



Stem breaks as an indirect measure of megafaunal herbivory in tropical forests: An experimental study

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Abstract

To simulate megafaunal (pig, tapir, and elephant) foraging, we cut 1228 saplings in a Sundaic rainforest. In total, 89%–94% of cut stems survived after 13.5 months. About 90% of naturally occurring break scars were at heights ≤ 1 m, implicating pigs, not elephants or tapirs, as the main source of stem damage in this forest.

Abstract in Malay is available with online material.

KEYWORDS

elephant, feral pigs, Gabon, Malaysia, megafauna, pigs, saplings, stem breaks

1 | INTRODUCTION

What we know about the ecology of extant megafauna comes largely from observations made in seasonal parts of Africa and India, where elephants and other large mammals still persist (Owen-Smith, 1988; Sukumar, 2003). We know relatively little about the roles played by megafaunal herbivores in closed-canopy evergreen forests (Hyvarinen et al., 2021). Large body mass allows giant herbivores to consume low-quality forage, giving them access to a wide range of plant species. Nevertheless, even elephants, the largest herbivores, are known to be highly selective in their foraging (Owen-Smith & Chafota, 2012; Sankaran et al., 2013). As selective foragers, megafaunal herbivores have the potential to alter species composition in two ways: by selecting for preferred species, and by inducing differential mortality on species sensitive to damage (Luskin et al., 2021).

Much of what we know about African savanna (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants has been learned because they can be safely observed at close range in open environments. Forest-dwelling megafaunal herbivores, however, are difficult to locate and can be dangerous, precluding direct observation of wild individuals. Consequences of foraging must therefore be inferred from indirect evidence such as the identification of plant fragments in dung deposits and the analysis of stem breaks (English et al., 2014; Terborgh et al., 2016; Yamamoto-Ebina et al., 2016).

Members of our group have investigated both African forest elephants (*Loxodonta cyclotis*) and Asian elephants in high canopy equatorial forests using stem break scars as evidence of foraging activity (Terborgh et al., 2016, 2018). Stems ≥ 1 –2 and < 5 cm dbh are routinely broken by foraging elephants and some other large herbivores, leaving a decapitated naked stem (Scheil &

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Salim, 2004). Many of these stems resprout and continue growing, as indicated by telltale scars at the break point, but an unknown fraction dies (Paciorek et al., 2000). Stems that do resprout leave break scars as evidence, but unknown numbers of stems die (Terborgh et al., 2018). Obtaining a better understanding of megafaunal impacts thus requires an evaluation of how many stems recover and how many die after being broken, and whether species are differentially affected by breakage. Here we report on an experiment designed to answer these questions by manually cutting saplings at diameters and heights corresponding to the patterns of breaks caused by megafauna in a Malaysian Sundaic forest supporting a largely intact fauna.

2 | METHODS

Stem breaks can result from multiple causes: megaherbivore foraging, crown dieback, and falling debris (Clark & Clark, 1991; Paciorek et al., 2000; Terborgh et al., 2016). Herbivore-caused breaks tend to occur within a height range typical of the herbivore, whereas breaks caused by dieback or falling debris are relatively unconstrained with respect to height. Herbivore-caused breaks can be isolated from the rest by subtracting the height-specific frequency of “background” breaks measured in a forest lacking megaherbivores (Terborgh et al., 2016, 2018). However, this procedure lacks species-level specificity and is blind to stems that died, so observations alone cannot answer questions about survival and selectivity.

These questions can be answered by experimentally cutting saplings and observing the consequences, as further described below. Normally, an experiment of this kind would be balanced by an equivalent set of untreated sites. However, an important member of the megafaunal community, wild pig (*Sus scrofa*), is ubiquitous in Malaysia, occurring in settled areas and plantations as well as in native forest, precluding the designation of control plots. Instead, we use data from a megafauna-free site in the Peruvian Amazon to provide a rough point of reference.

The experiment was conducted in the Royal Belum State Park (hereafter Belum; 1175 km², 5°35' N, 101°20' E). Belum is part of a much larger area of reserved forest extending into southern Thailand. Belum has not been logged, but has suffered some recent megafaunal extinctions: Javan rhinoceros (*Rhinoceros sondaicus*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), and banteng (*Bos javanicus*), and a sharp decline in the population of gaur (*Bos gaurus*). Belum retains healthy populations of Asian elephants, Malayan tapir (*Tapirus indicus*) and wild pig. Tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*) are the top predators in the system. Belum is relentlessly hilly, so the experimental plots were situated on ridges or slopes at elevations around 120–150 m in primary dipterocarp forest. Stem cuts were executed on June 21–25, 2018.

Using long-handled shears, we cut 1228 saplings (juvenile trees (≠ lianas) ≥ 0.5 cm diameter at 0.5 m height, to ≤ 3.5 cm diameter, and

7.0 m total height) at five locations within Belum. Roughly a third of the stems were cut at 0.5 m to simulate stem breakage by pigs, a third at 1.0 m to simulate tapir foraging, and the remaining third at 1.5 m to simulate elephant foraging (Ickes et al., 2003, Terborgh et al., 2016, Tok Sum Pot pers. comm.). Deer are present, including sambar (*Rusa unicolor*), but are not known for breaking saplings during foraging, so were not represented in the design.

All cut stems were marked with numbered tags (Figure 1). Prior to cutting, each stem was identified to species in the local Temiar language (Lim et al., 2017; Ong et al., 2021). In addition, we recorded the total height of each stem, its diameter at the height of the cut, and the presence and height of any prior break scars.

Cut stems were evaluated on August 9–11, 2019. We recorded whether each stem was alive or dead and, if alive, how long a leader it had produced during the 13.5 months allowed for recovery. A few stems (4%) that had not resprouted but that were still limber and appeared alive. These we scored as alive with 0 cm of regrowth. Some stems had lost their tags, probably mostly to curious animals, but these had an approximate location, a species identity, the diameter and height at the cut and the presence of prior break scars—in short, enough information to confidently identify them. Finally, there were stems we failed to find after diligent search (4.3%). We may have overlooked some of them, but the tag of one was found in a nearby pig nest, so whether the



FIGURE 1 Saplings severed at 1.0 and 1.5 m above the ground to simulate tapir and elephant browsing.

rest of these not-found stems had died, were browsed, or survived cannot be determined. For the purposes of analysis, we bracket the possibilities by presenting results assuming that these “lost” stems all lived, or all died.

3 | RESULTS

Of the 1228 stems cut experimentally, 1092 (89%) were alive when assessed after 13.5 months, 83 (6.8%) were confirmed dead, and 53 (4.3%) were not found (Table 1). Ninety percent of small saplings (a subset defined as those ≥ 1 m tall and < 1.0 cm diameter at 1.3 m height) were confirmed alive. As a point of reference, the annual survival of small saplings at Cocha Cashu, in Perú, where megaherbivores are lacking, is 94.5% (Terborgh et al., 2020).

The results at face value indicate that experimental stem cutting elevates the 1-year mortality of small saplings by about 4.5% (10% vs. 5.5% in Perú). However, the estimated additional mortality caused by stem cutting depends on whether not-found (“lost”) stems are regarded as all dead or all alive. If dead, then the treatment increased mortality by 4.5%, but if “lost” stems lived but were browsed or overlooked, the estimated additional mortality drops to zero. The true result is likely to be somewhere in-between. Regardless, the additional mortality imposed on small saplings by being broken is not much above the background mortality rate.

Valuable evidence is contained in the height distribution of breaks, as each foraging species addresses stems at a characteristic height. Sixty-two percent of the experimental saplings carried stem-break scars prior to cutting (Table 1). Stems cut at heights of 0.5, 1.0, and 1.5 m, were progressively taller and thicker with mean heights of 1.4, 2.2, and 3.7 m, respectively. Post-cutting survival of these three classes was independent of cut height at 0.88, 0.89 and 0.90, respectively (Table 1). More than 90% of the break scars found in the

smaller two classes were at heights < 1.0 m (mean 0.38 m), as were 70% of those cut at 1.5 m (mean 0.54), with the remainder at heights > 1.0 m in the expected range for elephant foraging.

High species diversity at Belum meant that only 15 species were represented by at least 20 individuals, a limit we set as minimally adequate for statistical purposes (Table S1). Survival in 13 of the 15 species was not statistically different from 89%, the survival rate (proportion confirmed alive) for the dataset as a whole. The two remaining species (“jerug” and “tanjung putih”) deviated sharply ($p < .0001$ by test for one proportion) from the overall mean with survival rates of 55% and 71%, respectively (Table S1). These two species (out of 172 total) accounted for 34% of all stems confirmed dead. Thus, there is some selective mortality resulting from stem break, but for the majority of species, stem cutting raised mortality only a few percent above background.

4 | DISCUSSION

Experimental severing of the stems of saplings in the understory of primary lowland dipterocarp forest in Belum, Malaysia, had only modest impact, reducing sapling survival by 7%–11% after 13.5 months. In a similar experiment conducted in Pasoh, Malaysia, where pig densities were reported to be 10–100 times higher, saplings experienced greater mortality (20%–30%) after 36 months (Ickes et al., 2003).

Perhaps we should not be surprised by low rates of damage-induced mortality. Plant communities that experience frequent wildfires are composed of species that have evolved various means of tolerance and recovery (Bond, 2005). Stem breakage may seem drastic to our sensibilities, but recovery appears to be an evolved trait, part of each species’ “persistence niche” (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). Thus, for most species, stem breakage has only minor consequences, a conclusion also reached

TABLE 1 Pretreatment measurements and survival of 1228 experimentally cut stems in Royal Belum State Park, Perak, Malaysia.

	Survival after 13.5 months		
	Cut at 0.5 m	Cut at 1.0 m	Cut at 1.5 m
Alive	0.876	0.885	0.904
Dead	0.072	0.057	0.074
Not found	0.052	0.057	0.022
N	387	419	418
Mean ht. pre-cut (m)	1.39	2.16	3.72
SD	0.47	0.60	1.07
Mean diameter at cut (cm)	1.01	1.13	2.10
SD	0.41	0.36	0.64
Mean length of resprout (cm) (live stems only)	20.39	29.32	39.71
SD	15.41	20.71	25.40
Proportion w/prior breaks	0.646	0.675	0.548
Proportion of breaks ≤ 1.0 m	0.980	0.919	0.703

by Cardoso et al. (2020) with respect to forest elephant foraging in Gabon, Central Africa.

Breaking stems is only one of several megafaunal foraging techniques used in tall evergreen forests. Other techniques, including leaf stripping, bark stripping, and uprooting, are invisible to forensic investigation and may add substantially to the overall mortality inflicted on saplings by elephant herbivory (Ong et al., 2023). For example, Ickes et al. (2005) evaluated the saplings used to construct pig nests in Pasoh and found that 45% of them had been uprooted, suggesting that assessing recovery from stem breaks considerably underestimates sapling mortality attributable to megafaunal foraging.

The distribution of stem breaks at Belum was strongly concentrated at heights of <1.0m, a height inconsistent with either elephant or tapir foraging but that fits with the breakage of stems by pigs. Evidence of pig foraging was obvious at all our sampling sites. Pigs cut stems at ca 0.5m to make maternal nests and perhaps for routine foraging (Ickes et al., 2003).

Relatively few stems at Belum were broken in the height range expected for either tapirs or elephants, in contrast to the situation in Gabon, where stem break rates overall were considerably higher, with a strong peak at 1.0–2.5 meters. The height distribution and high frequency of breaks in African forests has been interpreted as evidence that elephants are responsible for the low density and great size of trees ≥ 10 cm dbh in these forests (Berzaghi et al., 2019; Terborgh et al., 2016).

That pigs were the predominant source of stem breaks at Belum was an unexpected finding, and one with wider implications. Feral pigs are now well established on many islands and all the ice-free continents, including the Americas and Australia, where they have few predators and where there are no naturally occurring suids. The manifest ability of most species at Belum to recover from stem breakage may not be as great in many localities where feral pigs are novel to the ecosystem, opening the possibility that these animals could become drivers of unwelcome forest change in large parts of the world.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6djh9w17z>.

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SUPPORTING INFORMATION

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