

Defaunation and habitat disturbance interact synergistically to alter seedling recruitment

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Abstract. Vertebrate granivores destroy plant seeds, but whether animal-induced seed mortality alters plant recruitment varies with habitat context, seed traits, and among granivore species. An incomplete understanding of seed predation makes it difficult to predict how widespread extirpations of vertebrate granivores in tropical forests might affect tree communities, especially in the face of habitat disturbance. Many tropical forests are simultaneously affected by animal loss as well as habitat disturbance, but the consequences of each for forest regeneration are often studied separately or additively, and usually on a single plant demographic stage. The combined impacts of these threats could affect plant recruitment in ways that are not apparent when studied in isolation. We used wire cages to exclude large (elephants), medium, (sambar deer, bearded pigs, muntjac deer), and small (porcupines, chevrotains) ground-dwelling mammalian granivores and herbivores in logged and unlogged forests in Malaysian Borneo. We assessed the interaction between habitat disturbance (selective logging) and experimental defaunation on seed survival, germination, and seedling establishment in five dominant dipterocarp tree species spanning a 21-fold gradient in seed size. Granivore-induced seed mortality was consistently higher in logged forest. Germination of unpredated seeds was reduced in logged forest and in the absence of small to large-bodied mammals. Experimental defaunation increased germination and reduced seed removal but had little effect on seed survival. Seedling recruitment however, was more likely where logging and animal loss occurred together. The interacting effects of logging and hunting could therefore, actually increase seedling establishment, suggesting that the loss of mammals in disturbed forest could have important consequences for forest regeneration and composition.

Key words: Borneo; defaunation; granivore; logging; plant recruitment; plant–herbivore interactions; seedling; tropical forest.

INTRODUCTION

Defaunation, the loss or functional loss of large animals from natural communities, is receiving increasing interest from ecologists because it is globally widespread and can potentially disrupt important species interactions such as seed predation (Harrison et al. 2013, Dirzo et al. 2014). But the conditions under which disrupted plant–animal interactions alter the abundance, distribution, or persistence of plant species are not well understood (McConkey et al. 2012, Brodie et al. 2014). The impacts of animal declines on plant populations may be wide-ranging in highly biodiverse systems with complex webs of interactions, such as tropical forests (Wright 2003, Morris 2010, Canale et al. 2012, Kurten 2013, Terborgh 2013), implying that dramatic changes in

abundance in certain species could indirectly affect numerous other taxa (Wright 2003). Our lack of knowledge on the extent to which animals influence plant recruitment and persistence via interactions like seed predation makes it difficult to predict the ecological consequences of defaunation in these systems.

Animal mutualists and antagonists can affect seed survival (Ostfeld et al. 1997, Fragoso and Huffman 2000) and germination (Asquith et al. 1997, Nunez-Iturri et al. 2008, Sherry 2008, Sethi and Howe 2009, Harrison et al. 2013). However, reduced germination does not necessarily lead to reduced seedling establishment or plant recruitment (Paine and Beck 2007) and therefore might not influence trees at the population level (Brodie et al. 2009, Harrison et al. 2013). The plant vital rate altered by granivores is seed germination, and this demographic transition often has little impact on population growth in long-lived plants (Pfister 1998, Howe and Miriti 2004). In some cases, reduced granivory due to the loss or exclusion of vertebrates can increase

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germination rates and seedling emergence (Guariguata and Pinard 1998, Bricker et al. 2010, Beckman et al. 2011, Harrison et al. 2013). In other cases, the loss of vertebrates decreases seedling and sapling diversity (Harrison et al. 2013, Camargo-Sanabria et al. 2014) or leads to compensatory seedling consumption by other plant consumers such as invertebrates (Itoh et al. 1995). Impacts of defaunation may also be obscured if small-bodied granivores increase in abundance following the loss of larger species, resulting in unchanged or even increased levels of seed predation (Wright and Duber 2001, Mendoza and Dirzo 2007, Maclean et al. 2011, Galetti et al. 2015).

In addition to defaunation, tropical forests worldwide are often simultaneously threatened by human-induced habitat disturbances (Wright 2005, Dirzo et al. 2014). However, the impacts on plants are usually assessed in isolation or additively and the combined effects of habitat disturbance and defaunation on plant recruitment are not well understood. Selective logging, a common and widespread activity in tropical forests, alters forest structure and may reduce seed production, seedling establishment (Hautier et al. 2010, Bagchi et al. 2011), and animal abundance (Laurance and Laurance 1996). The decline or absence of large-bodied animals, in particular, can indirectly reduce the recruitment of certain trees (Terborgh et al. 2008, Melo et al. 2010), with variable consequences for tree population dynamics and forest regeneration (Forget and Jansen 2007, Paine and Beck 2007, Harrison et al. 2013). Although logging and defaunation often occur together, we have little understanding of their interacting effects on plant recruitment in tropical forests (Peres 2000, Guariguata et al. 2002, Poulsen and Clark 2011, Brodie et al. 2014).

Our knowledge of the conditions under which seed dynamics can influence long-lived tree abundance is limited because most studies focus on one or a few plant species (often short-lived taxa with similar ecological traits) or on a single demographic transition (usually seed germination; Comita et al. 2014, Visser et al. 2016). Here, we sought to assess the joint effects of defaunation and habitat disturbance on seed mortality, germination, and seedling establishment of five dominant tree species in disturbed and undisturbed tropical rainforest. We excluded large, medium, and small terrestrial mammals from three experimental enclosure blocks in logged and unlogged forest in Malaysian Borneo in 2014. Each block consisted of three exclusion treatments and one control. We also used camera traps to quantify the presence of large and small-bodied vertebrates (i.e., those highly vulnerable to anthropogenic defaunation and those not, respectively) in our logged and unlogged forest study sites. We expected a higher occurrence of vertebrate taxa in unlogged forest (Barlow et al. 2007, Poulsen and Clark 2011) and higher levels of seed mortality to occur in areas where more vertebrates were detected (Curran and Webb 2000, Beckman and Muller-Landau 2007). The predation of large-seeded species can also be lower where large

mammals are absent vs. where they are present (Mendoza and Dirzo 2007) so we expected reduced seed mortality among large seeded species within exclusion plots. Finally, we predicted that seed mortality for all tree species would be higher in control plots.

MATERIALS AND METHODS

Study system

We conducted our experiment at the Danum Valley Conservation Area (DVCA, 5.10189° N, 117.688° E) and the Sabah Biodiversity Experiment (SBE; 5.16727° N, 117.564° E) in Sabah, Malaysian Borneo in 2014; both areas are part of the Yayasan Sabah Forest Management Area. This region is characterized by lowland forest dominated by trees in the family Dipterocarpaceae. The DVCA (438 km²) is unlogged forest that has remained relatively undisturbed by human activity, with no accounts of logging or agriculture (Hazebrook et al. 2012). It is the largest expanse of intact primary lowland dipterocarp forest in Sabah (Hazebrook et al. 2012). Our logged forest study site is the SBE and adjacent forest (Malua Forest Reserve, 335 km², total area). This area is located 25 km north of the DVCA and was logged for dipterocarp trees >60 cm dbh in the late 1980s with the use of tractors and high lead cables (Berry et al. 2008, Tuck et al. 2016). The SBE itself is found within that area that was previously logged and consists of 124 plots; each plot is 200 × 200 m. From 1999 to 2007, parts of the Malua Forest Reserve were re-logged, although the SBE itself was not (Tuck et al. 2016). In this second logging cycle, a reduced impact logging regime was adopted and trees of 40 cm dbh or greater were targeted (Anon 2008, Ang et al. 2017). A 500-m unlogged area was left around the SBE during the logging in the early 2000s.

Most dipterocarp reproduction occurs in mast fruiting events every 2–10 yr, with minor fruit production that results in little to no seedling recruitment occurring in between (Appanah 1985, Ashton et al. 1988). Dipterocarp seeds are wind and gravity dispersed and several bird and mammal species consume their fruit and seeds (Curran and Leighton 2000). Dipterocarp seeds germinate very rapidly or else perish; delayed germination and seed banks are unknown.

Bearded pigs (*Sus barbatus*) are the largest major predator of dipterocarp seeds in our system (Curran and Leighton 2000, Curran and Webb 2000). Rodents (e.g., Murids: *Rattus*, *Maxomys* spp.) are important seed predators throughout the tropics, though their importance to plants can be habitat and species dependent (Blate et al. 1998, Wells and Bagchi 2005, Fleury and Galetti 2006, Wells et al. 2009). Bornean pygmy elephants (*Elephas maximus borneensis*) occur in our study area. They are generalist herbivores and the extent to which they consume dipterocarp seeds, if at all, is not known (M. Bernadus, *personal communication*). Other

locally common herbivore-granivores include sambar deer (*Rusa unicolor*), two species each of chevrotains (*Tragulid* spp.), and muntjac deer (*Muntiacus* spp.), all of which eat fruit and seeds to varying degrees (Hazebroek et al. 2012). Pig-tailed macaques (*Macaca nemestrina*) occur in the study and may consume dipterocarp seeds on occasion (Curran and Leighton 2000). Omnivores that may eat dipterocarp seeds include Malay civet (*Viverra zibethica*) and porcupine species (Malayan, thick-spined, and long-tailed porcupine *Hystrix brachyura*, *H. crassispinis*, and *Trichys fasciculata*, respectively). Finally, climbing animals such as squirrels and treeshrews (Sciuridae and Tupaiidae) occur in this system, with the former known to be granivorous (Phillips and Phillips 2016).

Habitat use by granivorous mammals in logged and unlogged forest

We quantified animal communities in our study area with camera traps to determine whether differences in occurrence among animals exhibiting varying levels of granivory might explain patterns in seed mortality, germination, or seedling establishment. Passive infrared Reconyx HC500 camera traps (RECONYX, Inc., Holmen, Wisconsin, USA) were deployed from May to November 2014, with 22 in the DVCA and 20 in the SBE. Cameras were active for an average of 100 d in DVCA and 90 d in SBE. Camera trap photos were date and time stamped, allowing us to estimate the average number of independent detections (photos) per 100 camera trap days, our metric of camera site usage. Detections of the same species at the same site were deemed to be independent if they were not consecutive (i.e., another species was photographed in between) or if they occurred at least 1 h apart; such methods are increasingly common in camera trap studies (e.g., Carter et al. 2012, Brodie and Giordano 2013).

We used generalized linear models (GLM) to determine if the number of independent animal detections at each camera trap station differed between forest types. Data were fit using a quasipoisson distribution to account for overdispersion. Detections at each camera trap station were pooled for the duration of the field season (May–November 2014). We focused our analyses on mammal taxa that may consume seeds to varying degrees. These taxa included bearded pigs, murid rodents, elephants, sambar, muntjac, chevrotains, pig-tailed macaques, Malay civets, porcupines (data pooled for common, thick-spined, and long-tailed porcupine), small climbing mammals (*Sciuridae* and *Tupaiidae* spp. pooled), and sun bears (*Helarctos malayanus*). *Tupaiidae* spp. are insectivorous and frugivorous (Phillips and Phillips 2016) but data were pooled with *Sciuridae* spp. because of difficulties in differentiating between taxonomic groups in photos. We determined that differences in occurrence between forest types for a given mammal species were significant if the 95% confidence intervals (CIs) of the regression coefficient for “forest type” did not include zero.

Influence of forest type, exclusion treatment, and seed size on seed fate

We collected seeds from five species of dipterocarp trees during a mast-fruiting event in August 2014: *Shorea macrophylla* (mean seed mass 13.80 g), *Parashorea tomentella* (2.95 g), *Dryobalanops lanceolata* (3.27 g), *Shorea leprosula* (0.74 g), and *Hopea nervosa* (0.65 g). These were selected to span a gradient in seed size, allowing us to assess seed fate across a range of values of this important plant reproductive trait (Moles and Westoby 2004), as well as across different scenarios of vertebrate exclusion. Seeds with evidence of insect damage or decay were not used.

We established three experimental blocks in the unlogged forest and three in the logged forest. Blocks were at least 1 km apart and their locations were selected to minimize microsite differences and environmental variation among blocks. Each block consisted of four treatments that excluded (1) large (elephant), medium (deer, bearded pigs), and small (porcupines, chevrotains) mammals, (2) elephants only, (3) small mammals only, or (4) no mammal species (control). The experimental design was partly factorial because deer and pigs could not be excluded without simultaneously excluding elephants. The arrangement of treatments in each block was not consistent between blocks or forest types as treatment orders were randomly assigned at the time of enclosure construction.

We used different construction materials for our experimental exclusion treatments based on which ground-dwelling vertebrates we intended to exclude. To simultaneously exclude large, medium, and small mammals, we used 2 m tall metal fencing with 2.2 cm mesh, coupled with two layers of barbed wire 2 m high around the perimeter of plots to deter elephants. Barbed wire was also placed 1 m off the ground around the perimeter of the metal fencing to further deter bearded pigs and deer from entering. To exclude only small mammals, we placed 50 cm tall fencing around the plot perimeter. To exclude only elephants, two layers of barbed wire 2 m high were placed around the plot perimeter with no other fencing. In the control plots, the corners were marked with flagging tape to delimit plot boundaries. During our experiment, we detected no breach of fencing or barbed wire, confirming that the animals we meant to exclude from plots were actually excluded. However, the enclosures were not covered so it is possible that climbing or arboreal mammals entered our plots.

We placed seeds in 1 × 1 m quadrats in the southeast corner of 7 × 7 m plots used for a concurrent study of seedling survival; quadrats were 1 m from the plot perimeter to minimize potential effects of metal leaching from the fencing. Five seeds of each tree species were placed within each quadrat, resulting in 25 seeds in each treatment and 20 seeds per species in each experimental block. One of our blocks in the logged forest did not have seeds placed in the control plot, resulting in an

uneven number of seeds between the logged and unlogged forest, but this was accounted for in the analysis. We placed seeds 10 cm apart, subject to the constraint that two seeds of the same species were never adjacent. Each seed was numbered with a unique ID in order to track its fate over time. A 1 m long string was attached to each seed and secured to a 10 cm nail, which was then placed into the soil to locate seeds that had been moved.

We visited plots approximately every 7 d for 60 d. These species germinate in <30 d (O'Brien et al. 2013) so the 60 d period allowed for germination and seedling establishment. Dipterocarp seeds do not form seed banks because of their sensitivity to desiccation and fast decomposition (O'Brien et al. 2013), so we assumed that seeds that had not germinated at the end of the study would not germinate at all. At each census, seed status was recorded as dead from granivory (i.e., browsed and radical damaged), eaten but alive (i.e., browsed with only cotyledon damage), removed or disappeared (i.e., no longer attached to the string and absent from the plot), germinated (i.e., radical emergence), or established as a seedling (i.e., established root and standing stem). Post-germination seed mortality caused by seed predation can occur (Terborgh et al. 1993), so more than one response was possible for an individual seed during a single visit. Also, granivory, whether leading to mortality or not, was possible both before and after germination. We did not quantify the mortality of seeds predated upon after removal from treatment plots. Rodents may transport seeds to burrows but scatter-hoarding in this system is unlikely due to the rapid germination of dipterocarp seeds (Wells and Bagchi 2005).

We aggregated responses of each species from all censuses in each treatment per block to calculate final proportions of seeds exhibiting each response. Therefore, all results represent the final fate observed for seeds exhibited at the conclusion of the experiment. Generalized linear mixed-effect models (GLMM) were used to assess the final proportions of seeds killed by granivores, eaten but alive, removed, germinated, or that established as seedlings as functions of exclusion treatment (a fixed factor with four levels), site (a fixed factor with two levels; logged and unlogged), and species identity of the seed (a fixed factor with five levels). We also tested for forest \times exclusion treatment, tree species \times exclusion treatment, and species \times forest interactions. We performed these GLMM analyses on final proportions using a binomial distribution weighted by the number of seeds of each species initially planted inside each treatment of each block. We included random effects for experimental block nested in forest site (a random term with six levels) and used model selection based on the Akaike information criterion corrected for sample size (AIC_c) to determine to which model best explained each response variable. We used R (version 2.15.2; R Development Core Team 2012) for all analyses. GLMM models were run using the lme4 package in R (Bates et al. 2015). Post-hoc

pairwise tests for fixed effects were performed for each response variable using the multcomp package (Hothorn et al. 2008) for models with the lowest AIC_c .

RESULTS

Habitat use by granivorous mammals in logged and unlogged forest

Bearded pigs, muntjac, and chevrotains were the most frequently detected granivores while elephants, sun bear, and arboreal granivores (squirrels and treeshrews) were among the least detected (Fig. 1). There were significantly more detections of bearded pigs in unlogged forest than in logged forest (regression slope = 0.9; 95% CI: 0.1–1.6).

Influence of forest type, exclusion treatment, and seed size on seed mortality, germination, and establishment

The proportions of seeds removed in unlogged and logged forest were 0.10 and 0.08, respectively. Removal was statistically unrelated to forest type ($P = 0.34$) and, overall, was higher in control plots than in plots that excluded large, medium, and small mammals ($F_{3,111} = 2.91$, $P = 0.05$). No species-related trends in seed removal were detected ($P < 0.41$). Granivore-induced seed mortality was only affected by seed species, treatment and forest site as main effects, so the interaction terms were dropped.

The overall proportion of seeds killed by granivores was greater in the logged forest (0.77) than in the unlogged (0.66; $F_{1,113} = 8.25$, $P = 0.03$; Fig. 2). Seed mortality was

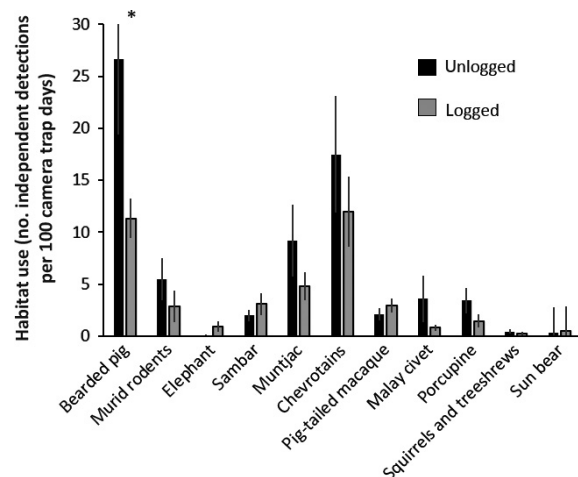


FIG. 1. Habitat use (average number of independent detections per 100 camera trap days) of terrestrial mammal taxa in Danum Valley (unlogged forest, black) and the Sabah Biodiversity Experiment (logged forest, gray), Malaysian Borneo from May to November 2014. Standard error bars are shown. Asterisks denote significant differences in relative site usage of animals between forest types based on model coefficients whose 95% confidence intervals do not include zero.

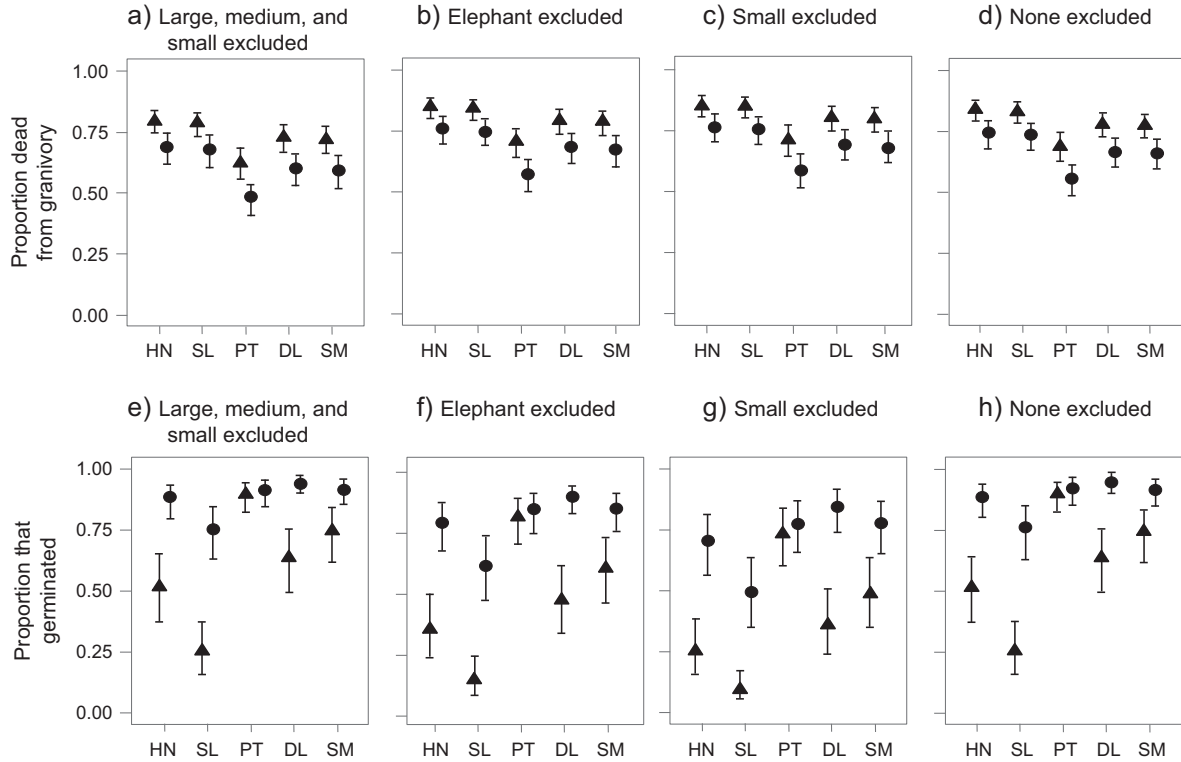


FIG. 2. Overall proportions (mean \pm SE) of dipterocarp seeds killed by granivores in experimental plots excluding (a) large, medium, and small mammals, (b) elephants only, (c) small mammals only, and (d) no species, in logged (triangles) and unlogged (circles) forest in Malaysian Borneo for five dipterocarp species (HN, *Hopea nervosa*; SL, *Shorea leprosula*; DL, *Dryobalanops lanceolata*; PT, *Parashorea tomentella*; and SM, *Shorea macrophylla*). Also shown are the overall proportions of seeds that germinated in plots excluding (e) large, medium, and small mammal herbivores, (f) elephants only, (g) small mammals only, and (h) no species. Dipterocarp seeds on the x-axes are ordered from smallest (left) to largest (right) seed mass. The proportion of seeds killed by granivores was greater in logged forest, but no significant differences among exclusion treatments were detected. Seed germination was higher in unlogged forest, in control plots, and for small-seeded species.

not significantly different between exclusion treatments ($P = 0.99$) and mortality was similar among large-seeded species (*P. tomentella* compared to *D. lanceolata*, $P = 0.44$; *S. macrophylla* compared to *D. lanceolata*, $P = 0.99$; *S. macrophylla* compared to *P. tomentella*, $P = 0.54$). The only size-related differences in mortality were between the smallest species (*H. nervosa* and *S. leprosula*) and *P. tomentella*, the species with the median seed mass. Mortality was less likely among *P. tomentella* seeds compared to the smaller species ($F_{4,110} = 2.58$; *H. nervosa*, $P = 0.03$; *S. leprosula*, $P = 0.05$). Seeds of the largest-seeded species (*S. macrophylla*) were more likely to survive granivore attack than either *S. leprosula* or *H. nervosa* ($F_{4,110} = 9.58$, $P < 0.01$). Also, both *H. nervosa* and *S. leprosula* were less likely to survive granivore attack than the second largest seeded-species, *D. lanceolata* ($P < 0.01$).

A smaller proportion of seeds germinated in the logged forest (0.54 of all seeds) than in unlogged forest (0.79 of all seeds; $F_{1,113} = 5.01$, $P < 0.01$). Germination was also lower in control plots than in large, medium, and small mammal exclusions treatments (proportion germinated in control = 0.60 and proportion germinated in large, medium, and small mammal exclusions

treatments = 0.73; $F_{3,111} = 5.34$, $P < 0.01$; Fig. 2e, h). There was a significant species \times site interaction ($F_{4,110} = 2.72$) for some of the pairwise comparisons: germination was greater for small-seeded species in unlogged forest (proportion of *H. nervosa* that germinated = 0.63 and *S. leprosula* = 0.78; $P = 0.04$) and was lowest for *S. macrophylla* in logged forest (*S. macrophylla* vs. *S. leprosula* in logged forest, $P < 0.01$).

Overall seedling establishment was greater in logged forest, but this difference was not significant (proportion of seeds that established in logged = 0.24, proportion that established in unlogged = 0.13; $P = 0.88$). No significant differences in establishment were found among treatments ($P > 0.76$ for all pairwise treatment comparisons). The best model for seedling establishment included a site \times treatment interaction (Table 1). Within logged forest, fewer seeds established in control plots than in treatments simultaneously excluding large, medium, and small herbivores ($F_{3,111} = 7.06$, $P = 0.02$). In the logged forest, establishment levels were higher in the absence of large, medium, and small mammals relative to treatments excluding only elephants ($P < 0.01$; Fig. 3). Small-herbivore exclusion plots experienced

TABLE 1. Number of model parameters, Akaike weights (w_i), and the change in the Akaike information criterion corrected for sample size (ΔAIC_c) for binomial general linear mixed effect models.

Model	No. model parameters	Response									
		Removed or missing		Dead from granivory		Eaten but alive		Germinated		Established as seedling	
		w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c
Site + treat + spp. + spp. \times treat + site \times treat + spp. \times site	28	0.00	38.82	0.00	25.93	0.00	28.34	0.00	14.20	0.06	5.35
Site + treat + spp. + site \times treat	12	0.04	5.99	0.28	1.38	0.09	0.10	0.26	1.03	0.93	0.00
Site + treat + site + spp. \times treat	21	0.00	21.62	0.00	14.72	0.00	20.19	0.00	9.21	0.00	13.03
Site + treat + spp. + spp. \times site	13	0.08	4.79	0.16	2.46	0.47	0.00	0.44	0.00	0.00	27.09
Site + treat + spp.	9	0.88	0.00	0.56	0.00	0.45	11.59	0.30	0.75	0.01	20.68

Notes: We tested forest ("site"; logged or unlogged forest), treatment ("treat"; large, medium, and small mammals excluded, elephant excluded, small excluded, and none excluded), and dipterocarp seed species ("spp."; *Hopea nervosa*, *Shorea leprosula*, *Parashorea tomentella*, *Dryobalanops lanceolata*, and *Shorea macrophylla*) on each response variable. We also tested for site \times treatment ("site \times treat"), species \times treatment ("spp. \times treat"), and species \times site ("spp. \times site") interactions. All models included the same random effects of (1|site: block). Akaike weights in boldface type represent the best model for each response variable.

more seedling establishment relative to treatments excluding only elephants within logged forest ($P < 0.01$). No treatment differences in seedling establishment were found within unlogged forest. Species-related differences in overall establishment were not found, with the exception for *P. tomentella*, the species with the median seed mass, which had the highest proportion of established seeds ($F_{4,111} = 0.64$, $P < 0.01$).

DISCUSSION

Most tropical forests are simultaneously affected by multiple human activities (Wright 2005), but considering only their additive effects could hinder our ability to understand consequences of these disturbances for forest regeneration. The combined impacts of habitat

disturbance and altered animal abundances could affect plant recruitment in ways that are not apparent when studied in isolation (Peres 2000, Guariguata et al. 2002, Poulsen and Clark 2011, Brodie et al. 2014). Though the effects of defaunation on plant recruitment may vary (Kurten 2013), our findings suggest that the interactive effects of defaunation and logging could influence forest regeneration by increasing the probability of seedling establishment and recruitment, in contrast to findings elsewhere (Asquith et al. 1997, Nunez-Iturri et al. 2008, Galetti et al. 2015, Rosin and Poulsen 2016). Our assessment of these interacting factors suggests two distinct patterns to seedling establishment that are dependent on logging history. Logged forests had higher seed mortality and lower germination but higher survival of germinated seeds that turned into seedlings (Fig. 4). Unlogged forests had lower mortality and higher germination but lower survival of germinated seeds (i.e., high mortality of young seedlings; Fig. 4).

At the seed stage, mortality was higher in the logged forest and the effects of logging outweighed those of experimental defaunation. However, lower seed mortality in the unlogged forest did not necessarily improve the chances of survival at future life stages, as seed establishment rates were statistically similar between forest types (Fig. 4). Herbivory by invertebrates or pathogen infection (which were not excluded from our plots) after seeds germinated may have contributed to overall mortality in the unlogged forest, compensating for the reduced mortality of ungerminated seeds. Herbivory by insects can increase following the seed germination stage in mature forest (Toy and Toy 1992, Lyal and Curran 2000, Notman and Gorchoy 2001, Nakagawa et al. 2005), whereas the removal of reproductive trees for logging can reduce invertebrate and pathogen populations (Intachat et al. 1997). Forest gaps created by tree removal in logged forest may also increase light availability to the understory, promoting seedling growth in disturbed forest (Ashton 2010), contributing to the similar establishment levels we observed between forest types.

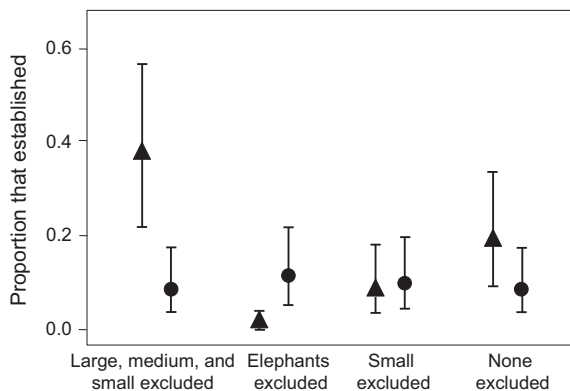


FIG. 3. Overall proportion of seeds (mean \pm SE) that established as seedlings out of initial seeds planted in experimental plots excluding large, medium, and small mammals, elephants only, small mammals only, and no species, in logged (triangles) and unlogged (circles) forest in Malaysian Borneo for five dipterocarp species: *Hopea nervosa*, *Shorea leprosula*, *Dryobalanops lanceolata*, *Parashorea tomentella*, and *Shorea macrophylla*. Data for these species were pooled because significant differences in establishment between species were not found, with the exception of *P. tomentella* seeds, which were more likely to establish.

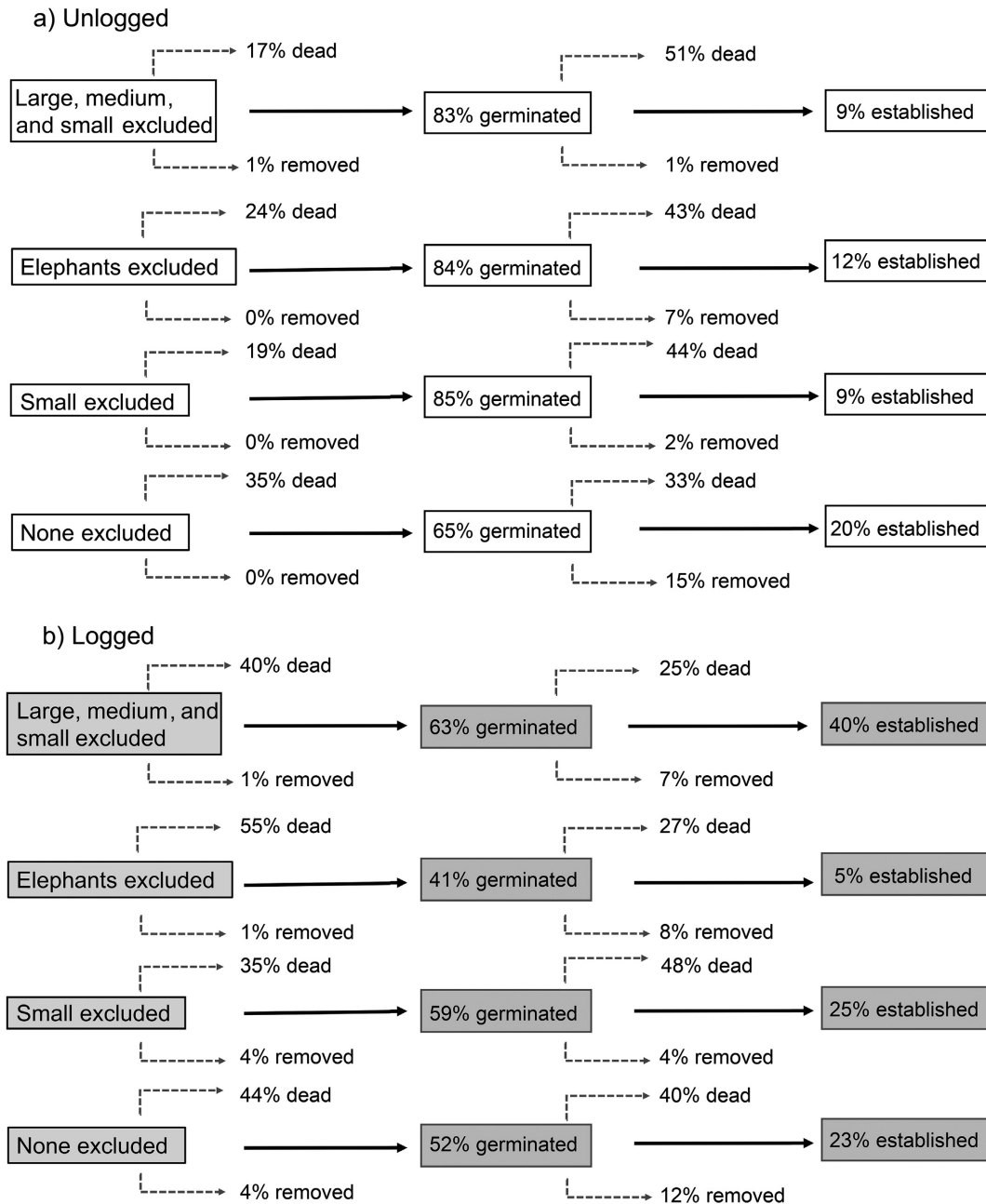


FIG. 4. Percentage of dipterocarp seeds killed and eaten by granivores (dead), germinated, removed, and/or that established as seedlings in animal exclusion treatments in (a) unlogged and (b) logged forest in Malaysian Borneo. Treatments excluded large, medium, and small mammals, elephants only, small herbivores only, or no species (control). Granivore-induced mortality and seed removal were possible both before and after germination. Data for five dipterocarp species (*Hopea nervosa*, *Shorea leprosula*, *Dryobalanops lanceolata*, *Parashorea tomentella*, and *Shorea macrophylla*) were pooled and percentages shown are out of the initial pool of planted seeds in each treatment within logged and unlogged forest. Overall percentages do not add up to 100% because more than one seed fate was possible for individual seeds (e.g., germination and establishment). Also, not all unpredated seeds successfully germinated.

Seed mortality was greater in logged forest despite lower usage of that habitat by bearded pigs. Differences in seed mortality between logged and unlogged forest could be related to changes in food availability and animal foraging patterns driven by logging rather than by

hunting-induced changes in seed predator abundance (Barnes et al. 1991, Chapman et al. 2000, Farwig et al. 2006). Hunting is limited in our study area and no hunters were detected by our camera traps in 2014 (nor in 2013 or 2015); this is partly due to the restricted access

and remoteness of this forest area. Seed production tends to be lower in selectively logged forest because of the reduced abundance of reproductive adult trees (Ghazoul and McLeish 2001), so the chance of large seed predators becoming satiated may be lower in logged forest. Where dipterocarp seeds are available, seed predators (e.g., bearded pigs or pig-tailed macaques) would therefore spend more time foraging in an area of logged forest than they would in an equivalent portion of unlogged forest, causing higher localized mortality in the former habitat (Curran and Leighton 2000).

Although seed removal was highest in control plots, excluding large, medium, and small-bodied mammals was not associated with reduced seed mortality, contrary to our initial predictions. The absence of large vertebrates could lead to increased seed predation by small taxa (e.g., *Rattus* spp.) if the latter is released from competition in the absence of large animal taxa (McCauley et al. 2006, Galetti et al. 2015). However, we found similar levels of seed mortality across treatments suggesting that small ground-dwelling animals were not released from competition in the absence of larger mammal taxa. Logged areas may contain higher rodent abundances compared to unlogged forest (Malcolm and Ray 2000) but our camera traps consistently captured fewer vertebrates, both small and large, in the logged forest, and rodent occurrence did not differ between forest types.

Logging reduced germination in seeds that were not predated, possibly by altering forest structure in ways that impacted the seedling microhabitat environment. Forest gaps created by logging, for example, increase the amount of light reaching the forest floor, thereby increasing the likelihood of seed desiccation (Itoh et al. 1995). Germination was also higher among small-seeded species (*H. nervosa* and *S. leprosula*) in the logged forest, illustrating that reduced mortality among large-seeded species does not necessarily lead to higher germination levels. In contrast to logging, experimental defaunation did not reduce seed survival, though reduced seed predation (Beckman and Muller-Landau 2007, Dirzo et al. 2007, Hautier et al. 2010) and increased germination in the absence of medium to large-bodied terrestrial mammals have been documented elsewhere (Paine and Beck 2007).

Unsustainable hunting of animals and habitat disturbance in the form of selective logging are two important threats facing wildlife throughout the tropics (Corlett and Primack 2011). Many tropical forests are simultaneously affected by both, but the consequences of each for forest regeneration are usually studied separately or additively, and usually on a single plant demographic stage (Wang and Smith 2002, Comita et al. 2014). We found that seed mortality was higher in logged forest, but the absence of medium and large mammals had little influence on seed mortality or on seedling recruitment. Instead, seedling recruitment was more likely where logging and animal loss occurred together. Our findings therefore suggest that defaunation could have important consequences for forest regeneration and community composition in logged

areas, a particularly striking result given that the overexploitation of both large mammals and trees continue to be widespread in tropical regions.

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DATA AVAILABILITY

Data available from Figshare: <https://doi.org/10.6084/m9.figshare.5106913.v2>