



Assessing the effects of elephant foraging on the structure and diversity of an Afrotropical forest

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Abstract

African forest elephants (*Loxodonta cyclotis*) are ecosystem engineers that browse and damage large quantities of vegetation during their foraging and movement. Though elephant trail networks and clearings are conspicuous features of many African forests, the consequences of elephant foraging for forest structure and diversity are poorly documented. In this study in northeastern Gabon, we compare stem size, stem density, proportional damage, species diversity, and species relative abundance of seedlings and saplings in the vicinity of seven tree species that produce elephant-preferred fruits ("elephant trees") relative to control trees that do not. Across 34 survey trees, with a combined census area of 2.04 ha, we recorded data on 26,128 woody stems in three sizes classes. Compared with control trees, the area around elephant trees had the following: (a) a significantly greater proportion of damaged seedlings and a marginally greater proportion of damaged saplings (with 82% and 24% greater odds of damage, respectively); (b) no significant difference in stem density or species diversity; and (c) a significantly greater relative abundance of seedlings of elephant tree species. Increasing distance away from focal elephant trees was associated with significantly reduced sapling stem damage, significantly increased sapling stem density, and significantly increased sapling species diversity. Considered in sum, our results suggest that elephants can affect the structure and diversity of Afrotropical forests through their foraging activities, with some variation based on location and plant size class. Developing a more complete understanding of elephants' ecological effects will require continued research, ideally with manipulative experiments.

Abstract in French is available with online material.

KEYWORDS

diversity, Elephant, Gabon, herbivory, *Loxodonta cyclotis*, physical damage, structure, tropical forest

1 | INTRODUCTION

Interactions between animals and plants drive many important ecological and evolutionary processes (Price, Lewinsohn, Fernandes, & Benson, 1991), with both beneficial (e.g., pollination, seed dispersal) and detrimental (e.g., seed and seedling predation, herbivory) consequences for plant reproduction and survival. In tropical forests, much of the research on these interactions focuses on their consequences for plant species diversity. Most evidence suggests that small, specialized plant “enemies”—such as fungal pathogens, arthropods, and rodents—play the largest role in promoting and maintaining species diversity by attacking plants at early life stages (Mangan et al., 2010; Paine, Beck, & Terborgh, 2016; Terborgh, 2012). However, large generalist herbivores might also shape species diversity and composition via frequency-dependent browsing (Clark, Poulsen, & Levey, 2012; Dyer, Letourneau, Chavarria, & Amoretti, 2010), affording rarer species an advantage by consuming the most common plants. Beyond their potential effects on species diversity, the largest herbivores can also influence vegetation structure, carbon storage, and broader ecosystem processes (Asner et al., 2009; Owen-Smith, 1992; Tanentzap & Coomes, 2012).

Elephants are the world's largest terrestrial herbivores, with massive ecological effects on their environment (Poulsen et al., 2018). African forest elephants (*Loxodonta cyclotis*) in particular are ecosystem engineers that contribute to fundamental processes including seed dispersal (e.g., Campos-Arceiz & Blake, 2011), nutrient cycling (e.g., Doughty et al., 2016), and herbivory and physical damage (e.g., Kortlandt, 1984). Combined, these actions likely shape forest structure, composition, and diversity, and might partially distinguish Afrotropical forests from Neotropical forests, where mega-herbivores have long been extinct (Berzaghi et al., 2019; Poulsen et al., 2018; Terborgh et al., 2016a, 2016b).

The extreme body size of elephants necessitates the consumption of a huge quantity and diversity of foods (Blake, 2002). In addition to browsing, elephants damage vegetation by trampling seedlings and saplings during their movement and foraging (Rosin, Poulsen, Swamy, & Granados, 2017). As a consequence of their passage through dense understories, elephants create and maintain forest clearings and vast trail networks (Blake & Inkamba-Nkulu, 2004; Campbell, 1991), shaping tropical forest vegetation communities (Hawthorne, Parren, & Hawthorne, 2000). Well-established trail networks connect large fruiting trees and other favored landscape features (Blake & Inkamba-Nkulu, 2004), though the consequences of elephant damage to the forest understory are not well documented.

Elephant browsing and related activity are likely to affect plant reproductive success, stem density, biomass, and perhaps species diversity. These effects will be especially prominent in areas near fruiting trees, where activity and damage are high. When elephant-preferred trees are fruiting, forest elephants visit them repeatedly to consume ripe fruit, while also browsing on vegetation and inadvertently trampling seedlings. These actions might reduce stem density, biomass, and species diversity in the short-term, but leave suitable sites for new seedlings to recruit by reducing competition and providing an influx of nutrients in dung. Elephant damage

might thus favor heterospecific recruitment, mirroring the expectations of the Janzen-Connell hypothesis (Connell, 1971; Janzen, 1970), though facilitated by a large generalist's trampling rather than small specialists' seed and seedling attack. Concomitantly, dung dispersal of seeds beneath the fruiting tree might promote conspecific recruitment if the elephant consumed conspecific fruits elsewhere, or further promote heterospecific recruitment if the dung contains seeds of other species. Understanding these complicated mechanisms requires a more explicit assessment of the patterns and consequences of elephant damage that has been conducted to date.

In this study, we compare stem density, proportional damage, species diversity, and species relative abundance of seedlings and saplings in the vicinity of seven tree species that produce elephant-preferred fruits (hereafter “elephant trees”) relative to non-diet control trees that are not preferentially visited by elephants. We tested four mutually compatible hypotheses:

1. The proportions of damaged seedlings and saplings will be higher around elephant trees than control trees, due to the increased frequency and intensity of elephant activity;
2. The stem densities of seedlings and saplings will be lower around elephant trees than control trees, assuming that elephant damage is sufficient to occasionally kill plants, and that the effects of this damage are stronger than the opposing effects of seed dispersal that promote new seedling recruitment;
3. The species diversity of seedlings and saplings will be lower around elephant trees than control trees, as reducing stem density likely reduces stem diversity (at least at small scales), and again assuming that the effects of damage are stronger than the opposing effects of seed dispersal that promote new seedling recruitment; and
4. The relative abundance of seedlings and saplings of elephant tree species—both heterospecific and conspecific—will be higher around elephant trees than control trees, as a result of the contagious dispersal of elephant tree species' seeds (Clark, Poulsen, Connor, & Parker, 2004).

2 | METHODS

2.1 | Study area and species selection

We conducted this study in the Ogooué-Ivindo province of north-eastern Gabon. The region is dominated by lowland forest, and receives approximately 1,700 mm of rain annually, with two rainy seasons (September–December and March–June). The study area includes the northern section of Ivindo National Park and the Ipassa Field Station, located within the park's buffer zone.

We selected seven tree species that produce fruits that have been observed with high frequency in elephant dung to serve as our focal elephant trees: *Annonidium mannii*, *Baillonella toxisperma*, *Dacryodes buettneri*, *Gambeya lacourtiana*, *Klainedoxa*

gabonensis, *Mammea africana*, and *Panda oleosa* (White, Tutin, & Fernandez, 1993, Poulsen unpublished data). As many of these fruits are also consumed by apes and other mammals (White et al., 1993), we selected individual adult trees of each species that had visible impacts of elephant browsing around their trunks, in order to maximize the likelihood that the observed effects were caused by elephants rather than by other species. In total, we conducted plant surveys around three individuals of each elephant tree species (21 total trees) and 13 control trees with the following criteria: (a) located within 200 m of one of the elephant trees, (b) had similar canopy-level height as the elephant trees, and (c) did not produce fruits commonly consumed by elephants. The control trees included two *Alstonia boonei*, two *Celtis tessmannii*, three *Dialium pachyphyllum*, one *Lophira alata*, two *Newtonia sp.*, and three *Pterocarpus soyauxii*.

2.2 | Survey methods

For each of the 34 survey trees, we recorded diameter at breast height (DBH, cm) and measured height (m) using a hypsometer. We also estimated canopy size by measuring the distance from the trunk to the end of the canopy at eight locations and then calculating the corresponding area. At the base of each tree, we established three 5 × 40 m plots radiating out along the 0°, 120°, and 240° axes. We marked each plot with ribbon at the corners and delimited them with Topofil thread so that the sides of the plot were clearly distinguishable. We then subdivided each plot into eight 5 × 5 m quadrats.

For each woody stem within the plots, we identified the plant to genus or species (see below) and recorded it as one of three size class categories for further measurement: seedling (0.5–2 m in height), sapling (>2 m in height but <6 cm DBH), or adult (≥6 cm DBH). We excluded lianas from our study with the exception of those within the seedling size class, which had not yet exhibited the typical climbing liana growth form and thus were as susceptible to elephant trampling damage as were tree seedlings. For seedlings, we measured the diameter of the plant at 5 cm and measured height from the ground to the terminal bud. For saplings and adults, we recorded only DBH. In the 0° plot, we measured all stems of all three size classes. In the 120° and 240° plots, we measured all saplings and adult trees, but only counted (and identified) the seedlings. In addition to species identification and stem measurement, we assessed all stems for the presence of damage, including breakages and irregular regrowth that may have occurred after being bent or snapped. All taxonomic identifications were conducted in the field by the same local botanist, in order to maintain consistency across survey trees. Plants that could not be identified to genus or species were assigned a unique code; all individuals that apparently belonged to the same unknown taxonomic group were given the same code, so that classification could be as specific as possible even when specific taxonomic identification was not possible.

2.3 | Statistical analysis

We used linear mixed (LMM) or generalized linear mixed (GLMM) models to test our hypotheses, including the focal tree species as a random effect in all models. For LMMs, we evaluated model fit by examining residuals and selected the best model based on the coefficient of determination, R^2 . For GLMMs, we employed the negative binomial distribution when the data were strongly overdispersed and selected among models using the Akaike Information Criterion (AIC). We performed statistical analyses in R 3.5 (R Core Team, 2018) using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) and followed the general recommendations for GLMMs outlined by Bolker et al. (2009).

To test whether elephant activity affects stem damage (H1) and density (H2), we modeled the proportion of elephant-damaged seedlings and saplings (binomial distribution) and the number of seedlings and saplings (negative binomial distribution) as functions of tree type (elephant tree vs. control tree) and distance from the tree (by quadrat), with species of the focal tree as a random effect.

To test whether elephant activity affects species diversity (H3), we computed Shannon–Wiener diversity indices (Magurran, 2004) for seedlings and saplings around elephant trees and control trees. We then assessed the effect of tree type (elephant tree vs. control tree) on diversity for both size classes, with species of the focal tree as a random effect. We did not account for differing levels of taxonomic identification in this diversity analysis, as even unidentified stems were given a unique identifying code in the field and were considered in the analysis as unique “species.”

To test whether elephant activity increases the proportion of elephant-dispersed species (H4), we modeled the proportion of seedlings and saplings of elephant tree species (binomial distribution) as a function of tree type (elephant tree vs. control tree) and distance from the tree (by quadrat), with species of the focal tree as a random effect. Although there are many other species that can be prominent in elephant diets, we considered only the relative abundance of the seven focal elephant tree species in this analysis.

3 | RESULTS

Across all 34 survey trees (with a combined census area of 2.04 ha), we recorded data on a total of 26,128 woody stems (Table 1). By size class (defined in Section 2), this included 14,413 seedlings, 10,527 saplings, and 1,188 adults. We identified 74% of stems to the species level (representing 146 unique species), 24% to the genus level (representing 51 unique genera), and 2% remained unidentified.

A significantly greater proportion of seedlings were damaged around elephant trees than control trees (GLMM: $z = 2.3$, $df = 4$, $p = .02$), with the odds of damage being 82% greater. Saplings were also more likely to be damaged around elephant trees than control trees (with 24% greater odds of damage), though not significantly so (GLMM: $z = 1.5$, $df = 4$, $p = .14$). Of the surveyed stems, 4.6% of

TABLE 1 The identity and relative abundance of stems of the ten most common taxa (top), and the seven focal elephant tree species (bottom) across all plots and size classes

Species	Family	% of stems
<i>Thomandersia congolana</i>	Acanthaceae	9.1
<i>Baphia leptobotrys</i>	Leguminosae	5.5
<i>Alchornea floribunda</i>	Euphorbiaceae	4.9
<i>Agelaea spp.</i>	Connaraceae	4.8
<i>Scorodophleus zenkeri</i>	Leguminosae	4.0
<i>Santiria trimera</i>	Burseraceae	3.2
<i>Crudia gabonensis</i>	Leguminosae	3.1
<i>Polyalthia suaveolens</i>	Annonaceae	2.9
<i>Quassia africana</i>	Simaroubaceae	2.7
<i>Rinorea spp.</i>	Violaceae	2.7
<i>Dacryodes buettneri</i>	Burseraceae	1.0
<i>Panda oleosa</i>	Pandaceae	0.35
<i>Anonidium mannii</i>	Annonaceae	0.22
<i>Klainedoxa gabonensis</i>	Irvingiaceae	0.1
<i>Mammea africana</i>	Calophyllaceae	0.02
<i>Baillonella toxisperma</i>	Sapotaceae	<0.01
<i>Gambeya lacourtiana</i>	Sapotaceae	<0.01

all seedlings (5.3% around elephant trees) and 2.8% of all saplings (3.6% around elephant trees) had evidence of damage. Seedling stem damage did not significantly differ with increasing distance (indicated by quadrat location) from elephant trees (GLMM: $z = -1.2$, $df = 3$, $p = .30$), though seedling damage decreased significantly with distance from control trees (GLMM: $z = -5.9$, $df = 3$, $p < .01$). Sapling stem damage significantly decreased with increasing distance from elephant trees (with the odds of damage decreasing by 4.3% every 5 m; GLMM: $z = -2.5$, $df = 3$, $p = .01$), but did not significantly differ with distance from control trees (GLMM: $z = -1.7$, $df = 3$, $p = .10$).

Neither seedling nor sapling stem density differed significantly around elephant trees compared with control trees (seedling GLMM:

$z = 1.3$, $df = 4$, $p = .20$; sapling GLMM: $z = -0.32$, $df = 4$, $p = .75$). Seedling stem density did not significantly differ with increasing distance from elephant trees (GLMM: $z = 1.4$, $df = 3$, $p = .17$), nor from control trees (GLMM: $z = 1.376$, $df = 3$, $p = .169$). Sapling stem density significantly increased with increasing distance from elephant trees (with 3.5% more stems every 5 m; GLMM: $z = 4.4$, $df = 3$, $p < .001$), but did not significantly differ with distance from control trees (GLMM: $z = 1.2$, $df = 3$, $p = .25$).

Neither the average height of seedlings nor the average DBH of saplings differed significantly between elephant trees and control trees (seedling LMM: $df = 4$, $p = .21$; sapling LMM: $df = 4$, $p = .28$).

Neither seedling nor sapling species diversity differed significantly between elephant trees and control trees (seedling LMM: $df = 4$, $p = .21$; sapling LMM: $df = 4$, $p = .89$). Seedling diversity did not significantly differ with distance from elephant trees (LMM: $df = 3$, $p = .88$), nor from control trees (LMM: $df = 3$, $p = .92$). Sapling diversity increased significantly with distance from elephant trees (with Shannon-Weiner diversity increasing by 1.3% every 5 m; LMM: $df = 3$, $p = .04$), and, to a lesser degree, from control trees (with Shannon-Weiner diversity increasing 0.7% every 5 m; LMM: $df = 3$, $p = .05$).

The proportion of seedlings of elephant tree species was significantly higher around elephant trees than control trees (GLMM: $z = 2.9$, $df = 5$, $p < .01$), representing 2.17% versus 1.45% of seedlings. The proportion of saplings of elephant tree species was also higher around elephant trees than control trees, representing 0.79% versus 0.58% of saplings, though this difference was not significant (GLMM: $z = 0.26$, $df = 4$, $p = .79$).

4 | DISCUSSION

We observed differences in the understory vegetation surrounding elephant trees compared with control trees, though not entirely as predicted (Figure 1). Both seedlings and saplings were more likely to be damaged around elephant trees than around control trees, though this relationship was only significant for seedlings, providing partial support for our first hypothesis. Higher damage around elephant trees

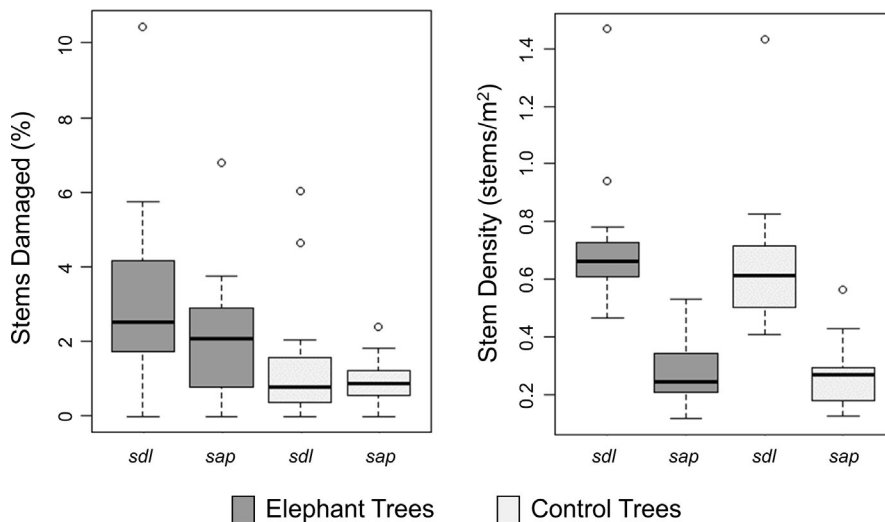


FIGURE 1 Stem damage and stem density around elephant trees versus control trees. Size classes represented include seedlings (sdl; 0.5–2 m in height) and saplings (sap; >2 m in height but <6 cm DBH)

did not translate to significant differences in stem density for either size class, contrary to the expectations of our second hypothesis. There was no significant difference in species diversity of seedlings or saplings around elephant trees versus control trees, contrary to the expectations of our third hypothesis. The relative abundance of both seedlings and saplings of elephant tree species was greater around elephant trees than control trees, though this difference was only significant for seedlings, providing partial support for our fourth hypothesis.

In analyzing the effect of quadrat location, we found that increasing distance from elephant trees was associated with significantly reduced sapling stem damage, significantly increased sapling stem density, and significantly increased sapling species diversity (Figure 2). For control trees, increasing distance had a lesser significant effect on sapling species diversity only, suggesting that elephant activity may be responsible for the observed effects. Using distance from the focal elephant tree as an indicator of the intensity of foraging, these results provide partial support for hypotheses that had been unsupported by comparisons of tree type alone. Considered in sum, our results suggest that elephants can affect both the structure and the composition of Afrotropical forests through their foraging activities.

The failure to find stronger differences between elephant trees and control trees might reflect the shortcomings of our study design, rather than the realities of forest elephant foraging. Our use of focal trees that produce elephant-preferred fruits was intended to isolate the effects of elephant damage, with elephant trees subjected to increased frequency and intensity of elephant foraging. However, there are many other potentially confounding differences between these tree types, including canopy size, soil nutrients and biotic communities, and phenology. These other differences may account for some of the observed effects and

highlight the limitations of this observational approach. In addition, it was impossible to determine the degree to which apes and other mammals may have generated some of the observed vegetative effects, which may more accurately reflect the combined effects of the large mammalian frugivore/folivore community. We were also unable to control for the presence of other preferred diet species or attractive landscape features in the vicinity of the trees we selected as controls, nor did we explicitly examine the relative abundance of the many species that can be prominent in elephant diets but that we did not include among our focal “elephant species.” Despite our best efforts, our study of diversity was further limited by the inherent difficulty in identifying all stems to the species level in the field. Lastly, hunting and poaching occur within our study area (Koerner, Poulsen, Blanchard, Okouyi, & Clark, 2017); although their full impact on elephants is unknown, lower than “natural” population densities could reduce the effects of elephants on this forest.

Given the significant influence of elephants on the process of tree recruitment in African forests (Terborgh et al., 2016a), plants of this region may be particularly tolerant of damage. If enhanced tolerance to damage affords plants more flexibility or an improved capacity to resprout, for example, elephant damage may not often translate to plant death and reduced stem density, as we had expected. Elephant trampling can undeniably result in dramatic local reductions in stem density, as evidenced by the many well-trodden trails kept free of any vegetation due to their frequent use (Blake & Inkamba-Nkulu, 2004; Campbell, 1991). However, the death of a significant proportion of plants may only occur in areas used frequently over extended time periods. The consequences for plant species diversity may likewise be variable, depending on the abundance of elephants and the intensity of the disturbance. As noted in our third hypothesis, the reduction of stem density may likely result in a reduction of stem species diversity, though only with sufficient damage at local scales.

Differences in the observed effects between seedlings and saplings reinforce the notion that the consequences of elephant foraging can be size dependent, and shed light on how these differences shape patterns in forest structure and diversity as a whole. Interestingly, mean Shannon–Wiener index values indicate that, at the quadrat level, saplings were always more diverse than seedlings (Figure 2). This supports the paradoxical observation of Terborgh et al. (2016b) that in Gabonese forests, larger size classes of trees tend to be more diverse than smaller size classes. We have little understanding of the degree to which elephants drive this phenomenon, though they might play a strong role in distinguishing African forests from Neotropical forests (Poulsen et al., 2018; Terborgh et al., 2016a, 2016b).

Across large spatial scales, Afrotropical forests with abundant elephants likely comprise a matrix of damage, with heavy and consistent damage on high-traffic trails, moderate and temporally variable damage under favored fruiting trees, and little to no damage elsewhere. The consequences of this matrix of damage likely contribute to increased heterogeneity of these forests. To fully understand the effects of elephants on forest structure, diversity, and composition will likely require manipulative experiments, as purely observational studies are unable to control for the myriad confounding factors in a natural forest environment. One suitable approach would be to use large size-selective

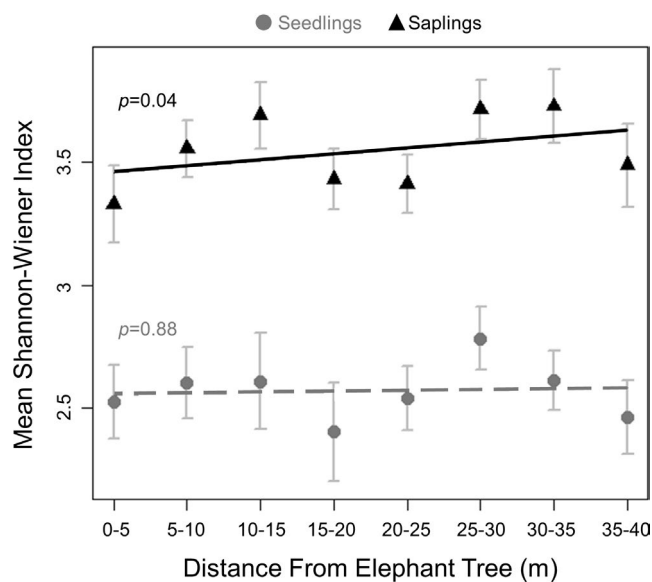


FIGURE 2 Plant diversity (as represented by mean Shannon–Wiener index per quadrat) of seedlings and saplings with increasing distance from the focal elephant tree. The error bars represent standard error, and the regression lines represent LMM predicted values with associated p -values (with the dashed line representing a non-significant result)

enclosures to isolate the specific ecological effects of elephants. Given their dramatic population declines (Maisels et al., 2013; Poulsen et al., 2017), research focused on African forest elephants has both ecological and conservation merit, and will lead to an improved understanding of the factors that shape and maintain these ecosystems.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x95x69pdr> (Rosin et al., 2019).

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