



Original Research Article

A pantropical assessment of vertebrate physical damage to forest seedlings and the effects of defaunation



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ABSTRACT

Many of the forces that shape tropical forest plant communities are facilitated by interactions with animals, which can either promote or inhibit plant reproduction and survival across ontogenetic stages. Hunting-induced defaunation can disrupt these interactions, altering tree recruitment, forest structure, and carbon storage, with strong effects at the seed and seedling stages. Research to date has largely focused on how changes to prominent interactions (especially seed dispersal) affect plant species and communities, while concurrent disruptions to less-studied processes may have opposing effects. With a particularly limited understanding of non-trophic interactions – such as physical damage to seedlings by vertebrate trampling, rooting, and digging – it remains difficult to predict the outcomes of defaunation for tropical forest plant communities. We established 1800 artificial seedlings in 18 intact and disturbed sites across the three main tropical forest regions – the Neotropics (Peru), the Afrotropics (Gabon) and the Indo-Malayan tropics (Malaysian Borneo) – to isolate non-trophic vertebrate physical damage from other causes of seedling mortality (herbivory, pathogens, abiotic desiccation, etc.), and to understand its effects in intact and anthropogenically-disturbed forests. We found that vertebrate physical damage is a consistent force in forests across the tropics, and that hunting significantly alters its strength, with a ~70% decrease in damage in hunted vs. intact sites that resulted in a ~3.5-fold (350%) increase in artificial seedling survival. Our results reveal an understudied mechanism that may contribute to changes in seedling survival, stem density, and plant community composition in tropical forests subjected to hunting.

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1. Introduction

Plant–animal interactions are prominent in tropical forests (Price et al., 1991), and can be beneficial (e.g. pollination, seed dispersal) or detrimental (e.g. herbivory, seed and seedling predation) to plant reproduction and survival. Disruptions to these interactions – such as defaunation resulting from hunting (Redford, 1992) – can generate broad changes in tree recruitment (Terborgh et al., 2008), forest structure (Dirzo and Miranda, 1990), and carbon storage (Osuri et al., 2016), with demographic filtering at the seed and seedling stages responsible for many of the effects (Kurten, 2013). Research to date has largely

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focused on a subset of prominent bi-trophic interactions (especially seed dispersal), while concurrent disruptions to other less-studied ecological processes may have unexpected or even opposing effects (Kurten, 2013; Wright, 2003).

Largely ignored in recent research are non-trophic interactions (Ohgushi, 2008), such as trampling, rooting, digging, and other incidental physical damage that occurs as animals use their habitat. The strongest of these ecological effects are obvious: elephants create vast networks of trails through repeated trampling (Blake and Inkamba-Nkulu, 2004), and maintain forest clearings called *bais* (Klaus et al., 1998); foraging herds of peccaries root and dig, disturbing the soil and vegetation over large areas and acting as “ecosystem engineers” (Beck et al., 2010). While extensive localized damage is conspicuous, multitudinous small effects – such as the trampling of many individual seedlings across large spatial and temporal scales – could have equally consequential effects for plant communities. With very limited understanding of these interactions, it remains difficult to predict the outcomes of defaunation for tropical forests.

Little is known about the role of vertebrate physical damage to seedlings in the tropical forest understory (Clark and Clark, 1989), as well as how this force may be altered by defaunation. The assessment of physical damage can be difficult, given that vertebrate and invertebrate herbivory, pathogen attack, abiotic desiccation, and other factors can produce visually similar forms of seedling mortality. To isolate the effects of physical damage (by both vertebrates and falling plant debris) from other causes of mortality, we used a modified artificial seedling model designed to replicate natural seedlings in general shape, flexibility, and resilience to damage (Clark and Clark, 1989, Fig. 1). The model provides an index of damage that is ideal for comparison across sites (Clark and Clark, 1989) and between forests with different human disturbances such as hunting (Roldán and Simonetti, 2001).

We sought to quantify physical damage to seedlings in biogeographically distinct forests across the tropics, and to compare these effects between intact forests (protected sites without any recent human disturbance) and those subjected to hunting and/or logging. We assessed damage to a total of 1800 artificial seedlings across 18 sites, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in Peru, Gabon, and Malaysian Borneo. We hypothesized that: 1) non-trophic vertebrate damage would be highest in Gabon and Malaysian Borneo, where megafauna remain abundant; and 2) hunting-induced defaunation would significantly reduce non-trophic vertebrate damage, resulting in proportionally greater debris damage but reduced damage overall.

2. Methods

2.1. Study sites

We conducted our study in both intact and disturbed forests of Peru, Gabon, and Malaysian Borneo (Fig. 1). In total, we established 18 experimental sites, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in each of

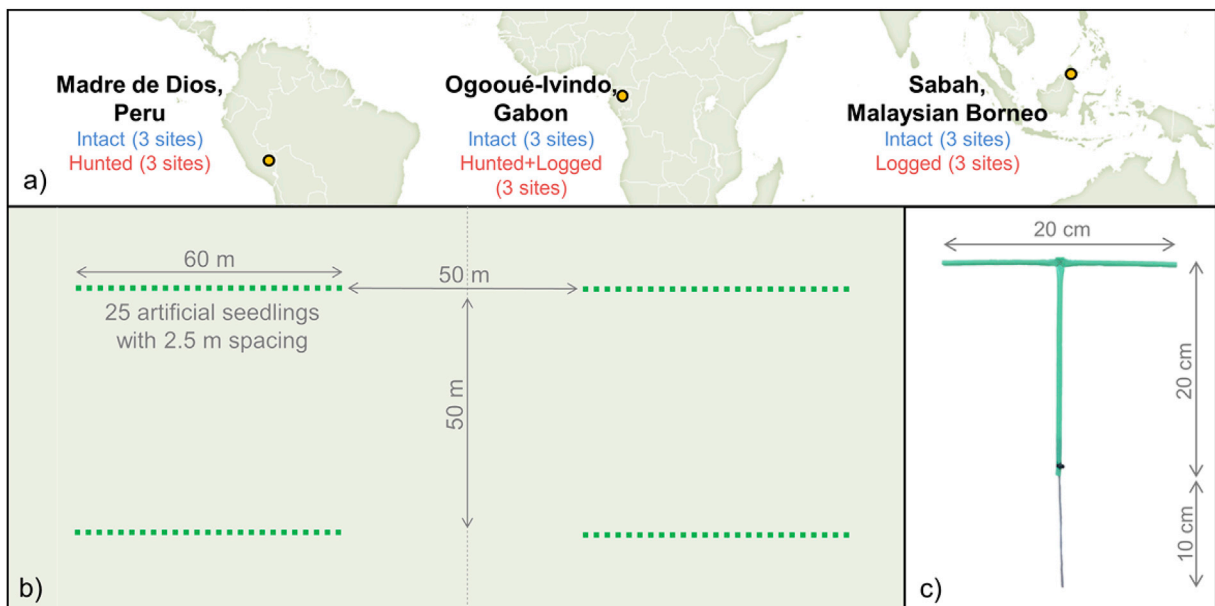


Fig. 1. a) Map of study areas, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in each of the three main tropical forest continents; b) The experimental design for a single site, made of four parallel lines of 25 artificial seedlings (green dotted lines; grey arrows indicate spatial scale and distance between seedling lines; central grey dashed line represents the access route) – in total, we established 18 sites and 1800 artificial seedlings; c) The artificial seedling model, constructed of two green plastic drinking straws attached to a stiff wire “root”.

the three regions. Sites within each forest condition were separated by at least 1 km (mean distance = 8 km; maximum distance = 34 km).

In Peru, our experimental sites were located in the Madre de Dios region in the southeast, and included: 1) three intact sites near the Tambopata Research Center in the Tambopata National Reserve, and 2) three disturbed sites subjected to heavy hunting, located within Reserva Amazónica, a small privately-owned forest approximately 16 km from the regional population center of Puerto Maldonado. Transect surveys of the disturbed forest sites have documented the substantial reduction in abundance of medium- and large-bodied mammals, with a near absence of white-lipped peccaries (*Tayassu* spp.), tapir (*Tapirus terrestris*), and deer (*Mazama* spp.; Rosin, unpublished data), and a highly impoverished primate community (Rosin and Swamy, 2013). The nearest distance between the intact and disturbed condition sites was approximately 90 km.

In Gabon, our experimental sites were located within the Ogooué-Ivindo province in the northeast, and included: 1) three intact forest sites in northern Ivindo National Park, and 2) three disturbed sites near the town of Makokou, with one site near a village, and two sites within the Wang Chuan Timber Sarl concession, all of which were selectively logged and subjected to heavy hunting. Transect surveys of the disturbed forest sites have documented substantially reduced abundances of medium- and large-bodied mammals, including elephants (*Loxodonta cyclotis*), red river hogs (*Potamochoerus porcus*), duikers (*Cephalophus* spp.), mandrills (*Mandrillus sphinx*), and apes (Koerner et al., 2016). The nearest distance between the intact and disturbed condition sites was approximately 22.5 km.

In Malaysian Borneo, our experimental sites were located in eastern Sabah, and included: 1) three intact forest sites within the Danum Valley Conservation Area, and 2) three disturbed sites within the Sabah Biodiversity Experiment (SBE), which was selectively logged for dipterocarp trees in the 1980s. This area has not been subjected to substantial hunting (Hector et al., 2011), in part due to security measures restricting forest access. In 2007, much of the surrounding forest was logged for a second time, though our specific study area was not (Hector et al., 2011). A comparative camera trap survey of the intact and disturbed sites indicated that despite differences in forest structure (Hector et al., 2011), the two areas have comparable abundances of terrestrial mammals, including bearded pigs (*Sus barbatus*), sambar (*Rusa unicolor*), yellow muntjac (*Muntiacus atherodes*), and pig-tailed macaques (*Macaca nemestrina*; Granados et al., 2016). The nearest distance between the intact and disturbed condition sites was approximately 20 km.

2.2. Artificial seedling construction, “planting,” and monitoring

We constructed 1800 artificial seedlings, following Clark and Clark (1989), with slight modification. Each artificial seedling was composed of two green plastic drinking straws (20 cm length x 0.5 cm diameter) stapled into a “T”, attached to a 13 cm “root” of 12-gauge wire with 3 cm of overlap, and secured with a plastic cable tie under a small duct tape lip (Fig. 1). We numbered each artificial seedling using black permanent marker. The model mimicked natural seedlings in general size, flexibility, and resilience to damage, and required a strong upward force to uproot.

At each of our 18 sites, we established four parallel 60 m lines, separated by 50 m (Fig. 1). For each line, we “planted” 25 artificial seedlings to a depth of 10 cm (so the cable tie attachment was flush with the soil), each separated by 2.5 m along the line. If a planting location was unavailable because of the presence of a tree bole, log, or stream, we avoided the obstacle and adjusted the rest of the line to maintain the separation among seedlings.

We censused all artificial seedlings monthly for a period of 12 months, during the following dates: December 2014 to December 2015 for Gabon; July 2015 to July 2016 for Malaysian Borneo, and November 2015 to November 2016 for Peru. Due to logistical limitations, we missed one census period in Peru and Gabon, and three census periods in Malaysian Borneo. In all cases, we continued with data collection at the following month’s census period.

Following Clark and Clark (1989), we classified artificial seedlings as “damaged” when the model was bent such that either of the two arms of the “T” touched the ground, or when the whole model was flattened, uprooted, or bitten off. We defined three categories of damage: 1) Plant debris – artificial seedlings found directly under fallen branches, trunks, large fruits, or other heavy debris; 2) Vertebrates – artificial seedlings that had been trampled, knocked over, or buried, with evidence of vertebrate activity including animal trails, tracks, scrapings and diggings, and tooth marks; and 3) Unknown – damaged artificial seedlings that couldn’t be assigned, with confidence, to either of the other categories. We categorized artificial seedlings as “Missing” for those that were uprooted and not found within a 10 m radius of their planting location. We categorized artificial seedlings as “Invertebrate damaged” for those with small cut marks and no evidence of vertebrate chewing. We removed all damaged artificial seedlings from their lines at the time of censusing.

2.3. Data Analysis

To test whether non-trophic vertebrate damage differentially affects the survival of artificial seedlings in intact vs. disturbed conditions for each of the three regions, we fitted generalized linear models (GLMs) with binomial error distributions. Our experiment consisted of a block design in which seedlings were planted along lines, and lines were located within sites. Therefore, we modeled artificial seedling fate (binary response: vertebrate damaged or survived) as a function of the total number of artificial seedlings established, including the fixed effects of forest condition (intact vs. hunted and/or logged), site, and line in our models. In the results, we focus on the effects of forest condition, as we had no intrinsic interest in the blocks. We performed all statistical analyses in R 3.2.3 (R Core Team, 2015).

3. Results

A total of 79% (of $n = 1800$) of all artificial seedlings were damaged during the 12-month study period; 71% ($n = 600$) were damaged in Peru, 65% ($n = 600$) in Gabon, and 100% ($n = 600$) in Malaysian Borneo (Fig. 3). We excluded all “Missing” ($n = 214$) and “Invertebrate Damaged” ($n = 120$) artificial seedlings from further analysis, as they likely represented an unnatural novelty response to the model itself (see below). Excluding these data resulted in reduced sample sizes of $n = 540$ artificial seedlings for Peru, $n = 592$ for Gabon, and $n = 334$ for Malaysian Borneo.

Across all sites, forest conditions, and regions, vertebrates predominantly drove artificial seedling losses (Table 1). Vertebrates damaged 49% ($n = 1466$) of all artificial seedlings, compared to just 16% ($n = 1466$) damaged by plant debris.

Hunting significantly reduced vertebrate damage to artificial seedlings, by 87% in hunted sites in Peru and 46% in hunted and logged sites in Gabon, compared to intact sites (Peru: $z = -7.22$, $df = 539$, $p < 0.001$; Gabon: $z = -4.265$, $df = 591$, $p < 0.001$). There was no significant difference in the level of damage by vertebrates in intact vs. logged sites in Malaysian Borneo ($z = -0.52$, $df = 333$, $p = 0.603$; see Table S1 for all model coefficients).

Artificial seedling survival was significantly greater in the hunted sites of both Peru and Gabon than in intact sites (Peru: $z = 6.1$, $df = 539$, $p < 0.001$; Gabon: $z = 3.94$, $df = 591$, $p < 0.001$). In Peru, 9% ($n = 278$) of artificial seedlings survived the year in the intact sites, while 57% ($n = 262$) survived in the hunted sites. In Gabon, 21% ($n = 297$) survived in the intact sites, while 50% ($n = 295$) survived in the hunted and logged sites.

4. Discussion

4.1. Patterns of damage

The magnitude of non-trophic vertebrate damage to the seedling layer was similar in intact sites across all three regions (Fig. 3), despite the substantial natural differences in their animal communities. Based on observations of the damaged artificial seedlings and their surroundings, opportunistic camera trap footage of animals, and knowledge of the foraging ecology of fauna in each region, we suspect that white-lipped peccaries (Peru), elephants and red river hogs (*P. porcus*, Gabon; Fig. 2), and bearded pigs (Malaysian Borneo) generated the strongest vertebrate effects.

The similarity in damage rates among continents contrasts with our hypothesis of greater damage in sites supporting abundant megafauna. There are several plausible explanations for this result. First, the artificial seedling model may not accurately capture differences in the quality of physical damage (for example, elephant trampling is a very different force than peccary rooting, though both damage artificial seedlings with quantitative equivalence). Second, trampling by megafauna not only damages vegetation but also compacts the soil, which may reduce the likelihood for seedling re-colonization; thus, the effects of megafauna on stem density may extend beyond the direct damage investigated by our study. Third, the expected geographic divergence in damage could occur for plants of larger size classes – an effect not captured by using the small artificial seedling model. No Neotropical forest vertebrates, except humans, are capable of inducing the physical damage necessary to kill woody plants with diameters ≥ 3 –5 cm, whereas elephants in the Afrotropics and Indo-Malayan tropics can and often do kill much larger trees (Kortlandt, 1984; Mueller-Dombois, 1972; Terborgh et al., 2016a). Plants in these forests may thus experience vertebrate damage for a much longer period and across multiple growth stages, only escaping this window of mortality at a relatively large size. Non-trophic vertebrate damage may contribute to the observed biogeographic divergence in stem density and forest structure across the tropics (Corlett and Primack, 2011; Terborgh et al., 2016b), though assessing this would require further study through later life stages, when the filtering mechanism exerted only by megafauna takes effect.

As with very large animals, falling branches or trees (categorized as “plant debris”) can kill plants much larger than our artificial seedling model. While most plants are susceptible to vertebrate damage for a relatively short period of time, the risk of death by plant debris may span several decades or more of the life of a slow-growing understory plant. Thus, while plant debris accounted for only relatively minor losses of artificial seedlings, the true lifetime impact of this damage is underestimated by our 12-month experiment. For comparative purposes, however, the observed differences in plant debris damage between regions are likely to reflect actual differences in debris damage to natural seedlings (Gillman et al., 2002). Debris damage was consistently lower across sites in Gabon than in Peru and Malaysian Borneo (Fig. 3). This may be a result of the lower overall tree density (Corlett and Primack, 2011; Lewis et al., 2013) and/or lower turnover (Lewis et al., 2004) in Central

Table 1

Damaged artificial seedlings, categorized by cause. The values represent average proportions across the three sites within each forest condition, with standard errors (averaged among all sites in the condition) in parentheses.

	Intact			Hunted and/or Logged		
	Vertebrates	Plant Debris	Unknown	Vertebrates	Plant Debris	Unknown
Peru (Intact $n = 278$; Hunted $n = 262$)	0.770 (0.044)	0.144 (0.036)	0 (0)	0.099 (0.029)	0.290 (0.049)	0.046 (0.021)
Gabon (Intact $n = 297$; Hunted+Logged $n = 295$)	0.593 (0.048)	0.047 (0.020)	0.152 (0.041)	0.322 (0.044)	0.061 (0.025)	0.115 (0.039)
Malaysian Borneo (Intact $n = 143$; Logged $n = 191$)	0.664 (0.069)	0.217 (0.061)	0.112 (0.030)	0.618 (0.060)	0.304 (0.057)	0.079 (0.031)



Fig. 2. a) Foraging elephants in Gabon approach an artificial seedling (in red square), monitored by an opportunistically-placed motion-sensitive video camera; b) Prior to trampling, the artificial seedling is undamaged (close up still photo from frame a); c) The artificial seedling is crushed under the elephant's foot; and d) Post-trampling, the artificial seedling and surrounding natural vegetation are flattened.

African forests than elsewhere in the tropics; with fewer trees and lower turnover to generate debris, the likelihood of physical damage to the seedling layer is lower.

The unexpectedly high proportion of missing artificial seedlings at sites in Malaysian Borneo (32% of $n = 600$) suggests that some of the observed vertebrate damage resulted from a novelty response of terrestrial mammals to the unnatural model. Based on local camera trap footage (A. Granados, unpublished data), macaques (*Macaca fascicularis* and *M. nemestrina*) were the most likely culprits, uprooting artificial seedlings and carrying them elsewhere. These losses reduced the sample sizes for Malaysian Borneo considerably, and may have inflated the rates of damage observed beyond those to be expected for natural seedlings. Uprooting and missing seedlings occurred rarely in Peru and Gabon, with even distribution across sites, and we have no other evidence that the model was treated in a non-natural way.

After excluding missing artificial seedlings, we are confident that the remaining observations represent an accurate index of non-trophic vertebrate damage for comparative purposes. Studies using the same model have demonstrated similar rates of damage between natural and artificial seedlings in tropical forests (Alvarez-Clare and Kitajima, 2009; Clark and Clark, 1989). However, rates of damage to artificial seedlings likely overestimate rates of mortality of natural seedlings by an unknown factor (Gillman et al., 2002), given the potentially greater resilience of natural seedlings to physical damage, particularly for those with large seeds and hypogeal germination (Harms and Dalling, 1997), and for older seedlings with large, flexible stems. Indeed, tropical forest seedling mortality by all causes is often substantially lower than the rates of artificial seedling damage reported here (eg Metz et al., 2008). Therefore, artificial seedlings are most useful as an index for comparing the potential for physical damage across forest conditions and regions, rather than as an absolute estimate of damage or mortality for natural seedlings in any locality (Clark and Clark, 1989; Gillman et al., 2002).

4.2. The effects of hunting and logging

As hypothesized, hunting strongly affected non-trophic vertebrate damage, reducing artificial seedling losses by 87% in hunted sites in Peru and 46% in hunted and logged sites in Gabon, compared to intact sites. In Malaysian Borneo, where the disturbed forest was selectively logged 30 years ago, but not hunted, there was no significant difference in the level of damage by vertebrates. Despite any logging-induced variation in forest structure and composition, the terrestrial mammal community composition in the disturbed sites was not significantly different from the intact sites (Granados et al., 2016), and vertebrate damage to artificial seedlings was nearly equal between the two forest conditions. Hunting generally affects animal

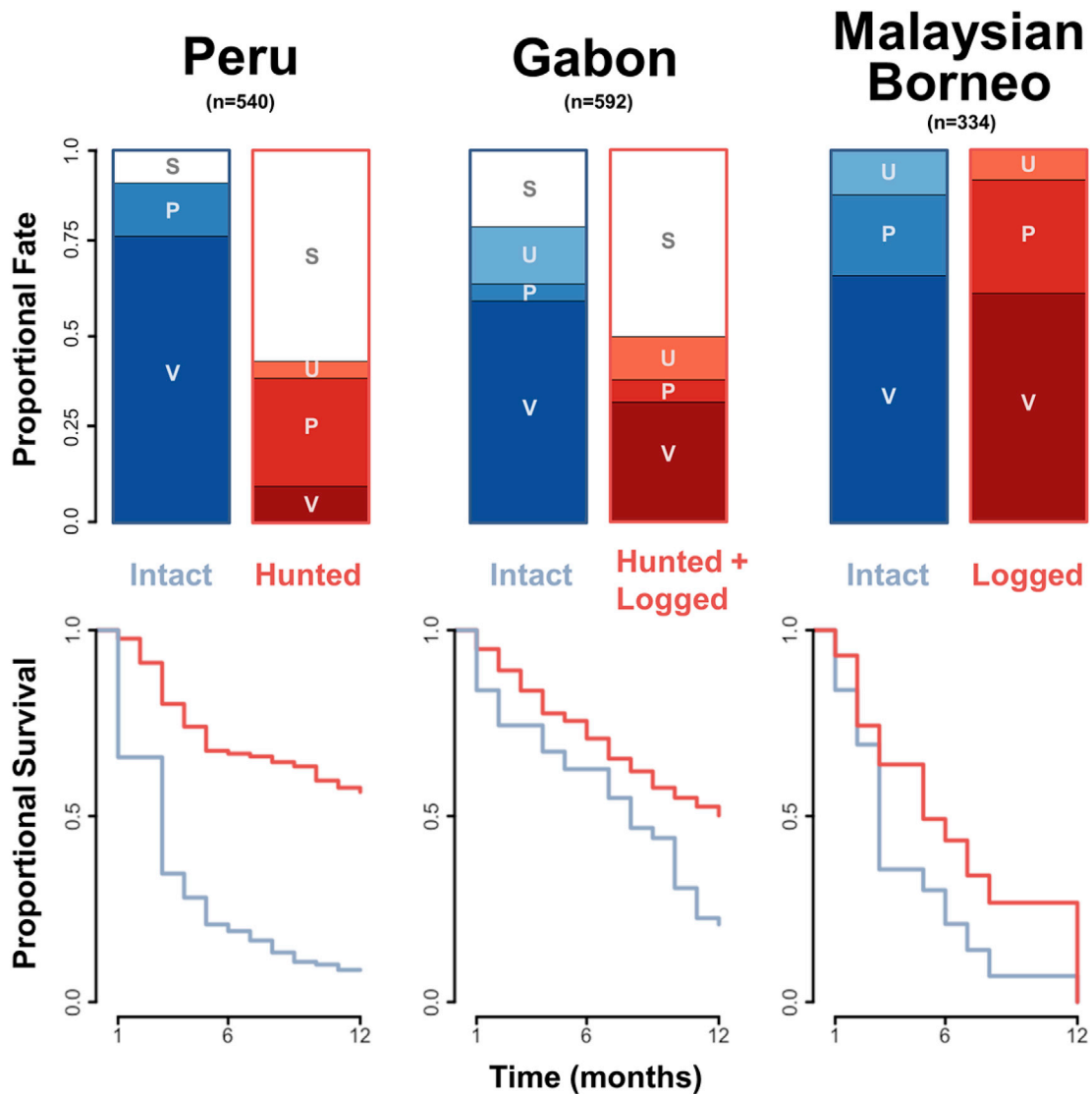


Fig. 3. Top row: The final proportion of artificial seedlings in each forest condition, categorized by fate, including damaged by vertebrates (V), damaged by plant debris (P), damaged by unknown causes (U), and survived (S). Unexpectedly high rates of damage in Malaysian Borneo are at least partly a result of a novelty response of vertebrates to the unnatural model (see Discussion). Bottom row: Kaplan-Meier survival curves, depicting the proportion of surviving artificial seedlings over time (blue line = Intact sites, red line = Disturbed sites).

abundance more strongly than do the direct effects of logging (Poulsen et al., 2011); in our study, hunting was also the key driver in modifying the rates of vertebrate damage to artificial seedlings.

As a consequence of reduced non-trophic vertebrate damage, artificial seedling survival was significantly greater in the hunted sites of both Peru and Gabon than in intact sites. In Peru, just 9% of artificial seedlings survived the year in the intact sites, while 57% survived in the hunted sites (a 6.3-fold increase). In Gabon, 21% survived in the intact sites, while 50% survived in the hunted and logged sites (a 2.4-fold increase). Several studies have demonstrated that hunting-induced defaunation can result in increased survival of natural seedlings (Dirzo and Miranda, 1990; Poulsen et al., 2013; Roldán and Simonetti, 2001), reflecting the trends presented here. While the absolute rates of survival of natural seedlings may be greater than those of artificial seedlings (as noted above), the relative differences in artificial seedling survival between hunted and intact forests presented here likely represent the relative survival differences for natural seedlings as well.

In addition to altering seedling survival and stem density, hunting-induced modifications to the physical damage regime could potentially alter plant community composition. As seedling responses to physical damage can differ among species (Clark and Clark, 1989), those most vulnerable to such damage could have disproportionately increased survival in hunted

sites (Roldán and Simonetti, 2001), with subsequent changes in seedling community composition. Specifically, this might favor fast-growing taxa that invest relatively few resources in strong stem structure, and have limited capacity to resprout.

Several studies have demonstrated that hunting-induced defaunation can result in community-level shifts in seedling stem density and diversity (Dirzo and Miranda, 1990; Kurten, 2013; Wright, 2003), though the mechanisms inducing change are not always well-established. Our study provides compelling evidence that the reduction of vertebrate physical damage to seedlings is an understudied mechanism that may contribute to changes in vegetation structure and composition in defaunated tropical forests. Determining the community-level importance of this ecological interaction – as well as its strength relative to others – will require its inclusion in future studies that seek to understand the drivers of plant recruitment in intact and anthropogenically-disturbed forests.

Author contributions

Conceptualization: C.R. and J.R.P. Data Collection: C.R., V.S., A.G., and J.R.P. Data Analysis: C.R. and J.R.P. Original Draft Writing: C.R. Review and Editing: C.R., J.R.P., V.S., and A.G.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.gecco.2017.06.001>.

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