LETTER

Consequences of defaunation for a tropical tree community

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Abstract

Hunting affects a considerably greater area of the tropical forest biome than deforestation and logging combined. Often even large remote protected areas are depleted of a substantial proportion of their vertebrate fauna. However, understanding of the long-term ecological consequences of defaunation in tropical forests remains poor. Using tree census data from a large-scale plot monitored over a 15-year period since the approximate onset of intense hunting, we provide a comprehensive assessment of the immediate consequences of defaunation for a tropical tree community. Our data strongly suggest that over-hunting has engendered pervasive changes in tree population spatial structure and dynamics, leading to a consistent decline in local tree diversity over time. However, we do not find any support for suggestions that over-hunting reduces above-ground biomass or biomass accumulation rate in this forest. To maintain critical ecosystem processes in tropical forests increased efforts are required to protect and restore wildlife populations.

Keywords

Biodiversity, bushmeat, conservation, defaunation, hunting, national park, rainforest, seed dispersal, spatial pattern, tropical.

Ecology Letters (2013)

Humans have hunted tropical forest vertebrates for millennia, but the scale and geographic extent of modern bushmeat hunting is unprecedented (Mittermeier 1987; Redford 1992; Peres & Palacios 2007; Galetti *et al.* 2009; Harrison 2011; Jenkins *et al.* 2011; Wilkie *et al.* 2011). Over the past 2–3 decades, the availability of firearms and affordable ammunition, on the one hand, and improved access to forests and markets, on the other, has resulted in widespread declines in wildlife populations throughout the tropics (Robinson & Bennett 2000). Beyond a concern for the future of many hunted species, understanding the functional consequences of these declines is important for the long-term conservation of tropical biodiversity. Nonetheless, general principles are difficult to infer. Hunted quarry include species involved in various ecological processes, including vertebrate predators, seed dispersers, seed predators and herbivores, and the extent of functional redundancy between hunting sensitive and more tolerant species is not known. Disentangling population responses of multiple animal species and integrating their effects on ecological functions to predict the impacts of hunting at an ecosystem level is thus extremely difficult, and unanticipated outcomes are to be expected (Wright 2003; Muller-Landau 2007; Stoner *et al.* 2007).

Studies comparing the performance of particular plant species across a gradient of hunting intensity have revealed some of the mechanisms behind functional loss or redundancy in biotic interactions. For example, large-bodied seed dispersers are particularly susceptible to hunting and studies have consistently reported reduced fruit removal and increased deposition of seeds, particularly large seeds, close to mother trees in hunted forests (Wright *et al.* 2000; Beckman & Muller-Landau 2007; Wang *et al.* 2007; Brodie *et al.* 2009; Holbrook & Loiselle 2009; Sethi & Howe 2009). However, hunting also tends to reduce populations of vertebrate seed predators (Wright *et al.* 2000; Roldan & Simonetti 2001; Beckman & Muller-Landau 2007), but not invertebrate seed predators or agents of plant disease, such as fungi. Thus, the consequences for recruitment are variable, with different studies reporting increased or decreased recruitment and an effect or no effect of seed-size (Wright *et al.* 2000; Galetti *et al.* 2006; Beckman & Muller-Landau 2007; Nunez-Iturri & Howe 2007; Nunez-Iturri *et al.* 2008; Brodie *et al.* 2009; Sethi & Howe 2009). Similarly, different studies have found that, as a consequence of reduced herbivory, seedling survival may increase or remain unchanged in hunted forests (Dirzo & Miranda 1991; Roldan & Simonetti 2001). Such idiosyncratic plant species responses have made it difficult to scale up results to the community-level.

Studies at the community-level are fewer and have been confined to once-off comparisons of hunted and non-hunted forests (Wright

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et al. 2007; Terborgh et al. 2008; Stevenson 2010; Vanthomme et al. 2010), which lack the time-dimension necessary to understand changes in plant population dynamics. Possibly as a consequence, these studies have also produced variable results, with overall sapling densities and the abundance of large-seeded plants reported as being both higher and lower in hunted forests. The only consistent result to emerge is a higher prevalence of plant species with abiotic seed-dispersal mechanisms in hunted forests.

In addition to complexities in the ecological responses to hunting, the relatively large spatial scales at which hunting affects tropical forests and the long temporal scales over which the impacts of defaunation may be manifested introduce methodological issues. Finding comparable hunted and less-hunted areas is difficult and inevitably many studies have been poorly replicated. Often studies compare a single patch of hunted forest with a single patch of non-hunted forest. At this level of pseudo-replication Type I error rates may be inflated by an order of magnitude in tropical forests (Ramage et al. 2012), thereby invalidating statistical inference. Hunting pressure also varies widely, and ecological impacts may vary in a non-linear manner with the level of defaunation. In large expanses of tropical forest, wildlife abundance has been found to decline with distance from the nearest access point (Peres & Lake 2003). However, hunting pressure is also related to local culture, with some communities hunting more sustainably or not at all, while in other communities hunting has extirpated successively smaller species (Mittermeier 1987; Robinson & Bennett 2000). Differences in the degree of defaunation among studies have so far thwarted attempts at meta-analysis. Lastly, there is high interannual variability in plant recruitment in tropical forests (Wright et al. 1999; Sakai et al. 2006), making it necessary to monitor trends in plant populations over an extended period of time.

In summary, while a picture is beginning to emerge as to how defaunation may be affecting certain processes, complex interactions among different ecological processes, variation in plant species responses, variation in the degree of defaunation, and the limited temporal perspective and oftentimes poor replication of existing studies, combine to restrict our understanding of how hunting affects tropical forests at a community-level.

Here, we present data tracking the performance of over 470 000 individual trees (> 1100 species) over a 15 year period since the approximate onset of intense hunting to provide a community-level study of the consequences of defaunation for a tropical forest. We investigated the impacts of hunting on the tree assemblage at Lambir in NW Borneo, one of the most diverse forests known. In 1984, when Lambir's vertebrates were first surveyed, the park supported a complete fauna, including several hunting sensitive species (Harrison R.D, unpublished data). However, in 1987 the road through the park was surfaced and in the early 1990s local urban bushmeat markets expanded dramatically (Bennett et al. 2000). One species (Helmeted hornbill) was extirpated by 1994 and several other hunting sensitive species (e.g. Rhinoceros hornbill, Bornean gibbon, Sun bear) were rare (Table 1, Shanahan & Debski 2002). By 1999, Robinson (1999) reported that all large animals were scarce and by 2004, when the next surveys were conducted, over 20% of the mammal and over 50% of the bird species > 1 kg had been locally extirpated (Harrison R.D, unpublished data). Almost all important large (> 1 kg) frugivores, including gibbons, six of seven hornbill species, and imperial-pigeons, were extirpated (Table 1), and the species-richness of frugivore assemblages feeding in figs

(Ficus spp.) declined by over 50% between 1996–1997 and 2005–2007 (Harrison 2011). Leaf monkeys, which are important pre-dispersal seed predators (Sun et al. 2007), were extirpated by 1998 (Table 1). A camera-trapping study in 2004 recorded only a single Bearded-pig (Sus barbatus Müller) in 1440 camera-trap days (Harrison 2011) – this species is normally one of the most abundant mammals in Bornean forests and is an important post-dispersal seed predator (Caldecott 1988; Curran & Leighton 2000). Thus, between 1987 and approximately 1999 Lambir was defaunated to the extent that all large (> 1 kg) animals are either scarce or extirpated (Robinson 1999, Harrison R.D, unpublished data).

The establishment of a 52-hectare ecological dynamics plot in 1992 approximately coincides with the start of the period of intense hunting that led to the declines in wildlife populations at Lambir. Hence, we are able to monitor changes in forest structure and composition starting from a minimally disturbed state to one increasingly affected by severe defaunation. The full impacts of defaunation at Lambir are only likely to be realised over several plant generations. Hence, the 15-year period covered in our study corresponds to the initial impacts of defaunation on a tropical forest. Moreover, tropical trees grow at very different rates and shade-tolerant seedlings, in particular, may be slow-growing. For example, Delissio et al. (2002) found that among six shade-tolerant species at Lambir between 5 and 95% of seedlings were ≥ 10 years old, but with high within-species variation in growth rates. So for tree species at Lambir, age of recruitment to the sapling size class may vary from < 1 year (Davies 2001) to > 50 year (Delissio et al. 2002) depending on species and conditions. Early results on the effects of defaunation may thus be somewhat biased toward faster growing species. Continued monitoring will be required to obtain a complete picture of the consequences of defaunation at Lambir. We also hope that longitudinal studies like this can be replicated elsewhere, so as to obtain a more general understanding of the impacts of defaunation on tropical forests.

Table 1 Functional roles with respect to plant population dynamics of large (> 1 kg) birds and mammals that have been extirpated from Lambir and year they were last recorded

Species		Year last recorded
Pre-dispersal seed predators		
Langurs	Presbytis hosei Thomas	1996
Seed dispersers		
White-crowned hornbill	Aceros comatus Raffles	1998
Wrinkled hornbill	Aceros corrugatus Temminck	1998
Wreathed hornbill	Aceros undulatus Shaw	1998
Bushy-crested hornbill	Anorrhinus galeritus Temminck	1998
Helmeted hornbill	Buceros vigil Forster	1984
Rhinoceros hornbill	Buceros rhinoceros Linnaeus	1994
Green imperial-pigeon	Ducula aenea Linnaeus	1998
Sun bear	Helarctos malayanus Raffles	1997
Bornean gibbon	Hylobates muelleri Martin	1996
Red-giant flying-squirrel	Petaurista petaurista Pallas	1996
Large flying fox	Pteropus vampyrus Linnaeus	1997
Post-dispersal seed predators and seedling predators		
Sambar	Cervus unicolor Kerr	1998

Surveys were conducted in 1984, 1994–1998, and 2004–2007. Data from Harrison R.D (unpublished data).

We investigated the following predictions about the effects of defaunation on plant population structure and dynamics (Wright 2003; Stoner *et al.* 2007). Reduced populations of seed and seedling predators should lead to increased survival through these critical stages. Hence, (1) we predicted overall sapling densities would increase. Reduced abundance of large frugivores is expected to cause a decline in seed dispersal distances and establishment of seedlings closer to the maternal parent. Hence, (2) we predicted there would be increased clustering in the spatial pattern among tree species with animal-dispersed seeds, but not those with abiotically dispersed seeds. In addition, one would anticipate that reduced dispersal would lead to increased density dependent seed and seedling mortality (Janzen-Connell effects) and reduced recruitment opportunities. Hence, (3) we predicted sapling recruitment would decline among tree species with animal-dispersed seeds relative to those with abiotic dispersal mechanisms. In addition, for (2) and (3) we predicted that (4) animal-dispersed tree species with larger seeds would be affected to a greater extent than those with smaller seeds. Other researchers have suggested that because wind-dispersed tree species and lianas often have low wood density and are expected to increase in abundance, (5) defaunation should result in declines in above-ground biomass over time (Brodie & Gibbs 2009; Jansen *et al.* 2010). Hence, we also investigated this hypothesis.

Our study examines the net effects of hunting on the tree community and the underlying mechanistic pathways may be complex. Ideally, one would be able to follow all the critical plant life-history stages from seed dispersal and seedling establishment, to growth of the plant from a seedling to reproductive maturity. However, the Lambir plot includes only trees of sapling size and above ($\geq$ 1 cm diameter-at-breast-height, dbh). Hence, we cannot directly measure defaunation effects on processes affecting younger plants. Compensatory processes may cancel out effects before the trees are recruited into our dataset. For example, increased density-dependent mortality might obscure the effects of decreased seed dispersal distances. Nevertheless, responses to hunting at these early life-history stages are often highly variable (Wright *et al.* 2000; Galetti *et al.* 2006; Beckman & Muller-Landau 2007; Nunez-Iturri & Howe 2007; Nunez-Iturri *et al.* 2008; Brodie *et al.* 2009; Sethi & Howe 2009) and, hence, by focusing on responses that emerge at the sapling stage, our study integrates across much of this variation.

We show that, consistent with our predictions, Lambir has experienced pervasive changes in tree population spatial structure and dynamics. We consider the potential role of other factors, such as global climate change or past large-scale disturbance, in driving these changes, but show that defaunation is by far the most plausible causal factor.

METHODS

Lambir (4°20′ N, 113°50′ E, ~ 50 m asl) is a lowland dipterocarp forest with an aseasonal climate and receives on average approximately 2900 mm of rain annually. In 1992, a 52 ha long-term ecological dynamics plot was established following standard Center for Tropical Forest Science (CTFS) protocols. All trees $\geq$1 cm dbh were individually tagged, measured (dbh), mapped and identified. Re-censuses, including enumeration of recruits, were conducted in 1997, 2003 and 2008.

We obtained data on seed dispersal syndromes from examination of herbarium material. Plants with animal-dispersed seeds were defined as those having fruits with edible parts that encourage the swallowing of seeds by animals or the transport of seeds during feeding. This includes tree species that are dispersed by terrestrial animals, particularly scatter-hoarding rodents, after the seeds have fallen to the forest floor (sometimes referred to as 'gravity' dispersal in previous publications, e.g. Seidler & Plotkin 2006). Abiotically dispersed seeds included species with plumes or wings and ballistic dispersed seeds. Where data on a particular tree species were not available, we used information from congeneric species, except in the rare cases where the same genus is known to include both animal and abiotically dispersed tree species. We were able to assign seed dispersal syndromes (animal; 984 spp. vs. abiotic; 162 spp.) for 1146 of 1245 tree species (see, Table S1). For more detailed analyses, based on species-level information only, we further classed tree species into those with small (< 20 mm long, 156 spp.), medium (20–< 50 mm long, 147 spp.) and large ($\geq$ 50 mm long, 46 spp.) seeds dispersed by canopy animals, seeds dispersed by terrestrial animals (32 spp.), gyration dispersed (95 spp.), wind dispersed (34 spp.) and ballistically (18 spp.) dispersed seeds. Although secondary dispersal by, for example, ants, dung beetles or small rodents, may be important for germination and seedling establishment, spatial patterns in tropical trees may be predicted from a knowledge of primary dispersal modes alone (e.g. Seidler & Plotkin 2006).

We used the standardised wavelet variance (SWV) as a measure of the aggregation of stems across a range of spatial scales (Detto & Muller-Landau in press). The SWV provides a measure of aggregation that is independent of abundance, thus enabling comparisons among species or between different censuses of the same population. The wavelet variance was calculated by counting the number of stems $N(\boldsymbol{x})$ in quadrats of area 2×2 m at position $\boldsymbol{x}$ (x, y), and applying a wavelet kernel, with specific scale s, according to:

$$v^2(s) = \int N(\omega)^2 \psi_s(\omega)^2 d\omega, \tag{1}$$

where $N(\omega)$ is the Fourier transformation of $N(\boldsymbol{x})$ (that is $N(\omega) = \int N(x)e^{-i\omega x}dx$ and $\boldsymbol{\omega}$ are the angular frequencies. The wavelet function is an isotropic exponential kernel given by:

$$y_s(\omega) = \frac{-1}{C_\psi S} \exp\left(\frac{-(S\omega - \omega_0)^2}{2}\right), \tag{2}$$

where C_ψ is a normalisation factor to ensure that the wavelet has unit energy at all scales and ω_0 (= 8) is a shape parameter that regulates the width of the support. Tree species with < 10 individuals were removed from analyses.

The wavelet variance represents how much each scale contributes to the total variability of the spatial process. To obtain the SWV, the resulting value is standardised by dividing by the mean density. For a completely randomly distributed population the SWV is equal to one at all scales. At small spatial scales the SWV of any population approaches unity as the probability of encountering two individuals in a given area declines to zero. In clustered populations, the SWV represents the variance between areas of high density inside the cluster and areas of low density outside the cluster and the scale can be interpreted as the cluster size. We calculated the SWV for saplings (dbh 1–2 cm) as we were interested in how recent recruitment had affected the population spatial pattern.

We calculated annualised tree population parameters by species. Recruitment was calculated as follows;

$$r = \frac{\ln N_t - \ln N_0}{t}, \qquad (3)$$

where N_t equals the number of individuals alive at the second census, N_0 equals the number of individuals alive at both censuses, and t equals the mean time-interval between censuses. For mortality and population growth we used the equivalent functions for these parameters. Tree species with $n < 30$ were removed from the analysis (animal-dispersed spp. = 694, abiotically dispersed spp. = 123; see, Table S1). We compared recruitment and population growth among tree species with different seed dispersal syndromes using linear models. To control for potentially confounding factors, we included mortality rate, initial population size, and adult size as covariates. Recruitment and mortality covary in relation to plant life-history strategy. Abundance may also covary with population parameters if, for example, compensatory mechanisms exist whereby rare tree species perform better in response to extreme climatic events, such as severe droughts (Potts 2003). Adult size is related to plant life-history strategy (King *et al.* 2006), but also covaries with seed dispersal syndrome (Table S2). Hence, including adult size as a covariate in the models was a conservative approach. Adult size was calculated as the 95th percentile of the dbh of all individuals $\geq 0.1 \times$ maximum dbh (D_{max95}) (King *et al.* 2006). Adult size was entered in alternate models as either a continuous variable or as a factor with five levels, with equivalent numbers of species (denoted shrub, treelet, subcanopy, canopy and emergent). Selection of alternative models and model simplification was conducted manually based on Akaike Information Criterion (AIC) values. All variables were log transformed and standard plotting functions were used to check model fit.

We considered incorporating phylogenetic autocorrelation into the population dynamics models. However, plant species cannot share an evolutionary response to defaunation through a common ancestor, because it is a recent phenomenon. Any correlation between population responses and phylogeny is likely to result from the fact that seed dispersal syndrome – the trait of interest – is a conserved trait. Hence, including phylogeny would have been inappropriate. We stress that our models were already conservative through incorporating traits related to plant life-history. However, we felt it necessary to include these covariates to control for possible effects of long-term change, such as global warming. Nonetheless, analyses incorporating phylogenetic autocorrelation produced qualitatively similar results.

For every 20×20 subplot, we calculated the number of saplings (dbh 1–2 cm) and sapling rarefied species-richness based on 99 random samples of 50 individuals. Comparisons among years were made using *apriori* contrasts. For the numbers of saplings we used a generalised linear model with a Poisson distribution of the error term. For rarefied species-richness we square-root transformed the response and used a Gaussian distribution for the error term. In both analyses, subplot was included as a random factor.

To calculate above-ground biomass, we developed a dipterocarp forest specific function derived from the dbh-biomass relationship using the combined dipterocarp forest datasets (Kalimantan 1, Kalimantan 2 and Malaysia) published in Chave *et al.* (2005) as follows;

$$B = 0.216 \; wsg \; dbh^{2.557}, \qquad (4)$$

where *wsg* equals the species-specific wood specific gravity and *dbh* is the diameter-at-breast-height measured in centimetres. Data on wood densities were obtained from the global database at http://datadryad.org. We summed across individuals to obtain the subplot level above-ground biomass. Lianas and epiphytes were not included in these calculations, because data on these groups are lacking for the Lambir plot. Although frequent in the forest at Lambir (Putz & Chai 1987), the contribution of lianas to the basal area is trivial. Epiphytes are rare in dipterocarp forests as compared with Neotropical or African rain forests (Corlett & Primack 2011), and presumably also make little contribution to above-ground biomass. Biomass accumulation rate was calculated as the difference in above-ground biomass between censuses. We use *t*-tests to test above-ground biomass and biomass accumulation rate between groups of tree species with animal or abiotic seed dispersal, and high ($\geq$ 75th percentile) or low ($\leq$ 25th percentile) population growth rates.

All statistical analyses were conducted in R v2.14 (R Development Core Team 2011).

RESULTS

In line with our first prediction, there was a consistent and substantial increase (25.7%) in the density of saplings over the 15 year study period (Fig. 1a).

Consistent with previous research, saplings of tree species with abiotically dispersed seeds showed high levels of aggregation at small scales (5–30 m), whereas pronounced aggregation occurred only at larger scales among animal-dispersed tree species and especially among those with the largest seeds (Fig. 2). However, in line with our second prediction, we found that saplings of species with animal-dispersed seeds, but not those with abiotically dispersed seeds, became significantly and substantially more clustered from one census to the next (Fig. 2). Furthermore, the effect was larger for tree species with larger seeds. For example, at the level of aggregation over which change was greatest (aggregation = 1.3) there was a 23 m (34%), 17 m (34%) and 12 m (27%) decline in mean cluster-size for tree species with large, medium and small animal-dispersed seeds respectively.

Again as predicted, we found that tree species with animal-dispersed seeds had significantly lower recruitment rates than species
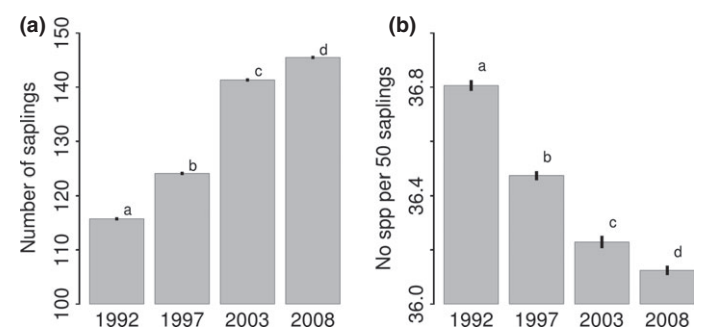
Figure 1 Change in (a) the mean (±SE) numbers of saplings (1–2 cm dbh) and (b) mean (±SE) sapling diversity (rarified species-richness) per 20×20 m subplot over four censuses at Lambir. Standard errors were calculated after controlling for random factors (subplot). Rarified species-richness was calculated based on 99 random samples of 50 individuals.
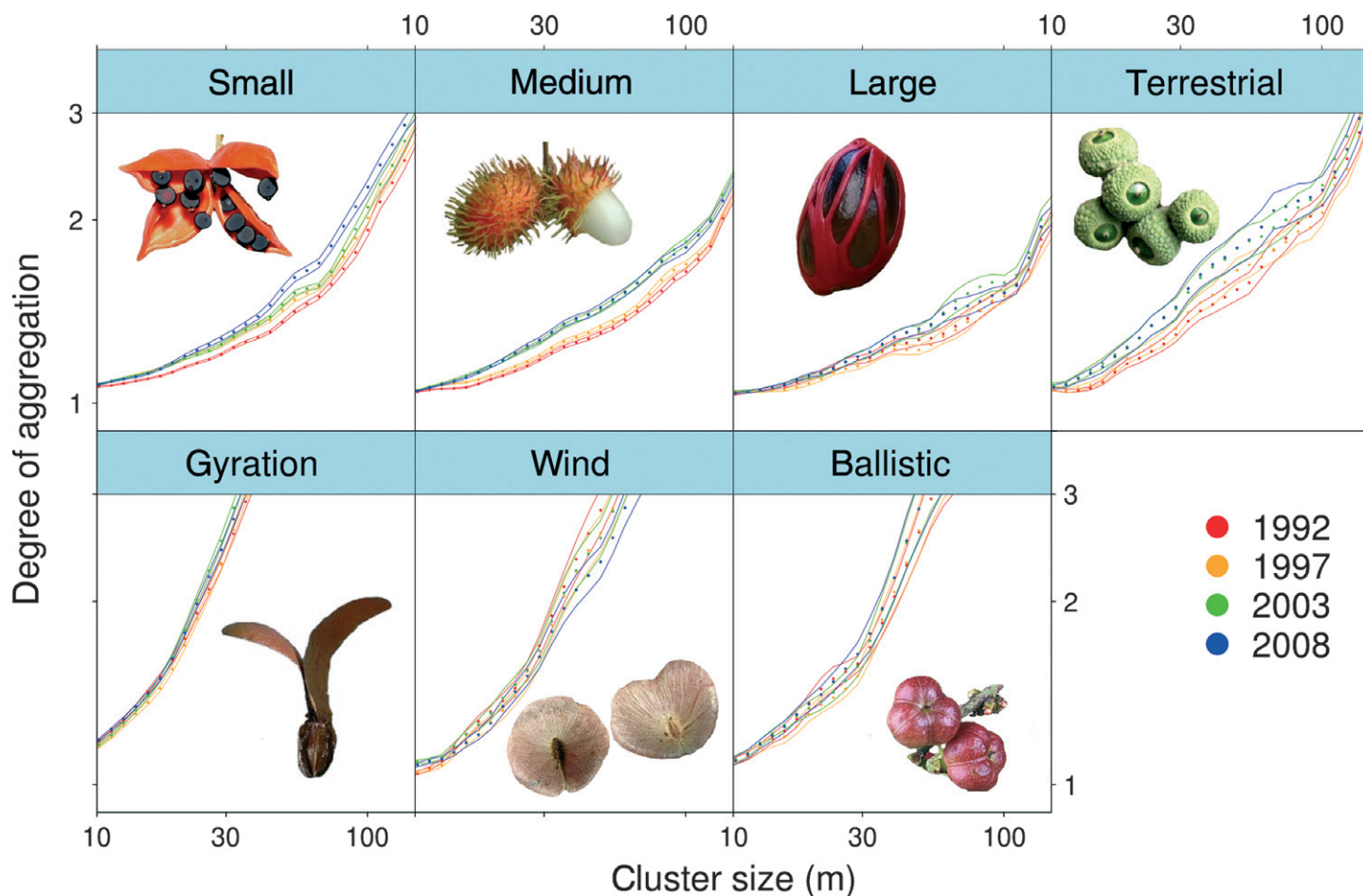
Figure 2 Degree of aggregation (*y*-axis) across a range of cluster sizes (*x*-axis) of saplings (dbh 1–2 cm) for tree species with different seed dispersal modes (see Methods for details). Points represent means across species and lines are the boundaries of the 95% confidence interval. Top row: small (< 20 mm long), medium (≥ 20– < 50 mm long), and large (≥ 50 mm long) seeds dispersed by canopy animals and seeds dispersed by terrestrial animals that initially fall from the canopy. Bottom row: tree species with gyration, wind and ballistically dispersed seeds. Tree species with animal-dispersed seeds show significantly (non-overlapping confidence intervals) increased clustering over time (curves move toward left), while species with abiotically dispersed seeds do not.

with abiotically dispersed seeds across all three census intervals (Table 2a, estimate = 0.144 ± 0.0251, *t* = 5.76, *P* < 0.0001). These differences in recruitment rates translated into a similar difference in population growth rates (see Table S3a). Moreover, tree species with medium and large animal-dispersed seeds had significantly lower recruitment rates than those with small seeds (Table 2b, estimate = 0.022 ± 0.0099, *t* = 2.21, *P* = 0.0275), although this did not translate into a significant difference in population growth rates (see Table S3b).

There was a small but consistent and significant decline in local diversity across the plot over the study period (Fig. 1b). At the 20 × 20 m subplot scale, this amounted to a 1.9% decline in diversity over 15 years.

However, contrary to earlier predictions (Brodie & Gibbs 2009; Jansen *et al.* 2010), above-ground biomass increased substantially over the study period through the growth of large trees. Moreover, there were no significant differences in wood density or relative above-ground biomass accumulation rate among tree species with animal-dispersed and abiotically dispersed seeds, or among tree species with high (≥ 75th percentile) and low (≤ 25th percentile) population growth rates (see Table S4). Indeed, because of the high

proportion of wind and gyration dispersed tree species in the canopy and emergent layers in Bornean forests, maximum individual tree biomass was on average substantially higher for abiotically dispersed tree species.

DISCUSSION

The tree community at Lambir has changed profoundly over a relative short period of time. Our study demonstrated a substantial increase in the total number of stems, increased clustering among saplings of species with animal-dispersed seeds, a relative decline in recruitment rates among tree species with animal-dispersed seeds as compared to those with abiotic dispersal mechanisms, and a reduction in local diversity across the plot. Coincident with these changes, > 20% of Lambir's large (> 1 kg) mammal fauna and > 50% of Lambir's large bird fauna were extirpated as a consequence of hunting (Harrison 2011, Harrison, R.D, unpublished data).

Potentially an increase in sapling densities could be driven by increased plant reproductive activity or an increased incidence of canopy gaps. Long-term monitoring of plant phenology at Lambir (Sakai *et al.* 2006) indicates reproductive activity has neither

Table 2 Coefficients table of the best statistical models for tree recruitment (log (r + 0.01)) for (a) all species ($\geq$ 1 cm dbh) comparing trees with animal (n = 733) and abiotic (n = 130) seed dispersal modes (adjusted R^2 = 0.2223) and (b) species (n = 477) with detailed seed dispersal information (adjusted R^2 = 0.2669)

	Estimate	Standard error	*t*-value	Pr(> |t|)
(a) Animal vs. Abiotic				
Intercept	−2.04	0.0811	−25.1	<0.0001
log(m + 0.01)	0.431	0.0186	23.1	<0.0001
log(N)	0.041	0.0075	5.51	<0.0001
Adult size				
emergent	0.008	0.0246	−3.39	0.735
shrub	0.147	0.0301	4.89	<0.0001
treelet	−0.039	0.0254	−1.54	0.124
subcanopy	−0.071	0.0237	−3.00	0.00272
Year				
1997–2003	−0.035	0.0207	−1.71	0.0869
2003–2008	−0.268	0.0215	−12.4	<0.0001
Dispersal mode : abiotic	**0.144**	**0.0251**	**5.76**	**<0.0001**
(b) Contrasts among canopy animal-dispersed species				
Intercept	−1.691	0.1080	−15.7	<0.0001
log(m + 0.01)	0.471	0.0245	19.2	<0.0001
log(N)	0.022	0.0097	2.25	0.0247
Adult size	−0.020	0.0075	−2.70	0.00707
Year				
1997–2003	−0.031	0.0276	−1.12	0.263
2003–2008	−0.264	0.0286	−9.23	<0.0001
Dispersal mode (i)	**0.117**	**0.0044**	**2.65**	**0.00816**
Dispersal mode (ii)	**0.022**	**0.0099**	**2.21**	**0.0275**
Dispersal mode (iii)	**−0.009**	**0.0214**	**−0.399**	**0.690**

The parameters of interest are highlighted in bold. In model (b) we tested three *apriori* orthogonal contrasts: (i) animal vs. abiotic; (ii) small vs. medium + large animal-dispersed; and (iii) medium vs. large animal-dispersed. Covariates included in the models were mortality rate (m), original abundance (N), adult size, census interval (year), and all two-way interactions. The two-way interaction terms were removed through model simplification. The factor baselines for adult size, census interval and dispersal mode were 'canopy', '1992–1997', and 'animal' respectively. The ΔAIC to the second best model was > 10.

increased over the study period nor is higher than historical records from elsewhere in the region. Similarly, the density of large trees has increased over the study period (Fig. S1), suggesting that the frequency of canopy gaps has actually declined. In a separate study focusing on seedlings, survival over a 10-year period was significantly higher at Lambir than at another site in Sarawak where wildlife is still abundant (Delissio *et al.* 2002). Hence, we suggest that reduced seed and seedling predation, as a consequence of reduced populations of vertebrate seed predators and herbivores, is the most likely cause of the substantial increase in sapling densities at Lambir.

Seed dispersal syndrome is an important life-history trait that is correlated with many other aspects of tree biology, including population spatial structure (Seidler & Plotkin 2006). Over the study period we observe a consistent increase in the level of aggregation for saplings of species with animal-dispersed seeds, but not for those with abiotically dispersed seeds. Our measure of aggregation was independent of abundance and both these groups include a broad phylogenetic diversity of plants (see Table S1). It is difficult to come up with plausible explanations for this pattern other than that

the functional extirpation of large frugivores has led to a decline in seed dispersal distances. Fruit that would formerly have been eaten by hornbills, gibbons or fruit pigeons, all of which are efficient long-distance seed dispersers, are now unlikely to be fed on by anything larger than a bulbul or a barbet. The fact that declines in cluster-size were greater for animal-dispersed tree species with the larger seeds further supports the notion that a loss of large seed-dispersal agents is the casual factor.

Long-distance seed dispersal is often viewed as a mechanism for escaping pathogens and other enemies, and increasing recruitment opportunities. Numerous studies have demonstrated declines in seedling survival close to the maternal plant (Janzen-Connell effects). Thus, as a result of reduced seed dispersal away from mother trees, we would expect animal-dispersed tree species to suffer higher seedling mortality. In the Lambir dataset we cannot observe seedling mortality directly as only individuals $\geq$ 1 cm dbh are recorded. However, as a consequence of increased seedling mortality we would predict reduced recruitment of tree species with animal-dispersed seeds relative to those with abiotically dispersed seeds. Across all three census intervals, the recruitment of tree species with animal-dispersed seeds was significantly lower than that of abiotically dispersed species. Moreover, among tree species with animal-dispersed seeds, species with medium or large seeds had significantly lower recruitment than species with small seeds. We note again that these groups comprise a broad phylogenetic diversity of plants and that we controlled for potentially confounding factors, including mortality rate, initial abundance and adult size, in our models. Thus, we suggest that reduced seed dispersal and a consequent increase in seedling mortality is the most likely explanation. However, we cannot rule out the possibility that long-term environmental change may be driving these responses through some unthought-of factor correlated with seed-dispersal syndrome.

Finally, we found a small but consistent decline in local tree diversity across the plot, which is an expected consequence of the observed relative decline in animal-dispersed species. However, because this is an observational study and not a manipulative experiment other factors, such as long-term climate change, cannot be ruled out.

Researchers have hypothesised that defaunation might drive reductions in carbon sequestration capacity in tropical forests (Brodie & Gibbs 2009; Jansen *et al.* 2010). We found no evidence to support this hypothesis. Indeed, because of the high proportion of wind and gyration dispersed tree species in the canopy, total biomass accumulation capacity was much higher for abiotically dispersed tree species, suggesting above-ground biomass might actually increase as a consequence of hunting at Lambir. We did not include lianas or epiphytes in our biomass estimates, because we lacked the data on these groups, but their main effect is expected to be through the suppression of tree growth and, as we showed, tree biomass increased substantial over the study period.

Our study was derived from an analysis of individuals larger than 1 cm dbh. This means we did not directly measure the effects of defaunation on seed-dispersal or seed and seedling survival, but examined changes in the tree community as emergent effects at the sapling stage. Indeed, in some respects, it is surprising that the effects we measured were so strong, given the expected time-lag between the impacts of defaunation on early life-history stages and recruitment to the sapling size-class. It suggests that the patterns we observed may become more pronounced

over time. Similarly, the changes we observed in sapling density and spatial structure may be taken as indicative of future changes among larger size classes as the trees continue to grow. However, changes in dynamics during the transition from sapling to adult tree could potentially exacerbate or erode the patterns we report. For example, increased density-dependent mortality among saplings could reduce the increase in clustering we observed among tree species with animal-dispersed seeds. As we have already indicated, our study corresponds to the initial impacts of defaunation and continued monitoring, potentially over several tree generations, will be necessary to understand the full implications of defaunation for the forest at Lambir.

Our results are based on a single site in Borneo. Moreover, one that has been particularly severely defaunated. Nevertheless, the situation at Lambir is increasingly prevalent throughout tropical Asia (Harrison 2011), and in other tropical areas with high human populations and a relatively low proportion of remaining forest, including West Africa (Fa & Brown 2009) and the Atlantic forests of Brazil (Galetti *et al.* 2009). Moreover, as access improves we can also expect increasing levels of defaunation in remaining large blocks of rain forest, such as the Amazon and Congo, unless the process is countered by strong conservation measures (Harrison 2011; Wilkie *et al.* 2011). Our results supported predictions that were based on a general conceptual framework of the impacts of defaunation on tropical forests (Wright 2003; Stoner *et al.* 2007). In particular, large-bodied frugivores are susceptible to hunting everywhere (McConkey *et al.* 2011) and hence we may anticipate increased clustering and reduced recruitment among trees with animal-dispersed seeds to be general characteristics of over-hunted forests. Indeed, a relative decline the abundance of tree species with animal-dispersed seeds in hunted forests is consistently reported from the few community-level studies available (Wright *et al.* 2007; Terborgh *et al.* 2008; Stevenson 2010; Vanthomme *et al.* 2010). Moreover, a decline in a large proportion of species at any site is expected to have a substantial impact on diversity. The role of seed size, however, is more equivocal. The importance of large scatter-hoarding rodents in Neotropical forests and presence of large terrestrial herbivores in Africa and parts of Asia (Corlett & Primack 2011) suggest effects of seed size may more site specific. Moreover, important large terrestrial seed predators, such as pigs, are often relatively hunting-tolerant and hence the extent of defaunation may be important in determining an effect. The possible impacts of defaunation on biomass are perhaps even less obvious (Jansen *et al.* 2010) and may vary substantially among regions. In addition, given the age of large trees it is clear that there will be a substantial time-lag before defaunation could have any appreciable effect on biomass. Other factors, such as the effects of increasing temperature on plant physiology or changes in rainfall regimes, are likely to be much more important. To obtain a general understanding of the impacts of over-hunting on tropical forests, it is clearly necessary that long-term studies, such as ours, are replicated across as many different forests, with different hunting histories, as possible.

Today vast areas of tropical forest, both inside and outside protected areas, are depleted of wildlife as a consequence of over-hunting. Our results strongly suggest this will have important consequences for ecological processes that structure plant diversity. Enhancing the protection of wildlife and restoring animal populations where they have been depleted will be essential for biodiversity conservation in tropical forest landscapes.

AUTHORSHIP

RH conceived the study, assembled the data, conducted the analysis and wrote the article. ST, AI and SD provided plot data. JP and FS provided data on seed dispersal syndromes. MD and TB developed the method for spatial analyses. All authors have reviewed and commented on the manuscript.

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