Experimental manipulation of seed shadows of an Afrotropical tree determines drivers of recruitment

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Abstract. The loss of animals in tropical forests may alter seed dispersal patterns and reduce seedling recruitment of tree species, but direct experimental evidence is scarce. We manipulated dispersal patterns of Manilkara mabokeensis, a monkey-dispersed tree, to assess the extent to which spatial distributions of seeds drive seedling recruitment. Based on the natural seed shadow, we created seed distributions with seeds deposited under the canopy (“no dispersal”), with declining density from the tree (“natural dispersal”), and at uniform densities (“good dispersal”). These distributions mimicked dispersal patterns that could occur with the extirpation of monkeys, low levels of hunting, and high rates of seed dispersal. We monitored seedling emergence and survival for 18 months and recorded the number of leaves and damage to leaves. “Good dispersal” increased seedling survival by 26%, and “no dispersal” decreased survival by 78%, relative to “natural dispersal.” Using a mixed-effects survival model, we decoupled the distance and density components of the seed shadow: seedling survival depended on the seed density, but not on the distance from the tree. Although community seedling diversity tended to decrease with longer dispersal distances, we found no conclusive evidence that patterns of seed dispersal influence the diversity of the seedling community. Local seed dispersal does affect seedling recruitment and survival, with better dispersal resulting in higher seedling recruitment; hence the loss of dispersal services that comes with the reduction or extirpation of seed dispersers will decrease regeneration of some tree species.

Key words: Bayesian analysis; Congo; experiment; Janzen-Connell hypothesis; loss of seed dispersers; Manilkara mabokeensis; seed dispersal; seedling emergence; seedling survival; seed shadow; tropical trees.

INTRODUCTION

In tropical forests, where animals disperse the majority of tree species, hunting and habitat conversion extirpate or reduce the abundance of seed-dispersing animals (Laurance et al. 2006, Peres and Palacios 2007, Poulsen et al. 2011). In particular, the unsustainable harvesting of wildlife is rapidly emptying tropical forests of large- and medium-bodied mammals (Milner-Gulland et al. 2003, Fa et al. 2005). The loss of seed-dispersing animals is predicted to dramatically alter patterns of seed deposition, with cascading effects for forest regeneration (Terborgh et al. 2008, Brodie et al. 2009). In order to predict how the loss of dispersers will affect tropical forests, however, we need to understand the relationship between spatial patterns of seed dispersal and the distribution, abundance, and diversity of tree species (Levine and Murrell 2003).

The consequences of hunting and consequent loss of dispersal services for forest regeneration depend on the extent to which spatial patterns of seed dispersal determine the distribution and abundance of trees. The spatial pattern of dispersed seeds of a plant, the seed shadow, is characterized by the pattern of seed density with respect to distance from the parent. Without dispersal, most seeds will fall under or close to the parent plant, accumulating in high densities. Seed dispersal increases the average distance of seeds from their parent and decreases the average density of seeds at any one location, with most seed shadows described by decreasing seed densities with distance from the parent plant (Nathan and Muller-Landau 2000). Seed dispersal is said to lay the template of seeds from which seeds germinate and seedlings recruit into adults (Schupp and Fuentes 1995). This line of argument suggests that information on dispersal patterns should thus allow one to predict the distribution of trees in space. However, several studies report a lack of concordance between patterns of seed deposition and seedling recruitment, demonstrating that post-dispersal processes act to dilute or erase the pattern arising from the original spatial distribution of seeds (Herrera et al. 1994, Harms et al. 2000, Balcomb and Chapman 2003).
Although we are quickly gaining a better grasp of the factors that affect local seed dispersal patterns (e.g., Clark et al. 1999), we still do not know whether these patterns have lasting consequences for plant abundance and diversity. In principle, by escaping from aggregated dispersal patterns close to the tree, dispersed seeds could avoid mortality from direct intraspecific competition and from the density- and distance-dependent behavior of seed and seedling predators (Janzen 1970, Connell 1971). In this way, seed dispersal could increase species recruitment and abundance. However, depending on the scale of favorable and unfavorable habitat patches, short-range dispersal may lead to greater rates of recruitment and higher abundance than more distant dispersal if seeds would otherwise disperse to unsuitable microsites (Bolker and Pacala 1999, Cheptou et al. 2008). At the community level, limited seed dispersal promotes diversity by slowing rates of competitive displacement and causing the spatial segregation of heterospecific individuals across a landscape (Hubbell et al. 1999, Wright 2002). Therefore, diversity should increase with short dispersal distances and decrease with longer dispersal distances.

The evidence that the spatial distribution of seeds determines juvenile and adult recruitment is mostly indirect and correlative (Levine and Murrell 2003). Seed shadow studies have demonstrated that dispersal mode partially explains among-species differences in patterns of seed deposition (Clark et al. 2005, Muller-Landau et al. 2008), and examinations of the spatial distribution of sapling and trees have shown that the aggregation of conspecifics is correlated with the mode of seed dispersal in tropical forests (Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006). However, directly linking the spatial distribution of seeds to tree abundance and diversity requires experimental approaches that decouple the distance and density components of the seed shadow and link them to patterns of seedlings and adult recruitment. In the only experimental study to date, Augspurger and Kitajima (1992) manipulated the distributions of seeds of two individuals of a wind-dispersed tree species to demonstrate that high seed density and proximity to the parent plant lowered seedling recruitment. Their experimental approach allowed them to directly examine the effects of seed distributions on seedling recruitment, but the low level of replication limited their ability to quantify the effects of different seed dispersal patterns and their distance and density components.

Here we build on Augspurger and Kitajima’s (1992) experiment to test whether the spatial distribution of dispersed seeds affects the recruitment of a monkey-dispersed tree species, Manilkara mabokeensis, and the diversity of the seedling community. Based on measurements of its natural seed shadow, we sowed seeds of M. mabokeensis under seven trees in three distributions to mimic scenarios that could occur with the extirpation of monkeys by hunting (“no dispersal”), low levels of hunting (“natural dispersal”), and high rates of seed dispersal (“good dispersal”). We then monitored the recruitment of seedlings over 18 months. By using a replicated, experimental approach, we directly examine how seed shadows affect seed survival and seedling recruitment, survival, and community diversity. We decouple the distance and density effects of seed shadows to assess their relevance, and we examine additional mechanisms (seed predation and herbivory) that limit seedling recruitment. Finally, we compare seedling diversity across the experimental seed distributions in order to assess whether the specific pattern of dispersed seed, and thus the abundance of seed dispersers, strongly determines the seedling community.

**Methods**

**Overview**

Our experiment entailed several steps. First we selected a tree species based on the criterion that its primary disperser (arboreal monkeys) was threatened by hunting. Second, we quantified natural patterns of seed dispersal around focal trees. Third, with the seed shadow data we calculated the density patterns of seeds to sow in the three experimental distributions (no dispersal, natural dispersal, and good dispersal). Fourth, we delimited wedges under seven individuals of Manilkara mabokeensis (see Plate 1) and sowed seeds in them according to the experimental distributions. Fifth, we monitored seedling recruitment and survival for 18 months. Finally, at the end of the experiment, we estimated the diversity of the seedling community in the wedges to examine the effects of the seed shadow on species coexistence.

**Study site and species**

We conducted this study in the Kabo logging concession in the northern Republic of Congo from July 2006 through July 2008. The logging concession is composed primarily of lowland, semi-deciduous tropical forest, and had been logged once in the late 1960s at a relatively low intensity (<2.5 trees/ha). Human population growth in the concession has dramatically increased hunting pressure on wildlife, including arboreal monkeys, to the point that some species may be unsustainably harvested (Poulsen et al. 2009). However, the study site is 20 km from the nearest village and is probably subject to only very low rates of hunting; in contrast to other areas in the same region in which we work, we witnessed no signs of hunting (hunters, gun shots, or shotgun shells) over the course of the study.

For this study, we created a list of all candidate species from lists of monkey diet species in the area (Poulsen et al. 2002; Wildlife Conservation Society, unpublished data), and experimented on the first species for which we could find several fruiting individuals. We randomly selected seven reproductive individuals of M. mabokeensis (Sapotaceae), a canopy-emergent tree whose fruits are primarily dispersed by arboreal
monkeys. Five species of monkeys feed on *M. mabokeensis* at least occasionally, although three species of *Cercopithecus* are the primary consumers and also tend to be the most frequently hunted monkey species in the concession (Poulsen et al. 2009). In the study area (10 000 ha), *M. mabokeensis* occurs at a density of 1.67 trees/ha. On average the focal trees were separated by 2061 m, with the smallest distance between two trees being 197 m. The trunks measured 121.5 ± 47.6 cm (mean ± SD) diameter at breast height and canopy radius varied among trees (8.5 ± 2.5 m, mean ± SD). The fruits are pulpy drupes, measuring 3–5 cm in diameter. Fruits hold 1–3 seeds per fruit that are an average of 12 mm in length.

**Quantification of seed shadow**

To quantify the seed shadow of *M. mabokeensis*, we placed seed traps under and around the canopies of four focal trees prior to fruit maturation. Traps were constructed of plastic mesh attached to wood frames and were elevated to a height of 1–1.5 m above the ground. Using the trunk as the point of origin, traps were placed along four lines at 1, 2.5, 5, 10, 20, 40, and 60 m from the tree. To avoid directional bias, we randomly selected a starting angle for the first trap line and then separated the four trap lines by 90° intervals.

We increased trap sizes with distance from the tree to sample 1% of the area at each trap annulus. We limited seed traps to 60 m from the parent because we were interested in seedling recruitment in the local neighborhood of the plant, not long-distance dispersal. Previous studies in the region have demonstrated that as much as 85% of seed crops of tropical trees are deposited within 20 m from a tree and only 3%, on average, are dispersed farther than 60 m (Clark et al. 2005). Fruits and seeds were collected from the traps and counted every two weeks until all fruits had fallen from the trees.

We fitted the negative exponential dispersal kernel, \( g(x, a) = (a) \exp(-ax) \), to the seed data, where \( g(x, a) \) is the density of seeds as a function of distance \( x \) from the source. Dispersal scale \( a \) determines how fast seed density falls off with distance from the source, and \( 1/a \) is the mean dispersal distance (Fig. 1). Given a dispersal kernel \( g(x, a) \), \( g(x, a) \, dx \) is the expected proportion of the total seedfall falling between distances \( x \) and \( x + dx \) from the parent tree. This is the one-dimensional probability distribution that describes the probability that a seed will land a particular distance from its parent. If a tree’s total fecundity is \( f \), the expected number of seeds in a trap at distance \( x \) is calculated by multiplying the expected proportion of seeds falling within the annulus between \( x \) and \( x + dx \) by the fecundity and then dividing by the proportion of the annulus covered, where \( A \) is the trap area, \( 2\pi x \, dx \): \( N = f g(x, a) \, dx \times A / (2\pi x \, dx) \). We assumed that observed seed numbers were negative binomially distributed with mean \( N \) and dispersion parameter \( k \). We used the negative exponential dispersal kernel as a simple description of the seed shadow, rather than exploring a greater variety of possible functions (e.g., Muller-Landau et al. 2008), because our goal was to find a phenomenological model of the seed shadow to inform the seed sowing experiment rather than to compare models or model parameters; the negative exponential performed well for monkey-dispersed trees in a previous study (Clark et al. 2005).

We calibrated parameters from the dispersal function by numerically maximizing the likelihood function using the default Nelder-Mead simplex algorithm in R 2.7.1 (R Development Core Team 2008). Confidence intervals were calculated for each parameter by numerical approximation of the Hessian, the matrix of second partial derivatives of the log-likelihood function with respect to the parameters at the maximum-likelihood estimate. The inverse of the Hessian, also called the observed information, is an estimate of the asymptotic variance–covariance matrix, from which standard errors were obtained to calculate 95% confidence parameters for all parameters (Wasserman 2004).

**Experimental seed distributions**

To examine the importance of patterns of seed dispersal for seedling recruitment, we experimentally planted seeds in three different distributions and...
monitored seedling recruitment and survival. Before sowing seeds, we first staked out seven “wedges” at 45° from each other under seven *Manilkara mabokeensis* trees (Fig. 2). We defined a wedge as a sector (188 m²) of a circle, with its origin at the trunk, a central angle of 6°, and a radius of 60 m. Together, the three wedges covered 5% of the area around the trunk. We delimited the radius of the sector into 5-m sections and planted seeds at the 12 different distance annuli. In three of the wedges, “Observed,” we monitored seedling recruitment derived from the natural seed rain. In the four remaining wedges, we removed all of the seeds from the canopy floor. One of these served as a seed-removal control (“Seed removal”). We sowed seeds in different distributions in the remaining three: (1) in the “No dispersal” wedge, seeds were sown within 10 m of the trunk (e.g., under the canopy of the tree); (2) in the “Natural dispersal” wedge, seeds were sown with decreasing densities from the tree following quantification of the seed shadow; (3) in the “Good dispersal” wedge, seeds were sown at uniform densities with distance from the tree.

Fig. 2. Depiction of the experimental design to evaluate the effect of three contrasting seed dispersal patterns on seedling recruitment and survival. Seven wedges were delineated under each of seven adult individuals of *Manilkara mabokeensis*. We defined a wedge as a sector (188 m²) of a circle, with its origin at the trunk with a central angle of 6° and radii of 60 m. In three of the wedges, “Observed,” we monitored seedling recruitment derived from the natural seed rain. In the four remaining wedges, we removed all of the seeds from the canopy floor. One of these served as a seed-removal control (“Seed removal”). We sowed seeds in different distributions in the remaining three: (1) in the “No dispersal” wedge, seeds were sown within 10 m of the trunk (e.g., under the canopy of the tree); (2) in the “Natural dispersal” wedge, seeds were sown with decreasing densities from the tree following quantification of the seed shadow; (3) in the “Good dispersal” wedge, seeds were sown at uniform densities with distance from the tree.

For the experimental wedges, we collected mature seeds and seeds from fruits from under the canopies of many different *M. mabokeensis* trees (~15 trees), mixing...
all the seeds together before sowing them. We monitored seedling recruitment 1, 3, 6, 9, 12, and 18 months after the sowing of seeds, recording the number of seeds in each of the wedges and distance annuli. We also noted the number of leaves on each seedling and the number of leaves with signs of insect damage and herbivory. To determine whether the spatial distribution of seeds influences the diversity of the seedling community, we counted and identified to morphospecies all of the seedlings <50 cm in height in the experimental wedges at the end of the experiment. Although we were able to identify many individuals to species, our primary concern was to correctly classify the number of individuals of different species in each distance by wedge combination.

Analysis

Our main interest was whether the spatial distribution of seeds determined seedling survival. We used survival analysis to analyze the data and Bayesian inference with Markov Chain Monte Carlo (MCMC) simulation to estimate posterior distributions of model parameters and test for significance. For the survivor function, we assumed a Weibull distribution for which the mortality rate is proportional to a power of time. The Weibull is commonly used in survival analysis because it is flexible and can model constant, increasing, and decreasing hazard rates (i.e., the instantaneous per capita mortality probability at a specific time), and can easily be extended to mixed survival models.

The seedling survival model included random effects for the replicate trees \( t_{ijk} \) and the experimental wedges \( e_w \) within trees as follows:

\[
t_{ijk} \sim \text{Weibull}(r_{jk}, \mu_{jk}) \quad i = 1, \ldots, N(j, k) \]
\[
j = 1, \ldots, 7 \]
\[
k = 1, \ldots, 3
\]

\[
\log(\mu_{jk}) = \beta X_{ijk} + \gamma D_{ijk} + \delta_k + \epsilon_{rj} + \epsilon_{ew}
\]

\[
\log(r_k) = \theta_{ew}
\]

where \( t_{ijk} \) is the failure time of the \( i \)th seed in wedge \( k \) around tree \( j \) and \( N(j,k) \) is the number of individuals in wedge \( (j,k) \). For censored observations (seedlings that survived past month 18, the last month of the experiment), we used the upper cumulative probability of the Weibull distribution (i.e., the probability of surviving \( \geq 18 \) months). The shape parameter \( r_k \) was allowed to vary by wedge with coefficient \( \theta_{ew} \). The shape parameter determines the shape of the hazard function: when \( r < 1 \), the hazard function decreases with time (early-life failures); when \( r = 1 \), the failure rate is constant; and when \( r > 1 \), the hazard function increases with time (wear-out failures). The scale parameter \( \mu_{jk} \) determines the range of the distribution and was described by a vector of regression coefficients (i.e., fixed effects), where \( \beta \) is the (log) linear effect of distance, \( X_{ijk} \); \( \gamma \) is the (log) linear effect of seed density, \( D_{ijk} \); and \( \delta_k \) represents the effect of the three-level factor of wedge, \( W_{ijk} \). Because the effects of distance and seed density were modeled on the log scale, their realized effects are exponential. The regression coefficients and the precision of the random effects were modeled with independent weak priors, with normally distributed priors (Normal\( (0, \tau = 10^6) \)): note that in Bayesian contexts normal distributions are typically specified in terms of the precision, or the reciprocal of the variance, \( \tau \) for fixed effects and means of random effects and uniform priors (Uniform\( (0, 100) \)) on the precisions of the variance components. So that all parameter estimates were interpretable on the same scale, we standardized distance and density (both here and in subsequent analyses) by subtracting the mean and dividing by the standard deviation to yield a Z score (Gelman and Hill 2007).

We used generalized linear mixed models (GLMMs) to gain insight into the spatial mechanisms (distance from tree, density, experimental distribution) that drive seedling recruitment and survival by modeling three different indicators of seedling recruitment. To assess their effects on seedling recruitment, we modeled the proportion of sowed seeds that germinated as a logistic regression using a logit link. To assess their effects on seedling health and growth, we modeled the number of leaves per seedling using a log link and Poisson error distribution. To assess their effects on herbivory, we modeled the proportion of leaves with herbivory damage as a logistic regression using a logit link. In all three tests we included tree and wedge within tree as random effects. Bayesian inference with MCMC simulation was used to estimate parameters and test for significance for the survival and GLMM models. We chose weak, proper prior distributions for all parameters (normal distributions with large variance), allowing the observed data to dominate inferences.

We fit our models using the software WinBUGS v. 1.4.1 (Spiegelhalter et al. 2003) run through the R Language, version 2.7.1 (R Development Core Team 2008) using the contributed package, R2WinBUGS (Sturtz et al. 2005). We ran three chains to monitor convergence and assessed convergence by visual inspection and with Gelman-Rubin statistics from the R contributed package, coda (Plummer et al. 2005). For the survival model, we achieved convergence after 100 000 iterations (the "burn-in") and based summary statistics on an additional 100 000 iterations. For the other models, the chains converged after 25 000 iterations and we based summary statistics on the next 25 000 iterations. Parameter estimates (means) and their 95% credible intervals were obtained from the quantiles of the posterior distribution of model parameters.

To assess the importance of parameters to our survival model, we tried to fit all possible candidate models and compared their deviance information criterion (DIC). DIC is analogous to information
criteria (e.g., Akaike Information Criterion, AIC) for hierarchical models and combines a measure of model fit and complexity to distinguish among models. For some models, we had difficulty achieving convergence of at least one parameter. Therefore, we instead ran the full survival model multiple times, each time setting a different parameter to 0 (i.e., effectively removing it from the model) to assess its contribution to the model. We used DIC to compare model fits, with lower DIC values indicating a better fit of a model to the data. To draw inferences from the GLMM models, we compared posterior means and 95\% credible intervals of the full models.

To evaluate whether patterns of seed dispersal affect species diversity of the seedling community, we computed Simpson’s diversity index, \( S = 1 - \sum n(n - 1)/N(N - 1) \), which takes the relative abundance of different species into account, where diversity \( S \) is a function of the number of individuals of a species \( n \), and the total number of individuals of all species \( N \). Specified in this way, a value of 0 represents no diversity and a value of 1 represents infinite diversity. We calculated Simpson’s diversity index for each wedge-by-distance combination, and then tested for differences in mean diversity by wedge to examine whether the spatial distribution of seeds affected species diversity. We compared mean diversity among wedges with a permutation test by shuffling the wedge identities (no dispersal, natural dispersal, good dispersal) within each tree and then calculating the average diversity for each wedge type across all seven trees. We ran 1000 permutations and compared the observed mean diversity, \( S_{\text{obs}} \), for each wedge to the 2.5\% and 97.5\% quantiles from the simulated mean diversity, \( S_{\text{sim}} \).

**RESULTS**

Of the 18,501 seeds sown in experimental wedges, 6.5\% (1203 seedlings) emerged and 1\% (192 seedlings) survived to 18 months. Seedling survival decreased over time, with the greatest decrease in survival occurring in the area closest to the tree for all seed distributions (Fig. 3).
Seedling survival was determined by the density of seeds sown, with lower seedling survival at higher seed densities ($\gamma = -1.73$, 95% CI = (-2.565, -0.9178); Fig. 4). Survival increased slightly with distance from the tree, but the credible interval of the effect overlapped 0 ($\beta = 0.260$, 95% CI = (-0.352, 0.822)). Similarly, the effects of the experimental treatments did not differ strongly, suggesting that any remaining treatment effects not absorbed by the density and distance parameters were weak (Fig. 4). As evidenced by the shape parameters, longer distance dispersal tended to have delayed mortality, although there were not strong differences among experimental distributions (no dispersal $r = -1.39$, 95% CI = (-1.481, -1.310); natural dispersal $r = -1.45$, 95% CI = (-1.541, -1.354); good dispersal $r = -1.51$, 95% CI = (-1.622, -1.404); see Fig. 4). Variation in survival was greater among trees ($\epsilon_T = 3.37$, 95% CI = (3.071, 7.244)) than it was among experimental wedges under the same tree ($\epsilon_W = 1.78$, 95% CI = (0.941, 3.170)). Comparing candidate models (by consecutively setting each parameter to 0 and comparing DIC values) demonstrated that seed density and random effect of wedge contributed strongly to seedling survival, whereas distance and experimental treatment parameters did not (Table 1).

To determine the mechanisms driving differences in seedling survival, we examined patterns of seed germination, leaf production, and leaf damage from herbivores in the experimental wedges. The advantage of low seed density for survival did not accrue until the seedling...
Table 1. Model comparison for survival analysis of seedlings of Manilkara mabokeensis trees in experimental wedge plots in the Congo.

<table>
<thead>
<tr>
<th>Model</th>
<th>ΔDIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full model</td>
<td>0</td>
</tr>
<tr>
<td>No wedge effect, ( \delta )</td>
<td>-2</td>
</tr>
<tr>
<td>No density effect, ( \gamma )</td>
<td>+1</td>
</tr>
<tr>
<td>No distance effect, ( \beta )</td>
<td>-1</td>
</tr>
<tr>
<td>No random effect of tree, ( \sigma_{tree} )</td>
<td>+2</td>
</tr>
<tr>
<td>No random effect of wedge, ( \sigma_{wedge} )</td>
<td>+32</td>
</tr>
</tbody>
</table>

Notes: M. mabokeensis seeds were sown in three patterns (no dispersal, natural dispersal, good dispersal) in wedges under seven trees (extending 60 m from tree; wedge area 188 m²). We delimited the radius of the sector into 5-m sections, and planted seeds at the 12 distance annuli. In the table, wedge effects signify the effect of the dispersal patterns on seedling survival; distance and density effects represent the distance from the tree and density of seeds in each annulus; and the tree effect indicates variation in survival across the seven trees. A low deviance information criterion (DIC) value indicates that the model fits the data better than a higher value. To assess the contribution of parameters to the survival model, we ran the model multiple times, each time setting one of the parameters to 0 (i.e., effectively removing it from the model). A parameter improves model fit when its removal from the model causes the DIC value to increase (positive ΔDIC); the removal of an important parameter should cause the model to get worse. The rule of thumb for evaluating models by DIC is as follows: DIC < 2 indicates little difference between models, DIC = 4−7 indicates that models are clearly distinguishable, and DIC > 10 indicates that models are definitely different (Bolker 2008).

stage, because the log-odds of seed germination did not strongly vary with distance from tree (log-odds ratio: 0.006, 95% CI = (−0.133, 0.143)) or density of sowed seeds (log-odds ratio: 0.086, 95% CI = (−0.050, 0.220)). Seed germination also differed little among experimental treatments, suggesting that there were no additional characteristics of the experimental treatments beyond distance and density that strongly affected seed germination (log-odds ratio: no dispersal = −4.84, 95% CI = (−6.10, −3.12); natural dispersal = −4.53, 95% CI = (−5.68, −2.84); good dispersal = −4.63, 95% CI = (−5.87, −2.92)). However, seed density did decrease the number of leaves per seedling, an indicator of seedling growth and health (log-odds ratio: −0.13, 95% CI = (−0.22, −0.04)), suggesting either that leaves are being removed by herbivores or that competition for resources with conspecific seedlings leads to a lower production of leaves. The number of leaves per seedling was not strongly affected by distance from tree (log-odds ratio: 0.051, 95% CI = (−0.01, 0.11)), nor was there a large difference in numbers of leaves among experimental distributions (log-odds ratio: no dispersal = −0.51, 95% CI = (−0.84, −0.16); natural dispersal = −0.31, 95% CI = (−0.54, −0.09); good dispersal = −0.33, 95% CI = (−0.55, −0.11)). Of the leaves on seedlings, the log-odds of insect damage to leaves decreased by ~7% with every 10 m away from the tree (log-odds ratio: −0.265, 95% CI = (−0.439, −0.095)). The density of seeds did not strongly influence the log-odds of leaf damage (log-odds ratio: 0.084, 95% CI = (−0.130, 0.293)), and there were no large differences (overlapping credible intervals) in leaf damage among the experimental distributions (log-odds ratio: no dispersal = −2.86, 95% CI = (−3.56, −2.19); natural dispersal = −2.79, 95% CI = (−3.22, −2.37); good dispersal = −2.67, 95% CI = (−3.12, −2.25)).

The higher survival that comes from recruiting into an area with relatively low seed density means that more uniform dispersal patterns will lead to higher seedling survival than aggregated patterns. By the end of our experiment, 4.85 ± 5.35 seedlings (mean ± SD) survived on average in the good dispersal wedges, 3.86 ± 4.60 seedlings survived in natural wedges, and 0.86 ± 1.21 seedlings survived in no dispersal wedges (Fig. 5). Scaling up to the local neighborhood of the tree (1.1 ha), good dispersal would result in 79.6 more seedlings than natural dispersal, and natural dispersal would result in 240.4 more seedlings than no dispersal. For M. mabokeensis, our results suggest that the extirpation of monkeys by hunting would result in a 78% decrease in recruitment at the end of 18 months.

Seedling diversity (based on Simpson’s index, \( S \)) within wedges decreased with longer dispersal distances (more even distributions), although seedling diversities in each treatment were not significantly different from the simulated diversity based on random dispersal patterns: for no dispersal, \( S_{obs} = 0.79 ± 0.23 \) (mean ± SD), \( S_{sim} = 0.76 \) (0.025 and 0.975 quantiles = 0.71, 0.81); for natural dispersal, \( S_{obs} = 0.76 ± 0.29 \), \( S_{sim} = 0.76 \) (quantiles = 0.70, 0.81); for good dispersal, \( S_{obs} = 0.74 ± 0.30 \), \( S_{sim} = 0.77 \) (quantiles = 0.71, 0.81).

![Fig. 5. Mean number of seedlings that survived over 18 months in the three experimental distributions (no dispersal, natural dispersal, and good dispersal) and the observed, nonexperimental distribution. Better rates of dispersal resulted in higher numbers of surviving seedlings.](image-url)
**Discussion**

The spatial distribution of dispersed seeds matters for seedling recruitment and survival for *Manilkara mabokeensis*, a monkey-dispersed tropical tree species. Compared to natural dispersal, good dispersal increased seedling survival by 26%, whereas the no dispersal treatment reduced seedling survival by 78%. With the transition from seed to seedling often acting as a bottleneck for recruitment (Chambers and MacMahon 1994), these differences in rates of seedling survival are probably important to the maintenance of the *M. mabokeensis* population: they represent 79.6 and 240.4 more seedlings at the neighborhood level, and 700,000 and 2,120,000 more seedlings at the scale of our study area. Seed shadows with more even distributions of seeds resulted in higher numbers of surviving seedlings. Survival of seedlings depended on the density of dispersed seeds but not the distance from the tree. These results support hypotheses that invoke density-dependent mortality as a limiting factor to recruitment, but fail to support the Janzen-Connell hypothesis in its contention that enhanced distance of seeds from conspecific adults improves survival (e.g., Hyatt et al. 2003).

Our results support previous studies indicating that local communities are seed limited (Turnbull et al. 2000, Clark et al. 2007), but that strong, density-dependent mortality limits post-dispersal survival (Poulsen et al. 2007, Norghauer and Newbery 2010). The shape of the seed shadow did not affect seed germination and seedling emergence, but had strong effects on seedling health and survival. The benefits of dispersal probably arose through higher probabilities of escaping herbivores (pathogens, insects, and vertebrates) that responded to seedling density. In a concurrent study, we caged seed addition plots of *M. mabokeensis* to protect seeds and seedlings from rodents and herbivores. Compared to uncaged plots, seedling survival in caged plots was 2.6 times higher after 3 months and 4.9 times higher after 24 months.

Janzen (1970) and Connell (1971) hypothesized that seeds dispersed away from the high densities of seeds aggregated under the parent canopy would avoid mortality from density- and distance-dependent behavior of seed and seedling predators. Previous studies have verified that higher seed or seedling density and greater proximity to the parent plant often lower seedling recruitment (Augspurger and Kelly 1984, Clark and Clark 1984, Howe et al. 1985, Augspurger and Kitajima 1992). Here we extended these findings by using a replicated design to decouple and quantify the effects of distance and density on seedling survival and the overall advantage of different dispersal patterns. We demonstrated effects of seed density on seedling recruitment and survival, but found no evidence of distance effects. The fact that we randomized genotypes, by mixing seeds from different trees in our experimental distributions, might have reduced the distance-dependent relationship if specialist pathogens build up near the parent tree; although phylogenetic range, at least of fungal pathogens, is probably wider than even a single species (Gilbert and Webb 2007). The distance component of Janzen and Connell’s hypothesis, however, has received little support (Hyatt et al. 2003), and might oversimplify the interaction between seeds, seedlings, and predators, which depends on the scale of movement of both offspring and their enemies (Adler and Muller-Landau 2005). It is also very likely that density-dependent mortality continues over time so that patterns of distance-dependent survival occur over several years.
and not the relatively short timescale (1–2 years) of most studies.

We expected that better (more uniform) dispersal would lead to lower community richness by increasing conspecific seedling establishment to the exclusion of heterospecifics. Connell (1971) argued that if propagule distance or density were to impact diversity, it should be seen most strongly in individual species at the seedling stage. Similarly, differences in diversity should be most detectable by comparing seed shadows that represent the extremes of seed dispersal patterns: only dispersal from seeds falling from the tree (no dispersal) and uniform rates of dispersal (good dispersal). Although we did find an inverse relationship between dispersal and seedling diversity, it was not strong enough to conclude that better dispersal would lead to lower diversity. Dispersal limitation may be less important for maintenance of species diversity than density dependence and habitat partitioning (Webb and Peart 2001). On the other hand, the contrasting seed shadows in our experiment resulted in dramatically different numbers of recruiting and surviving seedlings. However, we only evaluated the community results after a single dispersal season. Spatial patterns of seedlings that accumulate over several seasons would likely have a much stronger effect on the diversity of the seedling community.

This experiment was a first step in understanding how dispersal patterns influence population- and community-level diversity. Future experiments could build on it by following recruitment over multiple fruiting seasons and extending the results to additional species and plant forms. Moreover, we would encourage testing additional patterns of dispersal relevant to the dispersal patterns of the species under examination, including nonparametric dispersal patterns that incorporate contagious dispersal away from the parent plant and temporal pulses of seed arrival. To assess the spatial mechanisms that contribute to community diversity, we recommend either measuring the incoming heterospecific seed rain and incorporating it into comparisons of community diversity across experimental replicates, or more directly, manipulating seed dispersal patterns of multiple species in a single experiment.

From a conservation perspective, our results from one monkey-dispersed tree species suggest an impending disaster as the loss of seed dispersal resulted in much lower seedling recruitment and survival. The population success of tropical tree species like *M. mabokeensis* may be imperiled with the extirpation of their seed dispersers, which is currently underway. Compared to the site of this experiment, densities of frugivorous monkeys were 35% lower in adjacent forest, ~10 km away, subjected to moderate (~1 people/km²) subsistence hunting (Poulsen et al. 2011). Forests throughout the Afrotropics face threats similar to those in northern Congo (Fa et al., 30–45% of these forests are now occupied by logging concessions and fragment-
ed by roads, exposing additional forests to increased hunting pressure. Hunting threatens to leave many tree species without reliable dispersers, which may in turn leave some tree species with limited or no regeneration.

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**LITERATURE CITED**


