

# Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality

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**Abstract.** In tropical forests, resource-based niches and density-dependent mortality are mutually compatible mechanisms that can act simultaneously to limit seedling populations. Differences in the strengths of these mechanisms will determine their roles in maintaining species coexistence. In the first assessment of these mechanisms in a Congo Basin forest, we quantified their relative strengths and tested the extent to which density-dependent mortality is driven by the distance-dependent behavior of seed and seedling predators predicted by the Janzen-Connell hypothesis. We conducted a large-scale seed addition experiment for five randomly selected tropical tree species, caging a subset of seed addition quadrats against vertebrate predators. We then developed models to assess the mechanisms that determine seedling emergence (three months after seed addition) and survival (two years after seed addition). As predicted, both niche differentiation and density-dependent mortality limited seedling recruitment, but predation had the strongest effects on seedling emergence and survival. Seedling species responded differently to naturally occurring environmental variation among sites, including variation in light levels and soil characteristics, supporting predictions of niche-based theories of tropical tree species coexistence. The addition of higher densities of seeds into quadrats initially led to greater seedling emergence, but survival to two years decreased with seed density. Seed and seedling predation reduced recruitment below levels maintained by density-dependent mortality, an indication that predators largely determine the population size of tree seedlings. Seedling recruitment was unrelated to the distance to or density of conspecific adult trees, suggesting that recruitment patterns are generated by generalist vertebrate herbivores rather than the specialized predators predicted by the Janzen-Connell hypothesis. If the role of seed and seedling predation in limiting seedling recruitment is a general phenomenon, then the relative abundances of tree species might largely depend on species-specific adaptations to avoid, survive, and recover from damage induced by vertebrate herbivores. Likewise, population declines of herbivorous vertebrate species (many of which are large and hunted) may trigger shifts in species composition of tropical forests.

**Key words:** Congo Basin; density-dependent mortality; herbivory; Janzen-Connell hypothesis; niche differentiation; seedling recruitment; seed predation; tropical forest.

## INTRODUCTION

A central question in ecology is: What mechanisms control local species diversity? This question has been particularly compelling for tropical tree communities, as nearly 300 species can be packed into a single hectare of forest (Valencia et al. 1994, De Oliveira and Mori 1999). Although many mechanisms have been proposed to explain the coexistence of so many species (reviewed by Chesson 2000, Wright 2002; but see also Clark et al. 2010), two enjoy substantial empirical and experimental support: (1) resource-based niche differentiation, and (2) conspecific density-dependent mechanisms that lead to higher survival of locally rare species. Niche differentiation occurs when functional differences among species

influence their competitive rankings across heterogeneous environments, with trade-offs usually determining where a particular species does best (Chase and Leibold 2003, Silvertown 2004). If niche differentiation is strong, indefinite numbers of species may coexist when resources vary through space or time (Tilman 1994). Density-dependent mechanisms, on the other hand, facilitate coexistence when nearby conspecifics reduce individual performance, thus constraining populations of locally abundant species and creating an among-species, frequency-dependent recruitment advantage for rare species. Both of these mechanisms can operate at early stages in the life cycle (e.g., seed-to-seedling transition), a demographic bottleneck that can disproportionately impact the structure, dynamics, and species composition of communities (Chambers and Macmahon 1994) and could contribute to stable species coexistence (Chesson 2000). Rarely are they considered in concert (but see Kobe and Vriesendorp 2011).

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Support for resource-based niche differentiation has emerged from studies demonstrating habitat specialization of adult trees along environmental gradients of light, soil, water, and nutrient availability (Plotkin et al. 2000, Harms et al. 2001, Aiba et al. 2004, Valencia et al. 2004, Kraft et al. 2008). Niche partitioning, however, may also impact the distribution and abundance of seedlings, in which case niche differences at small spatial scales not relevant for adults could determine seed germination and seedling performance (Comita et al. 2007). If resource-based niche partitioning occurs among seedlings, species should differentiate by specializing on particular combinations of light, soil, water, and nutrients, across canopy openings and within the forest understory (Silvertown 2004).

Density-dependent mechanisms by which individual plants impair seed and seedling performance of neighboring conspecifics include allelopathy, intraspecific competition, and pest or pathogen facilitation. With respect to pests and pathogens, the Janzen-Connell hypothesis posits that host-specific pests prey on the high density of seeds and seedlings located near conspecific adults so that seeds dispersed farther have higher survival rates than those near them (Janzen 1970, Connell 1971). Host-specific predators of seeds and seedlings create a form of spatially mediated density-dependent mortality that opens space and resources for less-common species (but see Adler and Muller-Landau 2005). Under the Janzen-Connell hypothesis, two interacting mechanisms are thought to maintain diversity: (1) species-specific seed and seedling mortality increase as seed and seedling densities increase (density-dependent mortality); and (2) species-specific survival of seeds and seedlings increases with distance from the parent tree (distance-dependent survival). Numerous studies have documented support for the Janzen-Connell hypothesis by demonstrating disproportionate seed and seedling mortality near parent trees (Augspurger 1984, Clark and Clark 1984, Webb and Peart 1999, Packer and Clay 2000, Swamy and Terborgh 2010, Matthesius et al. 2011, Swamy et al. 2011; but see Hyatt et al. 2003). Furthermore, pervasive density-dependent mortality at early life history stages has sometimes correlated with increased species richness of seedlings (Harms et al. 2000).

Although the Janzen-Connell hypothesis initially focused on host-specific predators, recent work demonstrates that by suppressing common species generalized herbivores can also create the conditions for the recruitment of new species or the persistence of rare species (Dyer et al. 2010). Studies on mutualistic networks demonstrate that generalist species may drive the evolution of a community, while specialist species are involved in highly asymmetric interactions with generalists (Bascompte and Jordano 2007, Nielsen and Bascompte 2007). In forests with intact faunal communities, vertebrate seed predators and herbivores often act as generalists, foraging on multiple families of plants,

and induce high rates of mortality on seedling populations (Asquith et al. 1997, Terborgh et al. 2008, Swamy and Terborgh 2010). Vertebrate herbivores can forage over large areas, which may make them less likely to induce distance-dependent mortality on seeds and seedlings (Terborgh et al. 1993, Hammond and Brown 1998, Swamy and Terborgh 2010). But, if vertebrate herbivores target or more frequently encounter common species, they may create a form of frequency-dependent selection. The potential role of large vertebrate herbivores to drive patterns of seedling recruitment, irrespective of the distance- and density-dependent mechanisms proposed by the Janzen-Connell hypothesis, has been understudied, probably due to the paucity of studies conducted at sites where large, wide-ranging generalist herbivores remain abundant.

In summary, multiple mechanisms of postdispersal seed and seedling mortality likely operate in concert to determine which species will recruit and persist at a given location. Thus, understanding tropical forest diversity requires quantifying the relative importance of the various mechanisms that underlie species recruitment, a task most directly accomplished through large-scale experiments.

We conducted seed addition experiments on five randomly selected tree species across 21 heterogeneous study sites in the Republic of Congo. We relate seedling establishment and survival following seed addition to (1) light availability and soil fertility (variables of resource-based niche partitioning); (2) conspecific density- and distance-dependent performance (Janzen-Connell effects); and (3) the strength of seed predation and herbivory. We decouple and evaluate the relative importance of each of these mechanisms at two stages: the seed-to-seedling transition (three months after seed addition) and seedling survival to the second year of growth. The vast majority of studies on tropical tree species coexistence have been conducted in Neotropical forests (e.g., Carson et al. 2008). This study is one of the few examinations of these mechanisms in the Congo Basin and should help elucidate whether similar mechanisms of coexistence operate pantropically.

## METHODS

### *Study area*

This study was conducted in the north of the Republic of Congo (Brazzaville) in the Nouabalé-Ndoki National Park (NNNP) and the Kabo forestry concession (see map in Appendix A). The Republic of Congo is known for its relatively intact forests, rich in flora and fauna. The region is characterized as tropical lowland forest with highly weathered sandstone, quartzite, and schist bedrock, overlain in places by ancient basin alluvial deposits that have formed well-developed soils (Lanfranchi and Schwartz 1991). The relief is generally flat, with altitude varying between ~350 and 400 m. The climate is dominated by a pronounced dry season, typically beginning at the end of November and

TABLE 1. Ecological characteristics of focal tree species in the northern Congo Basin study area.

Species	Family	Regeneration guild	Dispersal mode	Mean seed length (cm)	Mean density (trees/ha)
<i>Pancovia laurentii</i>	Sapindaceae	shade bearer	P	1.0	2.37
<i>Staudtia kamerunensis</i>	Myristicaceae	NPLD	P, B	1.9	0.57
<i>Manilkara mabokeensis</i>	Sapotaceae	shade bearer	P	1.4	1.67
<i>Myrianthus arboreus</i>	Urticaceae	shade bearer	P, B, E	2.1	3.96
<i>Entandophragma utile</i>	Meliaceae	NPLD	W	0.8	1.17

Notes: Regeneration guilds include non-pioneer, light-demanding (NPLD), and shade-bearer (Hawthorne 1995). Dispersal categories include wind (W), primate (arboreal primates, chimpanzees, and gorillas; P), bird (B), and elephant (E). Mean seed lengths are the averages of 100 seeds of each species. Mean tree density was estimated from 30 1-ha plots in which all adults >10 cm dbh were measured, mapped, and identified to species.

extending through early March. The mean annual rainfall is 1700 mm. Minimum and maximum average temperatures range between 21.1° and 21.9°C and 26.5° and 26.8°C, respectively (Bomassa Research Station, unpublished data). Seven distinct vegetation types (Harris 2002) occur in this forest with mixed-species terra firma forest occupying 70% of the area. The forests of NNNP have never been commercially logged, although hunter-gatherer populations inhabited the region for ca. 40 000 years and iron smelting sites, which can degrade forest habitats, date as early as 800 BC (Lanfranchi et al. 1998). The Kabo concession was selectively logged (<2 trees/ha; Congolaise Industrielle des Bois 2006) ca. 30 years ago, and ~3000 people harvest its non-timber forest products for subsistence use. Combined, the NNNP and the Kabo concession provide a contiguous, yet heterogeneous landscape to evaluate how differences in biotic and abiotic conditions influence patterns of seed and seedling survival.

#### Site selection

We used satellite images to identify areas within the NNNP and the Kabo concession that contained dense terra firma forest. From these potential study areas, we used the geographic survey design component of the Distance 4.1 software (Thomas et al. 2002) to randomly select 30 sites, which collectively spanned an area of >3000 km<sup>2</sup> and individually were separated by at least 2.5 km to promote independence (Appendix A). At each site, we delineated a 100 × 100 m (1-ha) vegetation plot and marked, mapped, and identified all trees ≥ 10 cm dbh (diameter at breast height). For each tree ( $N = 11\,360$ ), we collected three voucher specimens for species verification, measured dbh, and estimated height. Within each vegetation plot, we also set up 21 1-m<sup>2</sup> seed traps ( $N = 630$  traps). The contents of the seed traps were collected, identified, and counted every two weeks to select potential study species and to estimate ambient seed rain densities for the seed-sowing experiment.

#### Experimental design

To evaluate the relative importance of the mechanisms that influence seedling recruitment, we established 63 stations in 21 sites, chosen randomly from among the 30 mapped study sites. In each station, we sowed seeds

of five randomly selected tree species: *Pancovia laurentii*, *Staudtia kamerunensis*, *Manilkara mabokeensis*, *Myrianthus arboreus*, and *Entandophragma utile*. Species were chosen from a list of all tree species for which we recorded at least five seeds in the first year of seed rain ( $N = 277$  species). Constraining the list in this way allowed us to collect sufficient numbers of seeds to conduct the experiment, while not biasing selection toward any particular species characteristic. The five focal species vary in regeneration niche, dispersal mode, seed size, and relative abundance (Table 1), and adult individuals of all species coexist across the study site (Appendix B). Random selection of species facilitates generalization of our results to the broader tree community, although inference from a sample of only five species merits caution.

We divided each 6 × 10 m station into 60 0.5 × 0.5 m quadrats with 0.5 m between each quadrat to provide access by field crews ( $N = 3780$  quadrats total; Appendix C). In each quadrat we scattered seeds of one species in one of seven densities ( $N = 46\,620$  seeds total). Each augmentation density was a multiple (0, 25, 50, 100, 200, 500, and 2000) of the average species-specific natural seed rain density observed in the previous year (Clark et al. 2007, Poulsen et al. 2007). By augmenting seeds at multiple densities we were able to span the range of observed seed rain and experimentally compare the strengths of seed and seedling density to other factors (light, soil, seed predation, herbivory) likely to influence seedling recruitment and mortality. Following seed addition, we monitored seedling emergence and mortality every three months for two years. At each observation period, we numbered each seedling and recorded its height, condition, and number of leaves.

#### Resource-based niche differentiation

Niche-based mechanisms most commonly posited to constrain successful emergence and survival of seedlings include light availability and soil fertility. Thus, we measured each of these characteristics at all stations.

*Light availability.*—We took hemispherical photographs at the center of each seed addition station, using a Coolpix 5000 camera with a Fisheye Converter FC-E8 lens (Nikon, Tokyo, Japan). To avoid overexposure by direct sunlight, photographs were taken 30 cm above the

ground, early in the morning (06:00–08:00 hours), late in the afternoon (16:00–17:30), or on overcast days (Montgomery and Chazdon 2002). Photographs were analyzed using the Gap Light Analyzer (GLA version 2.0; Frazer et al. 2001). We related seedling emergence and survival to estimates of transmitted diffuse light, which varied significantly among plots (mean = 10.18, SD = 4.02,  $F = 2.25$ ,  $df = 20, 42$ ,  $P = 0.013$ ).

*Soil sampling and analysis.*—We collected soil samples at three randomly selected locations in each station, using a soil probe ( $2.85 \times 83$  cm) at 15 cm depth. Samples were weighed (wet mass), and then air-dried and weighed again (dry mass). For analysis, the three samples taken at each station were pooled into a single composite and thoroughly mixed. The IFAS Extension Soil Testing Laboratory, University of Florida, analyzed soils for their characteristics (percentage sand, clay, and silt), nutrient availability (N, P, K, Al, Ca, Mg, Mn), and pH. Available cations and P were extracted using the Mehlich III solution (Tran and Simard 1993). Elemental analysis for the cations and P was done on the extracts by using inductively coupled plasma (ICP) spectroscopy. We extracted N as  $\text{NH}_4$  and  $\text{NO}_3^-$ . Nitrogen was estimated colorimetrically using a Technicon II auto-analyzer (SEAL Analytical, Mequon, Wisconsin, USA). The Kjeldahl method was used for the determination of total N (Hesse 1971). Soil pH was measured in an Adams-Evans buffer solution made up of one volume of soil diluted in two volumes of water. Subsoil samples were analyzed for soil texture, using a hydrometer method (Sheldrick and Wang 1993).

We used principal-components analysis (PCA) to identify major trends in the soil data and to reduce the number of variables describing soil factors for further statistical analysis.

#### *Conspecific density- and distance-dependent mortality (Janzen-Connell effects)*

*Density of seeds and seedlings.*—We examined the degree to which nearby conspecific seeds and seedlings constrain recruitment at two time steps for each species. First, we tested how initial seed density influenced the probability of an individual transitioning from seed to seedling by calculating the proportion of seedlings that recruited into each quadrat as a function of seed augmentation density. Second, we evaluated how the density of emerged seedlings influenced the probability of surviving to the second year of growth by calculating the proportion of seedlings that survived to the end of the experiment as a function of the maximum number of seedlings that emerged within the same quadrat. These values were used as response variables for statistical analyses (see *Data analysis*...).

*Distance to and density of conspecific adults.*—To quantify the degree to which the spacing mechanism proposed by the Janzen-Connell hypothesis influences seed and seedling recruitment, we measured the distance between each seed addition station and the nearest

conspecific adult ( $\geq 10$  cm dbh) as well as the density of conspecific adults within 100 m of each station for all five focal species. We then related seedling recruitment and survival to the distance to and density of conspecific adults. Seed and seedling recruitment must be positively related to distance from conspecific adults to establish distance-dependent survival and negatively related to the number of seeds sown to establish density-dependent mortality; both are necessary to fully support the spacing mechanism described by the Janzen-Connell hypothesis. We did not explicitly identify predators and their effects on seedling recruitment and survival; however, in the absence of the expected patterns of recruitment, nailing down the specific agent of mortality is not required to evaluate Janzen-Connell effects.

#### *Vertebrate seed predators and herbivores*

To quantify the strength of vertebrate seed predation and herbivory as potential postdispersal mechanisms limiting seedling establishment, we established caged treatments within all stations for three of the five focal species (*Entandophragma utile*, *Manilkara maboakeensis*, and *Myrianthus arboreus*; Appendix C). We caged only three species because of the logistical challenges of constructing and carrying cages to remote forest sites. Cages consisted of 0.75 m high wooden frames covered by 13-mm wire netting that allowed entry by invertebrates while protecting the quadrats from rodents, duikers, forest pigs, and other vertebrate predators. Elephants, which are not typically predators of the focal seeds and seedlings, could have removed or damaged the cages; however, elephant presence in the stations was extremely rare (as assessed by footprints, dung, and bark stripping) and only a handful of cages were damaged over the course of the study. By adding seeds into both caged and uncaged quadrats at each seed addition level  $\times$  site combination, we disentangled mortality resulting from vertebrate predation and herbivory from mortality caused by other microsite characteristics (e.g., soil pathogens, soil characteristics, invertebrate depredation, light availability), which we assumed to be constant between the paired caged and uncaged quadrats in a station. By replicating each seed addition level with a caged treatment, we also assessed how vertebrate seed predation and herbivory vary with seed and seedling density.

#### *Data analysis and the relative importance of multiple processes*

To examine the relative importance of specific mechanisms associated with resource-based niche differentiation, conspecific density- and distance-dependent mortality, and vertebrate herbivores, we fitted and evaluated generalized linear mixed models (GLMMs) to: (1) the proportion of seedlings that emerged as a function of the number of seeds added to a given quadrat; and (2) the proportion of seedlings that survived to 24 months as a function of the maximum

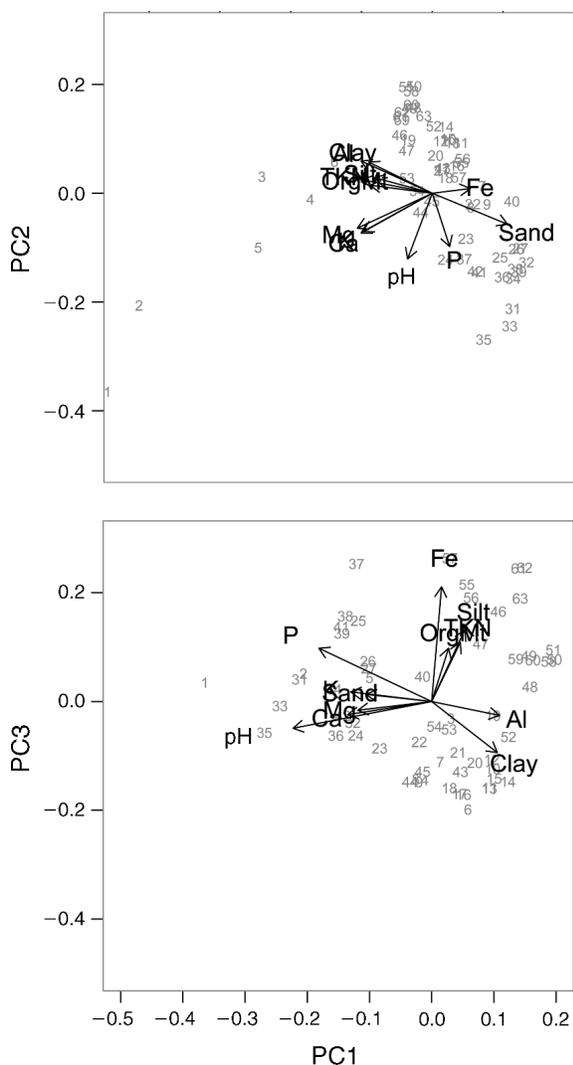


FIG. 1. Characteristics of soils from the 63 seed-augmentation stations in the northern Congo Basin study area. From the principal-component analysis, the first axis explained 26.7% of the total variance in soil data and was strongly correlated with soil texture (fractions of clay, sand, and silt), total N, and exchangeable cations. These parameters are strongly associated with soil fertility. The second axis explained an additional 17.5% of the variance and was most strongly correlated with pH. Axis 3 explained an additional 13.5% of the variance and was most strongly correlated with Fe and Al.

number of emerged seedlings in each quadrat. The experimental design, with quadrats located within stations, might cause seedling emergence and survival in a quadrat to depend on its spatial location within a station, and thus, not be independent of other quadrats. We examined model residuals for spatial autocorrelation and station effects, and found no evidence of either, suggesting the quadrats are an appropriate unit of replication (Appendix D). Our full set of explanatory variables for these models included: diffuse light transmission, soil PC1, soil PC2, soil PC3, seed augmentation level, density of conspecific adults, and distance to nearest conspecific adult. To make parameter

estimates comparable across explanatory variables, we standardized all continuous explanatory variables by subtracting the mean and dividing by the standard deviation to yield a Z score (Gelman and Hill 2007). We ran three sets of models for each of the response variables. First, we examined the effects of explanatory variables on species in general, by pooling data of all five species, but excluding the caged treatment. Second, we evaluated the effect of vertebrate exclusion by running the same models for the three species with the caging treatment, including caging as an additional variable. Finally, we ran species-specific models, including caging for those species with a caging treatment. We fit all models with a binomial error distribution and a logit-link. For the pooled analyses, we included species, site, and species-by-site random effects. For species-level analyses we included plot as a random effect. The random effects quantify variation in seedling emergence and survival among sites and species, and the species-by-site interaction examines the degree to which the emergence and survival of species depends on site identity. If strong, these interaction effects would provide evidence of niche differentiation in our study system. We used Laplace approximation (lme4 package) for maximum likelihood estimation of the parameters and tested the statistical significance of fixed effects with Wald Z statistics (Bolker et al. 2009). We estimated confidence intervals by calculating the denominator degrees of freedom for our study design and calculating Wald *t* confidence intervals. All statistical analyses were performed in R 2.7.2 (R Development Core Team 2005).

## RESULTS

Across all species, densities, and caging treatments, a total of 10 399 seedlings emerged and survived to three months following seed addition (22.3% of all seeds). Of these, 3355 survived the first two years of the study (7.2% of all seeds). Stated differently, 77.7% of sown seeds either did not germinate (likely because they were not viable or consumed) or their seedlings died within three months, and 67.7% of emerged seedlings died by the end of the second year.

### Soil characteristics

The first PC axis explained 26.7% of the total variance in soil data and was strongly correlated with soil texture (fractions of clay, sand, and silt), total N, and exchangeable cations (Fig. 1); these parameters are strongly associated with soil fertility. The second PC axis explained an additional 17.5% of the variance and was most strongly correlated with pH and phosphorous. PC axis 3 explained an additional 13.5% of the variance and was most strongly correlated with Fe and Al. Combined, these three axes explained 57.5% of the variance in soil conditions. Significant differences among plots were identified for PC1 ( $F = 33.49$ ,  $df = 18, 38$ ,  $P < 0.001$ ), PC2 ( $F = 11.65$ ,  $df = 18, 38$ ,  $P < 0.001$ ), and PC3 ( $F = 18.73$ ,  $df = 18, 38$ ,  $P < 0.001$ ).

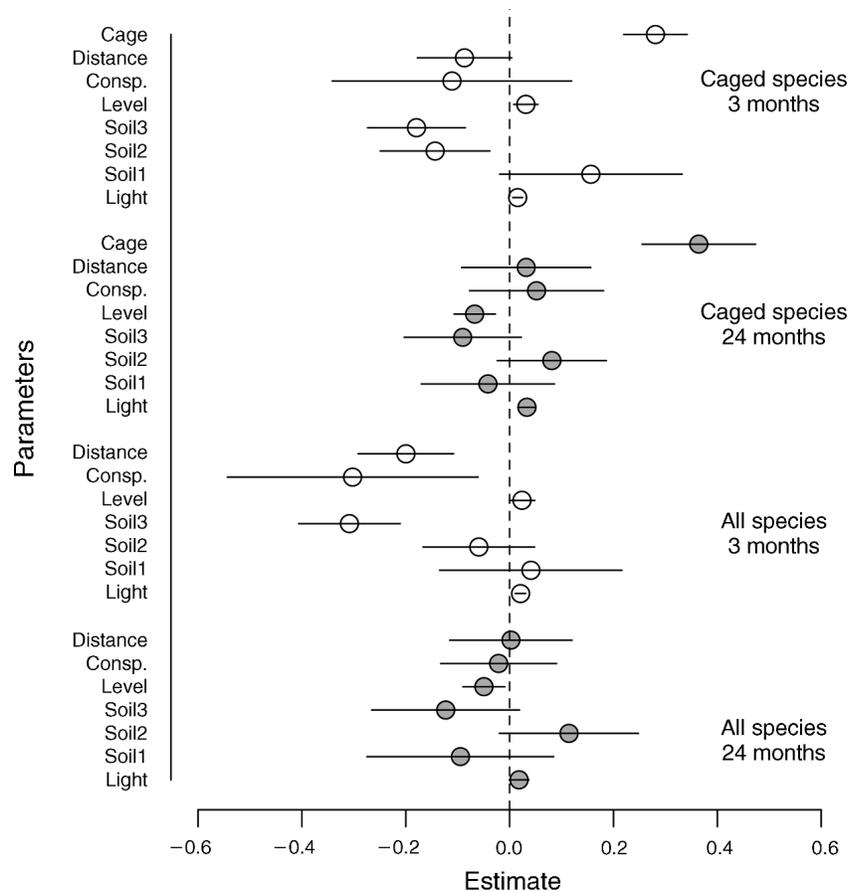


FIG. 2. Factors that influence seed recruitment to 3 months and survival to 24 months. Estimates are Z values of fixed effects from four generalized linear mixed models (GLMMs), including the effect of caging (Cage), distance from nearest conspecific adult (Distance), number of conspecific adults in the plot (Consp.), level of seed augmentation (Level), three composite variables taken from the principal-components analysis (Fig. 1; Soil 1, Soil 2, and Soil 3), and light availability (Light). Open circles are effects of recruitment after 3 months; filled circles are effects of survival up to 24 months. Horizontal lines indicate 95% confidence intervals.

*Resource-based niche differentiation*

Analysis of all species combined (excluding caging treatment) demonstrated that the strengths of random effects (species, site, and their interaction) were greater than other explanatory variables (soil, light, initial seed density, distance to and density of conspecific adults) at both life history stages, although the strength of the random effects was lower for seedling survival (SD of random effects: site = 0.49, species = 0.40, species × site = 0.31) than for seedling emergence (site = 0.59, species = 0.90, and species × site = 1.01). The strength of the species-by-site interaction suggests that species have asymmetric recruitment probabilities that vary with site characteristics, thus supporting niche differentiation as a driver of seedling emergence and survival. This interpretation is supported by the fact that across all species, the probability of seedling emergence was significantly influenced by light availability and soil characteristics (Fig. 2); all five species exhibited significant responses to one or both of these factors (Appendix E). Species responded differently to environmental variables, exhibiting neutral, positive, and negative responses to light

and soil PC1 and neutral or negative responses to soil PC2 and PC3. Overall, soil characteristics, particularly those associated with PC1 and PC3, exhibited stronger effects on seed-to-seedling transition probabilities than did light availability (Fig. 2; Appendix E). While environmental factors strongly influenced patterns of seedling emergence, they were less important for seed survival: neither soil nor light variables significantly influenced seedling survival to two years.

*Conspecific density- and distance-dependent mortality*

Across species, adding higher densities of seeds to quadrats slightly increased seedling emergence up to three months. Adding higher densities of seeds, however, decreased seedling survival up to 24 months. Thus, conspecific density-dependent mortality of seeds and seedlings required to support the Janzen-Connell hypothesis did not determine the probability of transitioning from seed to seedling but did occur at the seedling survival stage of plant recruitment (Fig. 2; Appendix E). However, contrary to hypotheses suggesting that conspecific density-dependent mortality should more

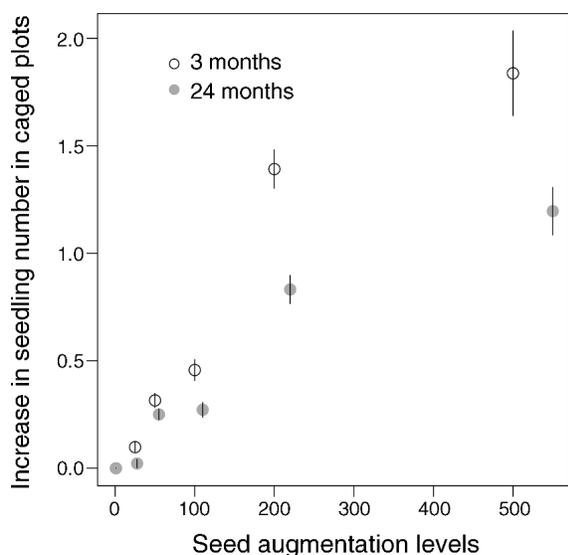


FIG. 3. Mean effect of caging on seedling recruitment in each experimental quadrat at 3 months and 24 months after seed augmentation. The  $y$ -axis is the effect of caging, the mean difference in seedling recruitment between caged and uncaged treatments over the different levels of seed augmentation. The  $x$ -axis refers to the levels of seed addition, not the number of seeds. It may be that the 500 augmentation level is only 29 seeds, because the natural seed rain density was less than 1. Thus the difference between caged and uncaged treatments is actually quite important. A positive value on the  $y$ -axis signifies that the caged treatment resulted in more seedlings than the uncaged treatment. Note that the symbols overlap at the 0 augmentation level, as there were no recruits at either 3 months or 24 months after seed augmentation.

strongly limit common than rare species, seedling survival of the most common species (*Myrianthus arboreus*) increased with higher densities of seed.

Our results failed to support the Janzen-Connell expectation of distance-dependent survival of seeds and seedlings. Distance to the nearest conspecific adult explained mortality at the seed-to-seedling transition stage, with the probability of seedling recruitment and survival decreasing, rather than increasing, with increased distance from conspecifics (Fig. 2).

#### *Seed predation and herbivory*

Vertebrate seed predation strongly limited seedling emergence: all three caged species had higher numbers of recruits with vertebrate exclusion (Fig. 3; Appendix E). Indeed, the large effect size of caging relative to all other variables suggests that seed predation more strongly limited the transition from seed to seedling than any other factor (Fig. 2). Similarly, the effect of caging on seedling survival was stronger than all other variables. The strengths of random effects were again lower for seedling survival (SD of random effects: site = 0.11, species = 0.11, species  $\times$  site = 0.16) than emergence (SD of random effects: site = 0.40, species = 0.33, species  $\times$  site = 0.79). These relatively small random effects for survival might indicate that the high species  $\times$  site

variation resulting from the analysis of uncaged, pooled species was largely due to across site variation in habitat characteristics like herbivore abundance that influence levels of seedling predation. To verify that Janzen-Connell effects did not operate through seed predation and herbivory, we also ran GLMMs that included an interaction between caging and distance to adult conspecifics. The interaction term failed to improve the model fit (seedling emergence model,  $\Delta$ AIC = 0; seedling survival model,  $\Delta$ AIC = 1). Together, these results clearly indicate that seed predation and seedling herbivory can strongly limit the size of seedling populations in this forest system.

#### DISCUSSION

Resource-based niche differentiation and density-dependent mortality simultaneously acted to limit recruitment of five randomly selected tree species. When three of the species were protected with vertebrate exclosures, seed predation and herbivory strongly dictated seedling emergence and survival, and resource-based niche differentiation and conspecific density-dependent mortality played secondary roles. Contrary to predictions of the Janzen-Connell hypothesis, seedling recruitment success was not related to the distance or density of conspecific adult trees, underscoring the importance of generalist predators and herbivores as drivers of patterns of seedling recruitment.

#### *Resource-based niche differentiation*

Our results support the notion that species coexistence is at least partially caused by species-specific habitat specialization to different abiotic conditions (Silvertown 2004, Kraft et al. 2008). Seedling emergence and survival varied among sites and species, indicating that seedling recruitment depends in a species-specific manner on the characteristics of the habitat into which seeds arrive. In general, soil and light characteristics acted more strongly on the transition of plants from the seed-to-seedling stage than they did on seedling survival. This result is somewhat surprising because the seed-to-seedling transition is strongly dependent on seed reserves for nutrients and water (Kitajima and Fenner 2000); therefore specific microsite characteristics should most strongly influence seedlings after a plant has exhausted its seed reserves (post-germination seedling survival). If seed reserves were exhausted in less than three months, it may be that we detected the effects of microsite characteristics on early establishment, not just seedling emergence. Alternatively, limitations to seedling emergence during the seed-to-seedling transition might be explained by either (1) the absence of appropriate physiological cues to stimulate germination (e.g., appropriate light cues) or (2) characteristics of the site that result in seed and early seedling mortality (e.g., desiccation, toxic levels of metals, soil pathogens).

While our results undeniably demonstrate the importance of biotic interactions, particularly seed and

seedling predation, for limiting seedling recruitment, the relative strength of niche differentiation might increase with a finer measurement of abiotic variables. Our measurements of light and soils at the level of the station ( $6 \times 10$  m) may have underestimated their effects if strong variation occurs over the scale of meters.

*Conspecific density- and distance-dependent mortality  
(Janzen-Connell effects)*

Of the hypotheses to explain the high diversity of tree species in tropical forests, the Janzen-Connell hypothesis is perhaps the most widely accepted, despite several critiques (Clark and Clark 1984, Hammond and Brown 1998, Hyatt et al. 2003). In brief, the Janzen-Connell hypothesis postulates that host-specific pests reduce recruitment near conspecific adults where conspecific seed density is greatest, thereby freeing space for establishment of other species. Tests of the Janzen-Connell hypothesis must therefore demonstrate that both mechanisms, density- and distance-dependent mortality, interact to determine patterns of seedling recruitment.

Three results from this study call into question the degree to which Janzen-Connell effects operate on seedlings at our study site. First, recruitment at the seed-to-seedling transition, when host-specific pathogens would be expected to strongly decrease recruitment probabilities, was positively, rather than negatively, related to density of conspecific seeds. Nonetheless, seedling mortality between 3 and 24 months was density dependent. Second, we observed no relationship between the distance to or density of conspecific trees and the probability of seedling establishment or survival. Third, the rarest species in the study experienced stronger effects of density-dependent mortality than the most common species, contradicting the expectation that species coexistence is promoted by stronger density-dependent mortality on common than rare species (Janzen 1970, Chesson and Warner 1981, Chesson 2000). Combined, these results contradict the Janzen-Connell hypothesis and weakly support the notion that intraspecific competition and density-dependent mortality in rare species may be the mechanisms that keep them rare (Klironomos 2002, Comita et al. 2010, Mangan et al. 2010). Although a study of three Neotropical species found no evidence of seedling competition (Paine et al. 2008), conspecific seed densities negatively impacted conspecific seedling densities for the first year of survival of 163 species in Ecuador (Metz et al. 2010). Our results from five African species also suggest that intraspecific seedling interactions might limit survival after recruitment.

Our failure to detect Janzen-Connell effects may be an artifact of our study design. We only followed seedling recruitment up to two years, whereas Janzen-Connell effects might emerge over time, due to predators or other causes of mortality that operate at later life stages or because predation events occur over longer time

scales (e.g., pest outbreaks; Carson et al. 2008). In addition, specialized predators may need a stronger signal, such as a flowering tree or the high densities of fruits and seeds that surround fruiting trees, to induce the distance-dependent behavior predicted by the Janzen-Connell hypothesis. In a different experiment, we manipulated patterns of seeds of *Manilkara mabo-keensis* at the scale of the tree (in wedges running from the tree trunk to 60 m away from the tree) to decouple the distance and density components of the Janzen-Connell hypothesis (Poulsen et al., *in press*). We similarly found that seed density determined seedling recruitment but was not significantly related to the distance from the tree.

Another explanation for differences observed between our study and those of other tropical forests (e.g., Swamy and Terborgh 2010, Swamy et al. 2011) with respect to Janzen-Connell effects could be the high numbers of medium- and large-bodied vertebrate seed and seedling predators in the Congo Basin (Clark et al. 2009, Poulsen et al. 2011). Unlike the host-specific seed and seedling consumers that drive the Janzen-Connell hypothesis, which are predominately invertebrates or fungal pathogens, large vertebrates typically act as generalist herbivores, consuming seeds and seedlings from multiple families. Our study suggests that vertebrate generalist herbivores may disproportionately impact common species, thus keeping their populations in check and facilitating coexistence, irrespective of a seedling's proximity to conspecific adults.

*Vertebrate seed predation and herbivory*

Results of our caging experiments demonstrated that vertebrate seed predators and herbivores more strongly influenced seedling recruitment and survival than abiotic factors of light and soil characteristics and than conspecific density-dependent mortality. Seed predation and herbivory reduced seedling recruitment to levels lower than those maintained by density-dependent mortality. This is the point at which seed predation and herbivory likely become important determinants of plant population size—when numbers of consumed seeds and seedlings surpass those otherwise doomed for mortality through density-dependent thinning (Crawley 1988, Hulme 1996).

At our site, the magnitude of seed predation and herbivory was related to the relative abundance of seedlings, with the most common species demonstrating greater effects of herbivory than rarer species (mean effect of seed predation, *Myrianthus arboreus*, 0.615; *Manilkara mabo-keensis*, 0.286; *Entandophragma utile*, 0.088; mean effect of herbivory, *M. arboreus*, 0.350; *M. mabo-keensis*, 0.168; *E. utile*, 0.129; Table 1). If herbivores and seed predators target the most common species, poorer competitors (presumably the less common species) can be maintained in the system (Dyer et al. 2010). Even though we randomized species selection, the small number of species in our study limits our

ability to generalize these patterns to the wider community. Future studies should include a wider range of species and life forms, including the random selection of liana and shrub species. Nonetheless, the tendency of more common species to be strongly impacted by vertebrate herbivory, coupled with a lack of support for conspecific distance-dependent effects leads us to speculate that generalist herbivores (rather than specialized seed predators, herbivores, and pathogens) might serve as a mechanism by which rare species can avoid competitive exclusion. If herbivory plays a predominate role in limiting seedling recruitment, then the relative abundances of tree species might largely depend on species-specific adaptations to avoid, survive, and recover from damage induced by vertebrate herbivores.

Our results have implications for conservation and management of tropical forests, where medium- and large-bodied herbivores are often heavily hunted, sometimes to local extinction (Poulsen et al. 2011). As these herbivores are lost, the relative importance of other mechanisms that control patterns of seedling recruitment would be expected to shift (Wright 2003, Bascompte and Jordano 2007, Muller-Landau 2007, Hautier et al. 2010; Poulsen et al., *in press*). The effects of density-dependent mortality were similar in both caged and uncaged treatments; therefore we would not expect its importance to dramatically change in the absence of herbivores. However, niche-based mechanisms may become increasingly important in the absence of mammalian herbivores. Because tropical forests worldwide are being degraded, research on species coexistence needs to not only assess the strengths of different mechanisms that drive patterns of diversity, but also evaluate the consequences of changes in their respective strengths with future disturbance.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Map of study area in the Republic of Congo, Africa (*Ecological Archives* E093-049-A1).

##### Appendix B

A table of the co-occurrence of adult trees of the focal species within study sites (*Ecological Archives* E093-049-A2).

##### Appendix C

A figure showing the experimental design of the seed addition stations (*Ecological Archives* E093-049-A3).

##### Appendix D

Methods and results for tests of spatial autocorrelation and independence of experimental quadrats (*Ecological Archives* E093-049-A4).

##### Appendix E

A figure showing the results of species-specific generalized linear mixed models (GLMMs) of seedling emergence and survival (*Ecological Archives* E093-049-A5).