

LOGGING AND HUNTING ALTER PATTERNS OF SEED DISPERSAL AND SEEDLING
RECRUITMENT IN AN AFROTROPICAL FOREST

By

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To my wife, Connie Clark,
who has explored tropical forests with me, and to my infant son, that the forests will survive so
that he will have the opportunity to experience their splendor

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Abstract of Dissertation Presented to the Graduate School
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Unprecedented rates of logging and hunting in Central Africa threaten to transform vast tracts of primary forest into a mosaic of degraded forest emptied of its animals. Reductions in abundances of seed-dispersing animals are hypothesized to alter patterns of seed deposition for many tree species, potentially limiting forest regeneration with long-term consequences for forest structure and composition. In northern Republic of Congo, I set up a large scale observational experiment to decouple the effects of logging and hunting on animal abundance and seed dispersal patterns by positioning 30 permanent transects, each linked to a 1 ha tree plot, in forest disturbed by logging and hunting, logging alone, and neither logging nor hunting. I found that the effects of hunting and logging on densities of animal guilds outweighed the effects of local forest structure and fruit resources. Logging and hunting sometimes interacted to reduce guild densities (ape, duiker, monkey, and pig) by as much as 71% and shifted the composition of the animal community away from large mammals towards squirrels and birds. With seed trap data collected from the tree plots, I used inverse modeling to quantify seed dispersal patterns of 26 tree species. Hunting reduced mean dispersal distances of animal-dispersed species by at least 20%, while hunting and logging both increased mean dispersal distances and dispersion of wind-dispersed species. To determine if changes in seed dispersal patterns reduce seedling recruitment

and survival, I experimentally manipulated seed dispersal patterns under several individuals of a monkey-dispersed tree, creating distributions to mimic scenarios of “no dispersal”, “natural dispersal” and “good dispersal”. After 18 months, “good dispersal” increased seedling survival by 26% over “natural dispersal”, whereas “no dispersal” reduced seedling survival by 78%. Survival of seedlings depended on the density of dispersed seeds but not the distance from the tree. This experiment demonstrated that seed dispersal patterns do matter for seedling recruitment and survival. Management of hunting is a priority for the conservation of tropical forests because forests emptied of their seed dispersers will have limited regeneration capacity.

CHAPTER 1 DECOUPLING THE EFFECTS OF LOGGING AND HUNTING ON A AFROTROPICAL ANIMAL COMMUNITY

Throughout tropical forests, logging and hunting are tightly interconnected: logging opens up frontier forest and hunting quickly follows in its wake. With the expansion of logging in Central Africa, conservation of animal populations depends on knowledge of the individual and combined effects of logging and hunting so that management efforts can be appropriately allocated. Our goals were first to decouple the effects of selective logging and hunting on densities of forest animal guilds, including apes, duikers, monkeys, elephant, pigs, squirrels, and large frugivorous and insectivorous birds, and second, to compare the relative importance of these disturbances to the effects of local scale variation in forest structure and fruit abundance. In northern Republic of Congo, we surveyed animals along 30 permanent transects positioned in forest disturbed by logging and hunting, logging alone, and neither logging nor hunting. Sampling bimonthly for two years, we observed 47,179 animals of 19 species and 8 guilds in 1154 passages (2861 km) over the transects. Densities varied by as much as 480% between forest types demonstrating the significant effects that human disturbance had on populations of some species. The landscape-level effects of hunting and logging on densities of animal guilds outweighed the effects of variation in local forest structure and fruit abundance. Logging and hunting sometimes interacted to reduce guild densities (e.g., ape, duiker, monkey, and pig) by as much as 71%; for other guilds, logging and hunting had opposite effects with positive impacts of one buffering the negative impacts of the other (e.g., squirrels, insectivorous and frugivorous birds). Logging and hunting shifted the relative abundance of the animal community away from large mammals towards squirrels and birds. The combination of logging and hunting had the strongest negative impact on tropical species, but both logging and hunting alone also negatively affected some species. Therefore the strategy of conserving biodiversity by managing hunting in

degraded forest will not stop reductions in animal populations by itself. To balance the loss of forest species and the ecological services they provide with the need for economic development and wild meat in tropical countries, we suggest that land use planning combine large tracts of pristine forest with resource use areas for either logging or hunting.

Introduction

Habitat loss from conversion of forest for agriculture, ranching and intensive logging has led to massive extinctions of tropical animals in some regions (Brook et al. 2003, Curran et al. 2004). Models predict that tropical animals will lose large proportions of their current habitat in the coming decades (Laurance 2001, Soares et al. 2006). In short, the extent of remaining old growth forest is likely insufficient to prevent further large-scale loss of species. The future of many animal species might thus depend on their ability to persist in secondary and degraded forests.

The conservation value of degraded forests has been at the center of the debate over the future of tropical species (Laurance 2007). Wright and Muller-Landau (Wright and Muller-Landau 2006a, b) state that secondary forests could rescue species unlikely to persist in remnants of primary forest, whereas Brook et al. (2006) argue that this is unlikely because tropical secondary forests support lower biodiversity, a predominance of generalist species, and act as reproductive sinks. To resolve this debate, we need a better understanding of the factors that limit the ability of animal species and communities to persist in the face of disturbance. Alarmingly, we seem to lack the field data necessary to translate the consequences of forest degradation into conservation and management policy (Gardner et al. 2007).

Logging is one of the primary drivers of tropical forest degradation. Most extant tropical forests have been logged or will be in the near future, with only relatively small fragments preserved (Whitmore 1997). Logging has been a significant contributor to the economies of the

Congo Basin since the post-colonial period; and at the turn of the century industrial logging expanded into the most remote forests of Gabon, Republic of Congo, and Democratic Republic of Congo (Laporte et al. 2007). Logging concessions now occupy 30-45% of all forests, reaching 70% of forests in some countries (Global Forest Watch 2002, Laporte et al. 2007).

Predicting the effect of logging on tropical forest animals is complicated because logging impacts the forest at multiple scales and its effects are usually confounded with other forms of disturbance. Commercial logging modifies landscape-scale forest structure, local environmental variables and resource abundance (reviewed in Putz et al. 2001). For example, at the level of the concession, logging can change the size, distribution and connectivity of habitat patches. At the level of the forest stand, logging alters canopy openness and light regimes. Changes in canopy openness can release fruit crop trees from competition and increase understory growth, modifying the composition and trophic structure of the stand. The environmental effects of logging alone are diverse, but logging rarely acts by itself. The net effect of logging on populations and communities of forest animals is further complicated to the extent that road construction, population growth and settlement, and hunting accompany and interact with timber extraction (Laurance et al. 2006, Blake et al. 2007, Laurance et al. 2008, Clark et al. 2009, Poulsen et al. 2009b). At best, unsustainable levels of hunting in tropical forest reduce populations of large-bodied animals; at worst they lead to local extinctions of species (Milner-Gulland et al. 2003).

Our goal was to decouple the effects of selective logging and hunting on densities of tropical forest animal guilds. To do this, we established a large scale observational experiment in lowland tropical forest in the Republic of Congo, positioning 30 transects in forest disturbed by logging, logging alone, and neither logging nor hunting. We then surveyed a broad range of

animal species over two years to quantify densities of animal species and guilds. Specifically, we sought to (1) quantify the effects of logging, hunting, and their combined effects on species and guild density, and (2) compare the relative importance of logging and hunting on guild densities to other variables like spatial heterogeneity, local scale environmental variables like forest structure and light availability, and fruit abundance.

Methods

Study Area

We conducted the study in the Nouabalé-Ndoki National Park (NNNP; 400,000 ha) and the Kabo logging concession (267,000 ha) in northern Republic of Congo (Clark et al. 2009, Poulsen et al. 2009b). The Kabo concession borders the NNNP to the south, and together they include a mosaic of logged and unlogged forest. Between 20-25 years before the study, the area was selectively logged at low intensity (<2.5 trees ha^{-1}) with four species, *Entandophragma cylindricum*, *E. utile*, *Triplochiton scleroxylon*, and *Milicia excelsa*, comprising 90% of the cutting volume (Congolaise Industrielle des Bois 2006). Approximately 3000 people inhabit the study site, most of whom live in the logging town of Kabo. Residents hunt with shotguns, and to a lesser extent with wire snares, to supplement their diets and for local trade (Poulsen et al. 2009b). Most hunting originates from the town of Kabo, resulting in a gradient of hunting intensity that decreases with distance from it with some variation with vegetation type (Mockrin 2008). The forests are classified as lowland tropical forest, and dominant tree families include Meliaceae, Euphorbiaceae, and Annonaceae. Rainfall averages about 1700 mm annually and is seasonal with peaks in May and October.

Animal Surveys

We established 30 2.5-km transects over an area of approximately 3000 km^2 . We located ten transects and tree plots (see below) in each of three forest types: unlogged and un hunted

forest, logged and unlogged forest, and logged and hunted forest. We minimized habitat variation among forest transects by positioning transects only in mixed lowland forest, with a buffer of 500 m to the nearest primary road and 100 m to the nearest water source. Using ArcView 3.2 and a 14 class habitat map, we extracted the areas that did not meet those criteria, and then randomly positioned transects on the remaining surface. Transects were oriented perpendicular to water drainage, and were separated by a minimum of 2.5 km. We cut narrow trails along each transect, and marked the trails every 20 meters with flagging tape. Following trail opening, we left all transects undisturbed for one month before sampling for animals.

We designed this study as a natural experiment to try to decouple the effects of hunting and logging. The strength of this design is that we can quantify the effects of hunting and logging while controlling for environmental variation, something that cannot be done with large scale one-off transect designs (e.g., Clark et al. 2009). The weakness of this design is that it is pseudo-replicated in the sense that we quantify the relative densities of animal species and guilds at a single site (a 3000 km² area in northern Congo). This site has particular characteristics, such as its spatial pattern of hunting and logging around the village of Kabo, which meant that hunted transects and logged transects were geographically grouped together and which may not be representative of all other sites in the Congo Basin.

Surveying forest animals, and in particular, assessing the effects of hunting and logging is complicated by the difficulty of observing animals in the forest. To obtain sufficient numbers of observations to estimate species densities, most surveys of tropical animals in the Congo Basin rely on indirect observations of nests for apes and dung for elephant and antelopes. Using indirect observations raises two problems: first, not all animals leave indices that can be counted limiting the number of species that can be surveyed; and, second, estimates of animal abundance

from indirect observations introduce a great deal of error by assuming constant rates of nest and dung production and decay (Walsh and White 2005). To bypass these difficulties, we surveyed permanent transects that were kept open so that we could make observations of live animals.

Three field teams, each composed of a researcher and a local guide, surveyed the 30 transects bimonthly over two years for diurnal mammals and a suite of large bird species (Table 1-1). Surveys began between 06:00 and 07:00 when animals were the most active. Observers walked slowly (ca. 1.2 km hr^{-1}), scanning the forest floor and canopy for direct and indirect observations of animals. For each observation, we recorded the distance along the transect and estimated the distance from the transect to the individual animal or center of an animal group following standard distance sampling protocol (Buckland et al. 2001). To survey birds, we conducted point counts at 200 m intervals along the transects. Upon arrival at the point count station, observers waited for two minutes, and then recorded visual observations of birds and the distance from the bird to the observer for two minutes. Although we surveyed several bird species, we only present data and results for large frugivorous and insectivorous birds for which we are confident that our survey methods were robust. In addition to observations of animals, we also counted signs of hunting encountered along transects, such as shotgun shells, wire snares, and camp fires, to assess the level of hunting pressure.

Environmental Variables

We measured canopy openness and light availability along transects with hemispherical canopy photographs. Photographs were taken every 200 m along a transect, 30 cm above the ground, in uniformly overcast conditions in the early morning or late afternoon with a leveled Nikon Coolpix P5000 camera body and Nikon FC-E8 Fisheye converter lens. We analyzed images for the percentage of transmitted diffuse light and canopy openness using Gap Light Analyzer 2.0 (Frazer et al. 2001).

We established 30 1-ha tree plots to examine whether forest structure influences animal abundance and distribution. The plots were positioned 50 m to the right or left (randomly selected) of the midpoint (1250 m) of each transect. Within each plot, we tagged, measured, mapped and identified to species all trees greater than 10 cm diameter-at-breast-height (dbh) (Harris and Wortley 2008). For each tree, we also recorded the canopy status of the tree (understory, midstory, canopy, and emergent) and the presence/absence of lianas in its crown. In addition, we quantified canopy openness and light availability for each plot, averaging the values of four pictures taken from each quadrant of the plots. Canopy heterogeneity was calculated for each plot and each transect as the standard deviation of canopy openness for the plot or transect.

We quantified fruit availability in each of the 30 plots by collecting fruits and seeds in 21 1m² traps. Seeds traps were centered along three lines at 25, 50, and 75 m from the plot border, with 10 m separating each trap. At the same time that transects were walked, we collected all seeds and fruits that fell into the traps and counted and identified them to species. When unknown fruits and seeds were collected, we searched the canopy over the seed trap for fruit, using the tagged trees to identify the propagule. We quantified fruit abundance as the monthly density of fruits per m².

Data Analysis

To quantify variation in habitat structure among sites, we summarized the plot data (presence/absence of lianas, number of trees, number of tree species, number of secondary forest trees, mean and standard deviation of diameter-at-breast height, number of understory, midstory, canopy, and emergent trees, and % diffuse light) into fewer variables using Principal Components Analysis (PCA). Three axes captured 95% of the variance and explained the main forest structure gradients (Figure 3). The first axis (51% of the variance) distinguished a gradient in the number of trees in a plot, with the number of understory, emergent, and canopy trees

contributing to the number of trees. The second axis (31% of the variance) identified a forest structure gradient in the number of lianas in the plot, with understory trees supporting few lianas relative to canopy trees. Finally, the third axis (10% of the variation) separated understory trees from canopy trees. We refer to these variables in subsequent analyses as “Number of trees”, “Number of lianas”, and “Understory”.

We estimated animal densities and calculated their associated coefficients of variation and 95% CIs with Distance 5.0 software (Thomas et al. 2006). To ensure robust estimation of detection and an effective strip half-width, the distance over which the probability of detection of an observation is estimated, we calculated densities for species for which we gathered at least 40 observations per site and we truncated observations farthest from each transect (Buckland et al. 2001). We fitted detection functions to the data sequentially with half-normal, uniform, and hazard-rate key functions that contained cosine, Hermite polynomial, and simple polynomial adjustment terms (Buckland et al. 2001). The best model was selected on the basis of the lowest Akaike information criterion score (AIC). We examined model fit with chi-square goodness-of-fit tests.

Animal species traits were directly linked to environmental variables with a three-table ordination method known as RLQ analysis (Doledec et al. 1996, Ribera et al. 2001, Dray et al. 2002). RLQ analysis is an extension of coinertia analysis that relates a plot-by-variable table (R) to a species-by-traits table (Q), with a plot-by-species table (L) serving as a link between R and Q. With RLQ analysis both species traits and environmental conditions affected by disturbance, as well as their interrelationships, can be assessed (Cleary et al. 2007). To visually assess the relationship between animal species traits and environmental characteristics of the plots, we used a three-table ordination method known as RLQ analysis (Doledec et al. 1996, Ribera et al. 2001,

Dray et al. 2002). RLQ analysis is an extension of coinertia analysis that relates a plot-by-variable table (R) to a species-by-traits table (Q), with a plot-by-species table (L) serving as a link between R and Q. With RLQ analysis both species traits and environmental conditions affected by disturbance, as well as their interrelationships, can be assessed (Cleary et al. 2007). For animal species traits we included body size (small, < 5kg; small-to-medium, < 10 kg; medium, <50 kg; large, >50 kg), feeding guild (brower, frugivore, frugivore-granivore, granivore, grazer, insectivore), and protected status (unprotected, partially protected, protected). For environmental traits we included type of disturbance (hunting, logging), fruit abundance, number of signs of hunting, mean diameter-at-breast height of trees > 10 cm, canopy heterogeneity, number of trees, number of trees topped by lianas, and number of understory and canopy trees.

Three separate ordinations of the R (environmental variables), L (species composition), and Q (species trait) tables were performed prior to the co-inertia analysis. First, the species abundance table containing the number of individuals of each species occurring at each site was analyzed by correspondence analysis (CA), an eigenanalysis approach that provides a joint scaling of sites and species scores. Only species with five observations or more were included in the analyses due to the sensitivity of correspondence analysis to “rare” species (Lesica and Cooper 1999). We also conducted the CA on the log₁₀ transformed abundances of species, but it did not alter the overall results. The sites and species scores were used to link the R and Q tables, as sites are shared by the R and L tables and species are shared by the Q and L tables (Ribera et al. 2001, Dray et al. 2002, Hausner et al. 2003, Choler 2005). Next, the relationship between sites and environmental attributes (i.e., R table) was analyzed. For the quantitative set of variables, PCA was applied using weights obtained with the correspondence analysis of

species, thereby linking the R to the L table. The final step in this initial procedure was the analysis of the Q table of categorical species traits with row weights obtained with the correspondence analysis of species using multiple correspondence analysis (MCA; Tenenhaus and Young 1985). After these three steps a single inertia analysis was performed on the cross-matrix of R, L, and Q. Co-inertia analysis selects axes that maximize covariance between the R and Q tables. As a result, the environmental attributes are directly related to species traits.

RLQ analysis is a symmetric analysis, in the sense of finding scores that are optimally related to each table, without emphasizing environmental variables or species traits. Scores are a compromise between maximizing the correlation and explaining the variation in each table. We investigated the significance of the relationship between the environmental attributes (R) and species traits (Q) with a Monte Carlo permutation test, permuting the R and Q tables 1000 times and comparing the results to observed values (Doledec et al. 1996). All analyses were carried out using the ADE4 software package within R (Dray et al. 2007).

We assessed the importance of disturbance (hunting and logging), geographic position, environmental variables, and fruit abundance on animal density by modeling these factors in relation to observations of animals for each of eight guilds. Modeling the number of animals in a given guild at a particular point in time (month) and space (site) is generally done by fitting a generalized linear mixed model (GLMM) using a Poisson distribution. However, a distinguishing characteristic of data from surveys is their tendency to contain a large proportion of zeros. Examination of the frequencies of counts of observations of animal guilds demonstrated that the data included more zeros than can be expected by either a Poisson or negative binomial distribution. A high frequency of zeros can arise in several ways (Kuhnert et al. 2005, Martin et al. 2005a, Martin et al. 2005b). Structural zeros result from a true ecological

effect; for example, a strong seasonal or environmental gradient will result in sites with no animals present in one season or under particular conditions (e.g., heavy hunting). Random zeros result from observer error and study design: the observer fails to detect the species or the species occurs but is not present in the survey period. These are false negative errors and arise when a species is not recorded when it is in fact present. Modeling of data with a high frequency of zeros can lead to spurious results if these factors are not taken into account (reviewed in Martin et al. 2005b).

Although multiple approaches can be used for modeling high frequencies of zeros (e.g., hurdle model, negative binomial model), when random zeros are present in the data, a zero-inflated mixture modeling approach is required (MacKenzie et al. 2002, Tyre et al. 2003). Our data certainly included random zeros because a species was sometimes not recorded on a transect at time t , even though it had been recorded at times $t-1$ and $t+1$. Therefore we employed a zero-inflated Poisson model (ZIP) comprised of a point mass at zero and a Poisson distribution (Lambert 1992). Using this approach, we model the probability that a zero comes from a Poisson distribution or alternatively as a random zero. The mean number of animals at a site is then estimated given the zeros are modeled in this way.

The mixture model is specified as:

$$Pr(y_{tjk} = 0 | x_t, z) = 1 - p(x_{tjk}) + p(x_{tjk}) \exp(-\lambda(z_{tjk})),$$

$$Pr(y_{tjk} = r | x_t, z) = p(x_{tjk}) \frac{\exp(-\lambda(z_{tjk})) \lambda(z_{tjk})^r}{r!}, \quad r = 1, 2, \dots,$$

where

$$\text{logit}(p(x_{tjk})) = \beta_0 x_{tjk} + \gamma_{0tjk}$$

$$\text{log}(\lambda(z_{tjk})) = \beta_1 z_{tjk} + \gamma_{1tjk} + \log(\Phi_{1j}).$$

In both equations, $p(x_{ijk})$ represents the probability that an observation i is modeled as a Poisson distribution. Above, $\lambda(z_{ijk})$ represents the mean expected number of individuals at site j and month k and is expressed as a function of the explanatory variables, z , through a log transformation. Similarly, p_{ijk} can be expressed as a function of the explanatory variables x , using a logit transformation. Here the parameters β_0 and β_1 are vectors representing the coefficients estimated for explanatory variables, x_{ijk} and z_{ijk} (fixed effects), and γ_{0ijk} and γ_{1ijk} are vectors for the grouping variables (random effects). To model animal density, we included the area sampled, Φ_{ij} , as an offset. We calculated Φ_{ij} for the i th species and j th site by multiplying the distance walked along a transect by twice the species-specific effect strip width estimated by Distance 5.0. We did not include a constant intercept term in the models as its inclusion sometimes made parameter optimization difficult.

We related the observations of animals of each guild to the following explanatory variables (x_{ijk} and z_{ijk}): 1) site (logged/hunted, logged/unhunted, unlogged/unhunted); 2) geographical coordinates (longitude and latitude); 3) number of trees (PCA 1); 4) number of lianas (PCA2); 5) number of understory trees (PCA 3); 6) canopy heterogeneity (standard deviation of transect diffuse light); and 7) monthly fruit abundance. All continuous explanatory variables were transformed into z -scores for analysis (Gelman and Hill 2007). So that fruit abundance would reflect the actual diet of an animal guild, we used diet lists from the literature to categorize fruit species by the types of animals that consumed them (Gautier-Hion et al. 1985, White et al. 1993, Tutin et al. 1997, Whitney et al. 1998, Clark et al. 2001, Poulsen et al. 2001, Poulsen et al. 2002, Morgan and Sanz 2006). We included the month that the survey was conducted and species as random effects (γ_{0ijk} and γ_{1ijk}).

To get the estimate of mean guild abundance for each site, we held all other covariates at their mean values and we multiplied the ZIP mixing probability, the probability that the number of individuals at a site has a Poisson distribution, by the predicted density of individuals at a site generated from a Poisson distribution. We then estimated the overall effect of logging, hunting, and logging and hunting as log-ratios of guild densities by dividing the posterior mean abundance of a guild at the disturbed site from the posterior mean abundance of the site where that disturbance was not present; for example, the effect size of logging would be:

$$Effect_{logging} = \log(Site_{logged,hunted}) / \log(Site_{unlogged,hunted})$$

Bayesian inference with Markov Chain Monte Carlo (MCMC) simulation was used to estimate posterior distributions of model parameters and test for significance. Statements of “significance” are made in the Bayesian context where a “significant” effect indicates that the 95% credible interval corresponding to that effect does not include zero, and an estimate that is “significantly less than” a proposed value has 5% probability of being equal to or greater than the proposed value. For the ZIP models, we used weakly informative, normally distributed priors for fixed effects, half-Cauchy priors for random effects and gamma priors on the precisions of the variance components (Gelman and Hill 2007). The ‘zeros trick’ rule allowed the specification of the truncated Poisson distribution (Spiegelhalter et al. 2003, Kuhnert et al. 2005, Martin et al. 2005a, Martin et al. 2005b). We fit our models using the software WinBUGS v. 1.4.1 (Spiegelhalter et al. 2003). For each model, we achieved convergence after 50,000 iterations (the “burn-in”) and based summary statistics on an additional 50,000 iterations. We ran three chains to monitor convergence based on variance components of multiple sequences and assessed convergence by visual inspection and with Gelman-Rubin statistics from the R contributed package, coda (Plummer et al. 2005). For point estimates, we extracted the means of

the posterior distributions and we derived 95% credible intervals based on the observed quantiles from the MCMC replicates.

With the exception of the ZIP models and estimation of species density, all statistical analyses and graphing were performed with the R Language, version 2.7.1 (R Development Core Team 2008).

Results

Densities of Animal Species

We recorded 9811 direct observations of animal groups (47,179 animals) in 2861 km of transects (n=1154 passages along transects) between June 2005 and May 2007 (Figure 2). We estimated the densities of 19 species at each of the 3 sites (Table 1-1). Several species demonstrated large differences in estimated densities among sites. For example, chimpanzee (*Pan troglodytes*) density was higher in the unlogged, unhunted forest than the logged, hunted forest. All four monkey species (*Lophocebus albigena*, *Cercopithecus cephus*, *C. nictitans*, and *C. pogonias*), ape species (*Gorilla gorilla* and *P. troglodytes*), blue duiker (*Cephalophus monticola*), and medium duikers (*Cephalophus* spp.) tended to have the highest densities in unlogged, unhunted forest and lowest densities in logged, hunted forest. By contrast, elephant (*Loxodonta africana*) density was highest in logged, hunted forest and logged, unhunted forest. Large frugivorous birds (*Bycanistes albotibialis*, *B. fistulator*, *Ceratogymna atrata*, *Corythaeola cristata*, and *Psittacus erithacus*) tended to have the highest densities in logged, hunted forest, whereas insectivorous birds (*Tockus albocristatus*, *T. cameras*, and *T. fasciatus*) had the highest densities in either the logged, unhunted or logged, hunted forest. Densities of both squirrel species (*Funisciurus lemniscatus* and *Protoxerus stangeri*) were highest in logged, hunted forest.

Relating Species and Guilds to Environmental Variables

The RLQ analysis revealed a significant (permutation test: $P < 0.001$) association between environmental variables and species traits. We consider the first two RLQ axes, which together explained 87.7% of variance in the analysis. Because the RLQ analysis represents the partial ordination of the environmental characteristics, the species abundances, and the species traits, we compared the proportion of variance attributed to each matrix to that resulting from their separate analyses. The first axis of the RLQ analysis accounted for 82.7% of the variance and for 53.5% of the variance in environmental variables and 56.0% of the variance in species traits (Table 1-2). The second axis of the RLQ analysis accounted for only 5.0% of the variance and for 56.0% of the variance in environmental variables and 79.2% of the variance in species traits. Overall, these results showed that the structure of tables R and Q were related to the species abundance gradients in L.

Along axis 1, hunted, logged forest with a low abundance of understory trees contained species with a different set of traits than logged, hunted and unlogged, unhunted forest (Figure 4). In addition to having a greater number of hunting sign, hunted, logged forest was characterized by having a greater number of secondary tree species. These forest sites tended to be occupied by small insectivorous and granivorous species; whereas unhunted forest tended to contain larger species and more grazers and browsers. Axis 2 explained very little of the variance, but separated plots and species by forest structure. Plots with high mean DBH were more heterogeneous and separated from those with greater numbers of canopy trees and a more even canopy cover. Abundance of large browsers was higher in the more heterogeneous forest and separated from the rest of the animal community.

Decoupling the Effects of Disturbance, Geographic Position, Forest Structure and Fruit Abundance on Guild Densities

ZIP models identified the factors that most strongly determine densities of animal guilds. The absence part of the ZIP model, quantifying the probability of a structural zero (i.e. species truly absent), varied across guilds (Appendix 1). Note that effects for the absence component presented in Appendix 1 are on the logit scale, where an effect of zero corresponds to a probability of 0.5. Here we focus on the abundance part of the models and the effects of hunting, logging, spatial variation, forest structure, and fruit abundance on the densities of guilds. Effects of abundance are guild densities so that effects that showed no change would be centered on zero. Because geographic coordinates were strongly correlated with logging presence and hunting intensity (see below), we present the results of models configured in two different ways: a full model which includes all factors and a disturbance model which excludes latitude and longitude from analysis.

In the full ZIP model, guild densities varied along a latitudinal gradient. Monkey, pig, duiker, and ape density increased with latitude; whereas frugivorous bird density decreased with latitude. In this model, the effect of disturbance, both logging and hunting, did not have a strong effect on most guilds. The logged guild densities predicted for each site (logged and hunted, logged and unhunted, and unlogged and unhunted) often had overlapping 95% credible intervals (Figure 5). Moreover, pig, elephant and monkey densities demonstrated differences among sites, but sometimes in an unexpected direction. For example, although Distance analysis found elephant to have a higher density in logged, hunted forest (which is in accordance with field observations), the full ZIP model predicted unlogged, unhunted forest to have a greater density than logged, hunted forest. This indicates that the effects of disturbance were confounded by the correlation between geographic coordinates and hunting indices (latitude: $r=-0.66$, $df=28$,

$p < 0.001$; longitude: $r = -0.53$, $df = 28$, $p = 0.002$): the intensity of hunting and the presence of logged forest both decreased with greater distance from the main logging village along a northeastern gradient. With spatial coordinates absorbing most of the effects of logging and hunting, any differences in guild densities among sites with different disturbance regimes, like those for pig, elephant, and monkey, were driven by other unmeasured differences among sites.

In the full model, the densities of several guilds varied according to forest structure and fruit resources. Elephant density was predicted to be higher in forest with a heterogeneous canopy with relatively greater numbers of large trees. Ape density was also higher in forest with variable canopy cover and with more lianas. Densities of frugivorous bird and monkey were higher in less heterogeneous canopy, with frugivorous bird having higher densities in forest without lianas and monkey having higher densities in forest with lianas. Both monkey and frugivorous bird density increased with increased fruit abundance.

The disturbance model (excluding latitude and longitude) decoupled the effects of hunting and logging. After running the ZIP models, we predicted guild density in the three sites keeping all other variables at their mean values and then calculated the effects of hunting, logging, and hunting and logging (Figure 6). Hunting negatively affected five of the eight guilds: elephant, frugivorous bird, and squirrel did not have significantly lower densities. Hunting had the largest negative effect on ape, reducing its density by 61%, and the largest positive effect on frugivorous bird, increasing its density by 77%. Logging lowered the densities of ape, duiker, monkey, pig, and frugivorous bird, but increased bird and elephant densities. The effect of logging ranged from a density reduction of 44% for pigs to a density increase of 90% for insectivorous birds. The combined effect of logging and hunting negatively affected guild

densities of ape, duiker, monkey and pig; elephant, bird, and squirrel guilds showed increases in density.

Discussion

In tropical forest, logging is nearly always accompanied by hunting, road construction, and population growth (Robinson et al. 1999, Wilkie et al. 2001, Laporte et al. 2007, Poulsen et al. 2009b). The entangled nature of these disturbances complicates our ability to resolve basic management problems. Can forest degraded by logging sustain communities of tropical forest animals? Can hunting be compatible with the conservation of forest biodiversity? To answer these questions the individual effects of disturbances must be decoupled from each other and separated from environmental variation. By comparing sites differentially affected by hunting and logging, we found the landscape-level effects of disturbance on densities of animal guilds to outweigh the effects of variation in forest structure, canopy cover and fruit abundance. The interaction between logging and hunting was not straightforward. Logging and hunting sometimes worked together to dramatically reduce densities of some guilds (ape, duiker, monkey, and pig). For other guilds (elephant, frugivorous and insectivorous bird, squirrel), hunting and logging worked against each other with positive impacts of one type of disturbance buffering negative impacts of the other. Together hunting and logging have shifted the composition of the animal community away from large mammals towards squirrels and birds.

Selective logging modifies both the large scale architecture of the forest and local scale environmental characteristics. At the landscape level, selective logging primarily alters the forest through the creation of felling gaps during timber extraction and the construction of roads and skid trails (Asner et al. 2004). Selective logging in the Congo Basin usually only damages 10-20% of the logged area (Durrieu de Madron et al. 2000, Van Gemerden et al. 2003), but canopy damage can be spatially distributed over the logged area, resulting in extensive

fragmentation and soft edge effects in contiguous forest (Broadbent et al. 2008). In our study we found the landscape level effects of selective logging to strongly influence densities of animal guilds. In a comparison of logged and unlogged sites, even logging conducted at low intensity (2.5 trees ha⁻¹) 25 years ago resulted in a detectable decline in densities of all animal guilds except insectivorous birds and elephants. Although we positioned transects so that they would be removed from the immediate influence of roads, logged forest is discontinuous, broken by active and inactive roads, and interrupted by felling gaps. These features can strongly influence animal density and distribution.

At the local scale, logging opens the canopy and changes forest structure, which has cascading effects on the light regime, vegetation regeneration and fruit production within the felling gap (Putz et al. 2001). Local scale environmental variation linked to habitat alteration by logging also played a role in animal density and distribution but to a lesser extent than landscape level characteristics. Canopy cover and forest structure explained variation in guild densities for several guilds. Notably, elephant and ape preferred forest with a heterogeneous canopy, whereas frugivorous and insectivorous birds and monkey preferred closed canopy forest. Resource abundance also determined densities of forest animals; frugivorous bird and monkey densities responded positively to fruit abundance. The creation of gaps released secondary species of fruiting trees like *Musanga cecropioides*, which is consumed by large frugivorous birds, and probably has a large effect on their densities. Our results demonstrate that logging by itself can impact densities of guilds and community composition.

Even moderate hunting pressure can markedly alter the structure of mammal communities in central Africa (Fa et al. 2005, Laurance et al. 2006, Clark et al. 2009). Despite low population pressure (1 person km⁻²) and active enforcement of hunting laws, hunting

reduced the densities of duiker, monkey and pig by 50, 30, and 31%. These declines in guild densities are consistent with market surveys of bushmeat demonstrating them to be the most commonly hunted animals (Poulsen et al. 2009b). On the other hand, hunting had a large positive effect on large frugivorous and insectivorous birds and squirrels suggesting that the decline in densities of other guilds might release birds and squirrels from competition for resources. Hunting shifts the animal community structure to be composed of higher numbers of birds and small mammals (Fa et al. 2005).

Change in the structure of the animal community may have cascading effects on forest dynamics through the modification or loss of ecological services. Fragmentation and selective logging can indirectly influence plant abundance by modifying the abundance and distribution of rodents and, in turn, seed predation (Asquith et al. 1997). Studies have also found the loss or reduction of large mammals from hunting to reduce seed dispersal rates for some plant species, to favor species dispersed abiotically and by birds and small mammals, and to alter seed banks and seedling and sapling recruitment (Wright et al. 2000, Wright et al. 2007a, Wright et al. 2007b, Terborgh et al. 2008). Large birds and monkeys in a Cameroonian forest had low dietary overlap and produced different seed shadow patterns, making it unlikely that the loss of arboreal monkeys from logging and hunting in this study could be replaced by the seed dispersal services of birds (Poulsen et al. 2002, Clark et al. 2005). The degree to which disruptions in ecological services affects tropical forests may depend on the time it takes animal communities to recover. If species composition of animal communities recovers within a few decades, degraded forest may help conserve animal species. On the other hand, if animal communities take much longer to recover, the recovery of plant communities and ecosystem processes may be slowed or fundamentally altered.

In this study we took advantage of a relatively long dataset (2 years of observations) for Central African forest animals so that our conclusions are not biased by seasonal and phenological changes. In addition, we only used direct observations of animals so that our estimates of species and guild densities do not include error introduced through estimates of nest and dung decay and production (Walsh and White 2005). We attributed the spatial gradient in guild densities to the effects of logging and hunting rather than topographic or floristic changes across the study area. This assumption is justified because the topography of this part of northern Congo is flat with little variation. In addition, except for a greater number of secondary trees in vegetation plots in logged forest, we did not detect major changes in tree species composition along the geographic gradient.

In our study, hunting pressure and presence of logging decreased with distance from the village. This spatial gradient in disturbance was reflected in a latitudinal gradient in densities for monkeys, duikers, and apes. The negative relationship between the abundance of vertebrate communities and hunting pressure or human activity has been observed in other tropical forests (Muchaal and Ngandjui 1999, Peres 2000). This pattern should be exploited in the design of forest management landscapes. To the extent possible, industrial towns should be kept out of forests to minimize the human pressure on forests and animals (Poulsen et al. 2009b). Where the construction of towns and sawmills is necessary in logging concessions, they should be located away from protected areas and positioned to minimize the area of forest accessible to residents.

With most of the forests of Central Africa either in the process of being exploited or already logged, degraded forest represents an increasingly important habitat for most tropical animals and needs to be protected from further destruction. Improvements in tropical logging practices and disincentives for illegal hunting are the most immediate ways to conserve

functional tropical forests. While our study demonstrates that even logging alone can significantly modify the density of animal guilds and the structure of the animal community, the conservation value of logged and degraded forests might depend largely on the interactions between different forms of disturbance (e.g., agriculture, fire, population pressure and hunting). To understand and mitigate disturbances, their effects need to be separated and quantified. Biodiversity management within logging concessions should focus on managing for hunting, maintaining large areas of unlogged forest and mitigating the adverse effects of logging on sensitive groups of species.

Table 1-1. Number of observations, density of individuals and 95% confidence intervals (CI), and the coefficient of variation (CV) for animal species in three types of forest stands: unlogged, unlogged forest; logged, unlogged forest; and logged, hunted forest. Asterisks indicate a significant difference in density between A) logged/hunted forest and logged/unlogged forest and B) logged unlogged forest and unlogged/unlogged forest. Densities between sites were compared as two-sided t-tests and corrected for multiple comparisons so that statistical significance is assessed as $p < 0.005$.

Species	No. observations per block	Density of individuals km ⁻² (95% CI)			CV
		Logged/Hunted	Logged/Unlogged	Unlogged/Unlogged	
Ape					
<i>Gorilla gorilla</i>	46, 79, 77	1.7 (0.8-3.7)	2.4 (1.6-3.6)	3.1 (2.0-4.7)	19.7-36.7
<i>Pan troglodytes</i>	50, 60, 104	1.7 (0.9-3.2)	1.9 (0.7-5.0)	6.2 (3.2-12.2)	32.5-49.3
Duiker					
<i>Cephalophus monticola</i> ^{A,B}	101, 163, 210	4.7 (3.2-6.9)	12.3 (6.94-21.84)	22.5 (16.2-31.2)	16.7-29.6
<i>Cephalophus</i> spp.	186, 226, 256	8.9 (5.6-14.3)	10.9 (8.3-14.2)	13.2 (10.3-17.1)	11.9-22.4
Elephant					
<i>Loxodonta africana</i>	48, 50, 32	1.5 (0.8-3.0)	0.9 (0.5-1.6)	0.4 [†] (0.2-0.9)	27.3-34.5
Large frugivorous bird					
<i>Bycanistes albotibialis</i> ^{A,B}	288, 236, 270	55.9 (41.1-76.1)	32.4 (22.4-46.9)	40.7 (26.3-62.9)	15.1-22.5
<i>Bycanistes fistulator</i> ^{A, B}	61, 63, 90	121.5 (84.0-175.8)	67.6 (39.8-114.7)	25.8 (17.6-37.7)	18.7-27.2
<i>Ceratogymna atrata</i> ^{A, B}	197, 172, 179	29.7 (20.6-42.9)	13.6 (10.6-17.5)	19.8 (14.9-26.31)	12.5-19.9
<i>Corythaeola cristata</i> ^A	198, 90, 80	26.7 (16.3-43.7)	5.4 (3.3-9.0)	11.4 (5.7-22.8)	23.9-34.9
<i>Psittacus erithacus</i> ^A	338, 280, 271	91.9 (59.3-142.3)	50.0 (33.2-75.4)	31.1 (23.1-42.0)	14.8-22.4
Bird					
<i>Tockus fasciatus</i> ^B	110, 89, 62	12.0 (6.23-23.2)	9.4 (5.4-16.4)	1.0 (0.6-1.7)	26.3-33.6
<i>Tockus camaras</i>	104, 126, 56	3.8 (2.5-5.9)	9.0 (6.2-13.1)	2.9 (1.8-4.7)	18.8-25.0
<i>Tockus albocristatus</i> ^{A,B}	133, 151, 134	7.1 (3.8-13.5)	17.0 (11.4-25.5)	9.8 (6.0-16.0)	20.3-32.6
Monkey					
<i>Cercopithecus nictitans</i> ^{A,B}	310, 336, 361	37.2 (24.4-56.8)	41.8 (32.8-53.1)	79.7 (62.1-102.3)	11.8-19.9

Table 1-1. Continued

<i>Cercopithecus pogonias</i> ^{A,B}	227, 252, 259	23.3 (15.9-34.2)	28.4 (20.5-39.4)	34.9 (24.8-49.1)	16.4-19.2
<i>Cercopithecus cephus</i> ^A	159, 184, 171	28.3 (15.9-50.1)	39.3 (17.2-89.3)	39.7 (27.8-56.6)	17.8-43.3
<i>Lophocebus albigena</i> ^{A,B}	171, 275, 318	14.9 (6.6-33.5)	26.1 (19.8-34.5)	49.5 (34.8-70.3)	13.9-42.4
Squirrel					
<i>Funisciurus lemniscatus</i> ^A	75, 80, 83	29.4 (17.4-49.7)	14.6 (10.1-21.1)	12.7 (8.4-19.1)	18.4-25.7
<i>Protoxerus stangeri</i> ^A	56, 43, 78	26.8 (11.9-60.1)	12.6 (5.6-28.3)	15.5 (9.1-26.5)	26.3-41.9

[†]Density estimated with less than 40 observations.

Other species encountered during the survey with insufficient observations for estimation of densities: *Panthera pardus* (Carnivore), *Cephalophus sylvicultor* (Duiker), *Cercopithecus neglectus*, *Cercocebus agilis*, *Ptilocolobus badius*, *Colobus guereza* (Monkey), *Hylochoerus meinertzhageni*, *Potamochoerus porcus* (Pig), *Atherurus africanus* (Rodent), *Syncerus caffer nanus*, *Tragelaphus euryceros* (Large ungulate).

Table 1-2. Results of multivariate analyses. A) Separate analyses: eigenvalues and percentages of the total inertia accounted for by axes 1 and 2. Ordinations were a principal components analysis (PCA) of R, multiple correspondence analysis (MCA) of Q, and a correspondence analysis (CA) of L. B) Summary of RLQ analysis: eigenvalues and percentages of the total co-inertia accounted for by RLQ axes 1 and 2, covariance and correlation between the site scores constrained by the environmental variables in R and species' scores constrained by the traits in Q, projected inertia of table R and Q onto the first two RLQ axes, and percentage of the inertia obtained in the separate analysis of R and Q along the same axes (e.g., RLQ axis 1 accounts for 53.5% of the projected inertia of R along PCA axis 1 $[(100 \times 1.39)/2.60 = 53.5\%]$).

Statistic	Axis1	Axis 2
A. Separate analyses		
R/PCA	2.60 (28.9%)	2.11 (23.4%)
L/CA	0.10 (47.5%)	0.03 (11.9%)
Q/MCA	2.39 (23.9%)	1.82 (18.2%)
B. RLQ Analysis		
Eigenvalues (and % total inertia)	0.148 (82.7%)	0.007 (5.0%)
Covariance	0.39	0.08
Correlation	0.21	0.05
Projected inertia		
Table R	1.95 (75.0%)	1.49 (70.5%)
Table Q	1.79 (74.6%)	1.76 (96.8%)

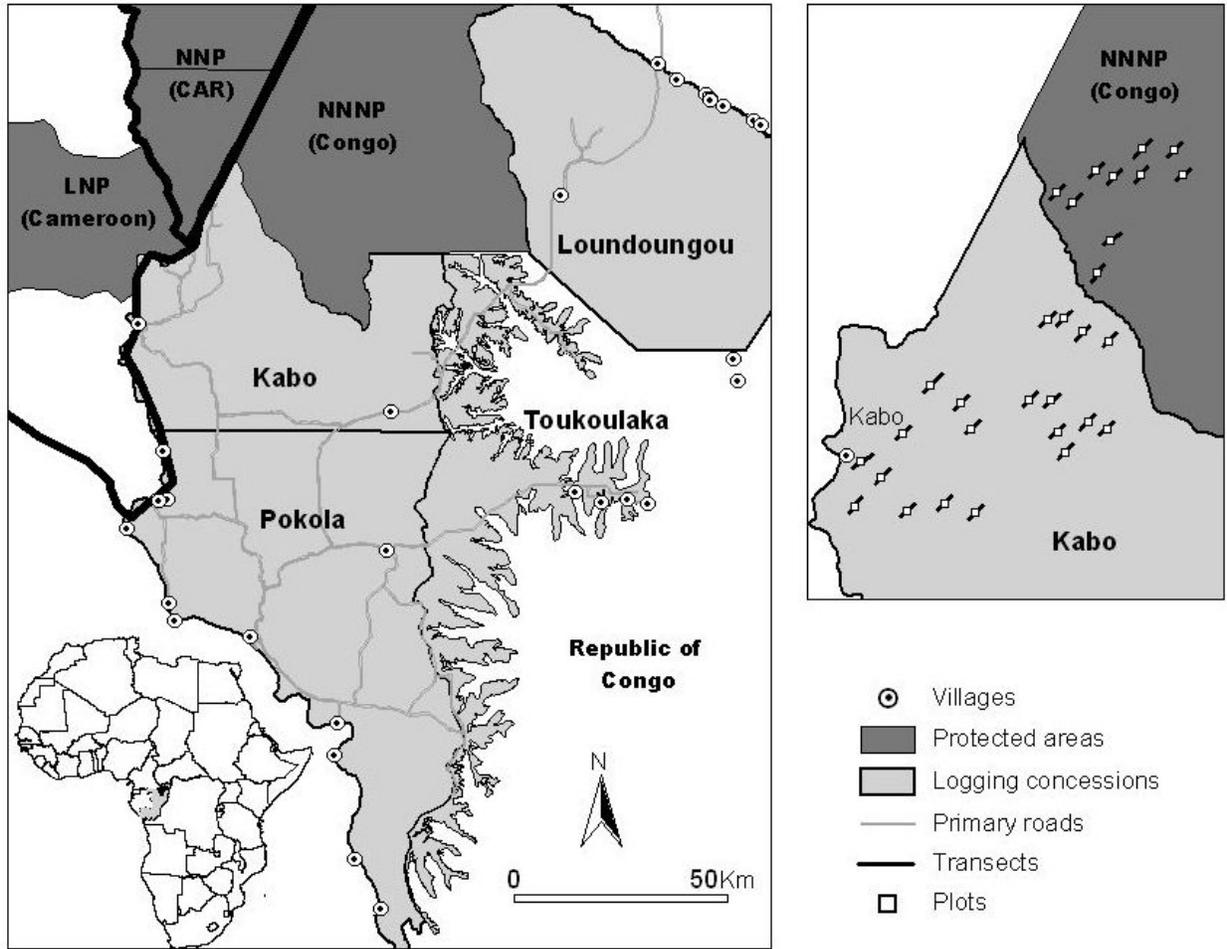


Figure 1-1. Map of study area in northern Republic of Congo. Thirty transects (2500 m) and 1 ha tree plots (open squares) were positioned in a random stratified manner in the Kabo concessions and Nouabalé-Ndoki National Park. All stations were separated by at least 2.5 km.

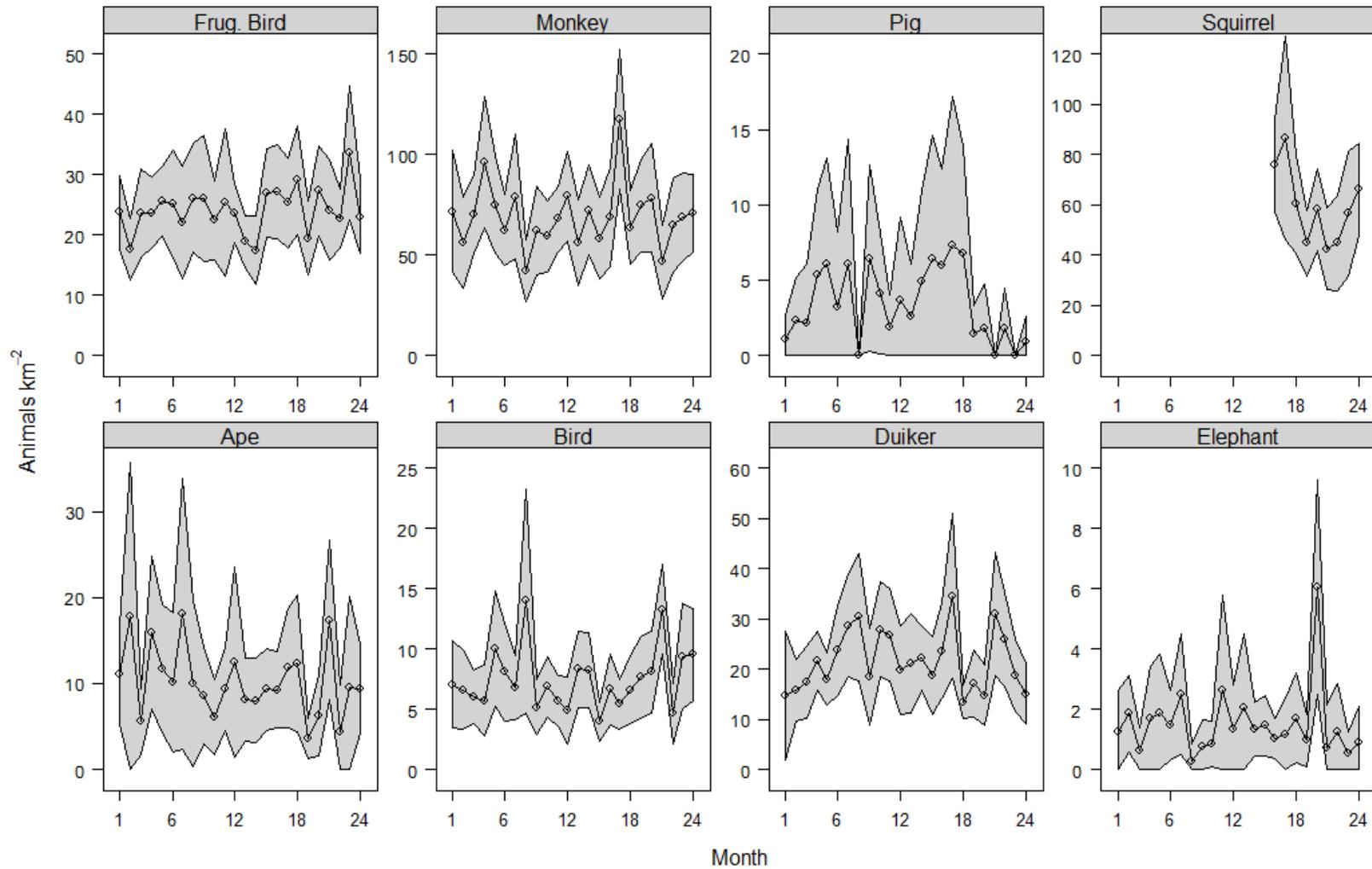


Figure 1-2. Densities of animal guilds averaged over all transect during the 24 months from June 2005 to May 2007. Shading represents the 95% confidence intervals around the monthly mean densities. Note that we only systematically sampled squirrels for the last 9 months of the study.

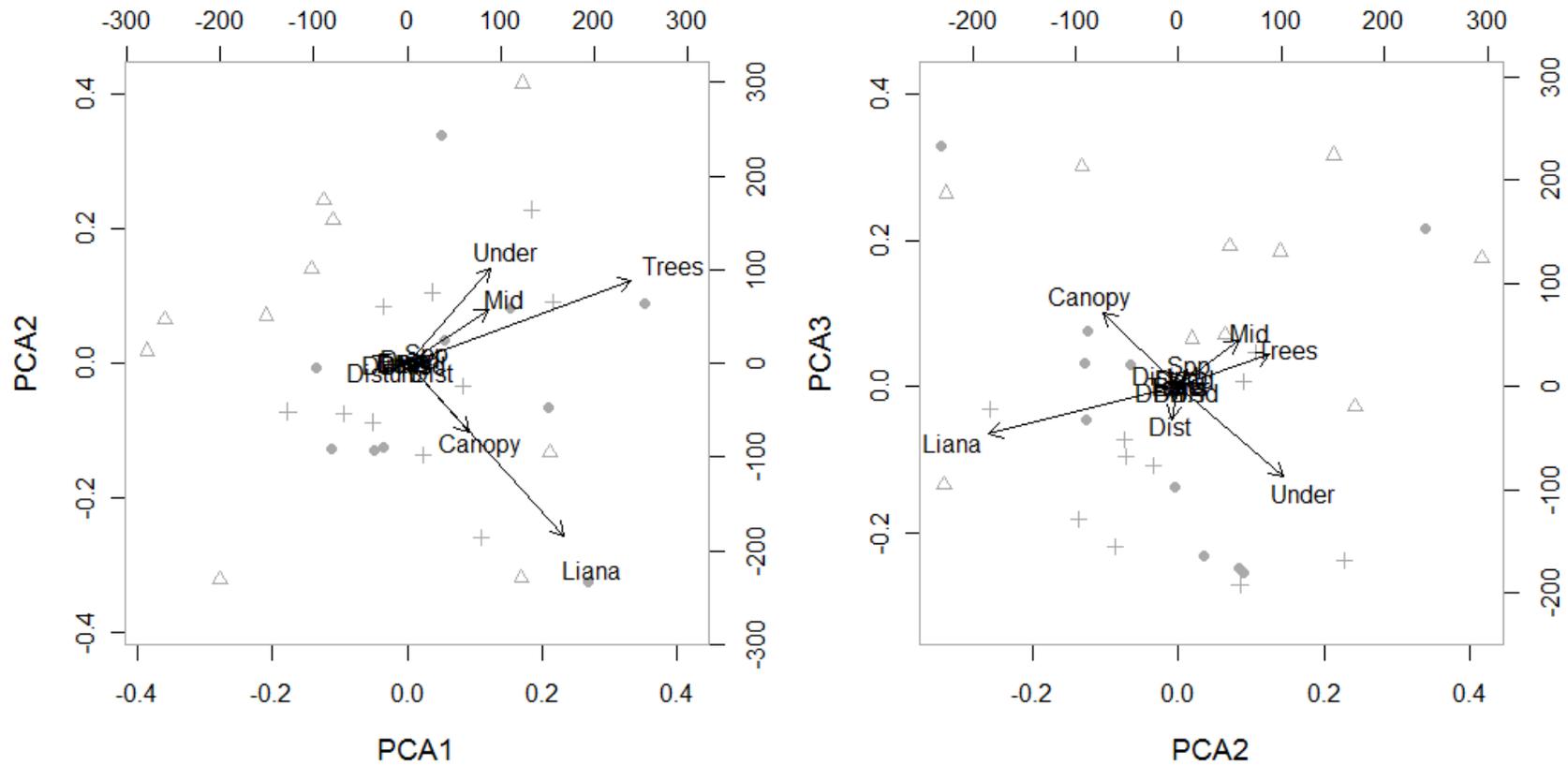


Figure 1-3. Ordination based on principal components analysis (PCA) of thirty 1 ha plots showing the first, second, and third axes. The biplot shows sites and environmental variables. Transects within sites are designated with different symbols (logged, hunted forest (open triangles), logged, unlogged forest (filled circles), and unlogged, unlogged forest (crosses). Arrows represent the most important environmental factors: under (no. of understory trees), mid (no. of midstory trees), canopy (no. of canopy trees), liana (no. of lianas), disturb (no. of secondary species), dist (distance of plot from village). Other variables that were included in the PCA, but did not importantly differentiate the plots included the number of trees, number of dead trees, average dbh, standard deviation of the average dbh, and the % of transmitted light in the plot.

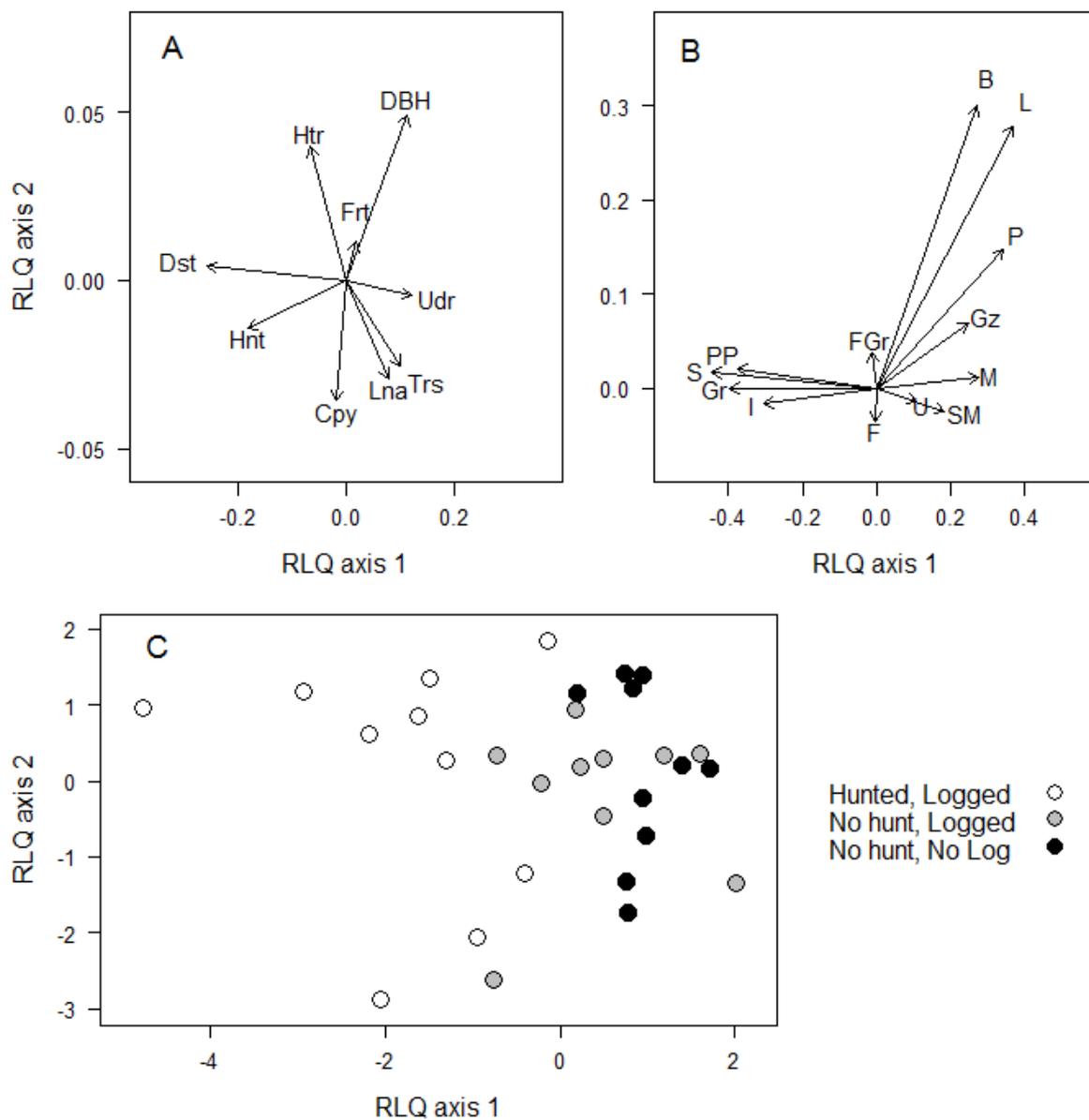


Figure 1-4. Display of (A) environmental variables, (B) species traits, and (C) plots along the first two RLQ axes. Each plot is represented by a symbol representing the forest type. Abbreviations for plot characteristics include: Dst (disturbance), Frt (fruit abundance), Hnt (signs of hunting), DBH (mean diameter-at-breast height of trees > 10 cm dbh), Htr (canopy heterogeneity), Trs (number of trees), Lna (number of trees topped by lianas), Udr (number of understory trees), Cpy (number of canopy trees). Abbreviations for species traits include size (S (small, < 5kg), SM (small-to-medium, < 10 kg), M (medium, <50 kg), L (large, >50 kg)), feeding guild (B (brower), F (frugivore), FG (frugivore-granivore), Gr (granivore), Gz (grazer), I (insectivore)), and protected status (U (unprotected), PP (partially protected), P (protected)).

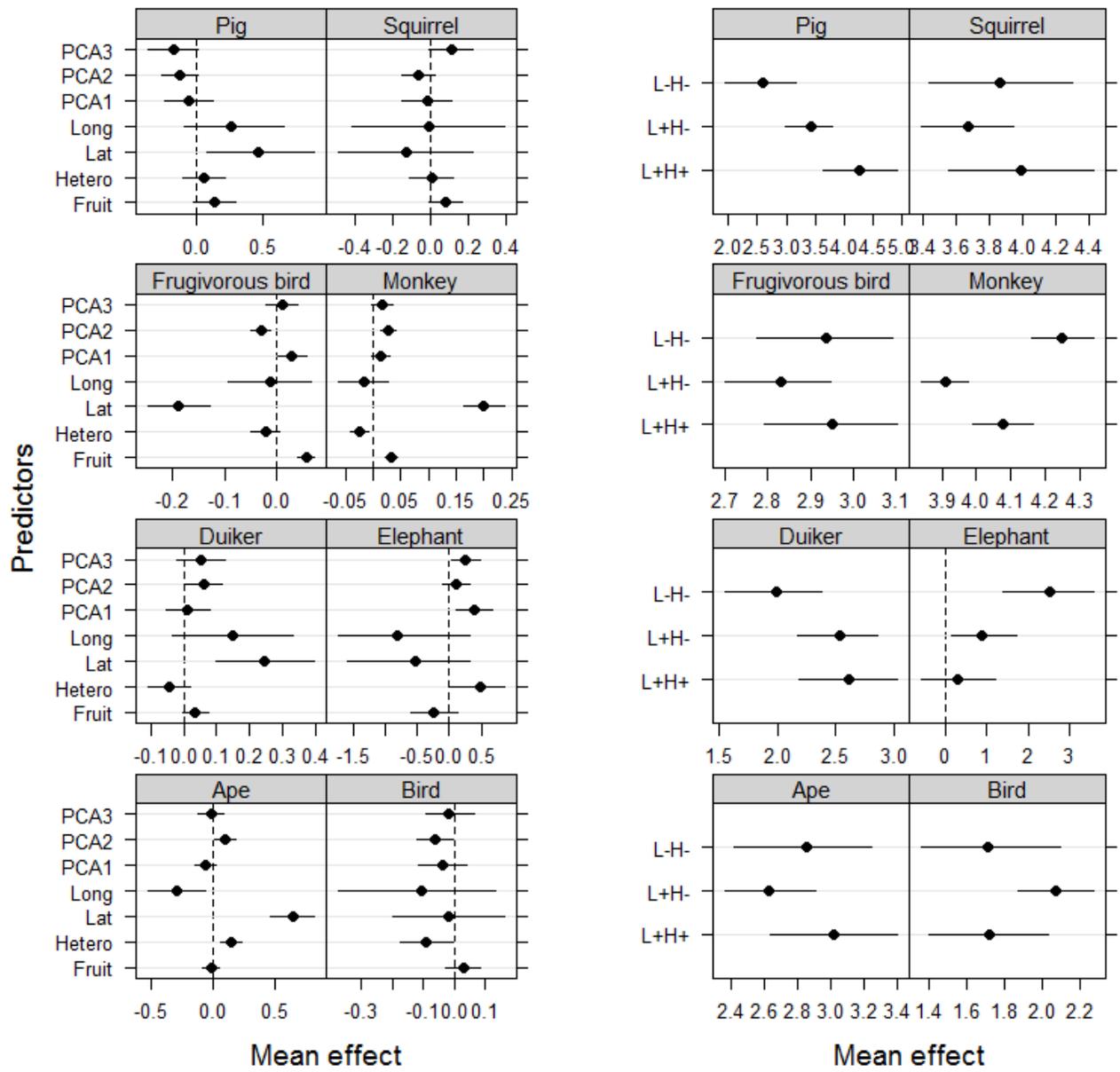


Figure 1-5. Dotplot of predictor values for animal guilds. Panel A depicts the effects of environmental (PCA1, PCA2, PCA3, and Hetero), spatial (Lat, Long), and resource (Fruit) variables on guild densities. Panel B demonstrates the effect of logging and hunting on each guild by depicting the difference in log(guild density) from the overall log(mean) in logged, hunted forest (L+H+), logged, unhunted forest (L+H-), and unlogged, unhunted forest (L-H-). In both panels, points are the posterior means from the ZIP models and bars are 95% credible intervals. Credible intervals that cross the dotted vertical line suggest that the effect is not different from zero.

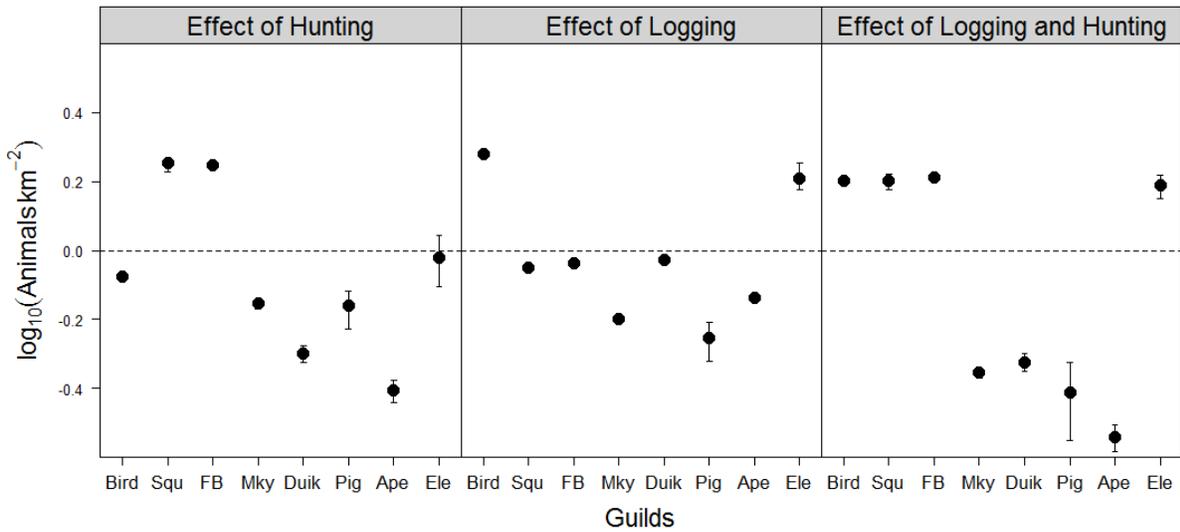


Figure 1-6. The effect of hunting, logging, and hunting and logging on guild density. The effects of disturbances were estimated as log-ratios of guild densities by dividing the posterior mean abundance of a guild at the disturbed site from the posterior mean abundance of the site where that disturbance was not present; for example, the effect size for logging would be:

$$Effect_{logging} = \log(Site_{logged, hunted}) / \log(Site_{unlogged, hunted})$$

Bars represent 95% credible intervals. Guilds are presented in order of increasing bodyweight and abbreviations are Bird (large insectivorous bird), Squ (squirrel), Fbird (frugivorous bird), Mky (monkey), Duik (duiker), Pig, Ape, and Ele (elephant).

CHAPTER 2

SEED DISPERSAL PATTERNS DRIVE SEEDLING RECRUITMENT IN AN EXPERIMENTAL MANIPULATION OF SEED SHADOWS

Unprecedented rates of logging and hunting in Central Africa threaten to transform vast tracts of primary forest into a mosaic of degraded forest emptied of its animals. Reductions in abundances of seed-dispersing animals are hypothesized to alter patterns of seed deposition for many tree species, potentially limiting forest regeneration with long-term consequences for forest structure and composition. To determine how logging and hunting affect seed dispersal, we measured seed rain in 30 1 ha tree plots in forest disturbed by logging and hunting, logging alone, and neither logging nor hunting. We used inverse modeling techniques with two years of seed rain data to quantify seed shadows for 26 tree species representing bird-, wind-, and mammal-dispersed species. Mean dispersal distance and degree of dispersion vary with dispersal vector, tree density and size, all of which are modified by hunting and logging. Across all forest types, wind-dispersed species had longer mean dispersal distances and greater dispersion relative to other dispersal modes. Hunting decreased mean dispersal distance of mammal- and bird-dispersed species by at least 20%. Logging decreased mean dispersal distance of bird-dispersed species by 37%, increased mean dispersal distances of mammal-dispersed species by 28%, and increased mean dispersal of wind-dispersed species by 49%. Both hunting and logging increased dispersion of wind-dispersed species. By altering seed dispersal patterns, human disturbance may provide an advantage for the regeneration of wind-dispersed species to the detriment of animal-dispersed species, with long-term consequences for forest structure and composition.

Introduction

Understanding seed dispersal is critical to understanding plant population and community dynamics (Nathan and Muller-Landau 2000, Levine and Murrell 2003). By determining the

spatial distribution of seeds, seed dispersal creates the template through which all other ecological processes that limit plant populations will be filtered. Many plant populations are limited for lack of seed (Poulsen et al. 2007), though the strength of seed limitation is usually small relative to post-dispersal factors like microsite limitation (John et al. 2007), density-dependence (Harms et al. 2000), and predation (Paine and Beck 2007) that kill seeds and emerging seedlings (Clark et al. 2007). Despite the diversity and strength of post-dispersal processes (Wang and Smith 2002), spatial patterns of tropical trees can be correlated with seed dispersal patterns, indicating that dispersal patterns can have lasting effects on the spatial distribution of trees (Seidler and Plotkin 2006).

In the last decade, our understanding of the mechanisms that influence seed dispersal processes has advanced considerably. Ecologists have employed a variety of tools including mechanistic models (Greene and Johnson 1989, Nathan et al. 2002, Greene et al. 2008), single source models (Clark et al. 2005), inverse modeling (Ribbens et al. 1994, Clark et al. 1999), and genetic sampling (Godoy and Jordano 2001, Hardesty et al. 2006) to quantify dispersal patterns. Mechanistic studies of wind dispersal have demonstrated the effects of wind speed, height of release, wind loading, and directionality on patterns of seed dispersal (Greene and Johnson 1989, Nathan et al. 2001, Nathan et al. 2002, Greene et al. 2008). Mechanistic models of dispersal by animals have presented a greater challenge because of the complexity of modeling animal behavior, but seed dispersal curves have been predicted taking into account seed passage times, movement rates, and some aspects of disperser behavior (Holbrook and Smith 2000, Westcott and Graham 2000, Levey et al. 2005, Russo et al. 2006). Comparisons of seed shadows of multiple tree species have demonstrated detectable differences in the spatial patterns of seed deposition produced by different dispersal vectors (Clark et al. 2005, Muller-Landau et al. 2008).

In addition to dispersal mode, substantial proportions of variation in interspecific patterns of seed rain can also be explained by plant traits like seed mass and tree height (Muller-Landau et al. 2008). Landscape traits such as plant aggregation and frugivore density also affect seed dispersal patterns, with greater plant aggregation reducing mean dispersal distances and greater frugivore density resulting in kernels with fat tails (Morales and Carlo 2006). Together these studies provide an idea of the most important mechanisms drive patterns of seed dispersal.

One of the most critical applications of these techniques is understanding how disturbance to forest affects seed dispersal patterns and the potential consequences for seedling recruitment, forest structure and diversity. Commercial logging is probably the most far-reaching anthropogenic disturbances in the tropics, fragmenting millions of square kilometers of tropical forest (Nepstad et al. 1999, Asner et al. 2005, Laporte et al. 2007). Selective logging primarily alters forest structure through the creation of felling gaps during timber extraction and the construction of roads and skid trails (Asner et al. 2004). The effects of logging depend on extraction techniques and intensities (Putz et al. 2001), but canopy damage can be spatially distributed over the logged area, resulting in extensive fragmentation and soft edge effects in contiguous forest (Broadbent et al. 2008). Because logging operations open remote forests to access by people (Poulsen et al. 2009b), timber exploitation is usually accompanied by hunting, dramatically reducing the abundance of tropical seed-dispersing animals (Wilkie et al. 2001, Peres and Palacios 2007, Poulsen et al. 2009a).

The goal of this study is to assess the effects of logging and hunting on community-level patterns of seed dispersal in a Central African forest. To decouple the effects of logging and hunting, we set up a large-scale observational experiment to quantify seed dispersal patterns in forest stands that were exposed vs. unexposed to logging and hunting. Over two years, we

collected seed rain data in thirty 1 ha tree plots that spanned a 55 km gradient capturing the landscape-scale variation in the density of plant species and community composition in northern Republic of Congo. To quantify seed dispersal on multiple species of trees, we employ inverse modeling, which is ideal for analyzing data from seed trapping studies within multi-species mapped stands (Ribbens et al. 1994, Clark 1998, Clark et al. 1999, Muller-Landau et al. 2008). We relate observed dispersal parameters to factors hypothesized to explain interspecific variation in seed production and dispersal distances including disturbance, dispersal mode, tree size and density.

Methods

Study Area

We conducted the study in the Nouabalé-Ndoki National Park (NNNP; 400,000 ha) and the Kabo logging concession (267,000 ha) in northern Republic of Congo. The Kabo concession borders the NNNP to the south, and together they include a mosaic of logged and unlogged forest. Between 20-25 years before the study, this area of the logging concession was selectively logged at low intensity (<2.5 stem ha^{-1}) with four species, *Entandophragma cylindricum*, *E. utile*, *Triplochiton scleroxylon*, and *Milicia excelsa*, making up 90% of the cutting volume (Congolaise Industrielle des Bois 2006). Approximately 3000 people inhabit the study site, most of who live in the logging town of Kabo. Residents hunt with shotguns, and to a lesser extent with wire snares, to supplement their diets and for local trade (Poulsen et al. 2009b). Most hunting originates from the town of Kabo creating a gradient of hunting intensity that decreases with distance from it, with some forest types used more than others (Mockrin 2008). The forests are classified as lowland tropical forest, and dominant tree families include Meliaceae, Euphorbiaceae, and Annonaceae. Annual rainfall averaged 1518 mm (SD = 96) from 2001 to 2006 and is seasonal with peaks in May and October.

Tree and Seed Census Data

We established 30 1-ha tree plots over an area of approximately 3000 km² to examine forest dynamics (Figure 1). We located ten plots in forest stands that were unlogged and unlogged and unlogged, logged and unlogged, and logged and hunted. Plots were only positioned in mixed lowland forest, with a buffer of at least 500 m to the nearest primary road and 100 m to the nearest water source. Using ArcView 3.2 and a 14 class habitat map, we extracted the areas that did not meet those criteria, and then randomly positioned plots on the remaining surface. Each of the plots was linked to a 2.5 km transect so that animal abundance could be related to seed dispersal. Within each plot, we tagged, measured, mapped and identified to species all trees greater than 10 cm diameter-at-breast-height (dbh) (species list and descriptions in Harris and Wortley 2008). For each tree, we also recorded the canopy status of the tree (understory, midstory, canopy, and emergent) and the presence of lianas in its crown. In addition, we quantified canopy openness and light availability for each plot, averaging the values of four pictures taken from each quarter of a plot. Photographs were taken every 30 cm above the ground, in uniformly overcast conditions in the early morning or late afternoon with a leveled Nikon Coolpix P5000 camera body and Nikon FC-E8 Fisheye converter lens. We analyzed images for the percentage of transmitted diffuse light using Gap Light Analyzer 2.0 (Frazer et al. 2001).

We quantified fruit availability in each of the 30 plots by collecting fruits and seeds in 21 1m² traps. Seeds traps were centered along three lines at 25, 50, and 75 m from the plot border, with 10 m separating each trap so that all traps were at least 20 m from the plot borders. Approximately every two weeks, we collected all seeds and fruits that fell into the traps and counted and identified them to species. When unknown fruits and seeds were collected, we searched the canopy over the seed trap for fruit, using the tagged trees to identify the propagule.

Seed Shadow Models and Parameter Estimation

We used an inverse modeling method that models the density of seeds at a single location (seed trap) as the summed contribution of seeds dispersed from all conspecific adult trees in the plot. We assumed that the contribution of each adult tree to the seed rain at a location depends only on its individual fecundity and its distance to the seed trap. Our approach is an adaptation of Ribbens et al. (1994) which was used to model the dispersion of seedlings, but has also been adapted to modeling seed dispersal (Clark 1998, Sagnard et al. 2007, Muller-Landau et al. 2008).

The expected number of seeds N_{ij} in seed trap i in plot j is the sum over each adult k of the product of its scaled fecundity F_k by the dispersal kernel f which gives the probability that a seed is dispersed at a distance d_{ik} from a tree:

$$N_{ij} = \sum_k F_k f(d_{ik})$$

We modeled adult fecundity by scaling seed production to tree size, $F_k = s_k^\beta$, where the number of seeds produced by a tree (F_k) is the size (diameter-at-breast height) s_k scaled by β which controls the dependence of fecundity on size. We assumed dispersal was isotropic and modeled the seed shadow as a negative exponential dispersal kernel, $f(x) = \gamma \exp(-d_{ik}/\alpha)$. Here γ is a normalization constant that controls overall seed density by constraining the dispersal kernel between 0 and 1 ($\gamma = \int_0^\infty \exp(-d_{ik}/\alpha) dd_{ik}$), and α is the scale of dispersal (average dispersal distance).

We assumed that the observed number of seeds in a seed trap followed a negative binomial error distribution with mean equal to N_{ij} and clumping parameter k (Hilborn and Mangel 1997, Clark 1998). We calibrated parameters for the dispersal model by searching numerically for the combination of parameter values that maximize the likelihood function, using the L-BFGS-B method (R Development Core Team 2008).

We analyzed interspecific variation in estimated mean seed dispersal distance (henceforth referred to as mean dispersal distance), the mean seed production per adult diameter (henceforth referred to as mean fecundity), and the κ parameter of the negative binomial distribution (henceforth referred to as the dispersion parameter). Smaller values of the dispersion parameter reflect more clumped distributions of seeds across traps, while larger values reflect greater dispersion of seeds among traps.

Plant Species Trait Data

We classified tree species by their dispersal mode based on fruit morphology and published and unpublished observations of fruit consumption (Gautier-Hion et al. 1985, Tutin et al. 1997, White and Abernathy 1997, Whitney et al. 1998, Clark et al. 2001, Poulsen et al. 2001, Poulsen et al. 2002, Hawthorne and Gyakari 2006, Morgan and Sanz 2006). Despite the use of broad categories, many of the animal-dispersed species were dispersed by both birds and mammals. We assigned a predominant dispersal syndrome of mammal or bird on the basis of fruit and seed traits for plant species with dispersal agents from multiple animal-dispersed categories (Gautier-Hion et al. 1985, Poulsen et al. 2002).

In addition to dispersal mode, we also quantified the mean dbh (cm) and tree density for each species by treatment combination to relate dispersal parameters to species characteristics. We used the log-transformed values of dbh and density to meet the assumptions of normality.

Comparison of dispersal parameters

To compare dispersal characteristics with plant species traits, we used linear mixed models to relate dispersal parameters (α , β , γ , κ) to dispersal mode (bird, mammal, and wind), disturbance (hunting, no hunting, logging, and no logging), density and dbh of the tree species. Linear mixed models were implemented in the nlme package in R 2.7.1 (R Development Core Team 2008). For comparisons of dispersal parameters by dispersal mode and disturbance level

significance determined with Tukey multiple comparisons of means (using a z-statistic) in the multcomp package (Hothorn et al. 2008). Note also that because we class trees by dispersal vector (bird-, mammal-, and wind-dispersed), we have low sample sizes and many of the comparisons of dispersal parameters are not statistically significant. In spite of the lack of statistical significance, we emphasize differences in dispersal patterns where we think they are biologically important (see Caveats).

Results

Twenty-six tree species met the minimum sample size for analysis. These included seven wind-dispersed species, 10 bird-dispersed species, and 11 mammal-dispersed species (Table 2-1). Wind-dispersed species (41.8 cm dbh) were larger than species dispersed by other vectors (bird-dispersed species = 29.5 cm dbh, animal-dispersed species = 26.9 cm dbh), and the log-transformed dbh of wind-dispersed species was significantly larger than that of mammal-dispersed species ($z = 2.66$, $p = 0.02$) but not bird-dispersed species ($z = 0.64$, $p = 0.23$). The densities of tree species did not differ significantly by dispersal mode (bird = 5.1 trees ha⁻¹, mammal = 9.1 trees ha⁻¹, wind = 5.6 trees ha⁻¹).

Mean dispersal distances were marginally negatively correlated with density ($r = -0.34$, $df = 26$, $p = 0.07$), but not dbh ($r = 0.17$, $df = 26$, $p = 0.38$). Dispersion increased with size (dbh) of trees ($r = 0.54$, $df = 26$, $p = 0.003$), but not with density ($r = 0.03$, $df = 26$, $p = 0.88$).

Effect of Dispersal Mode

Wind-dispersed trees dispersed the farthest, nearly 1.5 times farther than bird-dispersed species ($z = 1.43$, $p = 0.33$) and 2 times farther than mammal-dispersed trees ($z = 1.92$, $p = 0.13$; Table 2-2). Dispersion of wind-dispersed seeds was also 2 times greater than for bird- ($z = 0.14$, $p = 0.18$) and 3.5 times greater than for mammal-dispersed species ($z = 2.22$, $p = 0.02$). Although bird-dispersed species had the highest fecundity parameter (1.8), fecundity did not vary

significantly among trees dispersed by different vectors (mammal-dispersed = 1.4, wind-dispersed = 1.4).

Effect of Disturbance

Hunting tended to decrease the distance that seeds were dispersed. Seeds in hunted forest dispersed 33% farther than unhunted forest (Table 2-2, Table 2-3), although dispersal distances were not significantly different between the forest types. When differentiated by vector, dispersal distances of bird-dispersed trees in unhunted forest were 35% higher than in hunted forest. Mammal-dispersed trees in unhunted forest were dispersed 50% further than in hunted forest (Figure 2-3). There was only a 3% difference in dispersal differences of wind-dispersed species between hunted and hunted forest (Figure 2-4). Hunting increased the dispersion of seeds for wind-dispersed (72%) and animal-dispersed trees (44%).

Overall, mean dispersal distances in logged forest were 7% farther than unlogged forest (Table 2-2, Table 2-3). Logging decreased mean dispersal distance of bird-dispersed species by 37%, increased mean dispersal distances of mammal-dispersed species by 28%, and increased mean dispersal of wind-dispersed species by 49% (Figure 2-3). Dispersion rates were 21% higher in logged than unlogged forest, although not statistically different (Figure 2-4). Dispersion of bird-dispersed trees in logged forest was 63% lower than in unlogged forest, whereas seed dispersal of wind-dispersed trees was 42% more dispersed.

Discussion

We show that human disturbance of tropical forests alters the seed dispersal patterns of trees: hunting reduced mean dispersal distances of animal-dispersed trees whereas logging increased the dispersal distances and dispersion of wind-dispersed trees. Mean dispersal distance and degree of dispersion vary with dispersal vector, tree density and dbh, all of which are modified by hunting and logging. While our understanding of both the patterns of seed dispersal

and the mechanisms that drive those patterns has increased enormously over the last decade, most of the work has focused on intact forest systems. Our study is the first to examine seed dispersal patterns over a large, tropical landscape and to compare forest stands with different types of disturbances.

Previous studies have shown that hunting in tropical forests can disrupt seed dispersal mutualisms by reducing the quantity of seeds removed (Wright et al. 2000, Wright and Duber 2001, Wang et al. 2007, Brodie et al. 2009) or the distances over which they are transported (Chapman and Onderdonk 1998). We show that over a large tract of forest with hunting levels that are similar to or lower than most forests in West and Central Africa, hunting altered seed dispersal patterns by reducing dispersal distances. Although the forests of northern Congo still retain their full complement of frugivorous birds and mammals, these reductions in dispersal distances are a startling trend. Brodie et al. (2009) employed a structured population model to demonstrate that overhunting of tropical frugivores could create an extinction debt, whereby adults of long-lived trees may remain extant (sometimes even common), but slowly disappear through attrition as they fail to be replaced due to lack of seed dispersal. By selectively reducing populations of larger vertebrates (Fa et al. 2005, Poulsen et al. 2009a), timber exploitation and hunting likely have a disproportional negative impact on influence on large-seeded mature forest plant species.

The changes in wind dispersal dynamics in our study may be due to the impacts of logging on forest structure. Logging modifies canopy structure at the tree-scale through timber extraction or by causing residual damage to nearby trees. Selective logging in particular targets the largest trees, resulting in a more heterogeneous canopy with fewer canopy and emergent trees relative to midstory trees (Asner et al. 2006). Bohrer et al. (2008) found that in heterogeneous

canopy relatively short trees not overcast by canopy trees are more likely to encounter strong updrafts and more likely to be ejected above the canopy. Updrafts with high wind speeds are more likely to cause abscission of seeds from the tree (which requires drag or branch vibration) and to disperse seeds farther (Greene 2005, Schippers and Jongejans 2005). Logged forest in our study has a noticeably less even canopy, and therefore wind dynamics may explain the increase in mean distance and dispersion of wind-dispersed species.

The opposite seed dispersal patterns exhibited by mammal- and bird-dispersed trees in our study might be explained by the differential responses of mammals and birds to changes in canopy structure. We show mammal-dispersed species to have slightly longer mean dispersal distances in logged forest which may result from the greater distances between emergent trees; monkeys, in particular, use emergent trees as sleeping or resting trees and often deposit large numbers of seeds under them (Russo and Augspurger 2004). By contrast, logging reduced mean dispersal distances of bird-dispersed species and increased the spatial aggregation of seeds. This may occur if logging alters the distribution and abundance of trees that are preferred by frugivorous birds. At our study site, logged forest had a higher proportion of light-gap specialist trees (e.g., *Musanga* spp. and *Macaranga* spp., (Poulsen, Clark and Bolker, unpubl. data) fed on by large frugivorous birds than unlogged forest (Poulsen and Clark, unpubl. data). In a simulation study, Morales and Carlos (2006) simulated bird dispersal in artificial landscapes and found that mean dispersal distances declined as plant spatial aggregation increased. They reasoned that denser landscapes retained simulated birds that were more likely to spend time foraging or perching, and thus travel shorter distances before dispersing seeds.

In addition to investigating the effects of logging and hunting on seed dispersal patterns, our study highlights the importance of considering seed dispersal mode in conjunction with

forest structure. Seed dispersal mode plays a role in determining dispersal patterns, but its role is perhaps less influential than predicted by animal-focused seed dispersal studies (Holbrook et al. 2002). Clark et al. (2005) found only small differences in mean dispersal distances between bird-, monkey-, and wind-dispersed species in Cameroon. Muller-Landau et al. (2008) found that seed dispersal mode did not explain significant variation in seed dispersal distances, but did explain significant variation in clumping with animal-dispersed species showing higher aggregations of seed deposition. As our study suggests, the link between dispersal mode and dispersal pattern likely largely depends on forest structure which can influence the behavior of seed-dispersing animals and the velocity and movement of wind-dispersed seeds.

Caveats

Through inverse modeling of 26 tree species we have found compelling evidence that dispersal mode, logging and hunting alter patterns of seed dispersal. Given the relatively low number of tree species per vector, it is perhaps not surprising that we found few statistically significant differences in dispersal parameters in comparisons among different vectors and among comparisons of vector and disturbance type. We only included in our analyses 26 of 428 for which we could model dispersal in all disturbance types (logged, unlogged, hunted, and unhunted). We may be able to add more species to our analysis and increase our statistical power by searching the data more thoroughly for species that can only be modeled in one or two of these disturbance types. In the face of low statistical power, our inferences are based on what we interpret as biologically important trends.

Even so, the results presented in this chapter are informative albeit preliminary. Although we have worked out the broader framework for modeling the data, more intensive modeling is in order. First, we intend to compare the fits of multiple dispersal kernels rather than

just relying on the negative exponential model. Other promising models include the Gaussian (Clark 1998), two-dimensional exponential, Bessel function (Turchin 1998), full 2DT (Clark et al. 1999), lognormal (Greene et al. 2004), and Weibull functions (Tufto et al. 1997). Second, we will consider the role of species fecundity in more detail. Third, we will attempt to incorporate interannual and among plot variation in seed production by fitting mixed models across the entire dataset using a Bayesian framework. Finally, we would like to expand our consideration of plant traits and plot characteristics that might affect dispersal by incorporating data on fruit and seed size as well as the forest structure and animal abundance around each plot.

Future of Tropical Forests

What do changes in seed dispersal patterns mean for the future of tropical forests? This depends on two pieces of information: 1) the degree to which seed dispersers are lost and dispersal rates are reduced, and 2) the recruitment success of seeds and seedlings under parent plants. At our study site, the densities of some animal species have been reduced by logging and hunting, but no seed-dispersing animals have been extirpated to our knowledge (Poulsen et al. 2009a). With the changes in seed dispersal patterns that we identified we would not expect large changes in forest composition or structure. However, tropical forests in parts of West Africa, Asia, and the Amazon have been emptied of most medium- and large-bodied species (Brook et al. 2003, Fa et al. 2003, Curran et al. 2004, Peres and Palacios 2007), with one study of hunting from 36 sites in West and Central Africa finding that 82% of harvested species were frugivores (Fa et al. 2005). Therefore, seed dispersal rates have and will be further reduced across tropical forests (Webb and Peart 2001, Wang et al. 2007). What is not clear is to what extent frugivores can replace each other as seed dispersers, although low dietary overlap between functionally similar guilds suggests that replacement may be rare (Poulsen et al. 2002). Furthermore, we

need a better understanding of where the threshold lies between a population that can carry out ecological functions like seed dispersal and one that cannot (McConkey and Drake 2006).

The loss of seed dispersal function could have a limited effect on tree populations if seeds and seedlings can recruit under parent plants. So far, however, the evidence suggests that species that lose dispersal services have reduced recruitment of seedlings (Chapman and Onderdonk 1998, Balcomb and Chapman 2003). In experimental tests of recruitment under different seed distributions, Augspurger and Kitajima (1992) and Poulsen et al. (2009a) both found lower rates of seed dispersal to lower recruitment. Lower recruitment was largely due to density-dependent mortality which is pervasive in tropical forests (Harms et al. 2000). Note that negative density dependence does not usually result in the absolute mortality of all seedlings (Harms et al. 2000), and so there is the unlikely possibility that every tree could replace itself. In the extreme case where dispersers have been removed from forests, the loss of dispersal function allowed species dispersed abiotically and by small birds and mammals to substitute for those dispersed by large birds and mammals, at least to the sapling stage (Terborgh et al. 2008). We found both hunting and logging to increase the dispersion of wind-dispersed trees suggesting that not only do seed dispersal rates of animal-dispersed trees decline with disturbance, but wind-dispersed species will also gain an advantage of more even dispersal across the landscape.

Table 2-1. Species, dispersal modes and samples.

Species	Dispersal mode	Plots	Traps	Seeds	Trees	DBH (cm)	Stems/ha
<i>Albizia gummifera</i>	Wind	16	70	561.5	38	31.15	1.3
<i>Angylocalyx pynaertii</i>	Mammal	15	52	285	112	27.56	3.7
<i>Caloncoba welwitschii</i>	Mammal	11	23	277	46	14.78	1.5
<i>Celtis adolfi-friderici</i>	Mammal	26	80	627	164	30.49	5.5
<i>Cleistopholis patens</i>	Bird	15	27	71	49	31.18	1.6
<i>Diospyros bipindensis</i>	Mammal	17	32	214	382	12.67	12.7
<i>Diospyros canaliculata</i>	Mammal	16	31	403	195	14.35	6.5
<i>Entandrophragma cylindricum</i>	Wind	18	173	3174.5	104	59.5	3.5
<i>Erythrophleum suaveolens</i>	Mammal	25	119	904	56	54.93	1.9
<i>Garcinia punctata</i>	Mammal	13	37	980.5	38	20.62	1.3
<i>Greenwayodendron suaveolens</i>	Bird	30	315	3717	457	24.83	15.2
<i>Guarea cedrata</i>	Bird	18	47	173.5	40	28.59	1.3
<i>Guarea thompsonii</i>	Bird	17	49	362	165	22.95	5.5
<i>Lannea welwitschii</i>	Bird	19	29	217	20	27.52	0.7
<i>Macaranga barteri</i>	Bird	18	30	1790	86	30.81	2.9
<i>Manilkara mabokeensis</i>	Mammal	13	36	366	50	26.1	1.7
<i>Nesogordonia kabingaensis</i>	Wind	16	34	492	165	27.63	5.5
<i>Petersianthus macrocarpus</i>	Wind	30	338	1513	135	44.43	4.5
<i>Pteleopsis hylodendron</i>	Wind	15	61	216	30	34.96	1
<i>Pterocarpus soyauxii</i>	Wind	24	142	709.5	78	29.6	2.6
<i>Staudtia kamerunensis</i>	Bird	20	67	163	13	40.75	0.4
<i>Strombosia nigropunctata</i>	Mammal	22	63	582	323	20.37	10.8
<i>Strombosia pustulata</i>	Mammal	23	55	254.5	212	27.88	7.1
<i>Strombosiopsis tetrandra</i>	Mammal	26	83	480	143	32.27	4.8
<i>Terminalia superba</i>	Wind	30	501	14729.5	93	46.57	3.1
<i>Xylopia chrysophylla</i>	Bird	20	78	356	40	23.99	1.3
<i>Xylopia hypolampra</i>	Bird	21	105	936	17	39.61	0.6
<i>Xylopia phloiodora</i>	Bird	15	33	262	49	25.33	1.6

Table 2-2. Mean fitted values and their standard deviations of model parameters.

Model	α	SD	β	SD	γ	SD	κ	SD
Bird	18.1	11.3	1.8	1.7	2.9	6.4	0.11	0.08
Monkey	13.4	12.6	1.4	1.5	8.7	24.7	0.19	0.23
Wind	26.9	12.6	1.4	1.4	6.5	14.3	0.39	0.32
Hunt	15.6	12.9	1.7	1.7	5.7	13.2	0.22	0.25
No hunt	20.8	14.2	1.3	1.4	4.5	9.5	0.19	0.21
Log	16.8	11.8	1.4	1.1	4.2	9.5	0.29	0.21
No log	15.7	13.3	2.0	2.0	14.5	34.9	0.24	0.32
Bird, Hunt	15.2	12.5	1.8	2.0	2.0	2.6	0.17	0.11
Bird, No hunt	20.6	12.5	1.6	1.5	3.5	5.8	0.19	0.20
Bird, Log	12.5	9.3	1.6	1.5	5.5	12.3	0.14	0.08
Bird, No log	19.8	12.9	2.8	2.0	1.7	3.1	0.37	0.48
Mammal, Hunt	10.9	8.5	1.8	1.8	11.3	18.9	0.13	0.14
Mammal, No hunt	16.4	13.5	0.8	1.0	2.8	5.8	0.09	0.04
Mammal, Log	14.5	11.4	1.2	1.0	4.9	9.2	0.11	0.08
Mammal, No log	11.3	13.7	1.8	2.1	22.1	47.9	0.11	0.07
Wind, Hunt	28.3	17.2	1.3	0.5	0.2	0.3	0.55	0.42
Wind, No hunt	27.4	16.5	1.5	1.9	8.2	16.1	0.32	0.32
Wind, Log	29.3	9.0	1.1	0.7	0.4	0.5	0.47	0.33
Wind, No log	19.6	12.0	1.4	1.7	15.6	22.0	0.33	0.37

Table 2-3. Fitted parameters for full (F; all plots), hunted (H+), logged (L+), unhunted (H-) and unlogged (L-) models. For parameter estimates denoted as dashes (-), there were not enough trees or trap hits to parameterize the model (Mod).

Species	Mod	α	SE	Z	P	β	SE	Z	P	γ	SE	Z	P	κ	SE	Z	P
<i>Albizia gummifera</i>	F	38.9	17.83	2.18	0.03	0.8	0.39	2.18	0.03	0.12	1.21	-1.56	0.12	0.12	1.21	-11.29	0.00
	H+	15.7	7.36	2.13	0.03	0.9	0.56	1.61	0.11	0.34	1.29	-0.44	0.66	0.10	1.29	-9.00	0.00
	H-	52.0	33.51	1.55	0.12	0.7	0.44	1.67	0.10	0.15	1.32	-1.20	0.23	0.17	1.32	-6.41	0.00
	L+	29.9	13.94	2.14	0.03	0.5	0.58	0.91	0.36	0.47	1.23	-0.35	0.73	0.10	1.23	-10.96	0.00
	L-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Angylocalyx pynaertii</i>	F	35.4	19.96	1.78	0.08	0.6	0.89	0.62	0.53	0.12	1.23	-0.62	0.54	0.08	1.23	-11.97	0.00
	H+	21.2	11.95	1.77	0.08	2.9	1.10	2.63	0.01	0.00	1.53	-2.59	0.01	0.09	1.53	-5.72	0.00
	H-	26.4	17.83	1.48	0.14	0.0	1.01	0	1	1.25	1.27	0.05	0.96	0.09	1.27	-9.71	0.00
	L+	41.2	26.56	1.55	0.12	0.7	0.89	0.74	0.46	0.08	1.25	-0.77	0.44	0.09	1.25	-10.42	0.00
	L-	6.8	-	-	-	0.0	-	-	-	9.05	-	-	-	0.08	-	-	-
<i>Celtis adolfi-friderici</i>	F	18.1	3.94	4.61	0.00	2.3	0.67	3.41	0.00	0.00	1.17	-3.02	0.00	0.08	1.17	-15.54	0.00
	H+	23.3	9.53	2.45	0.01	2.8	0.90	3.09	0.00	0.00	1.23	-2.72	0.01	0.10	1.23	-11.35	0.00
	H-	11.6	3.12	3.73	0.00	1.5	1.01	1.44	0.15	0.01	1.32	-1.18	0.24	0.08	1.32	-9.14	0.00
	L+	18.5	4.70	3.93	0.00	2.7	0.79	3.39	0.00	0.00	1.19	-3.00	0.00	0.09	1.19	-13.93	0.00
	L-	16.3	7.41	2.21	0.03	0.8	1.32	0.64	0.52	0.07	1.55	-0.54	0.59	0.06	1.55	-6.43	0.00
<i>Cleistopholis patens</i>	F	8.4	2.30	3.65	0.00	0.6	1.08	0.59	0.56	0.44	1.53	-0.20	0.84	0.12	1.53	-4.98	0.00
	H+	4.5	2.47	1.84	0.07	0.8	-	-	-	1.61	-	-	-	0.38	3.03	-0.87	0.38
	H-	9.3	3.06	3.04	0.00	0.7	1.22	0.57	0.57	0.28	1.57	-0.29	0.78	0.11	1.57	-5.00	0.00
	L+	8.4	3.95	2.14	0.03	2.1	1.55	1.33	0.18	0.00	1.98	-1.14	0.26	0.20	1.98	-2.33	0.02
	L-	7.6	2.68	2.82	0.00	0.0	1.59	0.00	1.00	7.80	1.78	0.34	0.74	0.11	1.78	-3.77	0.00
<i>Diospyros bipindensis</i>	F	6.4	2.01	3.16	0.00	0.0	4.19	0.00	1.00	3.43	1.29	0.12	0.91	0.04	1.29	-12.32	0.00
	H+	8.6	14.07	0.61	0.54	0.0	17.91	0.00	1.00	2.72	2.53	0.02	0.98	0.04	2.53	-3.60	0.00
	H-	5.7	1.84	3.08	0.00	0.0	4.34	0.00	1.00	4.16	1.31	0.13	0.89	0.04	1.31	-11.62	0.00
	L+	6.1	2.81	2.18	0.03	0.0	7.90	0.00	1.00	5.17	1.52	0.08	0.93	0.04	1.52	-7.48	0.00
	L-	6.2	2.71	2.31	0.02	2.9	5.58	0.52	0.60	0.00	1.41	-0.47	0.64	0.04	1.41	-9.19	0.00

Table 2-3. Continued

<i>Diospyros canaliculata</i>	F	5.4	2.85	1.90	0.06	2.5	3.65	0.67	0.50	0.03	1.36	-0.36	0.72	0.03	1.36	-11.35	0.00
	H+	3.5	4.25	0.82	0.41	0.6	13.12	0.05	0.96	45.65	1.66	0.10	0.92	0.03	1.66	-6.88	0.00
	H-	8.8	4.56	1.93	0.05	0.0	3.79	0.00	1.00	2.43	1.49	0.09	0.93	0.04	1.49	-8.20	0.00
	L+	6.6	3.70	1.78	0.08	1.7	4.96	0.35	0.72	0.11	1.39	-0.16	0.87	0.03	1.39	-10.80	0.00
	L-	0.9	0.67	1.35	0.18	5.6	13.63	0.41	0.68	2.75	2.43	0.03	0.97	0.20	2.43	-1.84	0.07
<i>Entandrophragma cylindricum</i>	F	16.2	-	-	-	0.0	-	-	-	35.51	-	-	-	0.17	1.09	-20.32	0.00
	H+	23.1	6.87	3.36	0.00	1.4	0.97	1.45	0.15	0.03	1.23	-0.80	0.43	0.28	1.23	-6.11	0.00
	H-	14.7	-	-	-	0.0	-	-	-	43.00	-	-	-	0.15	1.11	-17.75	0.00
	L+	21.3	5.00	4.25	0.00	0.6	0.75	0.75	0.45	1.11	1.20	0.03	0.98	0.22	1.20	-8.13	0.00
	L-	14.8	-	-	-	0.0	-	-	-	46.93	-	-	-	0.16	1.12	-16.84	0.00
<i>Erythrophleum suaveolens</i>	F	11.6	1.27	9.13	0.00	1.6	0.46	3.47	0.00	0.01	1.16	-2.15	0.03	0.24	1.16	-9.93	0.00
	H+	7.4	0.97	7.63	0.00	1.9	0.63	3.05	0.00	0.01	1.29	-1.67	0.09	0.51	1.29	-2.64	0.01
	H-	14.2	2.38	5.97	0.00	1.4	0.62	2.19	0.03	0.03	1.20	-1.36	0.17	0.18	1.20	-9.36	0.00
	L+	10.1	1.18	8.61	0.00	2.3	0.57	4.11	0.00	0.00	1.22	-2.90	0.00	0.31	1.22	-6.06	0.00
	L-	15.5	3.90	3.97	0.00	0.2	0.71	0.24	0.81	2.99	1.26	0.36	0.72	0.20	1.26	-7.06	0.00
<i>Garcinia punctata</i>	F	15.7	5.39	2.92	0.00	0.4	1.60	0.23	0.81	4.69	1.25	0.29	0.77	0.06	1.25	-12.78	0.00
	H+	12.7	10.67	1.19	0.23	0.0	4.52	0.00	1.00	46.20	1.40	0.25	0.80	0.06	1.40	-8.40	0.00
	H-	36.5	26.85	1.36	0.17	0.7	1.58	0.42	0.67	0.12	1.43	-0.45	0.65	0.10	1.43	-6.55	0.00
	L+	14.1	5.94	2.37	0.02	0.0	2.12	0.00	1.00	26.08	1.33	0.46	0.65	0.05	1.33	-10.70	0.00
	L-	14.7	5.07	2.90	0.00	2.6	4.37	0.59	0.55	0.00	1.62	-0.54	0.59	0.22	1.62	-3.13	0.00
<i>Greenwayodendron suaveolens</i>	F	30.3	4.00	7.58	0.00	3.5	0.58	6.03	0.00	0.00	1.08	-5.63	0.00	0.27	1.08	-17.52	0.00
	H+	25.0	6.96	3.59	0.00	3.5	0.92	3.86	0.00	0.00	1.20	-3.65	0.00	0.29	1.20	-6.97	0.00
	H-	33.1	5.92	5.60	0.00	2.4	0.81	2.98	0.00	0.00	1.09	-2.73	0.01	0.28	1.09	-15.27	0.00
	L+	21.0	3.33	6.31	0.00	3.3	0.64	5.16	0.00	0.00	1.11	-4.61	0.00	0.31	1.11	-11.40	0.00
	L-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 2-3. Continued

<i>Guarea cedrata</i>	F	22.2	10.48	2.12	0.03	0.0	0.67	0.00	1.00	2.93	1.34	0.45	0.65	0.11	1.34	-7.61	0.00
	H+	7.9	2.53	3.12	0.00	0.4	0.83	0.51	0.61	5.07	1.47	0.61	0.54	0.12	1.47	-5.47	0.00
	H-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L+	7.9	2.53	3.12	0.00	0.4	0.83	0.51	0.61	5.07	1.47	0.61	0.54	0.12	1.47	-5.47	0.00
	L-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guarea thompsonii</i>	F	11.2	3.51	3.18	0.00	1.3	0.58	2.23	0.03	0.04	1.23	-1.69	0.09	0.07	1.23	-13.09	0.00
	H+	22.0	29.20	0.75	0.45	0.0	5.71	0.00	1.00	0.86	1.57	-0.01	0.99	0.09	1.57	-5.39	0.00
	H-	7.9	1.92	4.10	0.00	2.5	0.77	3.21	0.00	0.00	1.31	-2.70	0.01	0.07	1.31	-9.58	0.00
	L+	10.4	3.08	3.37	0.00	0.4	1.17	0.31	0.76	1.01	1.27	0.00	1.00	0.08	1.27	-10.65	0.00
	L-	11.1	6.67	1.66	0.10	3.2	1.53	2.09	0.04	0.00	1.49	-2.01	0.04	0.07	1.49	-6.83	0.00
<i>Lanea welwitschii</i>	F	21.1	9.53	2.22	0.03	2.7	2.27	1.18	0.24	0.00	1.50	-1.04	0.30	0.03	1.50	-8.87	0.00
	H+	6.6	3.20	2.05	0.04	2.5	2.06	1.21	0.23	0.00	2.25	-0.78	0.44	0.06	2.25	-3.48	0.00
	H-	28.2	21.69	1.30	0.19	0.0	4.92	0.00	1.00	4.90	1.64	0.08	0.93	0.03	1.64	-7.12	0.00
	L+	5.0	2.21	2.25	0.02	1.6	1.69	0.92	0.36	0.14	2.05	-0.29	0.78	0.06	2.05	-3.98	0.00
	L-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macaranga barteri</i>	F	7.7	2.02	3.79	0.00	3.5	1.97	1.75	0.08	0.00	1.32	-1.19	0.23	0.03	1.32	-12.43	0.00
	H+	2.2	0.79	2.81	0.00	3.0	2.08	1.45	0.15	0.01	1.83	-0.51	0.61	0.07	1.83	-4.46	0.00
	H-	8.1	2.47	3.30	0.00	4.2	2.53	1.65	0.10	0.00	1.40	-1.22	0.22	0.03	1.40	-10.30	0.00
	L+	2.3	0.73	3.22	0.00	4.2	1.70	2.44	0.01	0.00	1.70	-1.39	0.17	0.09	1.70	-4.46	0.00
	L-	8.1	3.26	2.47	0.01	3.5	3.41	1.04	0.30	0.0	1.44	-0.69	0.49	0.03	1.44	-9.70	0.00
<i>Manilkara mabokeensis</i>	F	16.3	8.08	2.02	0.04	0.2	1.04	0.19	0.85	3.5	1.38	0.31	0.76	0.08	1.38	-7.99	0.00
	H+	3.5	1.28	2.73	0.01	1.4	1.28	1.07	0.29	2.4	1.61	0.17	0.86	0.23	1.61	-3.10	0.00
	H-	41.2	58.12	0.71	0.48	0.0	1.69	0.00	1.00	0.7	1.67	-0.07	0.94	0.07	1.67	-5.09	0.00
	L+	13.0	5.22	2.50	0.01	0.0	1.02	0.00	1.00	17.1	1.46	0.70	0.48	0.16	1.46	-4.81	0.00
	L-	1.8	1.92	0.91	0.36	0.0	7.76	0.00	1.00	77.1	2.42	0.14	0.89	0.08	2.42	-2.83	0.00

Table 2-3. Continued

<i>Nesogordonia kabingaensis</i>	F	29.0	22.78	1.28	0.20	5.3	1.60	3.34	0.00	0.0	1.25	-3.53	0.00	0.03	1.25	-15.94	0.00
	H+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	H-	23.7	15.87	1.49	0.14	5.4	1.72	3.16	0.00	0.0	1.26	-3.31	0.00	0.03	1.26	-14.81	0.00
	L+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L-	15.5	8.28	1.87	0.06	4.1	3.43	1.19	0.24	0.0	1.52	-1.11	0.27	0.03	1.52	-8.34	0.00
<i>Petersianthus macrocarpus</i>	F	38.6	6.93	5.57	0.00	1.8	0.20	8.92	0.00	0.0	1.09	-7.90	0.00	0.59	1.09	-5.85	0.00
	H+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	H-	28.3	4.04	7.01	0.00	1.9	0.29	6.51	0.00	0.0	1.10	-5.45	0.00	0.61	1.10	-4.97	0.00
	L+	42.3	12.31	3.44	0.00	1.7	0.27	6.32	0.00	0.0	1.14	-5.77	0.00	0.50	1.14	-5.29	0.00
	L-	35.9	8.80	4.09	0.00	1.1	0.58	1.94	0.05	0.0	1.13	-1.43	0.15	0.70	1.13	-2.95	0.00
<i>Pterocarpus soyauxii</i>	F	22.9	3.43	6.70	0.00	0.9	0.16	5.36	0.00	0.3	1.15	-2.02	0.04	0.43	1.15	-5.97	0.00
	H+	21.0	3.74	5.61	0.00	0.9	0.16	5.32	0.00	0.5	1.27	-0.91	0.36	0.95	1.27	-0.21	0.84
	H-	45.4	25.65	1.77	0.08	0.3	0.42	0.77	0.44	0.3	1.25	-0.84	0.40	0.37	1.25	-4.45	0.00
	L+	20.4	3.13	6.53	0.00	1.0	0.17	5.95	0.00	0.2	1.19	-2.14	0.03	0.60	1.19	-2.90	0.00
	L-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Staudtia kamerunensis</i>	F	59.2	43.50	1.36	0.17	1.3	1.32	1.02	0.31	0.0	1.32	-0.92	0.36	0.21	1.32	-5.71	0.00
	H+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	H-	43.0	46.02	0.94	0.35	3.2	2.45	1.30	0.19	0.0	1.72	-1.35	0.18	0.42	1.72	-1.59	0.11
	L+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	L-	43.0	46.02	0.94	0.35	3.2	2.45	1.30	0.19	0.0	1.72	-1.35	0.18	0.42	1.72	-1.59	0.11
<i>Strombosia nigropunctata</i>	F	3.3	0.45	7.23	0.00	0.9	0.62	1.42	0.16	0.8	1.20	-0.10	0.92	0.10	1.20	-12.34	0.00
	H+	4.9	1.54	3.18	0.00	1.5	1.26	1.17	0.24	0.1	1.43	-0.63	0.53	0.13	1.43	-5.82	0.00
	H-	2.0	0.36	5.60	0.00	0.3	0.66	0.42	0.68	18.9	1.24	1.31	0.19	0.11	1.24	-10.24	0.00
	L+	3.9	0.64	6.05	0.00	1.8	0.85	2.10	0.04	0.0	1.25	-1.22	0.22	0.13	1.25	-9.37	0.00
	L-	1.5	0.53	2.85	0.00	0.0	1.64	0.00	1.00	149.4	1.47	1.11	0.27	0.09	1.47	-6.40	0.00

Table 2-3. Continued

<i>Strombosia pustulata</i>	F	7.5	1.29	5.80	0.00	1.5	0.62	2.44	0.01	0.0	1.28	-1.96	0.05	0.10	1.28	-9.36	0.00
	H+	1.4	0.90	1.58	0.11	0.9	1.60	0.57	0.57	15.5	1.98	0.42	0.67	0.08	1.98	-3.65	0.00
	H-	8.4	1.61	5.20	0.00	2.5	0.84	3.01	0.00	0.0	1.30	-2.73	0.01	0.12	1.30	-7.93	0.00
	L+	6.7	1.34	4.99	0.00	1.4	0.61	2.25	0.02	0.0	1.37	-1.66	0.10	0.11	1.37	-6.97	0.00
	L-	9.2	3.80	2.41	0.02	5.6	3.54	1.58	0.11	0.0	1.54	-1.47	0.14	0.10	1.54	-5.34	0.00
<i>Strombosiopsis tetrandra</i>	F	22.5	6.54	3.44	0.00	1.9	0.83	2.25	0.02	0.0	1.18	-2.10	0.04	0.07	1.18	-16.03	0.00
	H+	22.6	29.25	0.77	0.44	5.9	8.48	0.70	0.49	0.0	1.46	-0.68	0.50	0.05	1.46	-7.86	0.00
	H-	9.5	1.84	5.19	0.00	2.1	1.10	1.92	0.05	0.0	1.25	-1.54	0.12	0.13	1.25	-9.24	0.00
	L+	25.0	8.87	2.82	0.00	1.8	0.87	2.13	0.03	0.0	1.21	-2.01	0.04	0.08	1.21	-13.62	0.00
	L-	2.6	0.70	3.76	0.00	2.1	1.85	1.13	0.26	0.1	1.46	-0.34	0.74	0.12	1.46	-5.55	0.00
<i>Terminalia superba</i>	F	31.3	2.98	10.48	0.00	0.7	0.14	5.35	0.00	1.7	1.06	0.97	0.33	0.77	1.06	-4.07	0.00
	H+	53.7	13.68	3.92	0.00	2.0	0.26	7.47	0.00	0.0	1.11	-4.47	0.00	0.85	1.11	-1.58	0.11
	H-	22.8	2.02	11.29	0.00	0.3	0.16	1.87	0.06	13.3	1.08	4.04	0.00	0.86	1.08	-1.86	0.06
	L+	32.6	3.32	9.83	0.00	2.1	0.21	9.96	0.00	0.0	1.08	-5.70	0.00	0.93	1.08	-0.94	0.35
	L-	27.0	5.02	5.39	0.00	0.0	0.27	0.00	1.00	31.0	1.13	3.48	0.00	0.77	1.13	-2.07	0.04
<i>Xylopiya chrysophylla</i>	F	19.9	5.62	3.54	0.00	0.0	0.48	0.00	1.00	4.7	1.20	0.92	0.36	0.18	1.20	-9.58	0.00
	H+	23.8	9.97	2.39	0.02	0.0	0.53	0.00	1.00	3.3	1.22	0.59	0.55	0.21	1.22	-8.05	0.00
	H-	13.6	6.02	2.26	0.02	0.0	2.23	0.00	1.00	12.8	1.60	0.42	0.67	0.10	1.60	-4.90	0.00
	L+	19.5	5.85	3.34	0.00	0.0	0.53	0.00	1.00	5.4	1.21	0.91	0.36	0.17	1.21	-9.10	0.00
	L-	21.8	11.27	1.93	0.05	6.0	16.42	0.36	0.72	0.0	3.31	-0.36	0.72	1.34	3.31	0.24	0.81
<i>Xylopiya hypolampra</i>	F	26.7	6.21	4.30	0.00	2.5	0.39	6.27	0.00	0.0	1.16	-4.48	0.00	0.22	1.16	-10.04	0.00
	H+	38.3	24.82	1.54	0.12	5.6	3.17	1.76	0.08	0.0	1.32	-1.49	0.14	0.18	1.32	-6.06	0.00
	H-	24.7	4.36	5.68	0.00	1.5	0.34	4.27	0.00	0.0	1.30	-2.83	0.00	0.60	1.30	-1.95	0.05
	L+	30.7	10.49	2.93	0.00	2.4	0.43	5.65	0.00	0.0	1.19	-4.06	0.00	0.19	1.19	-9.43	0.00
	L-	29.3	11.97	2.44	0.01	3.1	1.39	2.24	0.03	0.0	1.43	-1.75	0.08	0.59	1.43	-1.45	0.15

Table 2-3. Continued

<i>Xylopiaphloiodora</i>	F	17.2	9.76	1.76	0.08	0.0	1.33	0.00	1.00	8.5	1.33	0.58	0.57	0.05	1.33	-10.56	0.00
	H+	6.3	2.45	2.56	0.01	0.0	2.51	0.00	1.00	7.0	1.77	0.23	0.82	0.11	1.77	-3.90	0.00
	H-	17.2	14.49	1.19	0.24	0.0	2.29	0.00	1.00	13.7	1.45	0.44	0.66	0.06	1.45	-7.69	0.00
	L+	7.0	2.26	3.11	0.00	0.0	1.41	0.00	1.00	37.7	1.41	0.97	0.33	0.07	1.41	-7.67	0.00
	L-	17.6	32.93	0.53	0.59	0.5	-	-	-	4.3	-	-	-	0.02	2.25	-4.59	0.00

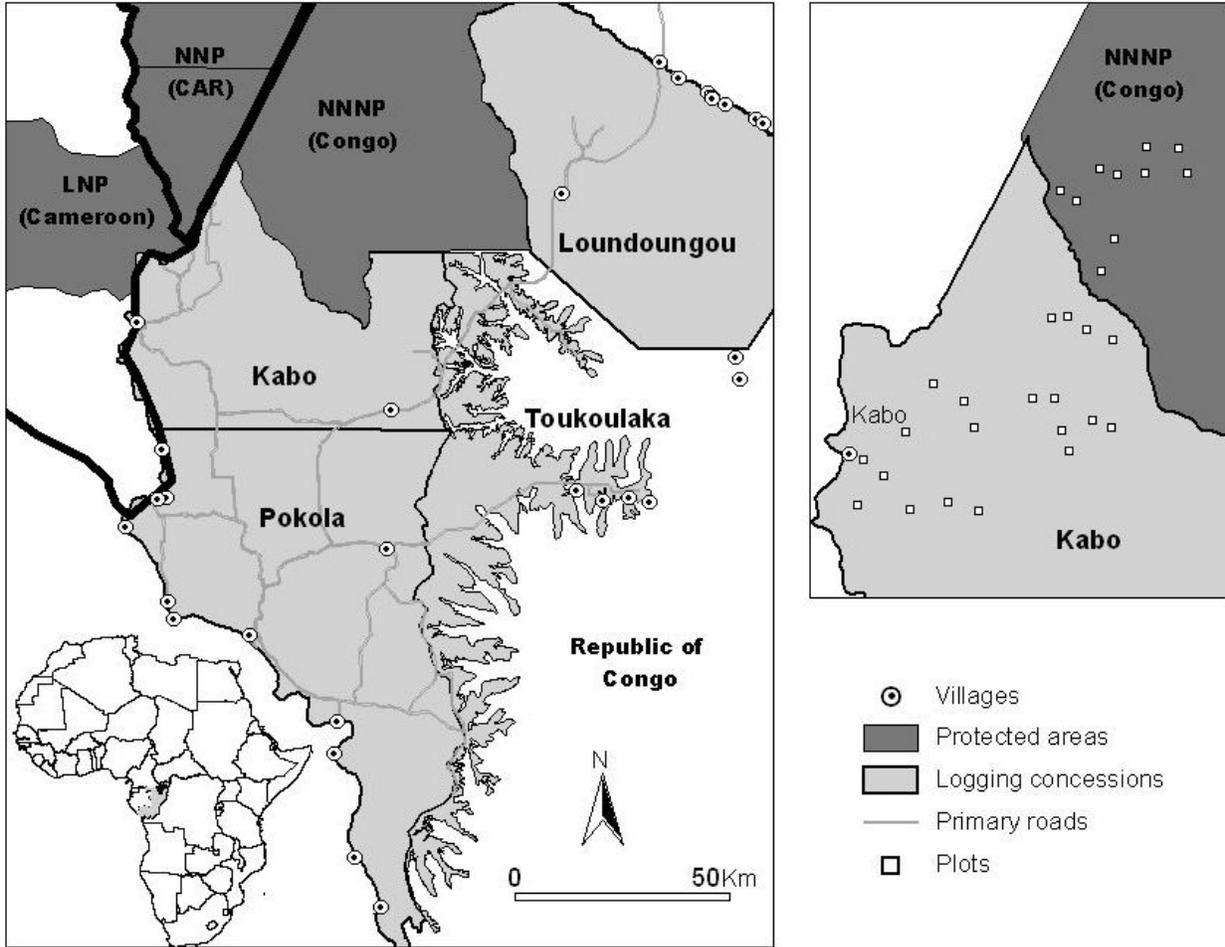


Figure 2-1. Location of the tree plots in the Kabo concession and Nouabalé-Ndoki National Park in northern Republic of Congo.

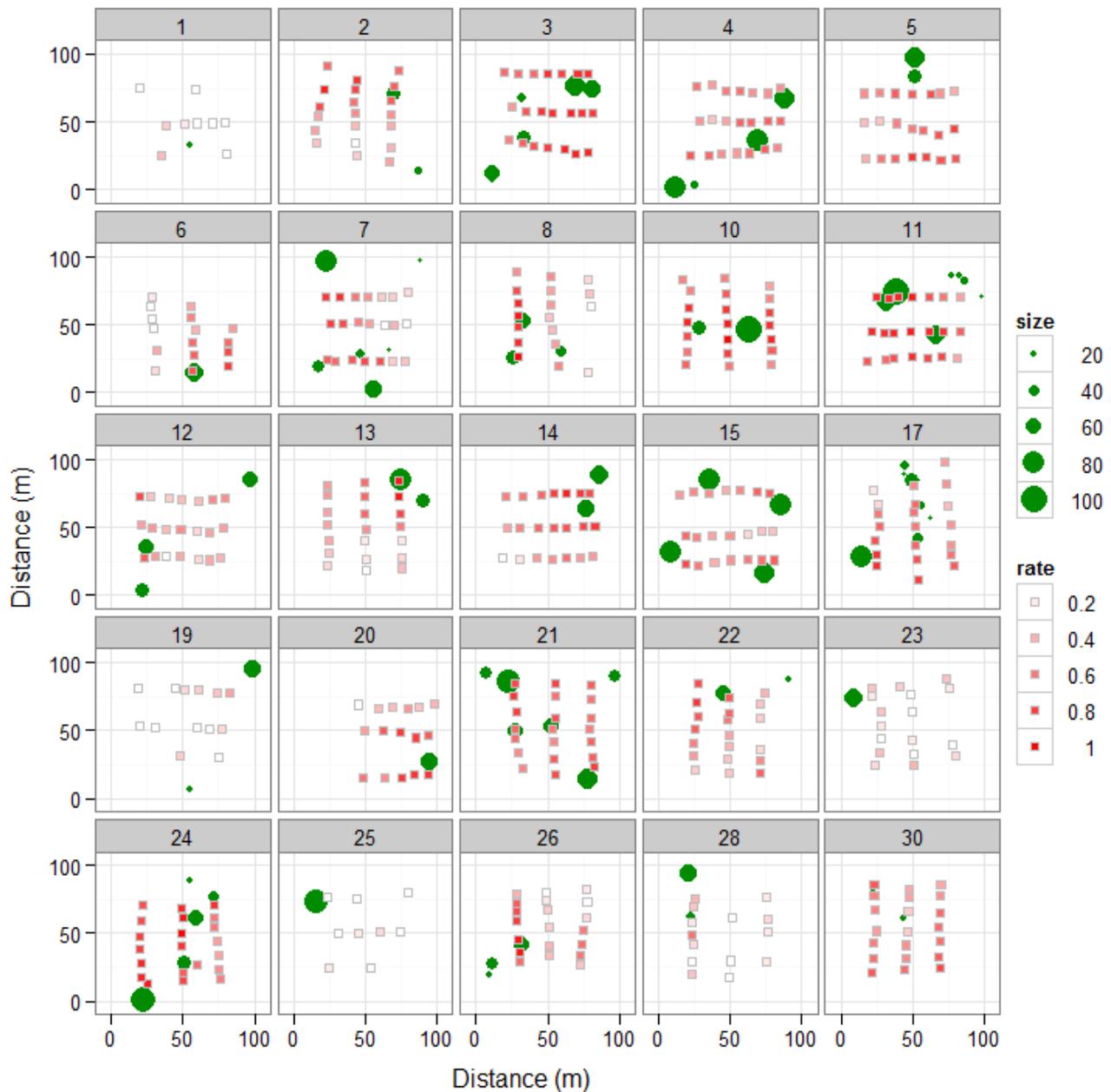


Figure 2-2. Seed dispersal for *Terminalia superba*, a wind-dispersed tree species, across the 30 tree plots. Each panel depicts a tree plot. Plots 1-10 are in logged, hunted forest; plots 11-20 are in logged, unhunted forest, and plots 21-30 and in forest that is neither logged, nor hunted. Trees (green circles) vary in size with the dbh (cm) of the tree. Seed traps (squares) which captured at least 1 seed of *Terminalia superba* are depicted with the intensity of red increasing with greater densities of arriving seeds.

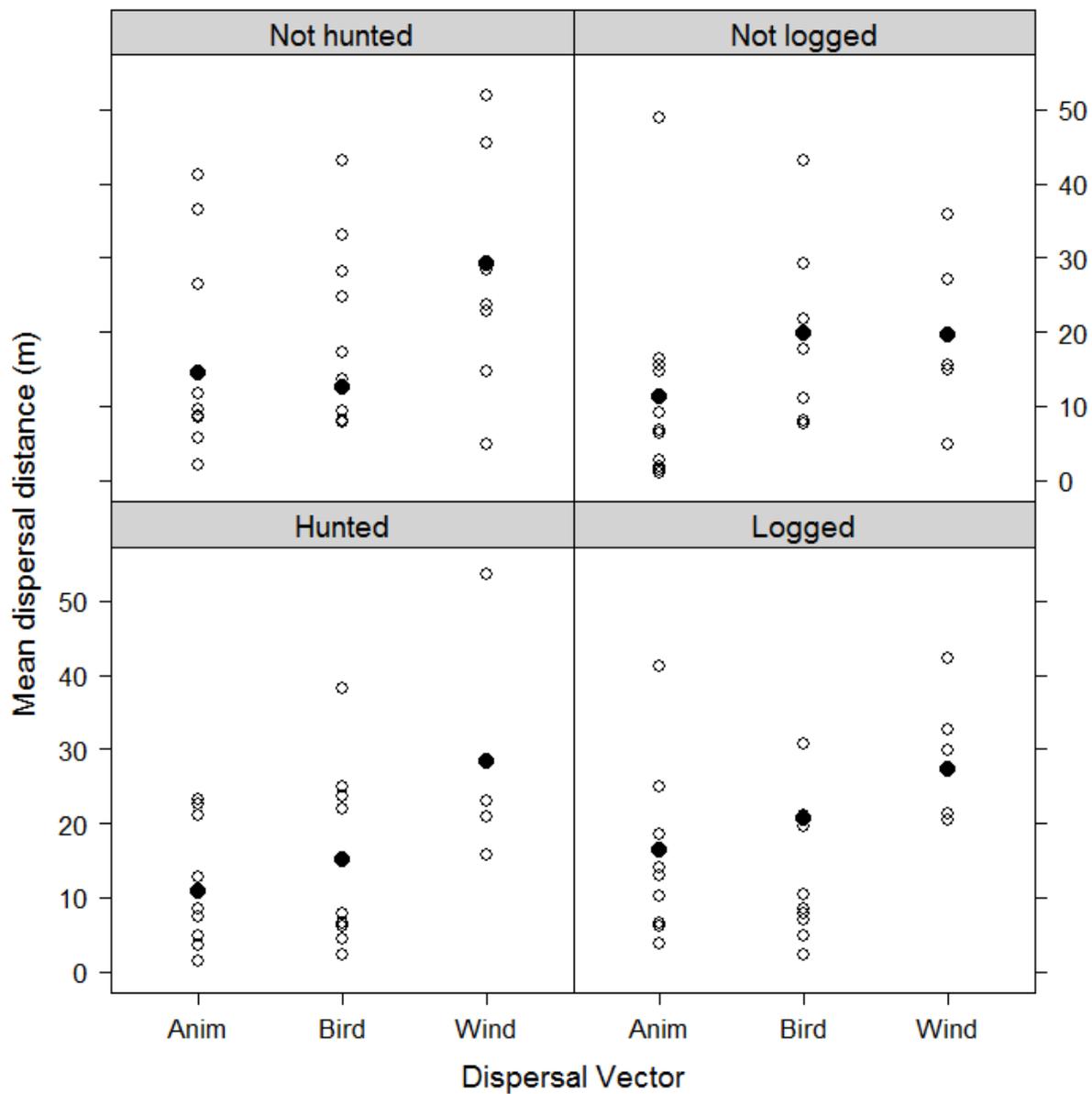


Figure 2-3. Mean dispersal distance (open circles) for each species within forest type combination grouped by dispersal vector (animal-, bird-, and wind-dispersed species). The closed, black circle is the vector mean dispersal distance over all the tree species.

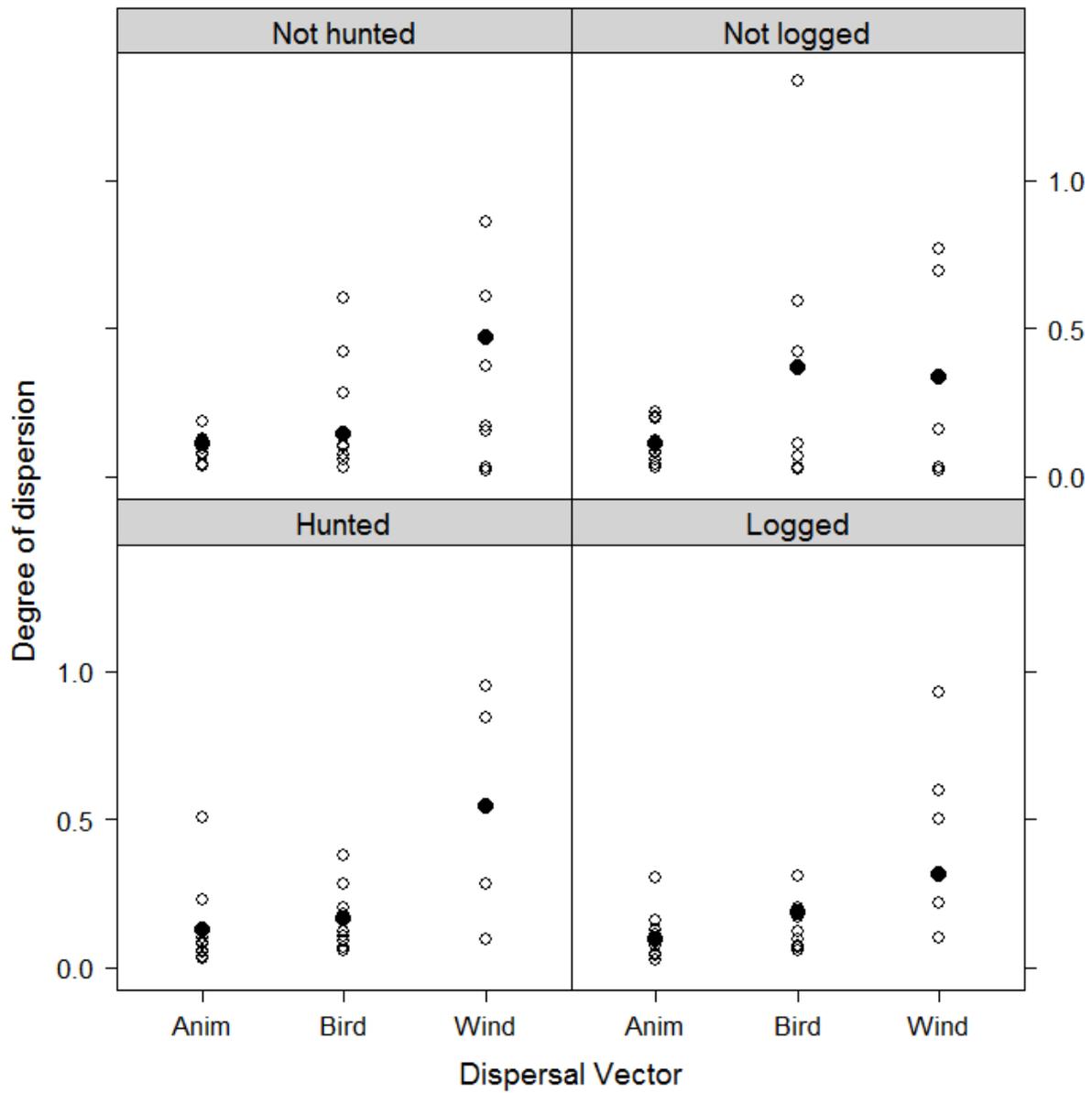


Figure 2-4. Mean degree of dispersion (open circles) for each species within forest type combination grouped by dispersal vector (animal-, bird-, and wind-dispersed species). The closed, black circle is the vector mean dispersion parameter over all the tree species.

CHAPTER 3
SEED DISPERSAL PATTERNS DRIVE SEEDLING RECRUITMENT IN AN
EXPERIMENTAL MANIPULATION OF SEED SHADOWS

African forests are being emptied of wildlife by unsustainable levels of hunting. The extirpation of seed-dispersing animals alters the spatial patterns of seed dispersal for many tree species, with unknown consequences for their regeneration. To test the extent to which spatial distributions of seed deposition drive seedling recruitment, we experimentally manipulated seed dispersal patterns under individuals of a monkey-dispersed tree, *Manilkara mabokeensis*. We created seed distributions with all seeds deposited under the canopy (“no dispersal”), with density declining (negative exponential curve) as a function of distance from the tree (“natural dispersal”), and at uniform densities (“even dispersal”). These distributions mimicked seed dispersal patterns that could occur with the extirpation of monkeys by hunting, 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 on all seedlings. Compared to “natural dispersal”, “even dispersal” increased seedling survival by 26%, whereas “no dispersal” reduced seedling survival by 78%. Survival of seedlings depended on the density of dispersed seeds but not the distance from the tree. These results support hypotheses that invoke density-dependence as a limiting factor to recruitment but they fail to support the Janzen-Connell hypothesis, which predicts that enhanced distance of seeds from conspecific adults improves survival. Our experiment demonstrates that seed dispersal patterns strongly influence seedling recruitment and survival. More generally, we concluded that management of hunting is a priority for the conservation of tropical forests because forests emptied of their seed dispersers will have limited regeneration capacity.

Introduction

In Afrotropical 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. 2009a). 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 (Wright et al. 2000, Terborgh et al. 2008, Brodie et al. 2009). But to predict how the loss of dispersers will affect tropical forests 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 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 distance and density at which seeds are located away from their 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; most seed shadows lead to decreasing seed densities as a function of 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). By this logic, tree recruitment is a deterministic process and knowledge of dispersal patterns should allow one to predict the distribution of trees in space. But 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 original

spatial distribution of seeds (Herrera et al. 1994, Harms et al. 2000, Balcomb and Chapman 2003).

While we are quickly gaining a better grasp of factors that affect local seed dispersal patterns (e.g., Clark et al. 1999), we still do not know whether these patterns have consequences for plant abundance and diversity. In theory, by escaping from aggregated dispersal patterns close to the tree, dispersed seeds avoid mortality from intraspecific competition and the density- and distance-dependent behavior of seed and seedling consumers (Janzen 1970, Connell 1971). In this way, seed dispersal increases species recruitment and abundance. However, depending on the scale of favorable and unfavorable sites for regeneration, short-range dispersal may lead to greater rates of recruitment and higher abundance than more distant dispersal if seeds are more likely to fall into unsuitable microsites at greater distances (Bolker and Pacala 1999). At the community level, high tree species diversity is promoted when seed dispersal is limited because limited dispersal slows rates of competitive displacement and causes spatial segregation of heterospecific individuals across a landscape (Hubbell et al. 1999, Wright 2002). Thus, even at the local scale, short-range dispersal should increase diversity and long-range dispersal should decrease diversity.

The evidence that the spatial distribution of seeds determines juvenile and adult recruitment is mostly indirect and correlative (Levine and Murrell 2003). Based on the knowledge that heterospecific differences in patterns of seed deposition can partially be explained by dispersal mode (Clark et al. 2005, Muller-Landau et al. 2008), the spatial aggregation of conspecific saplings and trees has been shown to correlate with the mode of seed dispersal in tropical forest (Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006). But to directly link the spatial distribution of seeds to tree abundance and diversity will require

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) compared distributions of seeds of two wind-dispersed trees 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 to separate distance- and density-dependent effects.

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 seed densities from its natural seed shadow, we sowed seeds of *M. mabokeensis* under seven trees in three different distributions to mimic scenarios of "no dispersal", "natural dispersal", and "even dispersal". These distributions mimicked seed dispersal patterns that could occur with the extirpation of monkeys by hunting, low levels of hunting, and extraordinarily high rates of seed dispersal. We then monitored the recruiting seedlings for 18 months to test whether seed shadows affect seed and seedling survival and community diversity. We had four specific objectives. First, we examined how different seed shadows affect seedling recruitment and survival. Second, we decoupled the distance- and density-effects. Third, we determined the mechanisms (seed predation, herbivory) that limit seedling recruitment. Fourth, we tested whether the seed shadow affects community diversity of seedlings.

Methods

Overview

Our experiment entailed several steps. First we selected a tree species based on the criterion that its primary disperser (arboreal monkeys) was being impacted by hunting. Second, we quantified natural patterns of seed dispersal around focal trees. Third, with the seed shadow data we calculated the densities of seeds to sow in the three experimental distributions (“no dispersal”, “natural dispersal”, and “even dispersal”). Fourth, we delineated wedges under seven individuals of our study species, *M. mabokeensis*, and sowed seeds into 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 (2°20' N, 16°25' E) in the northern Republic of Congo from July 2006 through July 2008. The logging concession is comprised primarily of lowland, semi-deciduous tropical forest, and had been logged once in the late 1960s at a relatively low intensity (<2.5 tree ha⁻¹). The study site is 20 km from the nearest village and subject to low rates of hunting. 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. 2009b).

For this study, we randomly selected seven reproductive individuals of *M. mabokeensis* (Sapotaceae), a canopy emergent tree whose fruits are primarily dispersed by arboreal monkeys. In the study area, *M. mabokeensis* occurs at a density of 1.67 trees per 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 cm (SD = 47.6) diameter at breast height and canopy radius varied among

trees (mean = 8.5 m, SD = 2.5). The fruits are pulpy, measuring 3-5 cm in diameter with 1-3 seeds per fruit.

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 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 of animal-dispersed species have demonstrated that as much as 85% of seed crops 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, $k(x) = (1/a)\exp(-x/a)$, to the seed data, where $k(x)$ is the density of seeds as a function of distance x from the source, and a describes the scale of the function (Figure 1). Given a dispersal kernel $k(x)$, $k(x)dA$ is the expected proportion of the total seedfall in an area dA at distance x from the parent tree. Dispersal scale a determines how fast seed density falls off with distance from the source. If a tree's total fecundity is f , we find the expected number of seeds in a trap at distance x by multiplying the dispersal kernel by the fecundity and the trap area and then dividing by the area of the annulus $2\pi x: N = f(x, a) \cdot A/2\pi x$. We assumed that observed seed numbers were

negative binomially distributed with mean N and dispersion parameter k . Although we used the negative exponential dispersal kernel, any number of dispersal functions could have fit the data, and some may have fit better than the negative exponential function. Our goal was to find a phenomenological model of the seed shadow to inform the seed sowing experiment, not to compare models or model parameters, and 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 searching numerically for the combination of parameter values that maximized the likelihood function using the default Nelder-Mead simplex algorithm in R 2.7.1 (R Development Team 2008). We estimated the scale parameter, α , to be 0.043, giving a mean dispersal distance of 23.3 m. Fecundity, f , was 77,135 fruits and the dispersion parameter, k , was estimated at 0.01 indicating strong overdispersion of seeds.

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 *M. mabokeensis* trees (Fig 1). 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 within 60 m of the tree. 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, we monitored seedling recruitment derived from the natural seed rain; we did not manipulate seed shadows in these “control” wedges. In the four remaining wedges, we removed all conspecific seeds from the canopy floor immediately after the fruiting

season so that our experimental seed distributions were not confounded by previously arriving seeds. One of these served as a seed removal control and we monitored it to verify that we had effectively removed conspecific seeds. Across all seven trees, an average of only 1.3 seedlings germinated in all seed removal control wedges, none of which survived to the end of the experiment; therefore because we successfully removed background conspecific seeds we do not discuss the seed removal control wedge further. We sowed seeds in different distributions in the remaining three wedges. In the “no dispersal” wedge, seeds were sown into the wedge in an aggregated distribution with all seeds dropped within 10 m of the trunk. The “no dispersal” distribution mimics the scenario in which monkeys are extirpated and dispersal is limited to seed and fruitfall from the canopy. In the “natural dispersal” wedge, seeds were sown according to the negative exponential dispersal kernel derived from quantifying the seed shadow, where seed densities decrease with distance from the tree. In the “even dispersal” wedge, seeds were sown in a uniform distribution to simulate high rates of dispersal where seeds are evenly dispersed across the landscape. We used the fitted negative exponential dispersal function to calculate the density of seeds to sow at each distance annulus for each experimental distribution (Figure 1). By multiplying the density of seeds by the sampling area of the experimental wedge (188 m²), we calculated a seed sowing number of 881 seeds for each wedge.

For the experimental wedges, we collected mature seeds and seeds from fruits from under the canopies of many different *M. maboensis* trees (~15 trees), mixing all the seeds together before sowing them. We wore plastic gloves when sowing the seeds to prevent leaving human odor and scattered the seeds on the ground within a wedge x distance block. 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 the seedlings less than 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 was used to estimate posterior distributions of model parameters and test for significance (see below for details). We assumed a Weibull distribution for the survivor function, and included random effects for the replicate trees ϵ_T and the experimental wedges ϵ_W within trees as follows:

$$t_{ijk} \sim \text{Weibull}(r_k, \mu_{ijk}) \quad i = 1, \dots, 9528, \quad j = 1, \dots, 7, \quad k = 1, 2, 3$$

$$\log \mu_{ijk} = \beta X_{ijk} + \gamma D_{ijk} + \delta W_{ijk} + \epsilon_{Ti} + \epsilon_{Wj}$$

$$\log r_k = \delta W_{ijk}$$

where t_{ijk} is the failure time of an individual at tree i and wedge k . In the data, time starts from the month after the seeds were sown and runs until month 18; we right-censored the data to account for seedlings that survived past the end of the experiment. The shape r_k was allowed to vary by wedge with coefficient δ . The scale μ_{ijk} was described by a vector of regression coefficients, where β is the (log-) linear effect of distance, D_{ijk} , γ is the (log-) linear effect of seed density, X_{ijk} , and δ represents the effect of the 3-level factor of treatment, W_{ijk} , which is the identify of the treatment. Because the effects of seed density and distance 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 ($Normal(0, 0.0001)$) for fixed and 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 below) 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 Markov Chain Monte Carlo (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 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 (i.e., Gelman-Rubin statistics < 1.2) from the R contributed package, coda (Plummer et al. 2005). For the survival model, we ran 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 compare their deviance information criterion (DIC). 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 compare 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 used Simpson’s diversity index $D = 1 - \sum n(n - 1)/N(N - 1)$ which takes the relative abundance of different species into account, where diversity D 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 is no diversity and a value of 1 is 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”, “even dispersal”) within

each tree and then calculated the average diversity for each wedge type across all seven trees.

We ran 1000 permutations and compared the observed mean diversity, D_{obs} , for each wedge to the 2.5 and 97.5% quantiles from the simulated mean diversity, D_{sim} .

Results

Of the 18,501 seeds sown in experimental wedges, 6.5% (1,203) seedlings emerged and 1% (188) survived to 18 months. Seedling mortality was highest in the area closest to the tree for all seed distributions (Figure 3).

Seedling survival was determined by the density of seeds sown, with higher seedling survival at lower seed densities (Mean = -1.73, CI = -2.565, -0.9178; Figure 4). Survival increased slightly with distance from the tree, but the effect was indistinguishable from 0 (Mean = 0.260, CI = -0.352, 0.822). Similarly, the overall 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 (Figure 4). The scale parameters differed among seed distributions (Mean = 391.2, df = 2, $p < 2.2e-16$), the instantaneous risk of death or log-hazard (instantaneous rate of change in the log of the number of survivors per unit time) decreased rapidly for the “no dispersal” distribution because mortality occurred early, followed by the “natural” and “good” dispersal distributions (Figure 4). Variation in survival was greater among trees than it was among experimental wedges under the same tree. Comparing candidate models (by consecutively setting each parameter to 0 and comparing DIC values) similarly demonstrated that the distance and treatment parameters did not contribute to seedling survival (Table 3-1).

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 before the seedling stage, as seed germination did not strongly vary with distance from tree, density of

sowed seeds, or experimental treatment (Table 3-2). However, seed density did affect the number of leaves per seedling, an indicator of seedling growth and health. The number of leaves per seedling decreased with seed density (Table 3-2), suggesting that leaves are either being removed by vertebrate herbivores or that competition for resources with conspecific seedlings leads to a lower production of leaves. Of the leaves on seedlings, the probability of insect damage to leaves decreased by approximately 1% with every 10 m away from the tree (Mean = 0.493, CI = 0.488-0.497).

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 seedlings (bootstrapped 95% CI = 1.71, 8.57) survived on average in the “good dispersal” wedges, 3.86 (bootstrapped 95% CI = 1, 6.86) seedlings survived in “natural” wedges, and 0.86 seedlings (bootstrapped 95% CI = 0.14, 1.71) survived in “no dispersal” wedges. Scaling up to the local neighborhood of the tree, “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. maboensis*, our results suggest that the extirpation of monkeys by hunting would result in a 78% decrease in recruitment at the end of 18 months.

More aggregated dispersal resulted in higher seedling diversity, although across-treatment differences in diversity were not significantly different from random (no dispersal $D_{obs} = 0.79$ (sd = 0.23), $D_{sim} = 0.76$ (quantiles = 0.71, 0.81); natural dispersal $D_{obs} = 0.76$ (sd = 0.29), $D_{sim} = 0.76$ (quantiles = 0.70, 0.81), good dispersal $D_{obs} = 0.74$ (sd = 0.30), $D_{sim} = 0.77$ (quantiles = 0.71, 0.81)).

Discussion

The spatial distribution of dispersed seeds matters for seedling recruitment and survival. Compared to “natural dispersal”, “good dispersal” increased seedling survival by 26%, whereas “no dispersal” reduced seedling survival by 78%. 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-dependence 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 (Hyatt et al. 2003).

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 more even dispersal patterns likely arose through escaping herbivores that responded to seedling density. In a concurrent study, we caged seed addition plots of *M. maboensis* to protect seeds and seedlings from rodents and vertebrate herbivores (Poulsen and Clark unpubl. data). Compared to uncaged plots, seedling survival in caged plots increased by 2.6 times after 3 months and increased by 4.9 times 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 distance component of Janzen and Connell's hypothesis has received little support (Hyatt et al. 2003), and likely oversimplifies 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).

From a theoretical perspective, 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"). While we did find an inverse trend 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 other mechanisms, such as density-dependence and habitat partitioning (Webb and Peart 2001). Alternatively, it is likely that interactions, particularly competition, among seedlings is too weak to drive patterns of diversity (e.g., Svenning et al. 2008). Our experiment consisted of a single dispersal season with different seed shadows resulting in dramatically different numbers of recruiting and surviving seedlings. We hypothesize that spatial patterns of seedlings that accumulate over several seasons would have a much more profound effect on the diversity of the seedling community.

From a conservation perspective, our results from one monkey-dispersed tree species demonstrate that the loss of dispersers could negatively affect the regeneration success of tropical trees. Once protected by their remoteness, 30-45% of Afrotropical forests are now

occupied by logging concessions, exposing an additional 29% of forests to increased hunting pressure (Laporte et al. 2007). Compared to our study site, densities of frugivorous monkeys were 35% lower in adjacent forest subjected to moderate (1 person km⁻²) subsistence hunting (Poulsen et al. 2009b). Hunting markedly alters the structure of mammal communities in central Africa (Fa et al. 2005, Laurance et al. 2006, Clark et al. 2009) and threatens to leave many tree species without reliable dispersers. The loss or reduction of seed dispersal services as a result of widespread hunting will leave some tree species with limited or no regeneration, thus altering forest composition with time. To maintain functioning forests, measures need to be taken to protect forest animals.

Table 3-1. Model comparison for survival analysis of seedlings. 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; the removal of an important parameter should cause the model to get worse. The scale for assessing DIC is approximately equal to the scale for the Akaike information criterion (AIC): <2 = little difference, $2-6$ = moderate, $6-10$ = substantial, and >10 = overwhelming (pg. 210, Bolker 2008).

Model	Δ DIC
Full model	
No β_{tree}	-2
No β_{density}	+16
No β_{distance}	-1
No σ_{tree}	+2
No σ_{wedge}	+32

Table 3-2. Parameters [and 95% credible intervals] from generalized linear mixed models (GLMMs) for seed germination, leaf growth on seedlings, and leaf damage. Density of seeds represents the difference in density from the average natural seed density. Distance from the tree represents the effect of moving 10 m farther from the tree. Random effects for tree and the experimental distribution are presented as σ_{tree} and σ_{wedge} .

Parameters	Probability of seed germination	Log ratio of leaves per seedling	Probability of leaf damage
Density of seeds	0.522 [0.488, 0.555]	-0.127 [-0.215, -0.043]	0.521 [0.468-0.573]
Distance from tree	0.502 [0.467, 0.536]	0.051 [-0.006, 0.108]	0.434 [0.392-0.476]
Aggregated distribution	0.008 [0.002, 0.042]	-0.506 [-0.844, -0.159]	0.054 [0.028-0.101]
Natural distribution	0.011 [0.003, 0.055]	-0.308 [-0.538, -0.086]	0.058 [0.039-0.086]
Uniform distribution	0.010 [0.003, 0.051]	-0.330 [-0.547, -0.107]	0.064 [0.042-0.095]
σ_{tree}	0.657 [0.593, 0.755]	0.182 [0.074, 0.336]	0.592 [0.533-0.668]
σ_{wedge}	0.795 [0.633, 0.956]	0.135 [0.012, 0.375]	0.545 [0.501-0.640]

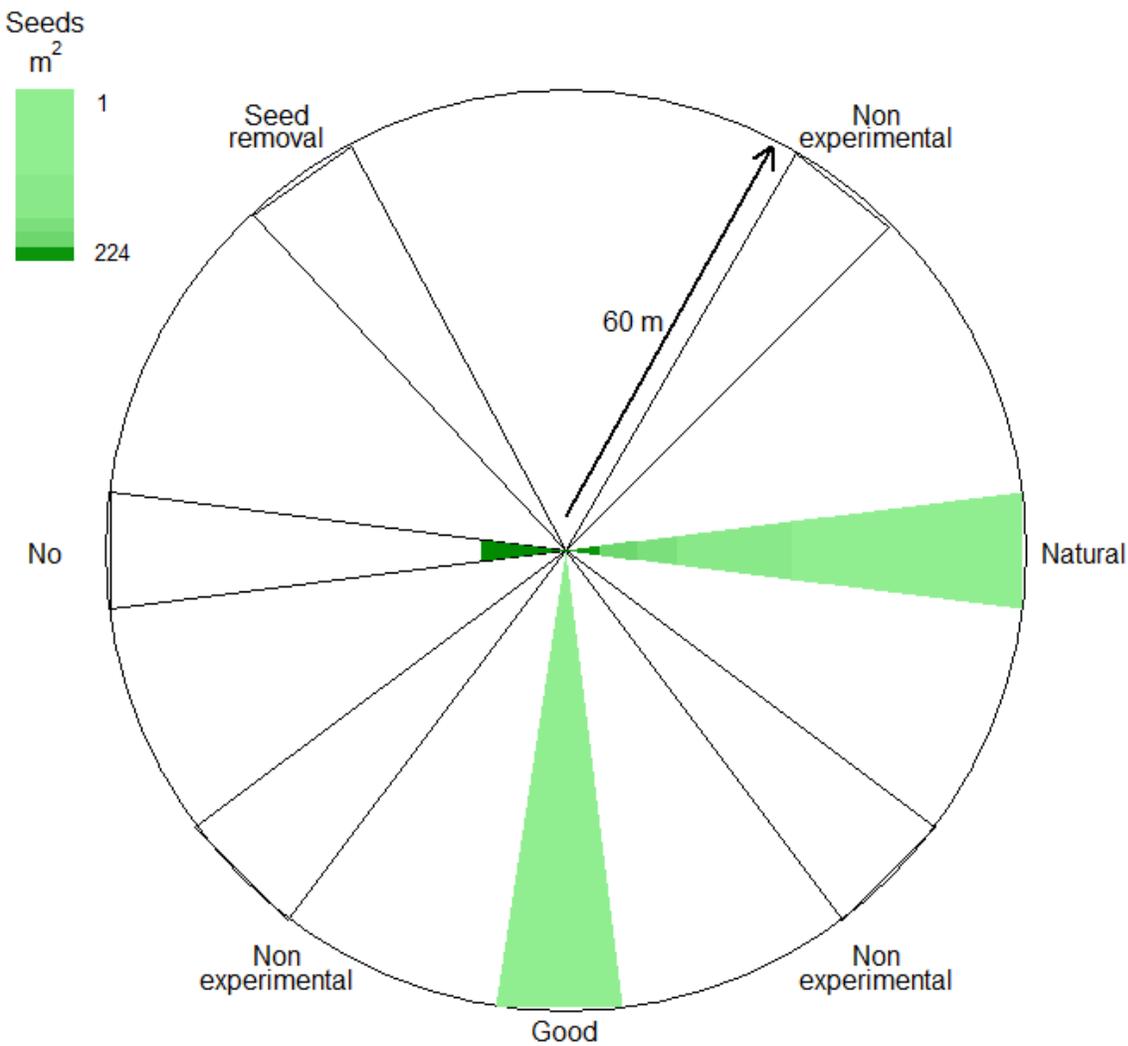


Figure 3-1. Depiction of the experimental design. Seven wedges were delineated under each of seven adult individuals of *Manilkara mabokeensis*. We defined a wedge as a sector (188 m^2) of a circle, its origin at the trunk with a central angle of 18° and radii of 60 m. We delimited the radius of the sector into 5 m sections, and planted seeds at the 12 different distance annuli. In three of the wedges (Non-experimental), we monitored seedling recruitment derived from the natural seed rain. In the four remaining wedges, we removed all 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; and 3) In the “Even” dispersal wedge, seeds were sown at uniform densities with distance from the tree.

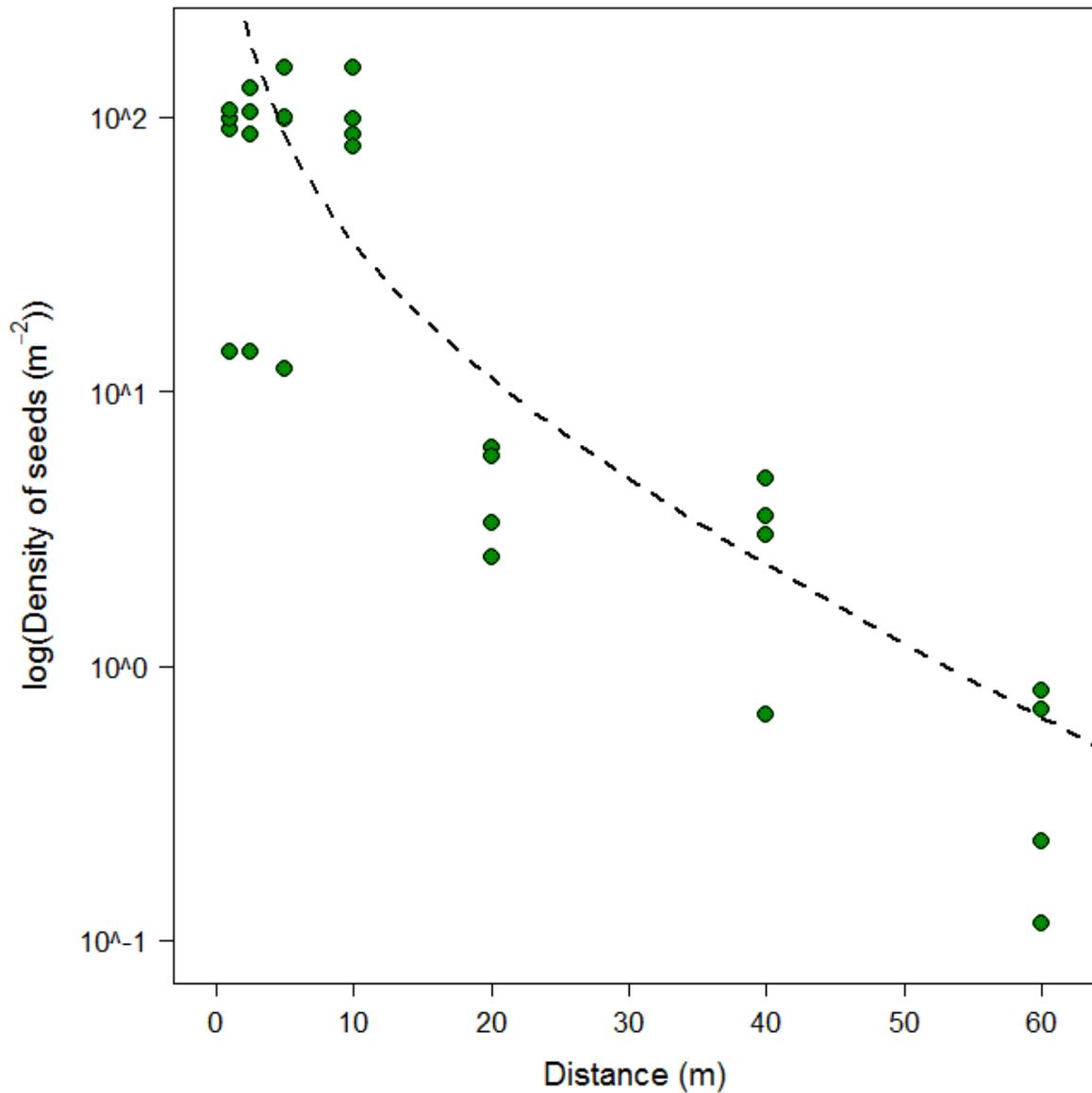


Figure 3-2. Fit of the negative exponential function to seed trap data from four individuals of *Manilkara mabokeensis*. Closed circles show seed densities in traps (on a logarithmic scale) in relation to distance from tree (N=4). Mean parameter values for the negative exponential dispersal function were $a = 0.44$ (scale), $f = 77,222$ (fecundity), and $k = 0.01$ (dispersion).

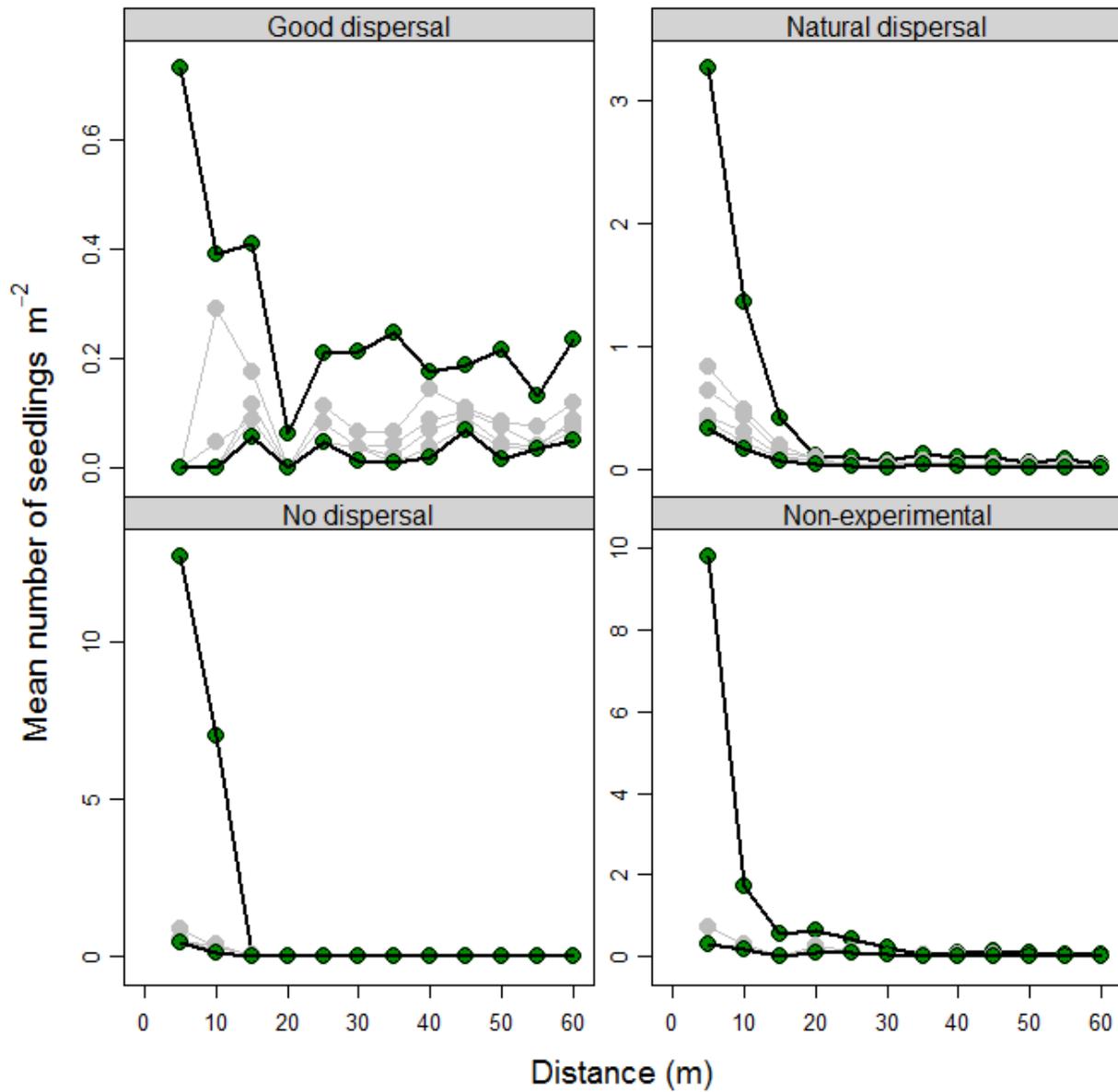


Figure 3-3. The density of seedlings surviving with distance from tree and in the different experimental and non-experimental wedges. The dark lines and dark green points represent the density of seedlings 1 month (top line) after seeds were sown and 18 months (bottom line) after sowing. Grey lines and dots indicate seedling densities during the months between the first and last seedlings censuses.

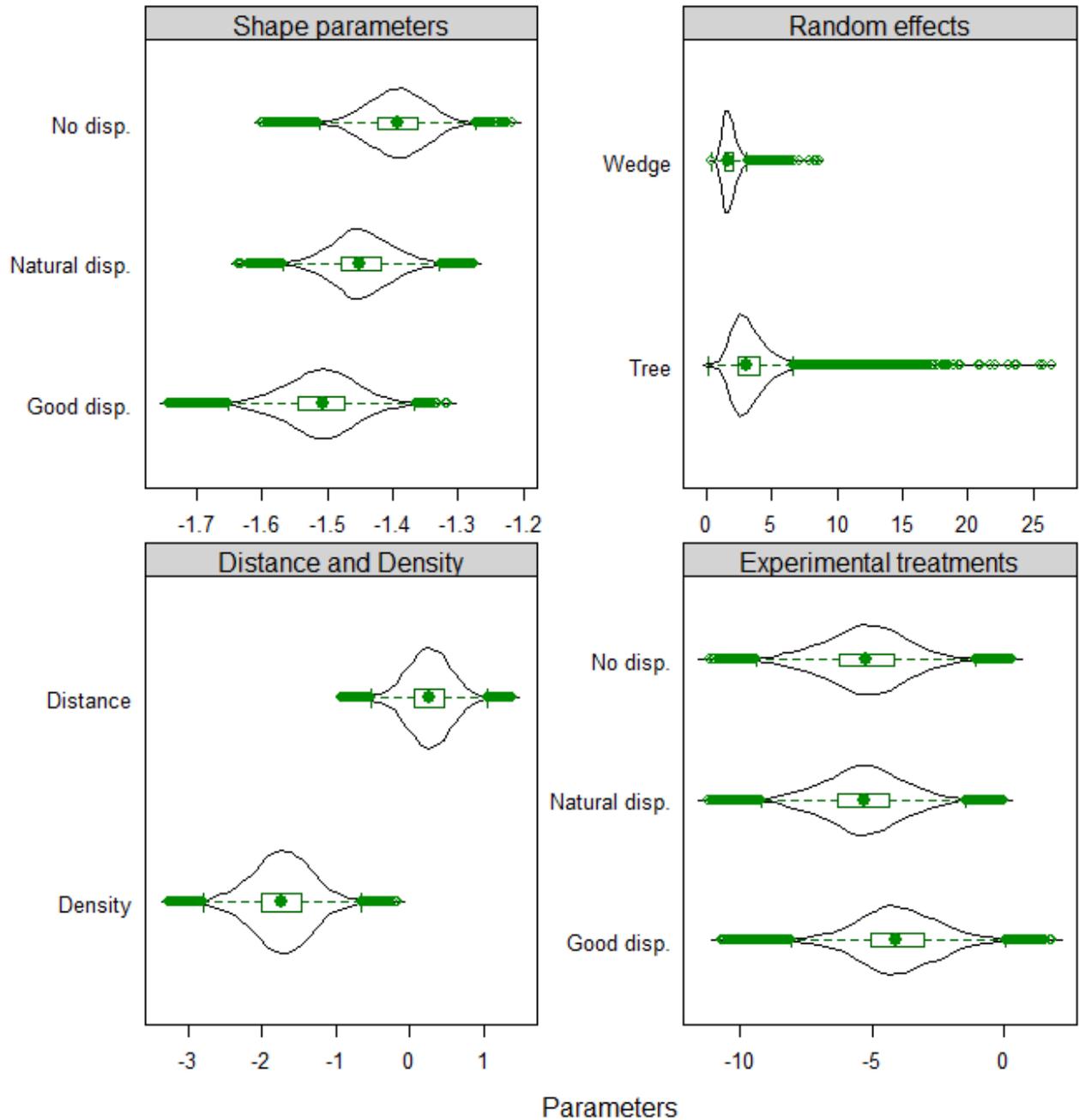


Figure 3-4. Violin plot of parameters from the seedling survival model, combining a box plot indicating the median (point) and interquartile range, with the probability density of the posterior distribution of parameters. Note that the distance parameter overlaps zero, whereas the density parameter does not. Similarly, shape parameters are significantly different among treatments, but the experimental treatments parameters do not.

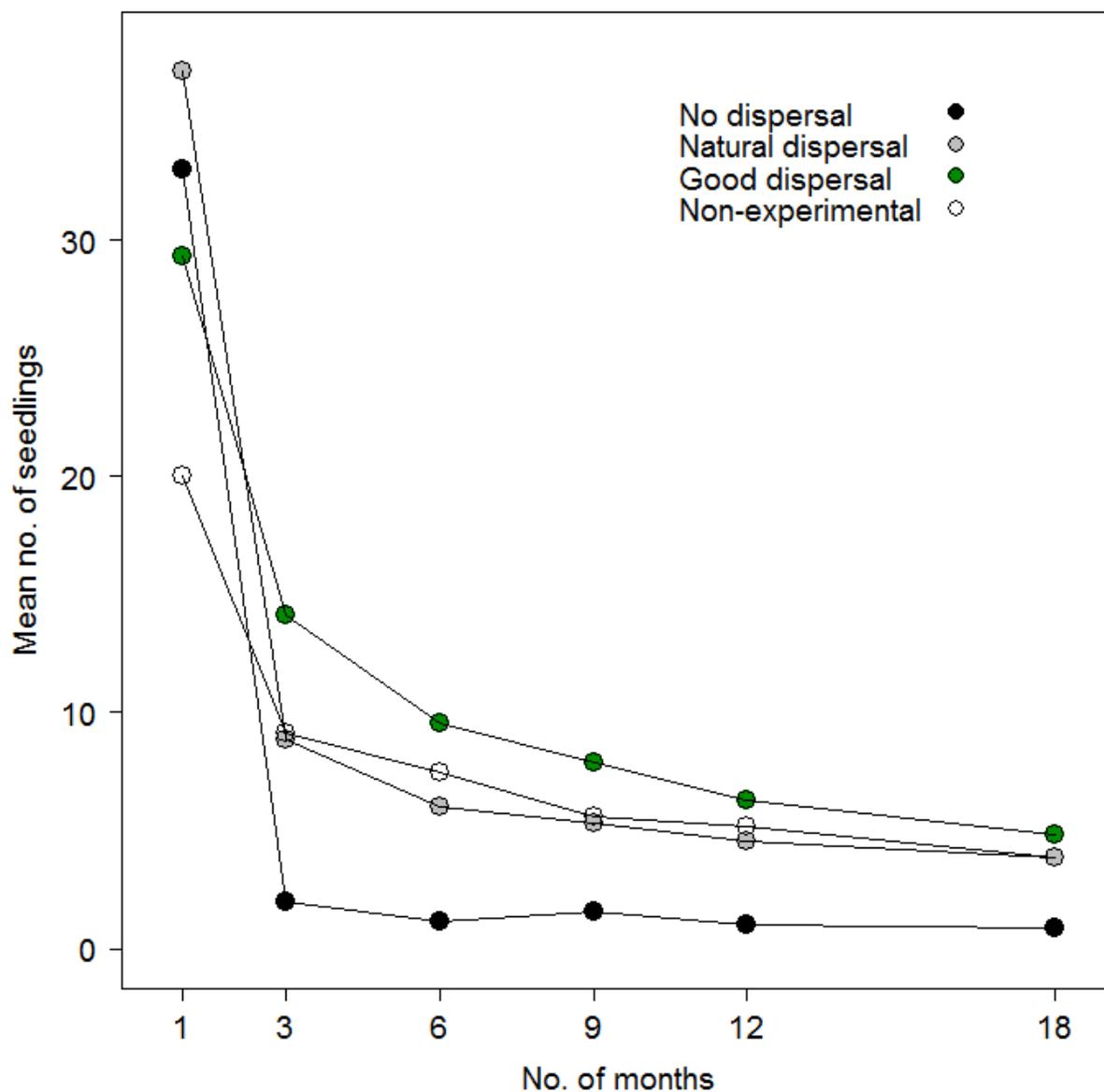


Figure 3-5. Number of seedlings that survived over 18 months in the three experimental distributions (No dispersal, Natural dispersal, and Good dispersal), the non-experimental distribution (Non-experimental), and the seed removal control (Seed removal).

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BIOGRAPHICAL SKETCH

John Poulsen was born in Texas. Having survived the Army and finished their own Ph.D.'s, his parents, Randy and Dorothy, moved him and his twin brother, Chris, to the mountains of Montana at the age of four. In Montana, he eventually learned how to flyfish and spent his childhood running around the mountains with Chris and his little sister, Melissa. After high school, John left behind small town life to join the Air Force Academy. Finding himself very good at following orders, but not so enthusiastic about killing people, after nine months John transferred to Willamette University where he studied international politics. During college, John returned to Montana in the summers to work for the U.S. Forest Service as a forest fire fighter and learned important life skills like using chainsaws and digging fire line that would serve him in his future endeavors. It was in his last year at Willamette that John met and fell in love with Connie Clark. Searching for an international experience, John worked for the US Peace Corps as a forestry volunteer in the Republic of Mali. In Mali he learned how to adapt and live in African cultures, learned to speak Fulfulde and French, and learned to contract and survive infectious diseases. After two and a half years John traveled to the rainforests of Cameroon where Connie had abandoned him to conduct research on hornbills. Reunited with Connie, he also fell in love with the tropical forest and gave up his ambitions to work in international politics to pursue ecology. Three years later John finished his master's degree in conservation biology at San Francisco State University. He then went to work for the Wildlife Conservation Society in the Republic of Congo as the co-director of the Lac Télé Community Reserve. Enjoying conservation work, but disappointed at not seeing Mokolé-Mbembé, the dinosaur said to inhabit Lake Télé, John left to start his Ph.D. at the University of Florida in 2002. He conducted three years of field work in northern Republic of Congo while working as the director of the Buffer Zone Project (PROGEPP) for the Wildlife Conservation Society.

Ironically, his experience in the Air Force served his well as he was largely responsible for managing 30 armed ecoguards. He received his Ph.D. from the University of Florida in 2009. The day after his dissertation defense, John and Connie flew to Ethiopia to pick up their 3 month old son. With son in tow, they moved to Falmouth, MA to join the scientific staff at the Woods Hole Research Center.

LOGGING AND HUNTING ALTER PATTERNS OF SEED DISPERSAL AND SEEDLING RECRUITMENT IN AN AFROTROPICAL FOREST

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Unprecedented rates of logging and hunting threaten the existence of the animals that inhabit tropical forests. Because animals perform ecological functions like seed dispersal their extirpation could hinder forest regeneration altering the structure and composition of the forest. I quantified the effects of logging and hunting on a tropical animal community, finding that they could reduce the abundance of some types of animals by as much as 71%. Both logging and hunting changed seed dispersal patterns of 26 tree species, reducing the dispersal distance of animal-dispersed trees while increasing dispersal for wind-dispersed trees. In an experimental evaluation of whether different dispersal patterns matter for seedling recruitment, more even distributions of seed across the landscape dramatically increased seedling survival. These results demonstrate that the loss of seed-dispersing animals is likely to inhibit forest regeneration. The conservation of tropical forests depends on the conservation of the animals that inhabit them.