



## Seed traits, not density or distance from parent, determine seed predation and establishment in an Afrotropical forest

Cooper Rosin<sup>1,2,3</sup> , and John R. Poulsen<sup>1</sup>

<sup>1</sup> Nicholas School of the Environment, Duke University, 9 Circuit Dr., Durham, NC, U.S.A.

<sup>2</sup> Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 550 N. Park St., Madison, WI, U.S.A.

### ABSTRACT

Seed predators drive patterns in seed mortality and seedling establishment and are posited to contribute to the maintenance of plant species diversity through several mechanisms. Negative density dependence and spatially restricted recruitment are apparently widespread in Neotropical forests, but are little studied in Afrotropical forests, where generalist vertebrates may contribute more to seed mortality than do specialized invertebrates and fungi. We experimentally assessed the roles of seed density and distance from the parent tree for ten tree species in a forest in northeastern Gabon, using exclosures to isolate the effects of different seed predator types. Vertebrates caused greater seed losses than all other mortality agents combined. Unexpectedly, seeds under fruiting conspecific trees had significantly lower removal and higher seedling establishment than those under heterospecific trees or in neutral non-fruiting locations. Seed density did not significantly affect seedling establishment. Vertebrate seed removal ranged from 0 percent to 100 percent among focal species and was positively correlated with seed mass but had no relationship with species commonness (adult tree density). Seed traits strongly affected patterns of seed removal and seedling establishment and may contribute more to the likelihood of success for an individual seed than do its density or distance from parent. Our results highlight an apparent divergence in patterns of seed mortality and seedling establishment between tropical forest regions and emphasize the need for further comparative study.

*Key words:* exclosure; Gabon; Janzen-Connell hypothesis; seed predation; tropical forest.

SEED PREDATION IS A PROMINENT ECOLOGICAL PROCESS DETERMINING PATTERNS OF SEED MORTALITY AND PLANT REPRODUCTIVE SUCCESS (Janzen 1971, Crawley 1992, Hulme 1998). In tropical forests, distance- and density-responsive seed predators may also contribute to the maintenance of high plant species diversity (Janzen 1970, Connell 1971, Bagchi *et al.* 2014). Mechanisms of distance and density dependence are not limited to the seed-to-seedling transition, though demographic filtering is often greatest at early life stages (Terborgh 2012, Green *et al.* 2014). Thus, seed density and distance from parent are likely major determinants of mortality and are posited to drive patterns of seed predation and seedling establishment (Howe & Smallwood 1982, Hammond & Brown 1998).

The process of seed predation is little studied in Afrotropical lowland forests, especially compared to forests of the Neotropics. With limited research, strong evidence for host-specificity and Janzen-Connell patterns of seed mortality is so far lacking (Clark *et al.* 2012), though there is some evidence of these patterns in seedling herbivory (Matthesius *et al.* 2011), and an apparent role of seed density (but not dispersal distance) in driving patterns of seedling recruitment and survival (Poulsen *et al.* 2012). Compared to Neotropical forests that house diverse and abundant invertebrates and fungi—the actors principally responsible for driving patterns of spatially restricted recruitment (Terborgh 2012, Bagchi

*et al.* 2014, Fricke *et al.* 2014)—Afrotropical forests tend to be drier and feature lower species diversity of plants and most other taxa (Corlett & Primack 2011). Lower tree diversity in Afrotropical forests may result in—or be caused by—a lower frequency and intensity of attack by specialized natural enemies. Indeed, in one Afrotropical forest, seed losses to generalist rodents were more than 5-fold higher than those to invertebrates and fungi combined (Rosin & Poulsen 2016). Despite low contribution to seed predation overall, specialized natural enemies may nonetheless generate distance and density effects for seedling establishment, but such patterns have not yet been documented in Afrotropical forests.

Generalist seed predators may also contribute to the maintenance of tree diversity through several mechanisms. In Borneo, Hautier *et al.* (2010) documented that small mammals significantly reduced the survival of seeds under conspecific—but not heterospecific—adult trees, as well as in high—but not low—densities; they suggested that small mammals maintain small home ranges and preferentially select local (conspecific) seeds, thereby acting functionally as specialists and generating Janzen-Connell patterns. In Peru, Paine and Beck (2007) and Paine *et al.* (2016) found that rodents preferentially removed common and large-seeded species from experimental plots and hypothesized that such selective seed consumption could generate a rare-species advantage. In Panama, Garzon-Lopez *et al.* (2015) demonstrated that generalist rodents with overlapping diets can act as ‘shared enemies’ of certain seed species, contributing in a

Received 11 June 2018; revision accepted 31 July 2018.

<sup>3</sup>Corresponding author; e-mail: crosin@wisc.edu

complementary manner to traditional host-specific Janzen-Connell mortality patterns. Whether any or all of these diversity-maintaining mechanisms are operating consistently, and in other tropical forest localities, remains to be seen.

We experimentally tested three mutually compatible hypotheses in a forest in northeastern Gabon: (1) rodents are the dominant seed predators and significantly reduce seedling establishment; (2) seed mortality by rodents and/or other biotic agents (including arthropods and fungi) is greatest for seeds under conspecific adult trees, and for seeds in high densities; and (3) rodents preferentially remove seeds from common and large-seeded species.

## METHODS

**STUDY SITE.**—We conducted this study in the forest surrounding the Ipassa Research Station, in the Ogooué-Ivindo region of northeastern Gabon. The region is dominated by lowland tropical forest and receives approximately 1700 mm of rain annually, with two rainy seasons (September–December and March–June). Despite its protected status as part of Ivindo National Park, the Ipassa forest is occasionally hunted. A few species of game animals—including bay duikers (*Cephalophus dorsalis*) and red river hogs (*Potamochoerus porcus*)—have been reduced in abundance as a result (Okouyi *et al.* 2001, van Vliet *et al.* 2007). Nonetheless, the forest boasts high mammal diversity (Okouyi *et al.* 2002, Koerner *et al.* 2017) and an apparently intact small mammal community (Markham 2015). The most prominent terrestrial seed consumers in this system are the Emin’s giant pouched rat (*Cricetomys emini*) and the African brush-tailed porcupine (*Atherurus africanus*), both of which primarily act as seed predators, though the latter of which sometimes acts as a scatterhoarder (Rosin & Poulsen 2017).

**EXPERIMENTAL DESIGN.**—We employed seed exclosures to experimentally assess the effects of (A) seed predator body size; (B) seed density; and (C) seed location on patterns of seed predation and seedling establishment for 10 tree species (Fig. 1). To isolate the effects of seed predator body size, we used three exclosure treatments: (1) *open*, leaving seeds unprotected from predators; (2) *partial*, excluding large ( $\geq 4$  kg) but not small vertebrates from accessing seeds; and (3) *closed*, excluding all vertebrates. For each treatment, we cleared approximately half the volume of leaf litter from the treatment’s ground area (0.6 m  $\times$  0.6 m) to facilitate visual seed monitoring. To construct the exclosures, we erected four 45 cm tall plastic-coated steel garden stakes to support galvanized 1.3 cm mesh hardware cloth walls and a roof, secured with zip ties. To exclude all vertebrates from the *closed* exclosure, we folded the base of the hardware cloth flush with the soil and secured it with 15 cm lawn staples. To allow the terrestrial entry of small mammals in the *partial* exclosure, we elevated the base of the hardware cloth 10 cm off the ground—this allowed for the entry of all rodents and other terrestrial mammals up to and including the African brush-tailed porcupine (*Atherurus africanus*; mass  $\leq 4$  kg), but excluded all larger

mammals, including duikers (*Cephalophus* spp.), red river hogs (*Potamochoerus porcus*), and mandrills (*Mandrillus sphinx*).

To assess the effects of seed density and location, we used a seed pairing approach modified from Hautier *et al.* (2010; Fig. 1). We repeated our experimental design for four consecutive experiments (establishing new locations for each), using seeds from a total of 10 tree species (Table 1). For each experiment, we placed seeds of two or three tree species at both *low* (one seed per species) and *high* (five seeds per species) density into each of the three exclosure types, creating six unique treatments of seed access and density. We established these treatments under one fruiting tree of each seed species and a neutral non-fruiting location haphazardly chosen at a minimum of 250 m from any other treatment. We surveyed each location to ensure that no other fruiting trees were present within a  $\sim 30$  m radius. The mean distance between nearest locations was  $\sim 400$  m (range = 177–794 m).

**FOCAL SPECIES.**—We conducted the experiments during the active fruiting period of each focal species, with experiments starting in September 2014 (Experimental Group 1; see Table 1), December 2014 (Experimental Group 2), February 2015 (Experimental Group 3), and March 2015 (Experimental Group 4). We selected species to encompass variation across several seed traits (size, diaspore type, and dispersal mode) as well as a range of adult tree abundance, from rare to common. Our focal species varied in seed mass 300-fold (0.1 g to  $\sim 30$  g), spanned a range in seed coat hardness from very soft to hard, ranged in adult abundance 71-fold (0.3–29.4 stems/ha), and included four animal-dispersed, three wind-dispersed, and three gravity/ballistically dispersed species.

We collected seeds from the ground beneath their parent trees. Prior to seed sowing, we cleaned flesh from fleshy-fruited seeds by hand or with a dull knife and inspected all seeds, discarding seeds with signs of fungal or arthropod damage. After placement, we assessed the condition of the seeds at days 15, 30, and 60, to allow sufficient time for seeds to either establish as seedlings or die. We noted germination as the visible emergence of a shoot and seed removal as the absence of the seed from the treatment area. We visually inspected all seeds that failed to germinate, identifying the apparent agent of mortality when applicable: fungal spores indicated fungus, while larvae, bore holes, or hollowed seeds indicated invertebrates. We defined seedling establishment as the point at which the rooted living seedling had no seed endosperm remaining.

**STATISTICAL ANALYSIS.**—We used generalized linear mixed-effects models (GLMMs) with binomial error distributions to model both seed removal (binary response: removed or not removed) and seedling establishment (binary response: established or died) as a function of seed density (*low* or *high*) and location (a proxy for dispersal, with heterospecific and neutral treatments combined to represent dispersed seeds, and conspecific treatments representing undispersed seeds), with seed species as a random effect. To increase statistical power, we pooled data from the *partial* and

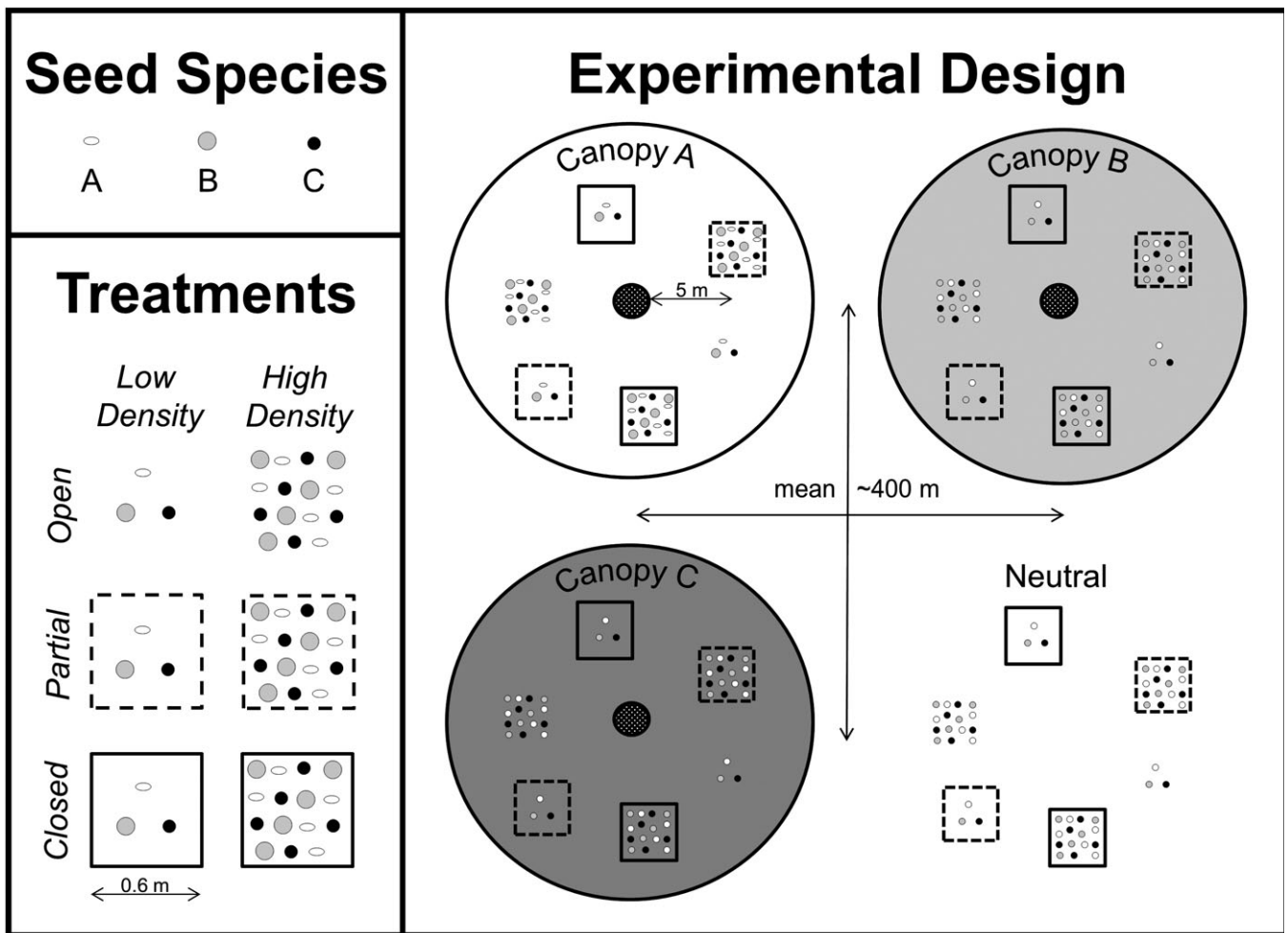


FIGURE 1. Experimental design. Using two or three seed species (upper left), and six treatments with varying seed density (*Low* = 1 seed per species, *High* = 5 seeds per species) and vertebrate access (*Closed* = no access, *Partial* = rodent access, *Open* = all access; lower left), we established treatment locations under one fruiting tree of each species, plus a random neutral non-fruiting location (with a mean distance of ~400 meters between nearest locations). We repeated this design for four consecutive experiments (each in a new location), using seeds from 10 tree species. Thus, we established a total of 10 focal tree locations and four neutral locations.

*open* treatments, given their similar results (see below). Our first model included an interaction between seed density and location. Because this interaction was non-significant, we developed a second, simplified model that included these variables as separate terms. Our third model assessed the three locations separately, rather than combining heterospecific and neutral locations. We treated individual seeds as independent of each other; while a seed in close proximity to other seeds is more likely to be discovered, seed predators evaluate each encountered seed independently, and the fate of two nearby seeds may not be the same, especially when they belong to different species.

We used generalized linear models (GLMs) to model three relationships between the following pairs of predictor and response variables across all seed species: (1) the proportion of seeds removed and the proportion established as seedlings; (2) seed mass and the proportion of seeds removed; and (3) adult tree abundance and the proportion of seeds removed.

We followed the recommendations for GLMMs outlined by Bolker *et al.* (2009) and performed statistical analyses in R 3.2.3 (R Development Core Team 2015), using the *lme4* package (Bates *et al.* 2015).

## RESULTS

We assessed seed mortality and seedling establishment for a total of 648 seeds from 10 species (Table 1). Across all species in the *open* treatments ( $N = 216$  seeds), 29 percent of seeds established as seedlings, 50 percent were removed by vertebrates, 10 percent killed by invertebrates, <1 percent killed by fungi, and 11 percent germinated but failed to establish for unknown reasons (Fig. 2). In the *partial* treatments ( $N = 216$  seeds), 29 percent of seeds established as seedlings, 46 percent were removed by vertebrates, 12 percent killed by invertebrates, 3 percent killed by fungi, and 10 percent germinated but failed to establish for unknown

TABLE 1. Experimental groupings and characteristics of focal seeds. Seed hardness was determined manually according to the following categories: very soft (easily crushed with fingernail), soft (dented with fingernail), medium (dented by metal nail held by hand), hard (dented with metal nail and hammer), and very hard (difficult to dent with metal nail and hammer). Adult abundance was calculated as the number of stems  $\geq 10$  cm within 14 local 1-ha plots that included a total of 6140 stems (J. R. Poulsen, unpubl. data).

Exp. group	Scientific name	Family	Adult abundance (stems/ha)	Seed mass (g)	Seed length (mm)	Seed hardness	Diaspore type	Dispersal mode
1	<i>Pycnanthus angolensis</i>	Myristicaceae	0.6	1.4	18	Medium	Fleshy	Animal
	<i>Pentaclethra macrophylla</i>	Fabaceae	1.8	29.4	64	Hard	Pod	Ballistic/gravity
	<i>Pentaclethra eetveldeana</i>	Fabaceae	3.7	2.4	31	Hard	Pod	Ballistic/gravity
2	<i>Cylicodiscus gabunensis</i>	Fabaceae	0.3	0.9	104	Very soft	Winged	Wind
	<i>Pseudospondias microcarpa</i>	Anacardiaceae	0.9	0.9	19	Hard	Fleshy	Animal
	<i>Diospyros crassiflora</i>	Ebenaceae	6.1	18.1	47	Medium	Fleshy	Animal
3	<i>Scorodaphloeus zenkeri</i>	Fabaceae	21.5	2.6	28	Hard	Pod	Ballistic/gravity
	<i>Piptadeniastrum africanum</i>	Fabaceae	0.9	0.1	42	Very soft	Winged	Wind
	<i>Daeryodes buettneri</i>	Burseraceae	2.6	4.6	34	Medium	Fleshy	Animal
4	<i>Pterocarpus soyauxii</i>	Fabaceae	0.3	0.3	73	Soft	Winged	Wind

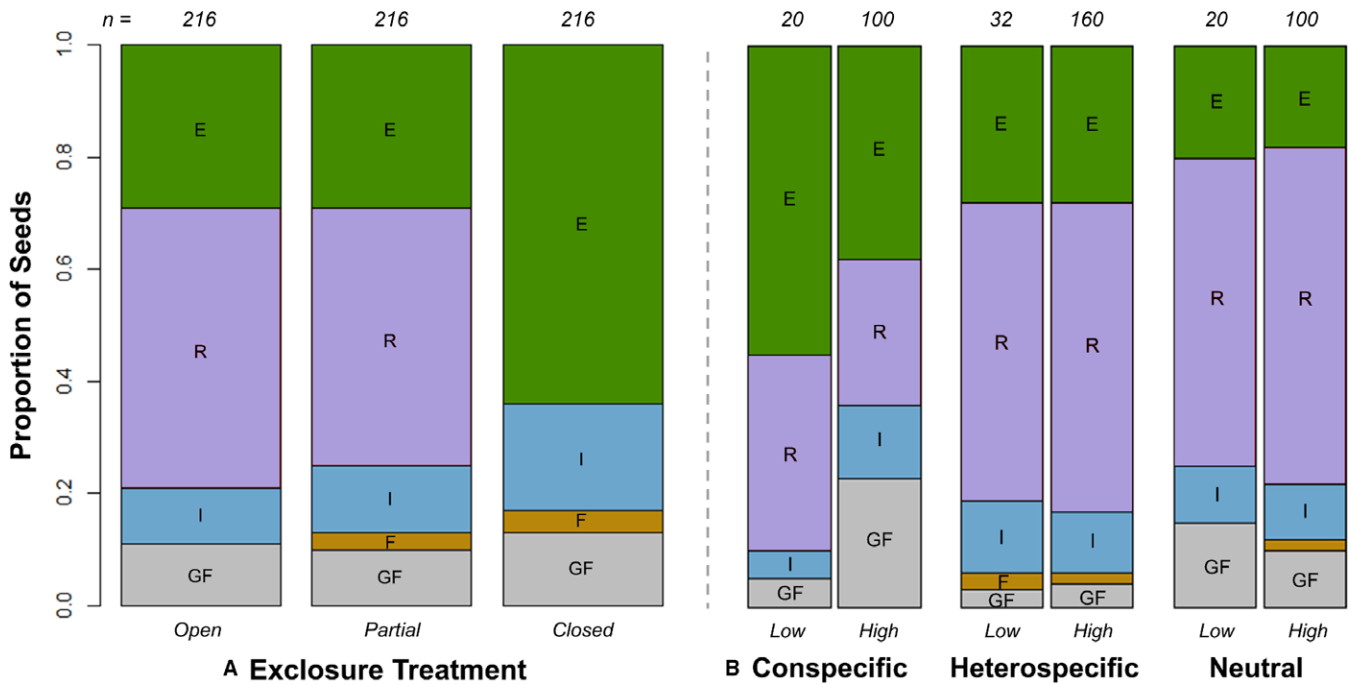


FIGURE 2. (A) Fate of all seeds across exclosure treatments (see Methods). Seed fate categories include established (E), removed (R), invertebrate killed (I), fungus killed (F), and germinated but failed to establish for unknown reasons (GF). Sample sizes are listed above each bar. (B) Fate of all seeds in the *Open* and *Partial* treatments (pooled together given their comparable fates) grouped by seed density (*Low* = 1 seed, *High* = 5 seeds) and location (beneath a conspecific fruiting tree, beneath a heterospecific fruiting tree, or in a random neutral non-fruiting location).

reasons. In the absence of vertebrates (*closed* treatments,  $n = 216$  seeds), 64 percent of seeds established as seedlings, 19 percent were killed by invertebrates, 4 percent killed by fungi, and 13 percent germinated but failed to establish.

Across all seeds of all species, there was no significant difference in removal between seeds placed at *high* versus *low* densities (GLMM:  $\chi = 0.09$ ,  $df = 647$ ,  $P = 0.931$ ; Fig. 2). Seed removal was significantly higher for seeds under heterospecific trees or

neutral locations (grouped as ‘dispersed’) than those sowed under conspecific trees (‘undispersed’; GLMM:  $\chi = -4.19$ ,  $df = 647$ ,  $P < 0.001$ ). Assessing the three seed locations separately, seed removal was significantly higher both for seeds under heterospecific trees (GLMM:  $\chi = 4.07$ ,  $df = 647$ ,  $P < 0.001$ ) and seeds in neutral non-fruiting locations (GLMM:  $\chi = 4.86$ ,  $df = 647$ ,  $P < 0.001$ ; Fig. 2) than for seeds under conspecific trees.

As with seed removal, there was no significant difference in seedling establishment between seeds placed at *high* versus *low* densities (GLMM:  $\chi = 1.60$ ,  $df = 647$ ,  $P = 0.111$ ; Fig. 2). Seedling establishment was significantly lower for seeds under heterospecific trees or neutral locations (grouped as ‘dispersed’) than those sowed under conspecific trees (‘undispersed’; GLMM:  $\chi = 2.53$ ,  $df = 647$ ,  $P = 0.012$ ). Assessing the three seed locations separately, seedling establishment did not differ significantly between seeds under heterospecific and conspecific trees (GLMM:  $\chi = -1.14$ ,  $df = 647$ ,  $P = 0.255$ ), but was significantly lower for seeds in neutral non-fruiting locations than under conspecific trees (GLMM:  $\chi = -3.74$ ,  $df = 647$ ,  $P < 0.001$ ; Fig. 2).

The proportions of seeds removed and established as seedlings varied widely among species (Fig. 3). Overall, the proportion of seeds that established as seedlings in the *open* and *partial* treatments declined significantly with increasing seed removal (GLM:  $df = 9$ ,  $P < 0.001$ ). Seed removal ranged from 0 percent (*C. gabunensis*;  $N = 36$  seeds) to 100 percent (*P. macrophylla*;  $N = 48$  seeds), while seedling establishment ranged from 0 percent (*P. macrophylla*;  $N = 48$  seeds) to 56 percent (*D. buettneri*;  $N = 36$  seeds). In the absence of vertebrates (*closed* treatment), seedling establishment ranged from 33 percent (*S. zenkeri*;  $n = 24$  seeds) to 96 percent (*P. macrophylla*;  $N = 24$  seeds). The proportion of seeds removed (*open* and *partial* treatments) increased with seed mass, though the relationship was only marginally significant (GLM:  $df = 9$ ,  $P = 0.081$ ). Seed removal had no relationship with adult tree abundance (GLM:  $df = 9$ ,  $P = 0.906$ ; Fig. 3).

## DISCUSSION

Vertebrates caused the greatest overall seed mortality in our study, preying on more seeds than all other mortality agents combined

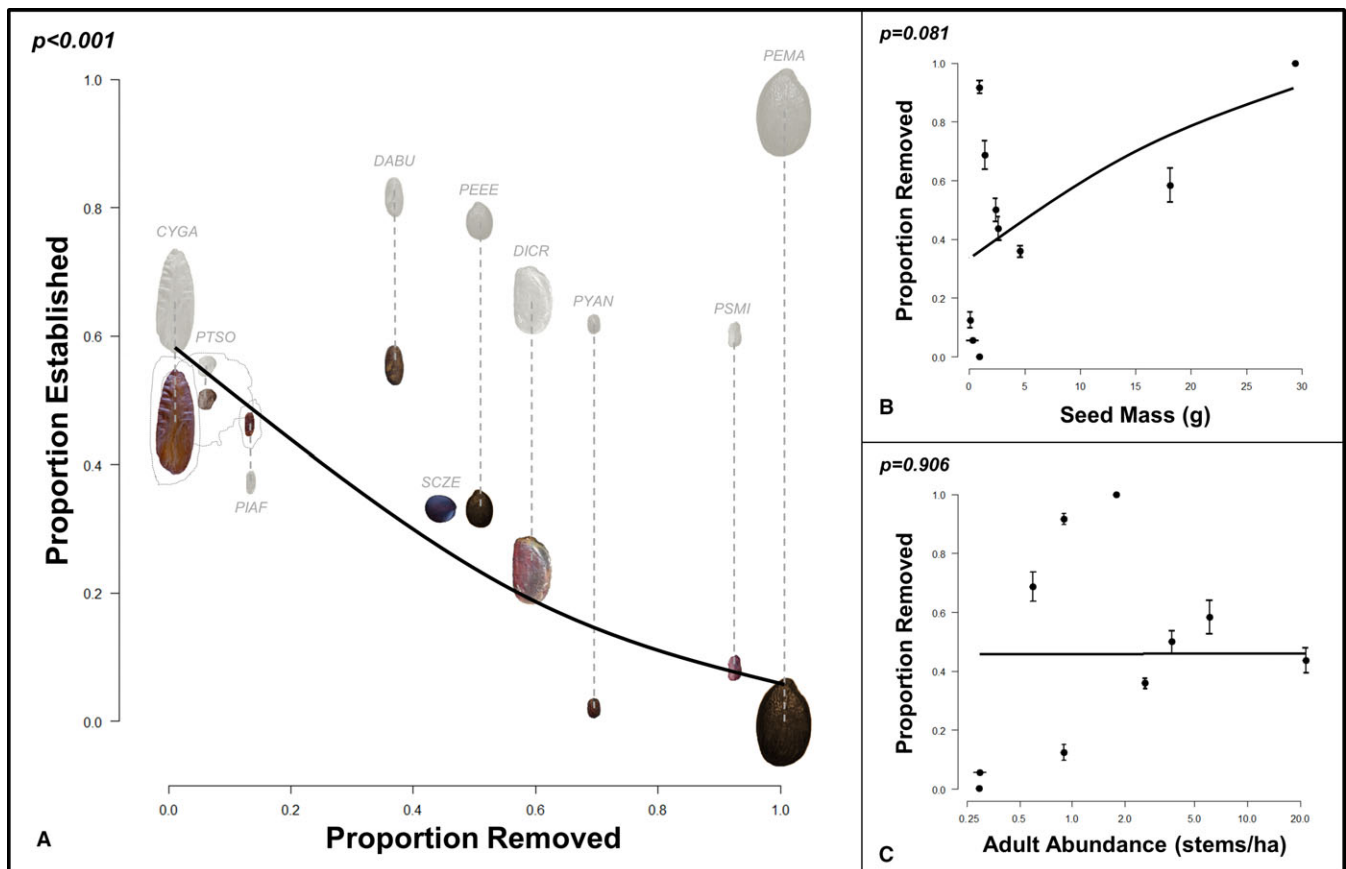


FIGURE 3. (A) Seed establishment versus removal by vertebrates, both in the presence of vertebrates (*Partial* and *Open* treatments: colored images) and in their absence (*Closed* treatment: gray images). Vertical dotted lines represent the degree to which vertebrate seed predators reduced establishment. Each species is identified by a four-letter species code. The wings of wind-dispersed seeds are outlined by gray dotted lines. (B) Seed removal versus seed mass. (C) Seed removal versus adult tree abundance (stems  $\geq 10$  cm  $ha^{-1}$ ). Fitted curves represent GLM model results, with  $P$ -values displayed in the upper left corner of each pane.



(Fig. 2). Rates of seed removal were similar between the *open* and *partial* treatments (50% [ $N = 216$ ] and 46% [ $N = 216$ ], respectively), suggesting that rodents are the dominant seed predators in this system. Though our study directly measured seed removal, not seed predation, prior research indicates that the vast majority of seeds removed by vertebrates are killed (Rosin & Poulsen 2017). Rodent seed removal significantly reduced seedling establishment (Fig. 2), resulting in 53 percent fewer established seedlings in their presence (30% of  $N = 432$  seeds, *open* and *partial* treatments) than in their absence (64% of  $N = 216$  seeds, *closed* treatment). These results support our first hypothesis and demonstrate the importance of vertebrate seed predators in Afrotropical forests (Clark *et al.* 2012, Rosin & Poulsen 2016).

With no significant difference in seed removal or seedling establishment between seeds placed at *high* versus *low* densities (Fig. 2), we found no support for seed density driving patterns of recruitment. However, we did not experiment with seeds at very high densities (*e.g.*, Clark *et al.* 2013), and our two density treatments were located close to each other at all locations (Fig. 1). So, while seeds in the *low*-density treatments represented a lower nutritional reward and were likely less detectable than seeds in the *high*-density treatment, they did not replicate long-distance dispersal in which a single or few seeds are isolated from all others. How often such isolation of dispersed seeds actually occurs in nature is debatable, but many seeds are likely subject to some aggregation via contagious dispersal (Howe 1989, Schupp *et al.* 2002, Clark *et al.* 2004). Inter-annual variation in natural seed rain may also influence how seed density affects seed removal and establishment (Curran & Webb 2000), though we did not assess that here. Additionally, the artificiality of the exclosures may have increased the conspicuousness of seeds within them, even at very low densities. Lastly, as a result of using ten tree species, three exclosure treatments, and multiple experimental locations, the sample sizes for individual species and for the study as a whole are relatively small, with only a single experimental fruiting tree location per species. These factors may partially explain why our study found no effect of seed density, while others using different methods (*e.g.*, Poulsen *et al.* 2012) have documented seed density to be a driver of patterns in recruitment.

Seed location (consppecific, heterosppecific, or neutral) did have a significant effect on seed removal and seedling establishment, but not as hypothesized. Using location as a proxy for dispersal and distance from the parent tree, dispersed seeds (those under heterosppecific trees and in neutral non-fruiting locations) had significantly greater removal and lower establishment than undispersed seeds (those under conspecific trees; Fig. 2). This trend was driven primarily by the significantly greater seed removal and lower seedling establishment of seeds in neutral locations than under conspecific trees. Our results contrast with those of Hautier *et al.* (2010), in which rodents disproportionately reduced conspecific—but not heterosppecific—seed mortality. Our results also fail to support the expectation of the Janzen-Connell hypothesis that seeds below the parent tree canopy face greater seed mortality and lower seedling establishment than those dispersed farther away. High densities of seeds from natural seed rain beneath fruiting trees may satiate seed predators, resulting in

higher rates of seedling recruitment than in neutral non-fruiting locations where food is scarcer. If a rodent's burrow and small home range do not include a fruiting tree at a given time, arriving dispersed seeds are almost certain to be found and eaten, even those that are small and undesirable under more favorable conditions. These results fail to support our hypothesis that seed mortality would be greater under conspecific trees than under heterosppecific trees or neutral non-fruiting locations. Janzen-Connell mortality patterns can operate over multiple life stages (Swamy & Terborgh 2010, Terborgh 2012), and thus, our study may not have fully captured them, given relatively small sample sizes and a focus on just the seed-to-seedling transition. Additionally, indirect interactions via shared generalist seed predators may better explain variation in seed predation than the density of conspecific seeds alone (Garzon-Lopez *et al.* 2015), though we did not evaluate these interactions in our study.

Seed removal was positively correlated with seed mass (with marginal significance), but was not correlated with adult tree abundance (Fig. 3). Higher removal of large seeds was expected because they provide a greater nutritional reward than small seeds (with smaller rodents generally consuming smaller seeds and larger rodents generally consuming larger seeds [Rosin & Poulsen 2017]). Although the mechanism of species maintenance by frequency-dependent seed selection is plausible (Paine & Beck 2007, Paine *et al.* 2016), we found no support for it in our study given the lack of correlation between seed removal and adult tree abundance. However, our results are limited to ten tree species and therefore may not capture community-wide trends. In a *post hoc* analysis of a related seed predation dataset with larger sample sizes and a partly overlapping but complementary suite of species (from Rosin & Poulsen 2016), we found no relationship between seed removal and adult tree abundance, supporting the results of this study.

On an individual species basis, the proportions of seeds removed and established as seedlings varied widely (Fig. 3). Vertebrates removed all *P. macrophylla* seeds—which are very large and dispersed ballistically—from *partial* and *open* treatments, resulting in zero seedling establishment, whereas 96 percent of seeds ( $N = 24$ ) established as seedlings when protected from vertebrates (*closed* treatment; Fig. 3). With such high seed losses to generalist vertebrates in all locations, strong patterns of spatially restricted recruitment are unlikely. By contrast, all three wind-dispersed species (*C. gabunensis*, *P. africanum*, and *P. soyauxii*) had very low removal by vertebrates in all locations, with greater proportional seed losses by invertebrates. The seeds of these species are small and papery, and are probably both inconspicuous and relatively undesirable to vertebrate seed predators. The proportional seedling establishment of these species varied little with respect to vertebrate access (~50% in all treatments; Fig. 3). Janzen-Connell mortality patterns may occur for tree species with seeds that are undesirable to vertebrates—and thus face proportionally greater seed losses by more specialized natural enemies—though we have insufficient data to test that possibility explicitly.

Seed traits clearly affect patterns of seed removal and seedling establishment, and may determine recruitment differences among species, contributing more to the likelihood of success for

an individual seed than do its density or distance from parent. Vertebrate seed predators likely play a strong role in driving these patterns, with preferential selection of certain seed species over others. It is challenging to establish an empirical basis for understanding seed preference among vertebrates, but it is likely a combination of the following factors: *seed size* (with larger seeds favored, within body size constraints; e.g., (Mendoza & Dirzo 2007, Rosin & Poulsen 2017); *seed conspicuousness* (related to size, but including characteristics of seed color, shape, and olfactory cues such as bits of fleshy fruit or seed deposition in dung; e.g., Janzen 1971, Hulme 1993); *physical defenses* (seed coat thickness and hardness, with thinner, softer seeds being more accessible to seed predators; e.g., Blate *et al.* 1998); *chemical defenses* (less defense means more palatable seeds, but this likely involves a trade-off with physical defenses; e.g., Janzen 1971); and *overall familiarity* (seed predators may develop a search image for common species, with adult abundance a good proxy for familiarity; e.g., Paine & Beck 2007). The divergence in seed traits among species likely reflects trade-offs in balancing traits that discourage seed predation with those that result in numerous and/or hardy seedlings.

Patterns of spatially restricted recruitment observed in Neotropical forests have not been well documented in Afrotropical forests. This may be due to the relative dearth of ecological research in the latter, or it may be an indication that these patterns are less prominent. Given the many diverging biogeographical characteristics of forests across continents, there should be little expectation of absolute consistency among processes that drive seed mortality and seedling establishment. Large-sample studies comparing ecological processes across regions are needed to address the many remaining questions of both ecological and conservation significance.

## ACKNOWLEDGMENTS

We thank Rachel Rosin for assistance in the field, and John Terborgh, Connie Clark, Roland Kays, C.E. Timothy Paine, and three anonymous reviewers for comments on the manuscript. We also thank the Gabonese Government for research support, including the Agence Nationale des Parcs Nationaux and the Centre Nationale de la Recherche Scientifique et Technique; and the Duke University Graduate School for financial support.

## DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qb35fd8> (Rosin & Poulsen 2018).

## LITERATURE CITED

- BAGCHI, R., R. E. GALLERY, S. GRIPENBERG, S. J. GURR, L. NARAYAN, C. E. ADDIS, R. P. FRECKLETON, AND O. T. LEWIS. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506: 85–88.
- BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* 67: 1–48.
- BLATE, G. M., D. R. D. PEART, AND M. LEIGHTON. 1998. Post-dispersal predation on isolated seeds: A comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82: 522–538.
- BOLKER, B. M., M. E. BROOKS, C. J. CLARK, S. W. GEANGE, J. R. POULSEN, M. H. H. STEVENS, AND J.-S. S. WHITE. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *TREE* 24: 127–135.
- CLARK, C. J., J. R. POULSEN, E. F. CONNOR, AND V. T. PARKER. 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia* 139: 66–75.
- CLARK, C. J., J. R. POULSEN, AND D. J. LEVEY. 2012. Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. *Ecology* 93: 554–564.
- CLARK, C. J., J. R. POULSEN, AND D. J. LEVEY. 2013. Roles of seed and establishment limitation in determining patterns of afrotropical tree recruitment. *PLoS One* 8: e63330.
- CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer and G. R. Gradwell (Eds.). *Dynamics of populations*. CAPD, Wageningen, The Netherlands.
- CORLETT, R. T., AND R. B. PRIMACK. 2011. *Tropical rain forests: An ecological and biogeographic comparison*. John Wiley & Sons Inc., New York, NY.
- CRAWLEY, M. J. 1992. Seed predators and plant population dynamics. In M. Fenner (Ed.). *Seeds: The ecology of regeneration in plant communities*, pp. 157–191. CAB International, Wallingford, UK.
- CURRAN, L. M., AND C. O. WEBB. 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruited Dipterocarpaceae. *Ecol. Monogr.* 70: 129–148.
- FRICKE, E. C., J. J. TEWKSBURY, AND H. S. ROGERS. 2014. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecol. Lett.* 17: 593–598.
- GARZON-LOPEZ, C. X., L. BALLESTEROS-MEJIA, A. ORDOÑEZ, S. A. BOHLMAN, H. OLFÉ, AND P. A. JANSEN. 2015. Indirect interactions among tropical tree species through shared rodent seed predators: A novel mechanism of tree species coexistence. *Ecol. Lett.* <https://doi.org/10.1111/ele.12452>.
- GREEN, P. T., K. E. HARMS, AND J. H. CONNELL. 2014. Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *PNAS* 111: 18649–18654.
- HAMMOND, D. S. D., AND V. BROWN. 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In D. Newbery, H. Prins, and N. Brown (Eds.). *Dynamics of tropical communities*, pp. 51–78. Blackwell Science, Inc., Malden, MA.
- HAUTIER, Y., P. SANER, C. PHILIPSON, R. BAGCHI, R. C. ONG, AND A. HECTOR. 2010. Effects of seed predators of different body size on seed mortality in Bornean logged forest. *PLoS One* 5: e11651.
- HOWE, H. F. 1989. Scatter- and clump-dispersal and seedling demography: Hypothesis and implications. *Oecologia* 79: 417–426.
- HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Ann. Rev. Eco. Syst.* 13: 201–228.
- HULME, P. 1993. Post-dispersal seed predation by small mammals. *Symp. Zoo. Soc. L* 65: 269–287.
- HULME, P. 1998. Post-dispersal seed predation: Consequences for plant demography and evolution. *Pers. Plant Eco. Evo. Syst.* 1: 32–46.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- JANZEN, D. H. 1971. Seed predation by animals. *Ann. Rev. Eco. Syst.* 2: 465–492.
- KOERNER, S. E., J. R. POULSEN, E. J. BLANCHARD, J. OKOUI, AND C. J. CLARK. 2016. Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *J. Appl. Ecol.* 54: 805–814.
- MARKHAM, I. 2015. *Of Mice and Men in Gabon: Changes in Rodent Communities Associated with Logging and Hunting*. Master's Thesis, Duke University.
- MATTHESIUS, A., H. CHAPMAN, AND D. KELLY. 2011. Testing for Janzen-Connell effects in a West African Montane forest. *Biotropica* 43: 77–83.

- MENDOZA, E., AND R. DIRZO. 2007. Seed-size variation determines interspecific differential predation by mammals in a Neotropical rain forest. *Oikos* 116: 1841–1852.
- OKOUI, J., P. POSSO, A. LEPETRE, AND P. SCAPS. 2002. Estimations des densités de populations de macro-mammifères de la Réserve d'Ipassa Makokou (Gabon). *Bull. Soc. Zool.* 127: 121–135.
- OKOUI, J., P. POSSO, AND P. SCAPS. 2001. La réserve d'Ipassa: constat d'une surexploitation de la faune. *Canopee* 21: 8–10.
- PAINE, C. E. T., AND H. BECK. 2007. Seed predation by Neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology* 88: 3076–3087.
- PAINE, C. E. T., H. BECK, AND J. TERBORGH. 2016. How mammalian predation contributes to tropical tree community structure. *Ecology* 97: 3326–3336.
- POULSEN, J. R., C. J. CLARK, AND B. M. BOLKER. 2012. Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment. *Ecology* 93: 500–510.
- R CORE TEAM. 2015. a language and environment for statistical computing. R. Found. Stat. Comput Vienne, Austria.
- ROSIN, C., AND J. R. POULSEN. 2016. Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest. *For. Eco. Mgmt.* 382: 206–213.
- ROSIN, C., AND J. R. POULSEN. 2017. Telemetric tracking of scatterhoarding and seed fate in a Central African forest. *Biotropica* 49: 170–176.
- ROSIN, C., AND J. R. POULSEN. 2018. Data from: Seed traits, not density or distance from parent, determine seed predation and establishment in an Afrotropical forest. Dryad Digital Repository. <https://doi.org/10.5061/dryad.qb35fd8>.
- SCHUPP, E., T. MILLERON, AND S. RUSSO. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In D. Levey, W. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 19–33. CAB International Publishing, Wallingford, UK.
- SWAMY, V., AND J. W. TERBORGH. 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *J. Eco.* 98: 1096–1107.
- TERBORGH, J. 2012. Enemies maintain hyperdiverse tropical forests. *Am. Nat.* 179: 303–314.
- van VLIET, N., R. NASI, L. EMMONS, F. FEER, P. MBAZZA, AND M. BOURGAREL. 2007. Evidence for the local depletion of bay duiker *Cephalophus dorsalis*, within the Ipassa Man and Biosphere Reserve, north-east Gabon. *Afr. J. Ecol.* 45: 440–443.