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SPECIAL ISSUE: The Role of Seed Dispersal in Plant Populations: Perspectives and Advances in a Changing World

Low-intensity logging and hunting have long-term effects on seed dispersal but not fecundity in Afrotropical forests

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Abstract. Hunting and logging, ubiquitous human disturbances in tropical forests, have the potential to alter the ecological processes that govern population recruitment and community composition. Hunting-induced declines in populations of seed-dispersing animals are expected to reduce dispersal of the tree species that rely on them, resulting in potentially greater distance- and density-dependent mortality. At the same time, selective logging may alter competitive interactions among tree species, releasing remaining trees from light, nutrient or space limitations. Taken together, these disturbances may alter the community composition of tropical forests, with implications for carbon storage, biodiversity conservation and ecosystem function. To evaluate the effects of hunting and logging on tree fecundity and seed dispersal, we use 3 years of seed rain data from a large-scale observational experiment in previously logged, hunted and protected forests in northern Republic of Congo (Brazzaville). We find that low-intensity logging had a meaningful long-term effect on species-specific seed dispersal distances, though the direction and magnitude varied and was not congruent within dispersal vector. Tree fecundity increased with tree diameter, but did not differ appreciably across disturbance regimes. The species-specific dispersal responses to logging in this study point towards the long-lasting toll of disturbance on ecological function and highlight the necessity of conserving intact forest.

Keywords: Anthropocene; dispersal; frugivory; habitat fragmentation; hunting; selective logging; tropical forest.

Introduction

Logging concessions now cover almost 56 million ha of forest in West and Central Africa (FAO 2016). Most concessions are subject to low-intensity, selective logging intended to reduce the negative ecological impacts of traditional, conventional logging operations. Studies across the tropics have demonstrated that selective logging techniques can substantially reduce the short-term

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effects of logging (Sist 2000; Sist *et al.* 2003; Medjibe *et al.* 2013), but few studies have considered the long-term effects of selective logging on critical forest processes (Brown and Gurevitch 2004; Meijaard *et al.* 2005). Tropical trees respond to environmental disturbance on timescales that usually surpass the duration of ecological studies (Gourlet-Fleury *et al.* 2013; Edwards *et al.* 2014; Berdanier and Clark 2015) and changes in tree fecundity and seed dispersal may persist long after disturbance has ended, potentially altering ecosystem function.

Logging directly disturbs tropical forest communities through the extraction of large trees (Laurance *et al.* 2000), residual damage to remaining trees (Kasenene and Murphy 1991) and disruption of seed-dispersing animal communities (Gutiérrez-Granados 2011; Haurez *et al.* 2016; Rosin and Poulsen 2016). Road construction fragments the forest and provides hunters access to previously inaccessible areas (Kleinschroth and Healey 2017). Unsustainable hunting is the major cause of defaunation in many parts of the world (Hoffmann *et al.* 2010), causing over a quarter of the world's vertebrate species to decline in abundance over the last four decades (Dirzo *et al.* 2014). Reductions in vertebrate dispersers may affect the approximately two-thirds of all woody plants that rely on animals for seed dispersal (Willson and Traveset 2000; Muller-Landau and Hardesty 2005; Beaune *et al.* 2013). Dispersal failure has consequences for community composition through density-dependent recruitment (Cannon *et al.* 1994; Bleher and Böhning-Gaese 2001) and competition at later life stages (Nathan and Muller-Landau 2000).

Studies investigating how hunting and logging affect seed dispersal have yielded mixed results (Theimer *et al.* 2011; Beck *et al.* 2013; Kurten 2013; Camargo-Sanabria *et al.* 2014; Comita *et al.* 2014; Rosin and Poulsen 2016) in part because the interacting effects of hunting and logging have not been quantified beyond their immediate responses to disturbances (Markl *et al.* 2012). In the short term, intermediate levels of disturbance from selective logging may increase light and nutrients available to survivors (Johns 1988; Kasenene and Murphy 1991; Cannon *et al.* 1994; Huante *et al.* 1998; John *et al.* 2007; Ewel and Mazzarino 2008; Gutiérrez-Granados 2011; Haurez *et al.* 2016), thereby increasing tree fecundity (Molino and Sabatier 2001; Clark *et al.* 2010, 2014b). Logging may even increase the dispersal distance of abiotically dispersed species following forest thinning due to greater wind speeds through the canopy (Gardiner 1994; Stacey *et al.* 1994; Gardiner *et al.* 1997). However, in the longer term, logging may reduce seed dispersal distance and fecundity through combinations of increased hunting pressure (Kleinschroth and Healey 2017), declines in vertebrate dispersal vectors (Poulsen *et al.* 2013; Haurez *et al.* 2016), soil compaction (Pinard *et al.* 2000) and invasion of fast-growing competitors (Schnitzer and Bongers 2002). Because declines in dispersal vectors and increases in fecundity can both follow disturbance, investigating the interactions of these processes is essential for understanding the underlying ecological process (Abernethy *et al.* 2013).

To evaluate the separate and combined effects of hunting and logging on both fecundity and dispersal for animal and abiotically dispersed trees, we collected 3 years of seed rain data from a large-scale observational experiment in previously logged, hunted and protected forests in northern Republic of Congo (Brazzaville). By controlling for logging and hunting in our sampling design, we offer a first opportunity to test their relative effects. We hypothesized that the fecundity and dispersal distances of tropical trees will be sensitive to both hunting and logging. Specifically, we expected that: (i) tree fecundity is greater in logged forests relative to protected forests, regardless of whether trees species are abiotically or animal dispersed; and (ii) hunting reduces dispersal distances of animal-dispersed species, but not the dispersal distances of abiotically (wind or ballistic) dispersed species. Understanding the separate and combined effects of disturbances on seed dispersal is critical to predict changes in forest species composition and diversity.

Materials and Methods

Study area

We conducted the study in the Nouabale Ndoki National Park (NNNP; 400 000 ha) and the Kabo logging concession (267 000 ha) in northern Republic of Congo (Fig. 1). The forests in this area are classified as lowland tropical forest. Dominant tree families include *Meliaceae*, *Euphorbiaceae* and *Annonaceae* (CIB 2006). Rainfall averages ~1700 mm annually and is seasonal with peaks in May and October. The Kabo concession borders the NNNP to the south, and together they include a mosaic of logged and unlogged forest. Twenty years before the study began, the logging concession was selectively logged at low intensity (<2.5 stems per hectare) with four species, *Entandophragma cylindricum*, *E. utile*, *Triplochiton scleroxylon* and *Milicia excelsa*, making up 90 % of the harvest volume (CIB 2006). Although we do not have data on rates of natural disturbance at our study site, a comparison of pantropical data ($n = 65$) report a range of natural stand mortality from 0.86 to 2.02 %, with a best estimate of adjusted stem turnover rate of 1.81 ± 0.16 % (Lewis *et al.* 2004). Approximately 3000 people inhabited the study site at the time of the study, most residing in the logging town of Kabo. Residents generally hunted with shotguns, and to a lesser extent with wire snares, for consumption and for local trade (Poulsen *et al.* 2009). A gradient of hunting intensity decreases with distance from Kabo, with some forest types being used more than others (Mockrin 2008).

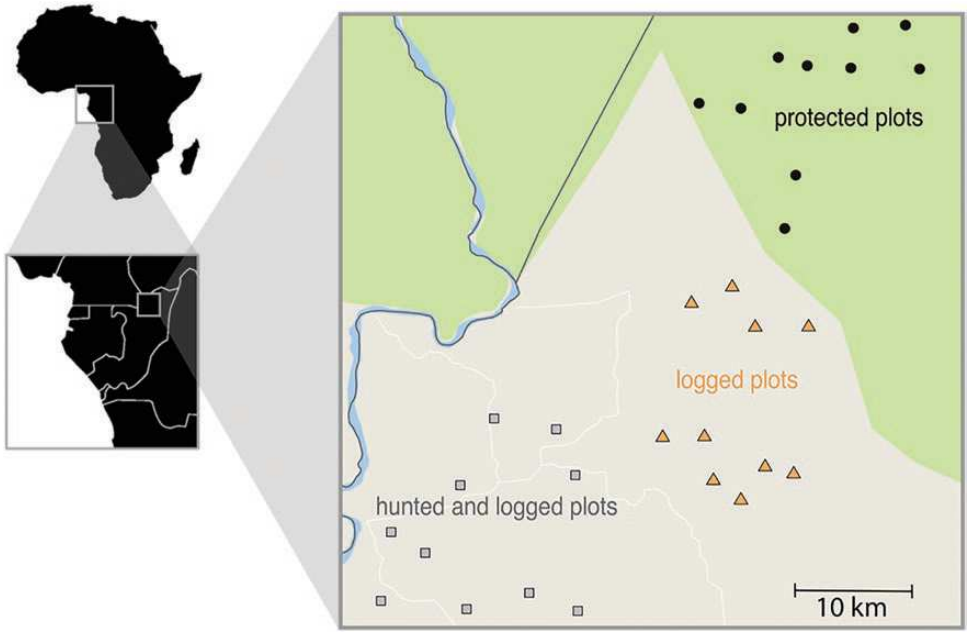

Figure 1. Location of 30 1-ha study plots in Northern Congo. Protected plots fall within the border of Nouabale-Ndoki National Park (green), whereas plots exposed to hunting and/or logging were located in the Kabo logging concession (grey) in northern Republic of Congo.

Tree census and seed rain data

We established 30 1-ha tree plots comprised of three equal-area groups, including 10 sites that were unlogged and unhunted, 10 sites that were logged and unhunted and 10 sites that were both logged and hunted. Using ArcView 3.2 and a 14-class habitat map (Laporte *et al.* 2007), we randomly located plots within each disturbance regime 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. Within each plot, all trees >10 cm diameter at breast height (DBH) were tagged, measured, mapped and identified to species (Wortley and Harris 2014). We additionally recorded canopy status (understory, midstory, canopy and emergent) and presence of lianas in the crown. Canopy openness and light availability were estimated for each plot by averaging values from four hemispherical pictures taken at each quarter of a plot. Seed traps 1 m^2 in area were centred along three transects at 25, 50 and 75 m from a plot border, with 10 m separating each trap. All traps were at least 20 m from the nearest plot border. Seeds and fruits were collected every 2 weeks and identified to species or genus level. Previous evidence demonstrates that parameter estimates are dominated by the relatively abundant seeds falling from within these distances (Clark *et al.* 1998).

We used seed rain data from 33 of the most common species to quantify fecundity and seed dispersal dynamics. Although seed rain was collected on many more species, we limited analysis to species that occurred in at least half of all plots. Tree density, size and species composition were approximately equivalent across plots and disturbance types **[see Supporting Information—Figs S1–S3]**. Of the 44 species that contributed seeds to at least half of the plots, 11 were lianas—woody vines that rely on trees for support. We omitted liana species from the present study despite their clear importance for frugivore diets, because they extend laterally tens of metres from their rooting stems, making the attribution of seeds to a censused stem challenging. The number of focal trees per 1-ha plot ranged from 50 to 253 with a median of 155 trees, and the number of seeds per focal species per plot ranged from 16 to 288 with a median of 96.

Plant species trait data

The dispersal mode for each tree species was assigned based on fruit morphology and observations of fruit consumption (Gautier-Hion *et al.* 1985; Tutin *et al.* 1997; White and Abernethy 1997; Whitney *et al.* 1998; Clark *et al.* 2001; Poulsen *et al.* 2001, 2002; Hawthorne and Gyakari 2006; Morgan and Sanz 2006) **[see Supporting Information—Table S1]**. Because many animal-dispersed species are dispersed by both birds and mammals, we report results by broad classes of animal and abiotic (wind or ballistic) dispersal mode. In addition to dispersal mode, the mean tree DBH (cm) and tree density (stems per hectare) for each species were also calculated by forest type to relate dispersal parameters to species characteristics.

Fecundity estimation and dispersal analysis

We use a state-space model for Mast Inference and Forecasting (available on CRAN as the R package MASTIF, http://rpubs.com/jimclark/281413) to determine the relative influence of hunting and logging on the fecundity and dispersal kernel of each tree (Clark, Nuñez and Tomasek, in revision). Mast Inference and Forecasting builds on the rich literature of seed dispersal models that employ a bivariate Student's t (2Dt) to relate the size and locations of reproductively active trees to numbers of seeds collected in seed traps in order to probabilistically estimate the seed production of each tree (Fig. 2; Clark *et al.* 1999, 2010, 2014a). Some authors use a two-parameter version of the 2Dt kernel; we do not fit a shape parameter due to the fact that it is poorly identified in data and it does not respond to the tail of the kernel as was originally hoped (e.g. Clark *et al.* 1999).

Not all seeds in seed traps must come from trees within the inventory plot. This possibility suggests an intercept proportional to basal area (Clark *et al.* 2010) or an integral over a large landscape area (Muller-Landau *et al.* 2008) as a rough accommodation of long-distance dispersal. In our comparisons an intercept can change estimates, without actually being sensitive to seeds outside the plot. This insensitivity to distant trees was demonstrated by Clark *et al.* (1998) by fitting the model without intercept to increasingly expanded plot areas. An intercept is insensitive to long-distance dispersal because distant trees do not affect the likelihood; the tail of the kernel has no impact on estimates except in cases where seeds are rare (Clark *et al.* 1999). The converse is also true: standard errors on estimates of fecundity increase with distance from seed traps. The intercept model further requires a strict assumption about forest composition outside the plot, e.g. extrapolating composition within the plot to infinite distance (Muller-Landau *et al.* 2008; Clark *et al.* 2010), which is unrealistic in many forests.

Mast Inference and Forecasting extends the model that has been extensively tested with predictive distributions to allow for uncertainty in seed identification, as well as time-dependence (Clark *et al.* 2004, 2010) and quasi-periodic variation and synchronicity in seed production (Koenig and Knops 2001; Boutin *et al.* 2006; Wang *et al.* 2017). Mast Inference and Forecasting uses Gibbs sampling—a Markov chain Monte Carlo (MCMC) technique—as well as Metropolis and Hamiltonian Markov chain (HMC) for posterior simulations of tree maturation state, fecundity, seed dispersal kernel and parameter estimates. Parameter estimates—the effects of hunting, logging and site-level covariates—are sampled directly from the posterior (Clark, Nuñez and Tomasek, in revision). We used non-informative flat priors for the dispersal parameter and variance in the dispersal parameter with fixed degrees of freedom as detailed in Clark *et al.* (2004, 2010, 2014a).

The broad dispersion of seed count data is accommodated in at least one of two ways. If accommodated at the data stage with a negative binomial distribution (Clark *et al.* 1998; Muller-Landau *et al.* 2008), then the dispersion parameter has no biological interpretation, and it cannot respond to the variables that are known to affect seed variability. Alternatively, a hierarchical specification

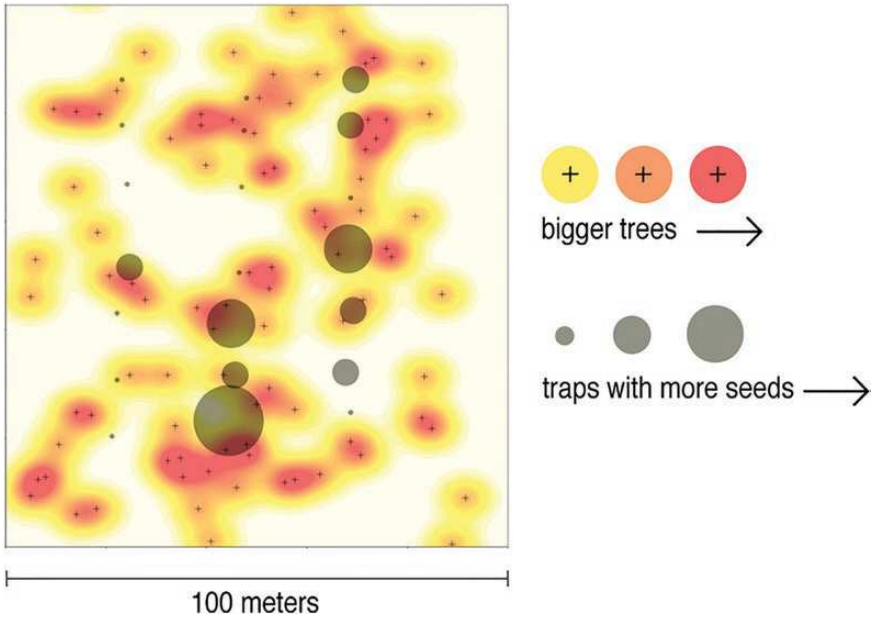

Figure 2. A schematic of seed shadow modelling, with spatially distributed trees of varying sizes acting as signal sources of varying strengths, and seed traps acting as stationary detectors through time.

helps to explain that variation, through individual differences in covariates and random effects and year or lag effects (Clark *et al.* 2004, 2013; Martínez and González-Taboada 2009; Uriarte *et al.* 2012). In other words, the overdispersion is taken up by the underlying process; the data are conditionally Poisson, but marginally overdispersed (Clark, Nuñez and Tomasek, in revision). Our model incorporates a Poisson likelihood for count data with seed production and dispersal, written as:

$$E(y_s) = A\lambda_s = A\sum_{i=1}^{n} S_{si}f_i$$

where $E(y_s)$ is the expected number of seeds counted in a trap at location s. λ_s is the expected seed density (seeds per m^2 per year) multiplied by the sampling effort A—the area of a seed trap times the fraction of the fruiting season it was deployed (m^2 per year). S_{si} is the density of seed (m^{-2}) produced by tree i dispersed to seed trap location s; and f_i is fecundity for an individual tree i at time t, which is the product of maturation status (ρ_{it}) and conditional fecundity (ψ_{it}) of tree i, ($f_{i,t}$) = $\psi_{i,t}\rho_{i,t} \geq 0$. Maturation and conditional fecundity are dynamic processes, modelled with fixed, random and year effects. Coefficients in the vector of fixed effects β^x include tree diameter, exposure to hunting or logging, and interactions (Clark 2010; Clark *et al.* 2013). Random individual effects accommodate the heterogeneity of responses among individual trees. The effect of year is random across species and within each of the three disturbance types, accommodating seed rain fluctuations that are coherent within, but not among the three groups.

Dispersal is summarized by the mean parameter of the 2Dt dispersal kernel (Clark *et al.* 1999), here termed the 'dispersal parameter'. A shape parameter is also sometimes fitted for this model, but we have found it to be unstable and unresponsive to long-distance dispersal (Clark *et al.* 2004, 2010).

Our modelling did not explicitly incorporate boundary effects because previous analysis demonstrated that trees tens of metres from seed traps have little impact on estimates (Clark *et al.* 1999). Muller-Landau *et al.* (2008), however, concluded that failure to account for boundary effects could bias models towards higher fecundity and fat tails (Muller-Landau *et al.* 2008), leading to overestimated fecundities and dispersal distances. However, this would not change inferences related to the relative effects of vectors or disturbance on seed dispersal patterns.

Gibbs sampling was used for posterior simulation. For each tree species **[see Supporting Information—Fig. S5]**, model estimates were taken from 50 000 iterations, discarding the first 1000 iteration as pre-convergence. We visually inspected trace plots to confirm convergence and adequate mixing **[see Supporting Information—Fig. S6A–C]**. Model fit was assessed with root mean squared prediction error (RMSPE) across species **[see Supporting Information—Fig. S4]**. Variable selection was based on Deviance Information Criterion (DIC). Model estimates reported in the text are posterior means and 95 % credible intervals (CIs) based on the Gibbs sampler realizations.

Results

Hunting and logging influenced the mean distances of dispersal kernels (hereafter average dispersal distance), with the greatest effects on animal-dispersed species, though the direction and magnitude varied. Two-thirds of all species (22/33) in disturbed forests had 95 % CIs for dispersal parameters that did not overlap with estimates from protected plots, indicating a role of disturbance. This trend held true whether a species relied on animals for dispersal entirely (13/18), in part (5/8) or not at all (4/7).

Of the 22 species affected by disturbance, 17 species showed an effect of logging alone: nine species had higher dispersal estimates in logged compared to protected forest (*Celtis mildbraedii*, *Diospyros canaliculata*, *Erythrophleum suaveolens*, *Greenwayodendron suaveolens*, *Lannea welwitschii*, *Pausinystalia macroceras*, *Rinorea oblongifolia*, *Staudtia kamerunensis*, *Strombosia nigropunctata*), and eight species had lower dispersal estimates (*Cleistopholis patens*, *Grossera macrantha*, *Myrianthus arboreus*, *Macaranga barteri*, *Nesogordonia kabingaensis*, *Strombosiopsis tetrandra*, *Thomandersia hensii*, *Terminalia superba*).

The combined effects of hunting and logging were consistent with logging alone for the majority of species, with the exception of six species that had dispersal estimates greater than (*Pteleopsis hylodendron*, *S. tetrandra*, *Guarea cedrata*) or less than (*G. macrantha*, *D. canaliculata* and *E. suaveolens*) logging alone. Notably, three species exhibited divergent effects of disturbance regime on dispersal estimates: logging positively affected *D. canaliculata* and *E. suaveolens*, whereas the combination of hunting and logging negatively affected dispersal estimates relative to protected plots. *Strombosiopsis tetrandra* displayed the opposite pattern (Table 1; Figs 3 and 4).

To reveal potential group-level effects of dispersal vectors, we clustered dispersal parameters from individual species by dispersal vector (i.e. animal, abiotic or mixed dispersal). Predictions were congruent within each dispersal vector, regardless of disturbance type (Fig. 5). Abiotically dispersed species had the greatest dispersal estimates overall, with 51.4 m [2.5th and 97.5th quantiles: 17.9, 75.5]. Species dispersed both by animals and abiotically had dispersal estimates of 41.1

Table 1. Predictive mean and 95 % CI for seed dispersal distances in metres.

	Mean predicted dispersal distance								
	Logged forests			Protected forests			Hunted and logged forests		
	Estimate	2.50 %	97.50 %	Estimate	2.50 %	97.50 %	Estimate	2.50 %	97.50 %
Abiotically dispersed									
Albizia gummifera	51.3	47.7	54.9	52.6	49.4	55.8	53.3	50.3	56.3
Erythrophleum suaveolens	42.6	40.2	45.0	31.8	30.0	33.7	23.4	22.1	24.7
Nesogordonia kabingaensis	12.4	9.5	16.5	41.1	38.1	44.1	37.0	33.5	40.6
Petersianthus macrocarpus	65.9	64.1	67.7	63.3	61.2	65.6	61.1	58.6	63.4
Pteleopsis hylodendron	43.9	39.0	48.6	36.5	28.4	43.6	57.5	54.0	61.2
Pterocarpus soyauxii	56.9	53.3	60.4	62.9	60.3	65.5	66.9	64.6	69.2
Terminalia superba	68.0	66.6	69.6	75.0	73.4	76.8	75.9	74.3	77.7
Animal dispersed									
Angylocalyx pynaertii	45.0	41.5	48.5	41.0	37.2	45.0	49.9	46.9	52.7
Celtis adolfi-friderici	18.0	16.0	20.3	14.5	13.2	15.9	13.8	12.9	14.8
Celtis mildbraedii	20.1	18.7	21.6	10.3	9.9	10.8	21.0	19.8	22.3
Cleistopholis patens	17.8	13.8	21.7	38.4	30.1	43.6	38.4	34.4	42.3
Diospyros bipindensis	41.9	38.7	45.2	39.8	36.7	43.1	39.5	35.2	43.8
Diospyros canaliculata	45.9	42.8	49.0	36.8	33.2	40.2	13.9	12.8	15.0
Greenwayodendron suaveolens	37.2	35.7	38.7	31.4	30.2	32.7	42.4	40.5	44.2
Guarea cedrata	35.3	31.0	39.7	28.0	19.5	35.1	39.2	35.9	42.6
Guarea thompsonii	40.7	37.5	44.0	40.2	36.4	43.9	46.9	43.7	50.1
Lannea welwitschii	42.5	37.3	47.6	2.2	1.0	8.7	16.9	14.0	20.6
Macaranga barteri	10.2	8.4	12.5	24.4	20.6	28.3	4.5	3.6	6.0
Staudtia kamerunensis	49.9	45.2	55.2	34.2	22.9	42.0	49.0	45.7	52.5
Strombosia nigropunctata	21.1	19.5	22.8	9.8	9.1	10.5	19.6	18.3	21.0
Strombosia pustulata	17.5	15.9	19.2	15.6	14.5	16.9	14.2	12.7	15.9
Strombosiopsis tetrandra	19.2	18.1	20.3	28.7	26.7	30.7	41.4	38.9	43.9
Xylopia chrysophylla	40.4	36.9	44.0	34.4	27.9	40.0	42.9	40.3	45.6
Xylopia hypolampra	98.5	95.3	100.0	98.8	96.1	100.0	98.0	93.6	99.9
Xylopia phloiodora	47.8	44.3	51.2	45.7	42.2	49.2	44.7	41.3	48.1
Abiotic and animal dispersed									
Camptostylus mannii	42.3	38.9	45.6	41.5	38.0	45.1	39.7	36.5	43.0
Grossera macrantha	40.5	35.6	45.0	51.9	49.2	54.5	43.9	40.1	46.9
Lepidobotrys staudtii	35.9	27.9	42.1	45.7	41.9	49.4	51.1	47.9	54.3
Myrianthus arboreus	34.2	28.8	39.0	43.3	39.8	46.6	25.3	22.7	28.1
Pausinystalia macroceras	37.1	34.0	40.3	31.2	28.8	33.7	39.0	35.6	42.4
Radlkofera calodendron	41.3	37.4	45.1	45.7	42.1	49.0	42.4	38.9	46.0
Rinorea oblongifolia	46.7	43.6	49.8	31.7	27.0	36.3	46.7	43.3	50.0
Thomandersia hensii	38.0	31.9	43.2	54.0	50.9	57.2	37.9	31.5	43.1

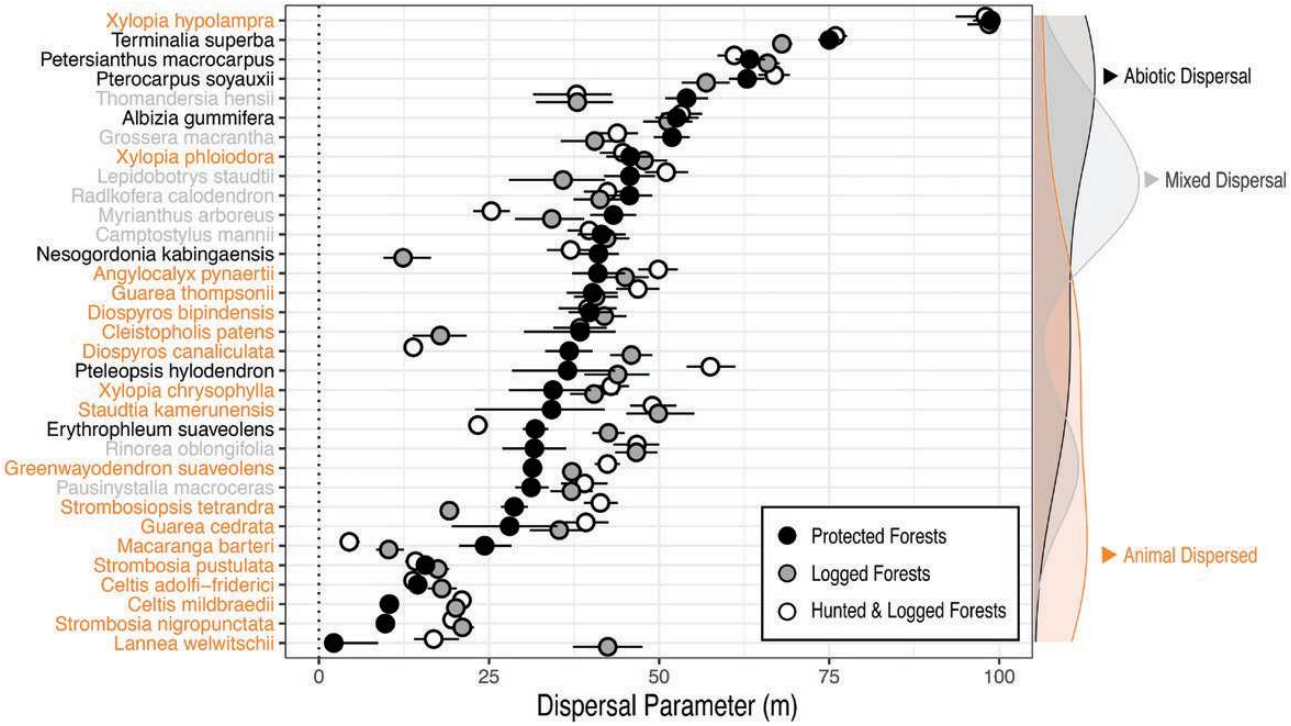

Figure 3. Comparison of average dispersal distance parameters among species in plots that were hunted and logged, logged, or protected from hunting and logging. Species are ordered by mean dispersal distance parameter in protected plots. Densities on right *Y*-axis show distribution of the dispersal type for species on left *Y*-axis.

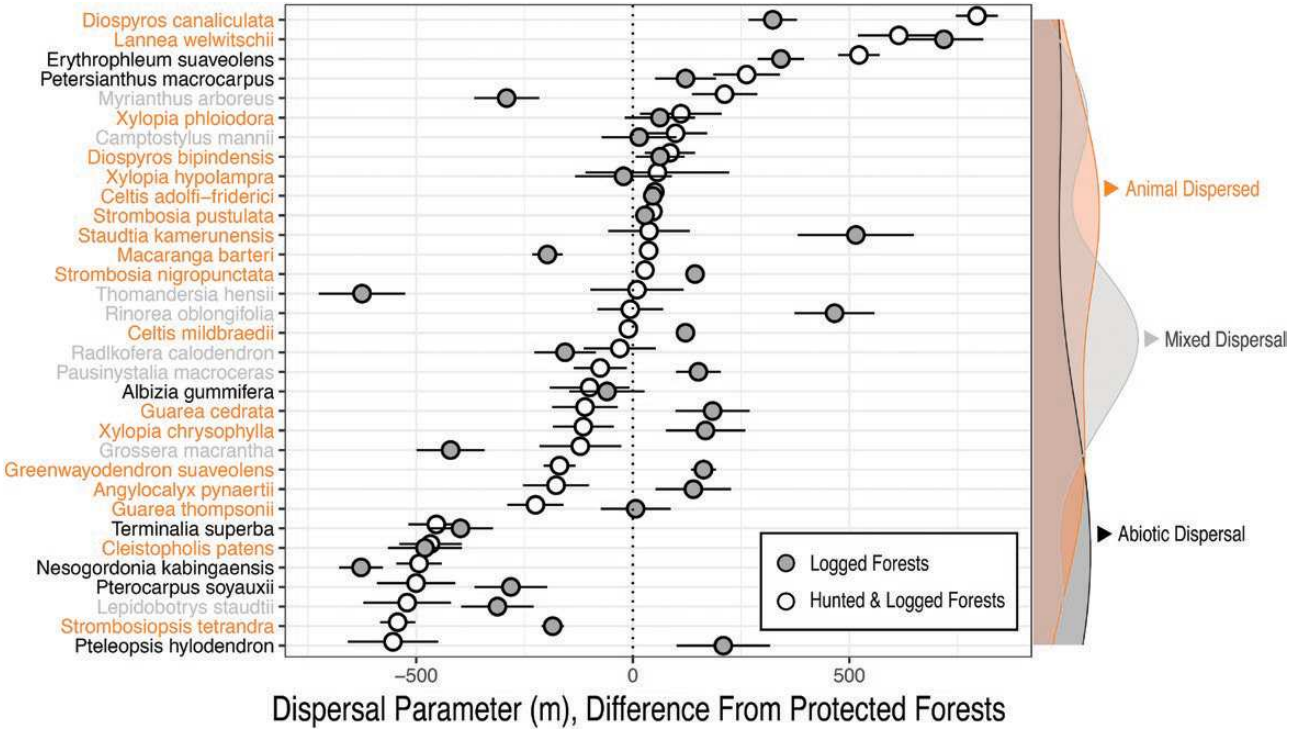

Figure 4. Comparison of difference in average dispersal distance parameter from protected forests among species in plots that were hunted and logged, or logged. Species are ordered by mean dispersal distance in hunted and logged plots. Densities on right *Y*-axis show distribution of the dispersal type for species on left *Y*-axis.

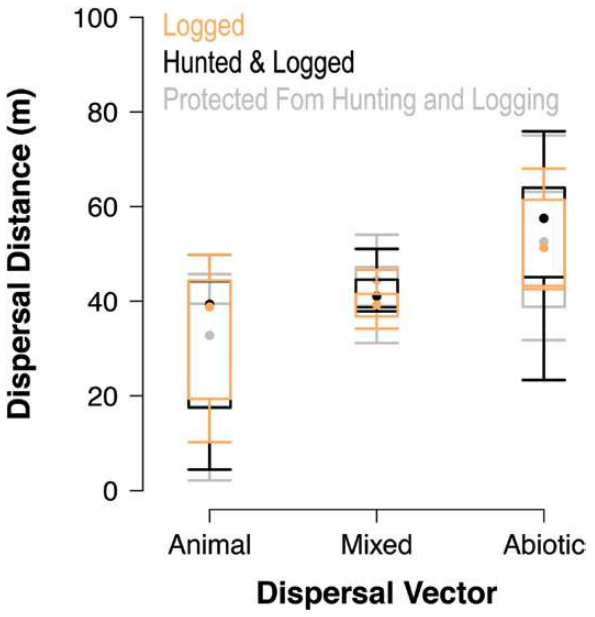

Figure 5. *Post hoc* comparison of the mean predicted dispersal distances for all species grouped by dispersal vector. Error bars show the 2.5th and 97.5th quantiles of mean dispersal distance in forests that were logged, hunted and logged, or protected from hunting and logging.

m [28.7, 52.8], and animal-dispersed species had the lowest dispersal estimates of 34.4 m [6.2, 98.3].

To evaluate the group-level effects of disturbance, we clustered dispersal estimates of all species by disturbance type, including protected (38.9 m [8.2, 79.8]), hunted and logged (40.5 m [12.0, 80.3]) and logged forests (39.6 m [11.9, 74.1]). The large overlap in dispersal estimates among forest types indicates a lack of consistent effects of disturbance on dispersal distance.

Estimated tree fecundity increased with tree diameter (Fig. 6), but was not affected by disturbance regime (Table 2; Figs 7 and 8). A majority of species (25/33) exhibited a positive effect of tree diameter on fecundity, with the exception of *Radlkofera calodendron*, *Lepidobotrys staudtii*, *S. kamerunensis*, *R. oblongifolia*, *Xylopia chrysophylla*, *Diospyros bipindensis*, *Camptostylus mannii* and *D. canaliculata*. Logging only influenced fecundity estimates of three species (*D. bipindensis*, posterior mean and 95 % CIs: −1.78 [−3.51, −0.03], *G. macrantha* −1.49 [−2.96, −0.08] and *M. arboreus* 2.30 [0.67, 3.84]).

Discussion

We find that low-intensity logging affected seed dispersal two decades after the logging event. Guidelines aimed at reducing the ecological damage stemming from logging can substantially reduce short-term impacts (Sist 2000; Sist *et al.* 2003), but our study suggests that impacts of low-intensity logging on ecological processes like seed dispersal are long term and may linger for decades. The difficult-to-detect effects on a key ecological process could have direct consequences for forest species composition through density-dependent recruitment (Janzen 1970; Connell 1971; Cannon *et al.* 1994; Bleher and Böhning-Gaese 2001) and competition at later life stages (Nathan and Muller-Landau 2000), potentially altering the diversity and function of forest ecosystems.

Contrary to our expectations, the dispersal vector of a seed type, abiotic or animal, was not a reliable indicator of the magnitude or direction of the responses of tree species to disturbance. Our results do not support the argument that dispersal decreases for animal-dispersed species following perturbation of the disperser community (Terborgh *et al.* 2008; Markl *et al.* 2012), at least several decades after the fact. It further does not support the notion that dispersal increases for abiotically dispersed species following forest thinning due to increased canopy wind speeds (Gardiner 1994; Stacey *et al.* 1994; Gardiner *et al.* 1997). Our results are more consistent with dispersal effects that are species-specific, as might be expected from the fact that each species has a unique relationship to unmeasured abiotic variables that contribute to its response to disturbance.

Despite a design specifically implemented to detect it, our study did not find evidence for an interaction between hunting and logging for most species, suggesting instead that dispersal following disturbance primarily responds to logging, but not hunting. Using the same data set, Poulsen *et al.* (2013) modelled seed dispersal of nine mammal-dispersed species finding that mean dispersal distance was farther in logged than unlogged forest for five species and farther in unhunted than hunted forest for six species. The disparity between the two studies could be due to the fact that we modelled dispersal for 33 tree species, separating them into animal and abiotic vectors, whereas Poulsen *et al.* (2013) only modelled nine mammal-dispersed species for which they had adequate seed numbers.

Limited evidence for a hunting effect on dispersal could come from the fact that hunting pressures were too low, even where present in our data set. Although hunting has clearly reduced the abundance of large vertebrates in the area (Poulsen *et al.* 2011), all species still exist throughout the landscape (Clark *et al.* 2009)—the vertebrate community is degraded, not defaunated. Alternatively, large frugivorous birds may have replaced the seed dispersal services of large, arboreal mammals. Bird species richness can increase with logging intensity (Burivalova *et al.* 2014), which can aggravate the negative effects of disturbance on seed dispersal due to the reduction in seed dispersers (Moran *et al.* 2004; Kirika *et al.* 2008a, b; Neuschulz *et al.* 2011) or mitigate the

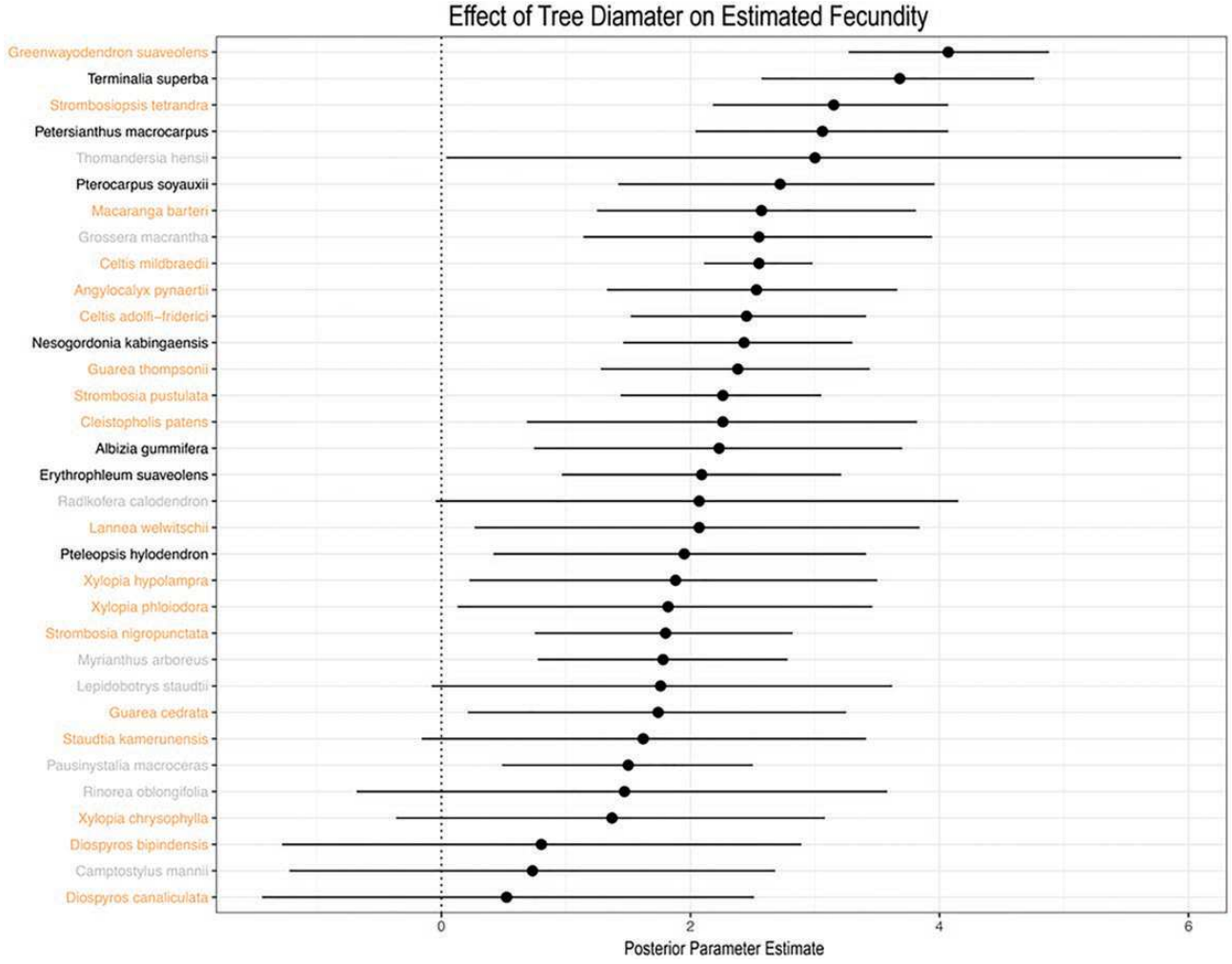

Figure 6. Comparison of posterior parameter estimates and 95 % CI show a positive effect of tree diameter on tree fecundity for a majority of species. Species names are colour coordinated here as elsewhere in the manuscript to denote dispersal vector: animal dispersed (orange), abiotically dispersed (black) or both animal and abiotically dispersed (grey).

effects of disturbance if generalist bird dispersers replace lost or reduced dispersal services (Putz *et al.* 2001; Gray *et al.* 2007; Burivalova *et al.* 2014; LaManna and Martin 2017; Trolliet *et al.* 2017). Indeed, in our study area, there was a 77 % increase in the density of large frugivorous birds following logging (Poulsen *et al.* 2011), a result that is consistent with other sites in the region (Koerner *et al.* 2017). Birds are not commonly hunted in our study site, and 2/3 of the mammal-dispersed species were also dispersed by birds **[see Supporting Information—Fig. S2]**, meaning that the full effects of hunting could be attenuated by an expanded bird community.

It is also possible that seed trap data inadequately sample long-distance seed dispersal by animals. A majority of seeds fall locally (Clark *et al.* 1999, 2005; Muller-Landau and Hardesty 2005; Muller-Landau *et al.* 2008), and studies that have combined seed traps with direct observations of seed counts from the canopy (LaDeau and Clark 2001, 2006) or the ground (Minor and Kobe 2017) find seed traps estimate fecundity well. However, seed dispersers may forage over large areas—over 4000 ha in some hornbills (Holbrook and Smith 2000). Seed trap data do not fully capture the dispersal of seeds that are consumed and dispersed outside of the plot. Although long-distance dispersal events may be rare, fully estimating the effects of disturbance on seed dispersal may require combined methods that can account for both local and long-distance dispersal. Nevertheless, our findings indicate that once a forest is disturbed by logging, seed dispersal may be altered regardless of the effect hunting has on seed disperser communities. This is consistent with other studies that found animal guild densities were negatively affected by logging even in the absence of hunting (Poulsen *et al.* 2013), but contradicts studies that found hunting and logging amplified the negative effects of either in isolation (Poulsen *et al.* 2011; Markl *et al.* 2012).

Table 2. Posterior mean and 95 % CIs of covariate effects on conditional fecundity.

	Covariate effects on conditional fecundity								
	Diameter			Logging			Hunting and logging		
	Posterior mean	2.50 %	97.50 %	Posterior mean	2.50 %	97.50 %	Posterior mean	2.50 %	97.50 %
Abiotically dispersed									
Albizia gummifera	2.4	0.9	3.8	0.2	−3.1	3.7	1.3	−1.1	3.7
Erythrophleum suaveolens	2.3	1.2	3.4	1.4	−0.6	3.4	0.3	−2.4	3.0
Nesogordonia kabingaensis	2.3	1.4	3.2	−0.6	−1.7	0.5	−0.5	−1.5	0.4
Petersianthus macrocarpus	3.3	2.3	4.3	−1.5	−3.1	0.1	−1.0	−2.3	0.3
Pteleopsis hylodendron	1.5	0.0	3.0	−1.3	−4.0	1.3	−2.0	−5.1	1.2
Pterocarpus soyauxii	2.8	1.5	4.1	−1.3	−3.0	0.5	−1.1	−2.8	0.6
Terminalia superba	3.9	2.8	4.9	0.0	−1.9	1.8	−1.3	−3.0	0.4
Animal dispersed									
Angylocalyx pynaertii	2.4	1.3	3.5	−0.2	−1.8	1.4	−0.2	−1.8	1.4
Celtis adolfi-friderici	2.9	2.0	3.8	0.0	−1.2	1.2	−0.3	−1.4	0.7
Celtis mildbraedii	2.4	2.0	2.9	−0.2	−1.0	0.5	−0.8	−1.4	−0.1
Cleistopholis patens	2.4	0.9	4.0	−1.1	−3.3	1.2	−2.0	−4.1	0.1
Diospyros bipindensis	0.8	−1.4	2.9	−1.8	−3.5	0.0	−1.8	−3.7	0.1
Diospyros canaliculata	0.3	−1.6	2.3	0.1	−1.5	1.8	−1.0	−2.4	0.4
Greenwayodendron suaveolens	4.2	3.4	5.0	−0.1	−0.9	0.7	−0.3	−1.0	0.4
Guarea cedrata	1.8	0.2	3.3	−0.7	−3.0	1.5	−0.1	−3.3	3.3
Guarea thompsonii	2.3	1.3	3.4	−1.1	−2.2	0.1	−1.0	−2.1	0.1
Lannea welwitschii	2.1	0.3	3.8	−0.2	−4.5	4.0	0.6	−4.4	5.2
Macaranga barteri	2.4	1.1	3.7	−1.0	−2.6	0.6	−0.8	−2.4	0.8
Staudtia kamerunensis	1.6	−0.2	3.4	−0.3	−4.1	3.6	0.0	−6.2	6.2
Strombosia nigropunctata	1.6	0.6	2.6	−0.5	−1.5	0.5	−0.6	−1.5	0.4
Strombosia pustulata	2.2	1.4	3.0	−0.6	−1.5	0.2	−0.3	−1.2	0.6
Strombosiopsis tetrandra	3.2	2.2	4.1	−0.9	−2.1	0.3	−0.6	−1.7	0.6
Xylopia chrysophylla	1.3	−0.4	3.0	0.1	−3.0	3.2	−2.5	−5.1	0.2
Xylopia hypolampra	1.8	0.2	3.4	1.6	−2.0	5.1	0.9	−2.4	4.2
Xylopia phloiodora	1.7	0.0	3.3	0.8	−1.4	2.9	1.6	−0.9	4.0
Abiotic and animal dispersed									
Camptostylus mannii	0.9	−1.1	2.8	0.7	−1.3	2.7	0.3	−1.6	2.1
Grossera macrantha	2.3	0.9	3.7	−1.5	−3.0	−0.1	−0.7	−2.2	0.8
Lepidobotrys staudtii	1.7	−0.1	3.6	−0.2	−3.0	2.6	0.1	−2.2	2.4
Myrianthus arboreus	1.7	0.6	2.7	2.1	−0.3	4.5	2.3	0.7	3.8
Pausinystalia macroceras	1.1	0.1	2.1	−0.1	−1.5	1.3	0.3	−1.0	1.6
Radlkofera calodendron	2.1	0.0	4.2	−1.9	−4.3	0.7	1.5	−2.4	5.4
Rinorea oblongifolia	1.6	−0.5	3.8	1.7	−1.7	5.0	−1.9	−5.2	1.1
Thomandersia hensii	2.9	0.0	5.9	1.1	−4.8	6.9	0.0	−6.2	6.2

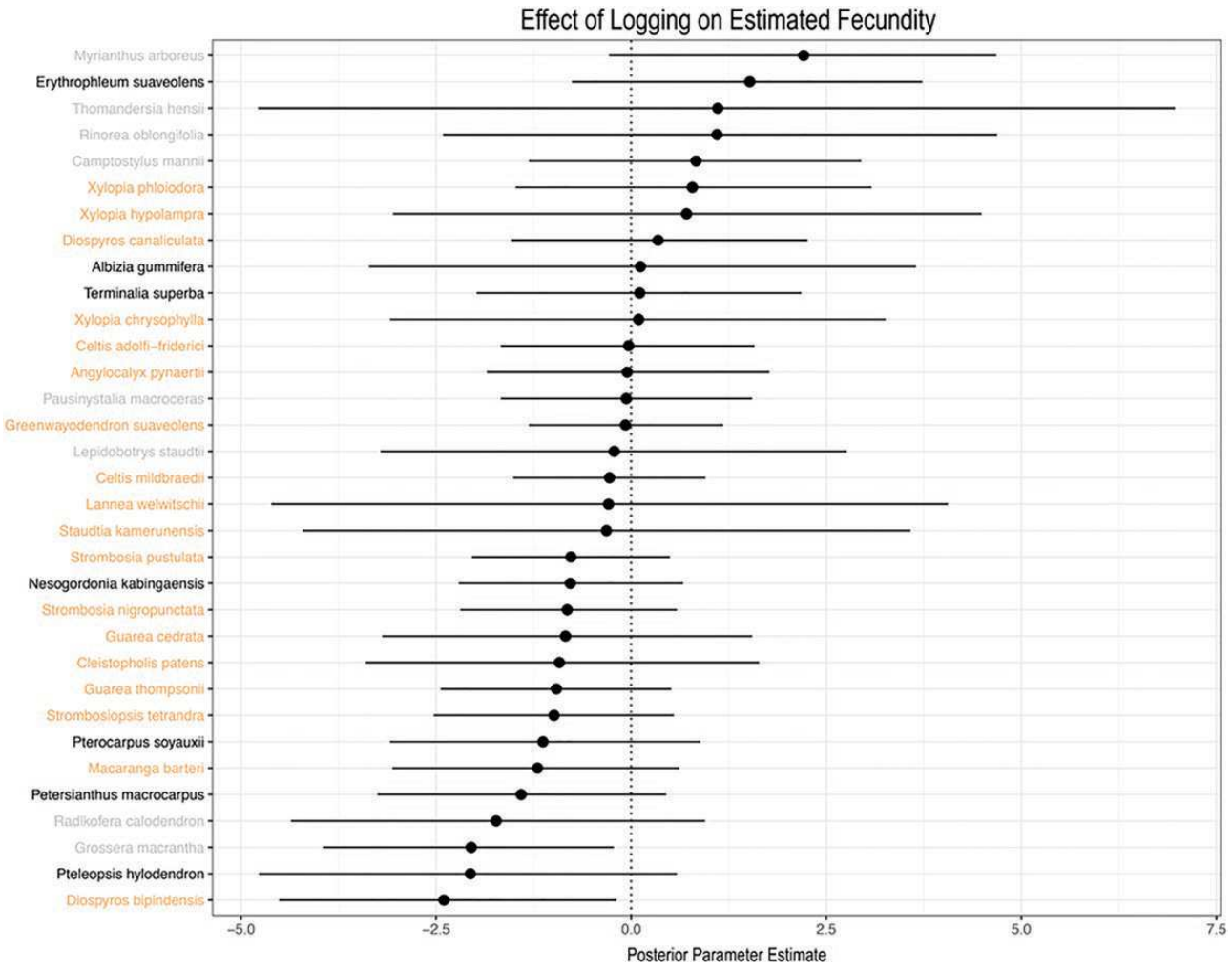

Figure 7. Comparison of posterior parameter estimates and 95 % CI show no effect of logging on tree fecundity for a majority of species.

Although dispersal vector was not predictive of how dispersal would respond to hunting or logging, there was a clear distinction in dispersal kernel estimates. Abiotically dispersed seeds moved farthest from the parent tree, animal-dispersed seeds generally fell closest and species dispersed both by animals and abiotically arrived at intermediate distances. Differences in dispersal distance between vectors (Venable and Brown 1988; Greene and Johnson 1989, 1993; Cornelissen *et al.* 2003; Clark *et al.* 2005; Thomson *et al.* 2011) are partly a result of mechanical properties. Abiotically dispersed seeds tend to have small mass that facilitate passive dispersal by wings, plumes, samaras and other adaptations for flight (Greene and Johnson 1989, 1993). Seeds reliant on animal dispersers must develop fleshy fruit mass to entice seed dispersers (Cao *et al.* 2016) limiting their passive dispersal distance.

Estimated fecundity long after disturbance did not differ across disturbance regimes to the extent found in studies immediately following disturbance (Markl *et al.* 2012; Uriarte *et al.* 2012; Berdanier and Clark 2016). Low-intensity logging in resource-limited tropical forest environments may have limited effects on crowding, light and soil moisture levels (Molino and Sabatier 2001; Bongers *et al.* 2009). However, our results suggest that any fecundity benefits from disturbance are unobservable 20 years post-logging. Lack of a long-term effect on fecundity may also be a result of studying only relatively large trees (≥10 cm DBH), which have already made it through the competitive gauntlet of the understory to attain adulthood, and can access resources that facilitate resilience to competitive environments in ways that smaller plants cannot (Clark *et al.* 2004).

Tree size was an important determinant of fecundity making large trees especially important for forest regeneration (Plumptre 1995; Freitas and Pinard 2008). Fecundity of large trees should encourage their protection during logging campaigns (CIB 2006). In addition to their outsized contribution to longer-distance dispersal events (Norghauer *et al.* 2011), large trees store a

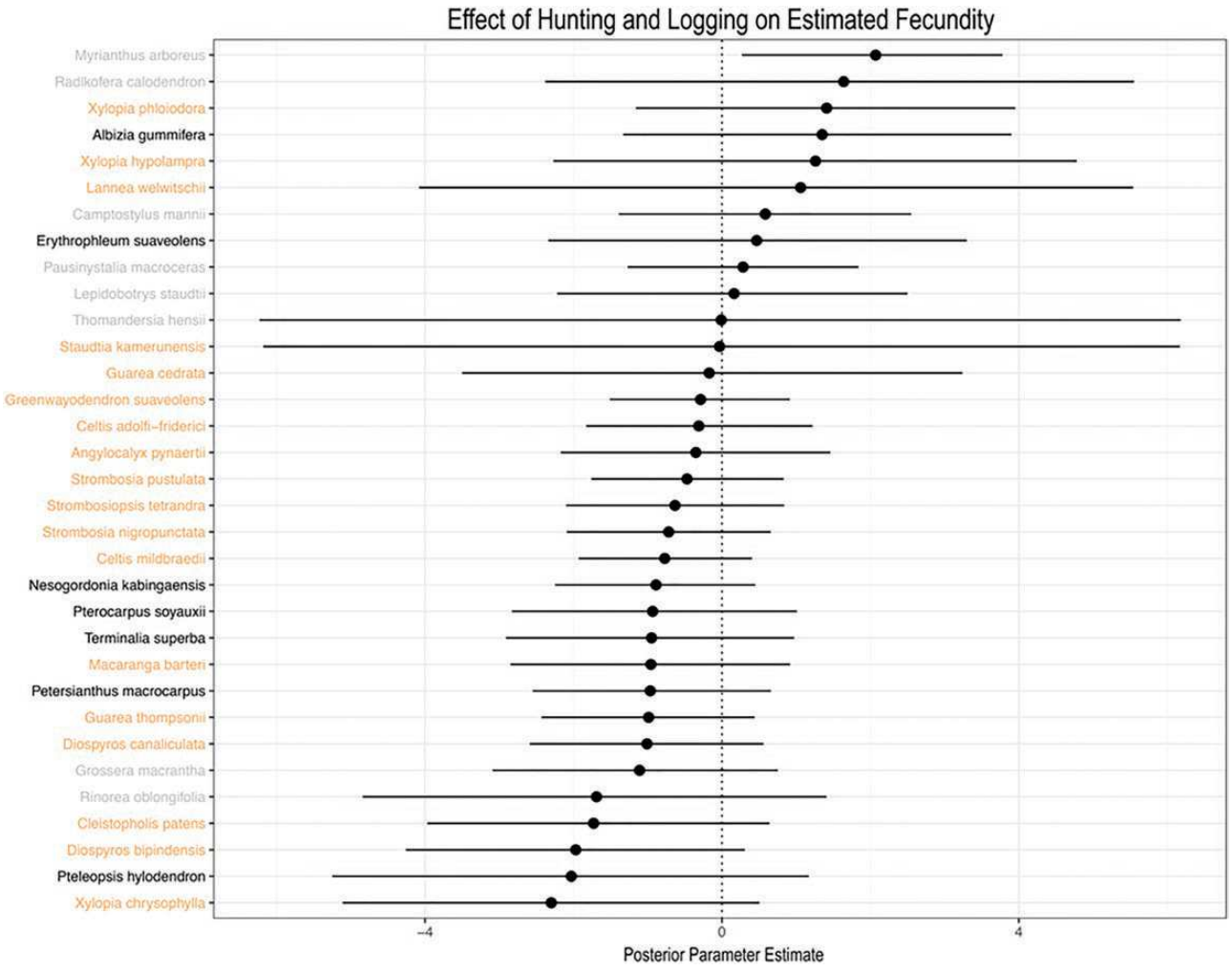

Figure 8. Comparison of posterior parameter estimates and 95 % CI show no effect of hunting and logging on tree fecundity for a majority of species.

disproportionate amount of above-ground carbon (Clark and Clark 1996; Lutz *et al.* 2012; Slik *et al.* 2013; Stephenson *et al.* 2014) and are crucial for maintenance of forest structure (Lindenmayer *et al.* 2012; Lutz *et al.* 2013) and animal habitat (Tews *et al.* 2004; Lutz *et al.* 2012, 2013).

Our study demonstrates that disturbances to forests and animal communities contribute to seed dispersal patterns even decades after the initial logging event. In this case, the responses in seed dispersal to disturbance varied across species with weak patterns related to dispersal vector or disturbance type. Our lack of a clear directional effect of hunting and logging on seed dispersal could be partially due to our study design, which was pseudoreplicated: study plots affected by the same disturbance type were geographically grouped together out of necessity. This was a direct result of the study area, particularly the spatial pattern of hunting and logging around the village of Kabo (Poulsen *et al.* 2011), and means that other, unmeasured environmental gradients could influence our results.

The limitations of our study should serve as a challenge to dispersal ecologists and modelers—what are the best methods or combinations of methods for disentangling the effects of multiple disturbances that can operate over disparate spatial and timescales?

Logging concessions cover much of West and Central Africa (FAO 2016), yet the long-term impacts of low-intensity logging techniques on fundamental ecological processes like seed dispersal have been largely overlooked. This work advances our understanding of how the separate and combined effects of hunting and logging affect seed dispersal in the understudied Afrotropics. Although care needs to be taken before extrapolating our results to other contexts, the species-specific dispersal responses to logging in this study point towards the long-lasting toll of disturbance on ecological function. Whereas the effects of disturbance on forest structure and animal communities are easily measured, the effects on ecological processes may be more cryptic, long-lasting and difficult to decipher.

Data

https://github.com/chasenunez/2018.AOBP.

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Contributions by the Authors

C.L.N. posed the central questions, wrote the original manuscript, and analyzed the data; J.S.C. wrote the the R and C++ code for the MASTIF model with testing and feedback by C.L.N. through development; J.R.P. and C.J.C. collected data with help from those in Acknowledgements section; J.R.P. and J.S.C. edited for content and provided guidance on structure and style.

Conflict of Interest

None declared.

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Supporting Information

The following additional information is available in the online version of this article—

Figure S1. Boxplots comparing the distribution of tree diameters within each plot type show no systematic difference across plot types.

Figure S2. Boxplots comparing the distributions of total stems per plot show significant overlap across plot type.

Figure S3. Stacked bar plots comparing community composition show a consistent distribution of 33 focal species across plots.

Figure S4. Comparison of standardized root mean squared prediction error (individual RMSPE/average number of seeds per trap) with size of circle indicating relative number of seeds from that species present in the study.

Figure S5. (A–D) Example of individual results (*Nesogordonia kabingaensis*) that were amalgamated across species for in-text summary figures.

Figure S6. (A–C) Examples of model diagnostics for *Nesogordonia kabingaensis*.

Table S1. Table of species information and dispersal vectors.

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