cleaning seeds
403 may have shaped the outcome of our experiment in two ways: our seeds may have been less
404 likely to be found by mammalian seed predators than ones reeking of dung, and seeds buried by
405 dung beetles or scatter-hoarding mammals were counted as dead. The former effect would lead
406 us to underestimate the effects of mammalian predation, because more seeds would have been
407 consumed, had they been covered in dung. The latter, on the other hand, would lead us to

408 overestimate the effects of mammalian predation, because seeds that were removed or buried,
409 and subsequently germinated, were considered by us to have died. The relative magnitude of
410 these countervailing effects remains unclear. Nevertheless, we stand by our decision to clean
411 seeds prior to their placement in the exclosures. To have done otherwise would have been
412 impractical.

413

414 **Conclusions**

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

423

424 **Acknowledgements**

425 The Peruvian Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP)
426 granted us permission to conduct research in Manu National Park. We thank the many people
427 involved in the establishment and monitoring of this study, including Gabriela Nuñez, Cornelio
428 Machaca, Pamela Weisenhorn, Patricia Alvarez-Loayza, Cecilia Carrasco, Beth Pringle, and
429 Karim Ledesma. Comments from Kirsten Hazelwood improved the manuscript.

430

431 **Literature Cited**

- 432 Alvarez-Loayza, P., and J. W. Terborgh. 2011. Fates of seedling carpets in an Amazonian
433 floodplain forest: intra-cohort competition or attack by enemies? *Journal of Ecology*
434 99:1045–1054.
- 435 Andresen, E., and D. J. Levey. 2004. Effects of dung and seed size on secondary dispersal, seed
436 predation, and seedling establishment of rain forest trees. *Oecologia* 139:45–54.
- 437 Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition
438 control recruitment in neotropical forests? Evidence from Panama. *Ecology* 78:941–946.
- 439 Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton,
440 and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and
441 composition. *Nature* 506:85–88.
- 442 Bates, D. M., M. Maechler, B. M. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects
443 models using Eigen and S4. R package.
- 444 Beck, H. 2005. Seed Predation and Dispersal by Peccaries throughout the Neotropics and its
445 Consequences: a Review and Synthesis. Page 77 in P. M. Forget, J. E. Lambert, P. E.
446 Hulme, and S. B. Vander Wall, editors. *Seed Fate: Predation, Dispersal and Seedling*
447 *Establishment*. CABI Publishing, Wallingford, UK.
- 448 Beck, H., J. W. Snodgrass, and P. Thebpanya. 2013. Long-term exclosure of large terrestrial
449 vertebrates: Implications of defaunation for seedling demographics in the Amazon
450 rainforest. *Biological Conservation* 163:115–121.
- 451 Beck, H., and J. W. Terborgh. 2002. Groves versus isolates: how spatial aggregation of
452 *Astrocaryum murumuru* palms affects seed removal. *Journal of Tropical Ecology* 18:275–
453 288.

- 454 Chave, J. J., D. A. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009.
455 Towards a worldwide wood economics spectrum. *Ecology letters* 12:351–66.
- 456 Chave, J., and E. G. Leigh. 2002. A spatially explicit neutral model of beta-diversity in tropical
457 forests. *Theoretical Population Biology* 62:153–168.
- 458 Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual review of Ecology*
459 and *Systematics* 31:343–366.
- 460 Daubenmire, R. F. 1940. Exclosure technique in ecology. *Ecology* 21:514–515.
- 461 DeMattia, E. A., L. M. Curran, and B. J. Rathcke. 2004. Effects of Small Rodents and Large
462 Mammals on Neotropical Seeds. *Ecology* 85:2161–2170.
- 463 Dexter, K. G., J. W. Terborgh, and C. W. Cunningham. 2012. Historical effects on beta diversity
464 and community assembly in Amazonian trees. *Proceedings of the National Academy of*
465 *Sciences of the United States of America* 109:7787–92.
- 466 Endo, W., C. A. Peres, E. Salas, S. Mori, J. L. Sanchez-Vega, G. H. Shepard, V. Pacheco, and D.
467 W. Yu. 2010. Game vertebrate densities in hunted and nonhunted forest sites in Manu
468 National Park, Peru. *Biotropica* 42:251–261.
- 469 Gentry, A. H. 1990. *Four Neotropical Forests*. Book, Yale University Press, New Haven, CT.
- 470 Green, P. T., K. E. Harms, and J. H. Connell. 2014. Nonrandom, diversifying processes are
471 disproportionately strong in the smallest size classes of a tropical forest. *Proceedings of the*
472 *National Academy of Sciences* 111:18649–18654.
- 473 Harms, K. E., S. J. Wright, O. Calderón, A. Hernandez, and E. A. Herre. 2000. Pervasive
474 density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*
475 404:493–495.
- 476 Harrison, R. D., S. Tan, J. B. Plotkin, F. Slik, M. Detto, T. Brenes, A. Itoh, and S. J. Davies.

- 477 2013. Consequences of defaunation for a tropical tree community. *Ecology letters* 16:687–
478 694.
- 479 Hautier, Y., P. Saner, C. D. Philipson, R. Bagchi, R. C. Ong, and A. Hector. 2010. Effects of
480 seed predators of different body size on seed mortality in Bornean logged forest. *PLoS one*
481 5:e11651.
- 482 Hirsch, B. T., R. Kays, V. E. Pereira, P. A. Jansen, and M. Rejmanek. 2012. Directed seed
483 dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent.
484 *Ecology Letters* 15:1423–1429.
- 485 Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. S. Condit, B. Wechsler, S. J. Wright,
486 and S. L. de Lao. 1999. Light-Gap disturbances, recruitment limitation, and tree diversity in
487 a neotropical forest. *Science* 283:554–7.
- 488 Janson, C. H., and L. H. Emmons. 1990. Ecological structure of the nonflying mammal
489 community at Cocha Cashu Biological Station, Manu National Park, Peru. *Four Neotropical*
490 *Rainforests*:314–338.
- 491 Kuprewicz, E. K. 2013. Mammal Abundances and Seed Traits Control the Seed Dispersal and
492 Predation Roles of Terrestrial Mammals in a Costa Rican Forest. *Biotropica* 45:333–342.
- 493 Kurten, E. L., S. J. Wright, W. P. Carson, and T. M. Palmer. 2015. Hunting alters seedling
494 functional trait composition in a Neotropical forest. *Ecology* 96:1923–1932.
- 495 Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Publishing Ltd.
- 496 Norghauer, J. M., J. R. Malcolm, B. Zimmerman, and J. M. Felfili. 2006. An experimental test of
497 density- and distant-dependent recruitment of mahogany (*Swietenia macrophylla*) in
498 southeastern Amazonia. *Oecologia* 148:437–446.
- 499 Notman, E., and A. C. Villegas. 2005. Patterns of Seed Predation by Vertebrate versus

- 500 Invertebrate Seed Predators among Different Plant Species, Seasons and Spatial
501 Distributions. Pages 55–75 Seed Fate: Predation, Dispersal and Seedling Establishment.
502 CABI Publishing, Wallingford, UK.
- 503 Paine, C. E. T., and H. Beck. 2007. Seed predation by Neotropical rain forest mammals increases
504 diversity in seedling recruitment. *Ecology* 88:3076–87.
- 505 Peres, C. A., E. Thaise, J. Schietti, S. J. M. Desmoulieres, and T. Levi. 2015. Dispersal limitation
506 induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the*
507 *National Academy of Sciences of the United States of America* 113:892–897.
- 508 Peres, C., and E. Palacios. 2007. Basin-Wide Effects of Game Harvest on Vertebrate Population
509 Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal.
510 *Biotropica* 39:304–315.
- 511 Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Book, Springer
512 Verlag.
- 513 R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation
514 for Statistical Computing, Vienna.
- 515 Reyna-Hurtado, R., E. Rojas-Flores, and G. W. Tanner. 2009. Home Range and Habitat
516 Preferences of White-Lipped Peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico.
517 *Journal of Mammalogy* 90:1199–1209.
- 518 Richard-Hansen, C., N. Surugue, K. Khazraie, M. Le Noc, and P. Grenand. 2014. Long-term
519 fluctuations of white-lipped peccary populations in French Guiana. *Mammalia* 78:291–301.
- 520 Silman, M. R., J. W. Terborgh, and R. A. Kiltie. 2003. Population regulation of a dominant rain
521 forest tree by a major seed predator. *Ecology* 84:431–438.
- 522 Swamy, V., J. W. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, F. Cornejo, and P. Alvarez-

- 523 Loayza. 2010. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling
524 recruitment in a tropical forest. *Ecology letters* 14:195–201.
- 525 Terborgh, J. W. 2012. Enemies Maintain Hyperdiverse Tropical Forests. *The American*
526 *Naturalist* 179:303–314.
- 527 Terborgh, J. W., G. Nuñez-Iturri, N. C. a. Pitman, F. H. C. Valverde, P. Alvarez-Loayza, V.
528 Swamy, E. G. Pringle, and C. E. T. Paine. 2008. Tree recruitment in an empty forest.
529 *Ecology* 89:1757–1768.
- 530 Theimer, T. C., C. A. Gehring, P. T. Green, and J. H. Connell. 2011. Terrestrial vertebrates alter
531 seedling composition and richness but not diversity in an Australian tropical rain forest.
532 *Ecology* 92:1637–47.
- 533 Vickers, W. T. 1991. Hunting yields and game composition over ten years in an Amazon Indian
534 territory. *Neotropical wildlife use and conservation* 400:53–81.
- 535 Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005. Seed Removal, Seed Predation, and
536 Secondary Dispersal. *Ecology* 86:801–806.
- 537 Wright, I. J., D. D. Ackerly, F. Bongers, K. E. Harms, G. Ibarra-Manriquez, M. Martinez-Ramos,
538 S. J. Mazer, H. C. Muller-Landau, H. Paz, N. C. a. Pitman, L. Poorter, M. R. Silman, C. F.
539 Vriesendorp, C. O. Webb, M. Westoby, S. J. Wright, M. Martínez-Ramos, S. J. Mazer, H.
540 C. Muller-Landau, H. Paz, N. C. a. Pitman, L. Poorter, M. R. Silman, C. F. Vriesendorp, C.
541 O. Webb, M. Westoby, S. J. Wright, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-
542 Landau, H. Paz, N. C. a. Pitman, L. Poorter, M. R. Silman, C. F. Vriesendorp, C. O. Webb,
543 M. Westoby, and S. J. Wright. 2007. Relationships among ecologically important
544 dimensions of plant trait variation in seven neotropical forests. *Annals of Botany* 99:1003–
545 1015.

546 Wyatt, J. L., and M. R. Silman. 2004. Distance-dependence in two Amazonian palms: effects of
547 spatial and temporal variation in seed predator communities. *Oecologia* 140:26–35.

548

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

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

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

553 **Figure Legends**

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

561

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

567

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

574

575 **Figure 4** Predation by mammals led to changes in plot-mean A) seed mass, B) wood
576 density and C) adult density. The effects of mammals are represented as the \log_{10} ratio of the
577 response variable in exclosures to which the mammals had access, versus those from which

578 they were excluded. Predicted effects and confidence intervals are derived from mixed-effect
579 models. Note that the Y-axis scales vary among panels.

580

581 **Supplemental Information**

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

583

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

590

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

593