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How selective are elephants as agents of forest tree damage in Bwindi Impenetrable National Park, Uganda?

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Abstract

Elephants are locally concentrated in Bwindi Impenetrable National Park. Vegetation damage attributable to elephants appears to be increasing and may result in the modification of the forest. We examined the implied selectivity of stem damage due to elephants. We followed 26.84 km of recent elephant trails and used 122 plots to document tree damage in relation to species, stem sizes and locations. Of 897 trees (DBH ≥ 2 cm), 542 (60.4%) were intact, 22 (2.5%) debarked, 274 (30.5%) toppled and 172 (19.2%) had broken branches. Small trees were more likely to be pushed over or have their branches broken, whereas large trees were more commonly debarked. The species most frequently selected for damage included mid-successional species such as *Newtonia buchananii*, *Myrianthus holstii* and *Chrysophyllum albidum*. These species may be vulnerable to increasing elephant numbers. Our analyses using general linear models indicate that elephants are selective concerning where, how and what tree stems they damage. We found a higher incidence of elephant damage per-tree stem in open areas than in more closed areas, suggesting feedback in which elephants maintain open habitats that may be conducive for other species such as mountain gorillas. More work is needed to better determine how changing elephant numbers may influence Bwindi's conservation values.

Key words: Bwindi, elephants, generalized linear models, selection, tree damage

Résumé

Dans le Parc National de la Forêt Impénétrable de Bwindi, les éléphants se concentrent par endroits. Les dommages qu'ils causent à la végétation semblent augmenter et pourraient entraîner la modification de la forêt. Nous avons étudié la sélectivité implicite des dégâts dus aux éléphants. Nous avons suivi 26,84 km de pistes d'éléphant récentes et nous avons eu recours à 122 parcelles pour illustrer les dégâts causés aux arbres en fonction des espèces, de la taille des plants et de leur emplacement. Sur 897 arbres (DBH 2 cm), 542 (60,4%) étaient intacts, 22 (2,5%) étaient écorcés, 274 (30,5%) étaient renversés et 172 (19,2%) avaient des branches cassées. Les arbres les plus petits étaient plus susceptibles d'être renversés ou d'avoir des branches cassées alors que les plus gros étaient plus souvent écorcés. Les espèces les plus souvent choisies comprenaient des espèces post-pionnières telles que *Newtonia buchananii*, *Myrianthus holstii* et *Chrysophyllum albidum*. Ces espèces pourraient être vulnérables face à l'augmentation du nombre d'éléphants. Nos analyses au moyen de modèles linéaires généraux indiquent que les éléphants sont sélectifs en ce qui concerne où, comment et quels plants ils attaquent. Nous avons relevé une plus grande incidence de dégâts d'éléphants par plant d'arbre dans les zones ouvertes que dans les zones plus fermées, ce qui suggère un effet en chaîne par lequel les éléphants gardent ouverts des habitats qui peuvent alors être propices pour d'autres espèces, comme le gorille de montagne. Il faudra de nouvelles recherches pour mieux déterminer comment l'évolution du nombre d'éléphants pourrait influencer les valeurs de conservation de Bwindi.

Introduction

Human activities have forced elephants (*Loxodonta africana*, Blumenbach, 1797) to alter their ranges with many animals now concentrated in protected areas (Western, 1989; Poole *et al.*, 1992). Such concentrations can impact the vegetation (Kortlandt, 1984; Western, 1989). Much of

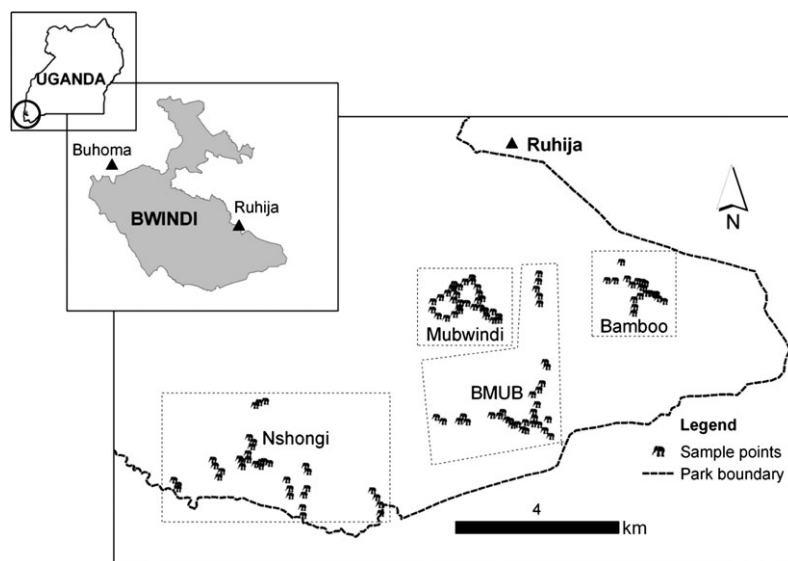*Correspondence*: E-mail: ssalifb@yahoo.co.uk

Fig 1 The location of study sites in Bwindi Impenetrable National Park, Uganda

this involves the direct impacts of elephants on trees: stems can be pushed over, uprooted, snapped, debarked or have their branches removed (Barnes, 1983; Calenge *et al.*, 2002; Kohi *et al.*, 2011). When such impacts are sustained and selective, they can lead to changes in habitat structure, cover and composition (Jachmann & Bell, 1985; Smallie & O'connor, 2000; Kohi *et al.*, 2011). Nonetheless the effects of elephants on ecosystems remain only partially understood.

Although elephants are considered unspecialized feeders (Kingdon, 1997), some plant species appear preferentially selected by elephants feeding in forests and woodlands (Viljoen, 1989; Sheil & Salim, 2004; Boundja & Midgley, 2009; Ihwagi *et al.*, 2009). Such selective impacts have implications for habitat composition and dynamics but are poorly characterized for closed high-altitude forests.

Elephants in Bwindi Impenetrable National Park ('Bwindi') are little studied, and their impacts remain poorly documented (Butynski, 1986; Babaasa, 1994, 2000). Bwindi's elephants occur principally in the southern part of the park (Fig. 1) and are commonly seen in and around the Bamboo forest during wet seasons and in the forest around Mubwindi Swamp during dry periods (Babaasa, 2000). The rugged terrain appears to restrict elephant movements to specific areas and paths. The elephant population has been estimated at 20 (Butynski, 1986), 22 (Babaasa, 2000) and more recently 40–50 (Plumptre *et al.*, 2008) with these numbers and more

casual observations (many footprints being of young animals) suggesting that the population is increasing.

We carried out this study to assess the selectivity of tree damage in Bwindi because of elephants in relation to species, stem sizes and locations. The dense herbaceous understorey made direct observations challenging and potentially dangerous, but also ensured that we were able to follow these animals by their fresh trails. The freshly trampled understorey was easily identified and elephants followed just as surely as if they were radio-collared. This means we knew where the animals had passed and could observe and sample the same vegetation that they had observed. Although we acknowledge limits to the explanatory power of this approach, we believe our results can be robustly interpreted to indicate patterns of damage and associated selectivity. As in any complex correlative study, causal reasoning remains speculative but all such patterns once revealed are available for further study.

Materials and methods

Bwindi Impenetrable National Park ('Bwindi') is located in south-western Uganda (0°53′–1°08′N and 29°35′–29°50′E). It is a diverse natural forest and covers approximately 331 km^2 with altitude ranging from 1160 to 2607 m (Howard, 1991). The landscape is rugged, with steep ridges and narrow valleys, and a general incline

from the high deeply dissected south and south-east to the lower north and north-west. The vegetation is classified as 'medium-altitude moist evergreen forest' and 'high-altitude submontane forest' (Langdale-Brown, Osmaston & Wilson, 1964) with an area of <0.4 km^2 of mountain bamboo *Arundinaria alpina* (Butynski, 1986).

Field work was conducted between September and November 2009 in four areas known to be frequented by elephants (Fig. 1): the Bamboo forest (*Bamboo*), the forest near Mubwindi Swamp (*Mubwindi*), the forest near Nshongi River (*Nshongi*) and the forest between the Bamboo forest and Mubwindi Swamp (*BMUB*). The forest's dense herbaceous understorey ensures that the elephants cannot move through the forest without leaving detailed signs of where they have been. This means that once a trail is located, it can be followed for evaluation of just what vegetation the animals have walked through. Our approach was to record fresh signs of elephant damage in elongated plots laid along fresh trails (0–5 days old). We searched for these trails after obtaining information regarding elephants' presence from park staff and others. To determine whether the trail was fresh enough and whether the damage was by elephants, we sought and examined any elephant dung, flattened vegetation, churned earth, footmarks and tusk marks on tree stems (guided by field staff of Institute of Tropical Forest Conservation who are experienced with tracking elephants).

A series of plots of 20 m × 4 m (running lengthwise along the trail) were laid out at 200-m intervals along the trail. At the centre of each plot, we recorded GPS coordinates and altitude. A Suunto PM-5 clinometer was used to measure slope and a densitometer to estimate cover. Each tree species in the plot larger than 2 cm DBH was identified, its stem diameter measured and any recent bark stripping, tree toppling and branch breaking along the main stem carefully examined and recorded. Plant identification was carried out by Robert Barigyira – the ITFC herbarium technician and botanist.

Data analysis

Using Arcview 3.2 (ESRI, 2000), we determined the shortest distance between each plot and the forest edge, and the distance to the closest permanent or ephemeral surface water source (i.e. rivers, streams and wetlands). Data layers were obtained from a reference GIS database of Bwindi and Mgahinga National Parks (Van Heist & Mugisha, 1995).

We calculated the 'preference ratio' (PR) for each species – the null hypotheses being that all species were equally impacted – as described by Viljoen (1989), as a simple measure of damage selectivity;

PR = PU/PA,

where PU = percent utilization and PA = percent availability.

PA = 100 × (n_{sp}/N), PU = 100 × (n_u/N_u), where n_{sp} = number of stems of a species in the plots, N = total number of all species in the plots, n_u = number of utilized trees of a species and N_u = number of utilized trees of all species in the plots. In this sense, 'utilization' means elephant damage. A 'selected species' (PR > 1) was defined as one that was damaged proportionately more frequently by elephants than the proportion of available trees of that species, whilst 'avoided species' had PR < 1 (Smallie & O'connor, 2000).

We used generalized linear models (GLM; McCullagh & Nelder, 1989; Barnett, 2004; Sheil & Salim, 2004) fitted in R version 2.6.0 (R Development Core Team, 2007), with a logit link function (logistic regression) to estimate the probability of a stem being damaged. We assessed effects of all single, two and three factor models giving the likelihood of a tree stem being damaged. A total of 144 models were generated with bark stripping, tree toppling and branch breaking as the response variables (i.e. 48 models for each). Explanatory factors considered were site, DBH, species, stem abundance, distance to forest edge, tree cover, altitude, terrain slope, distance to nearest ephemeral water source, distance to nearest permanent water source, nearest distance to any water source and basal area. We identified the best models as those with the lowest Akaike Information Criterion (AIC; Akaike, 1974). We followed the logistic function:

$$(Z) = \frac{e^z}{e^z + 1} = \frac{1}{1 + e^{-z}} \tag{1}$$

Here z is defined as

$$Z = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \cdots \beta_k X_k \tag{2}$$

where β_0 is the 'intercept' and β_1, β_2, β_3 and β_k are the 'regression coefficients' of the tree and site characteristics (categorical and continuous variables) X_1, X_2, X_3, and X_k respectively. For continuous variables, the intercept is the value of z when the value of all independent variables is zero. For nominal variables, the intercept is the reference

class of each variable. Each regression coefficient describes the size of the contribution of the explanatory factors X_1, to X_k in Eq. (2). The form of a regression coefficient if positive or negative means that the explanatory variable increases or decreases the probability of the outcome, respectively. The magnitude of the regression coefficient indicates the strength of influence of the explanatory factor (for more clarification concerning model specification see McCullagh & Nelder, 1989; Barnett, 2004).

Results

General summary

We walked a total of 26.84 km of elephant trails. A total of 122 sample plots (sum = 0.976 ha) were located in the four sites with 33 plots in *Mubwindi*, 36 in *Nshongi*, 20 in *Bamboo* and 33 in *BMUB*. *Mubwindi* had 29 species with a total of 303 stems (DBH ≥ 2 cm), 230 saplings (DBH 2–9.9 cm) and 73 large trees (DBH ≥ 10 cm). *Nshongi* had 38 species, 295 total stems, 227 saplings and 68 large trees. *Bamboo* had 25 species, 75 total stems, 49 saplings and 26 large trees. *BMUB* had 25 species, 224 total stems, 129 saplings and 95 large trees.

Eight hundred and 97 tree stems (DBH ≥ 2 cm) representing 55 species were recorded in 113 sample plots with nine plots being empty, and six hundred and 23 saplings (DBH 2–9.9 cm) representing 48 species recorded in 100 plots (with 13 more being empty). Two hundred and 74 stems (present in 96 sample plots) were ≥ 10 cm DBH representing 45 species. The most abundant tree species overall were *Neoboutonia macrocalyx* Pax (Euphorbiaceae; n = 194), followed by *Galiniera saxifraga* (Hochst.) Bridson (Rubiaceae; n = 84), *Xymalos monospora* (Harv.) Warb. (Monimiaceae; n = 59), *Psychotria mahonii* C. H. Wright (Rubiaceae; n = 55) and *Macaranga kilimandscharica* Pax (Euphorbiaceae; n = 54). Overall, 542 stems (60.4%) appeared fully intact, whereas 274 (30.5%) had been toppled, 172 (19.2%) had been broken and 22 (2.5%) had had their bark stripped (n = 897). All these impacts were attributed to elephants due to the nature of the damage (e.g. tusk marks on tree stems) and the evidence that the animals had recently been present.

How does elephant damage vary with openness of the forest?

Elephant damage was evident along trails across the study sites but was especially common in more open areas with vigorous pioneer growth (F. Ssali, pers. obs.). There was a markedly higher incidence of damage in plots nearer to the forest edge (Spearman rank correlation: r_s = −0.299, n = 111, P = 0.001, Fig. 2a) and in plots with low tree cover (Spearman rank correlation: r_s = −0.298, n = 111, P = 0.015, Fig. 2b).

Single-factor analyses explaining damage across sites

Generalized linear models indicated significant differences in per-stem probabilities of a given tree stem being damaged among sites. For bark stripping, a tree stem from *BMUB* and *Nshongi* had a significantly higher likelihood of selection compared to a tree from *Bamboo*. With respect to branch breaking, a stem from *Mubwindi* and *BMUB* had a significantly higher likelihood of selection compared to a tree stem from *Bamboo*. For tree toppling, a stem from *Nshongi* and *Mubwindi* had a significantly higher likelihood of selection compared to a tree from *bamboo*. The likelihood of a tree being toppled was markedly higher at *Nshongi* than at others. Generally, these models showed that elephants preferentially selected trees in *Nshongi* for toppling but had no other favoured sites for tree damage (Table 1).

Damage by DBH as explained by single-factor GLM

In single-factor logistic models, DBH was positively related to bark stripping but negatively related with tree toppling and branch breaking (Table 1: models 1b, 2b and 3b). Thus, stem-by-stem, larger trees were more frequently debarked compared to smaller trees, whereas smaller trees were more frequently toppled or had branches broken when compared with larger stem.

Which species of small trees were selected or neglected by elephants?

Out of the available 623 stems of small trees (DBH 2–9.9 cm), 255 were toppled, 152 had broken branches and three were bark stripped. *Newtonia buchananii* (Baker) Gilbert & Boutique, *Myrianthus holstii* Engl., *Chrysophyllum albidum* G. Don and *Macaranga kilimandscharica* Pax were more likely to be toppled or branch broken than most other stems. *Psychotria mahonii* C. H. Wright was more often bark stripped. *Cassipourea gummiflua* Tul., *Teclea nobilis* Del. and *Neoboutonia macrocalyx* Pax were comparatively neglected and thus escaped damage (Table 2).
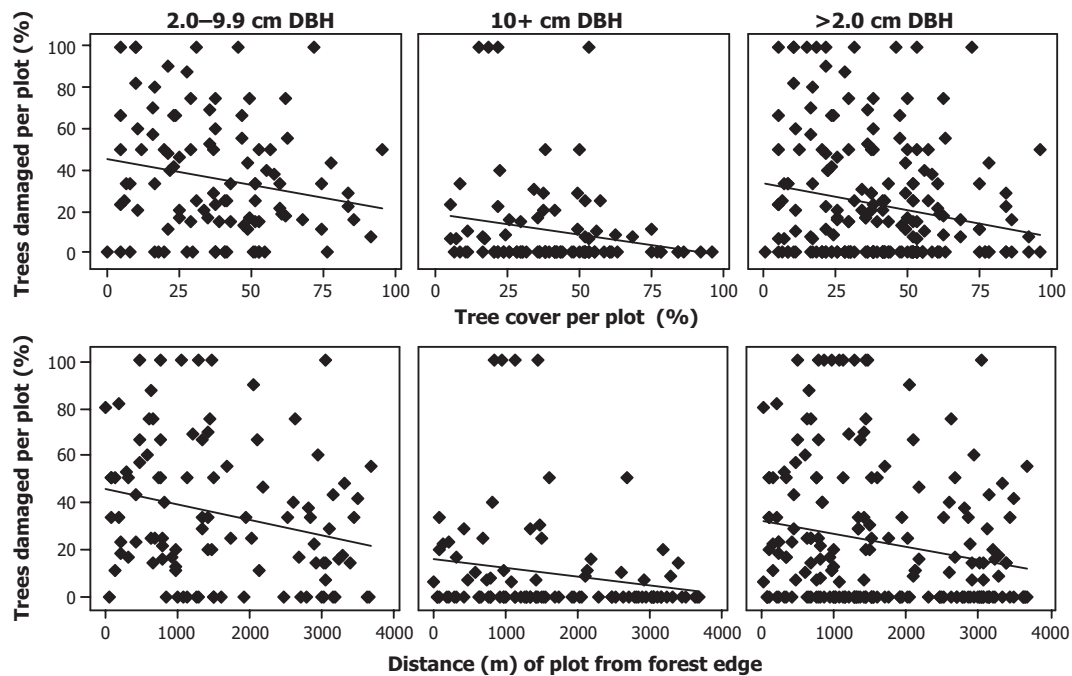
Fig 2 Variation of elephant impacts with tree cover and distance of plot from the forest edge

Tree toppling, branch breaking and bark stripping as explained by combined GLM

The AIC of the top three models for tree toppling differed substantially (Model 1, AIC = 810.7, Model 2, AIC = 812.4 and Model 3 AIC = 814.4). The best GLM (i.e. Model 1) suggests that the per-stem probability of a tree being toppled was influenced by DBH, species and location (Table 3). All three models confirmed that the likelihood of tree toppling was dependent on species identity and negatively related to stem size with smaller trees more likely to be toppled. With respect to branch breakage, the AIC of the top three models differed notably (Model 1, AIC = 723.59, Model 2, AIC = 729.48 and Model 3 AIC = 731.48). The best GLM (i.e. model 1) showed that per-stem probability of a given tree's branches being broken decreased as stems became larger. For instance, increasing a stem by 5 cm decreased the probability of its branches being broken by 27–28% – but damage patterns were also substantially nonrandom with respect to site and species identity with *Myrianthus holstii* being especially impacted.

The AIC of the best three models for bark stripping was only marginally different (Model 1, AIC = 167.41, Model 2, AIC = 167.68 and Model 3 AIC = 168.32; Table 3). All

three showed a consistent relationship, with respect to form and magnitude, of the probability of bark stripping and DBH. As in the single-factor analyses, these models showed that the probability of a given stem's bark being stripped increased with stem size. For Model 1, adding 10 cm to a stem increased its probability of being bark stripped by approximately 1%. In addition, Model 1 suggests that bark stripping occurred more frequently on a per-stem basis if a tree was located further away from permanent water sources – but this relationship remains only weakly supported as it is not part of the second best model (Table 3).

Discussion

The elephants that we have followed by their tracks through the undergrowth have caused damage to trees. On a stem-by-stem basis, these patterns of damage appear to be influenced by stem size, by species and by location. Our data indicate that elephants selectively topple and break branches of smaller trees with larger trees seldom subjected to such damage. This can be attributed at least in part to stem strength and accessibility. Larger stems possess greater strength and resistance that helps them to

Table 1 Per-stem probabilities of trees being impacted with each damage type based on (a) site and (b) DBH

	Estimate	Error	Probability
Model 1a: P(tree toppling$_i$) = constant + as.factor (site$_i$) + noise$_i$, AIC = 1060.2, N = 897			
Intercept	−0.816	0.250	0.001
BMUB	−0.381	0.296	0.199
Nshongi	0.660	0.276	0.017
Mubwindi	−0.522	0.288	0.07
Model 2a: P(branch breaking$_i$) = constant + as.factor (site$_i$) + noise$_i$, AIC = 867.24, N = 897			
Intercept	−0.8792	0.2536	0.001
BMUB	−0.8765	0.316	0.006
Nshongi	−0.233	0.2873	0.417
Mubwindi	−0.8934	0.3015	0.003
Model 3a: P(bark stripping$_i$) = constant + as.factor (site$_i$) + noise$_i$, AIC = 180.88, N = 897			
Intercept	−1.9924	0.3553	2.06×10^{-08}
BMUB	−1.181	0.492	0.016
Nshongi	−2.2946	0.6162	0.0002
Mubwindi	−18.5736	1018.583	0.986
Model 1b: P(tree toppling$_i$) = β_1DBH$_i$ + noise$_i$, AIC = 957.36, N = 897			
Intercept	0.2953	0.1345	0.028
DBH	−0.1587	0.02098	3.90E-14
Model 2b: P(branch breaking$_i$) = β_1DBH$_i$ + noise$_i$, AIC = 835.59, N = 897			
Intercept	−0.8732	0.1244	2.27E-12
DBH	−0.0697	0.0144	1.24E-06
Model 3b: P(stripping$_i$) = constant + β_1DBH$_i$ + noise$_i$, AIC = 191.79, N = 897			
Intercept	−4.3874	0.3066	2.00E-16
DBH	0.0394	0.008	8.73E-07

NB: For models 1a, 2a and 3a, the intercept represents the reference site (i.e. *Bamboo*).

withstand elephant damage (Sheil & Salim, 2004). In contrast, smaller stems are vulnerable and can easily be pushed over by elephants to bring foliage into easy reach during feeding. In addition, branches are more likely to be out of reach on the bigger stems. Our results also suggest that while elephants only rarely strip bark from tree stems they preferentially select larger trees when they do so. One plausible explanation of this finding is that elephants do not seek out smaller trees for bark because they do not have much bark available (Gadd, 2002). The observation that bark stripping occurred more frequently on a per-stem basis if a tree was located further away from permanent water sources is suggestive but remains inconclusive because of our small sample size, and the similar (only marginally reduced) degree of fit demonstrated by other models.

Our study and previous studies in Bwindi (Babaasa, 1994) and Kibale forest (Kasenene, 1980, 1984; Lwanga, 1994) show that when all damage is considered, elephants preferentially impact small trees. All these studies report relatively consistent patterns in terms of relative differences in how species are impacted (Table 4). From these studies, we conclude that elephants selectively inflict damage on small trees of *Newtonia buchananii*, *Chrysophyllum* sp., *Strombosia scheffleri* and *Alangium chinense* but, in a stem-by-stem comparative sense, avoid impacting stems of *Psychotria* sp. and *Teclea nobilis*. Such selective impacts indicate that elephants may selectively disadvantage some tree species over others. However, the nature of these effects is not certain because consequences may also differ among species, and the interactions of elephants and trees can produce feedback loops in which faster-growing tree species selected for damage actually benefit relative to others that may initially appear less impacted (Sheil & Salim, 2004). A good example was noted in the Shimba Hills, Kenya, where Höft & Höft (1995) reported that by feeding more frequently on the light demanding, gap colonizing species of *Leptonychia usambarensis* K. Schum.,

Table 2 Small trees (DBH 2–9.9 cm with >10 stems in all plots) selected or neglected by elephants

Species	Preference ratio tree toppling (n of n)	Preference ratio branch breaking (n of n)	Preference ratio bark stripping (n of n)
Newtonia buchananii (Baker) Gilb. & Bout.[b]	2.55 (15/15)[a]	2.44 (9/15)	0.00 (0/15)[a]
Myrianthus holstii Engl.[b]	2.35 (12/13)[a]	2.50 (8/13)	0.00 (0/13)[a]
Chrysophyllum albidum G. Don[b]	2.18 (24/28)[a]	1.02 (7/28)[a]	0.00 (0/28)[a]
Macaranga kilimandscharica Pax[b]	1.89 (32/43)[a]	2.74 (29/43)[a]	0.00 (0/43)[a]
Carapa grandiflora Sprague[b]	1.62 (8/11)[a]	1.85 (5/11)	0.00 (0/11)[a]
Strombosia scheffleri Engl.[b]	1.60 (17/27)	1.50 (10/27)	0.00 (0/27)[a]
Xymalos monospora (Harv.) Warb.[b]	1.15 (21/42)	2.03 (25/42)	0.00 (0/42)[a]
Psychotria mahonii C. H. Wright[d]	0.72 (9/32)[a]	1.27 (10/32)	16.63 (3/32)[a,*]
Bersama abyssynica Fresen.[c]	1.45 (8/14)	0.87 (3/14)[a]	0.00 (0/14)[a]
Galiniera saxifraga (Hochst.) Bridson[c]	1.07 (34/76)	0.75 (14/76)[a]	0.00 (0/76)[a]
Drypetes gerrardii Hutch.[e]	0.17 (1/15)[a]	1.08 (4/15)	0.00 (0/15)[a]
Cassipourea gummiflua Tul.	0.67 (9/34)[a]	0.24 (2/34)[a]	0.00 (0/34)[a]
Teclea nobilis Del.	0.13 (3/20)[a]	0.20 (1/20)[a]	0.00 (0/20)[a]
Neoboutonia macrocalyx Pax	0.36 (23/161)[a]	0.20 (8/161)[a]	0.00 (0/161)[a]

[a] significant χ^2, $P < 0.05$, df = 1.
[b] selected for tree toppling or branch breaking.
[c] selected for tree toppling
[d] selected for branch breaking or bark stripping
[e] selected for branch breaking
* the only debarked small trees.

elephants were also favouring its regeneration. Similarly, elephants in Bwindi may favour persistence and growth of fast-growing damage tolerant pioneer tree species such as *Neoboutonia macrocalyx*, *Macaranga kilimandscharica* and *Polyscias fulva*. More research would be required to understand these dynamics.

The most selected species in our results seem to be neither fast-growing pioneer nor slow-growing late-successional shade-tolerant species but rather to be what we judge to be 'mid-successional species' like *Newtonia buchananii*, *Myrianthus holstii* and *Chrysophyllum albidum*. Hawthorne (1995) and Sheil, Jennings & Savill (2000) describe pioneer species as those consistently well exposed ('early successional'); shade-tolerant species as those consistently found in shade ('late successional') and mid-successional (or 'non-pioneer light demander' after Hawthorne, 1995) species as those relatively shaded at seedling stage but become relatively exposed at larger sizes. Sheil & Salim (2004) proposed that mid-successional species are least tolerant of elephants as these species are poor at both resisting damage and recovering from it. Thus, elephants in Bwindi may selectively disadvantage mid-successional species shifting overall competitive processes to benefit

other, early and late-successional, species. Therefore, as elephant numbers increase, mid-successional species may be depleted in habitats selected by elephants.

Plant damage has been widely used to infer animal feeding selectivity (e.g. for elephants, Tchamba & Seme, 1993; Lwanga, 1994; Babaasa, 2000; Theuerkauf *et al.*, 2000). Strictly, these data refer to the observations of damage that could be caused by other (nonfeeding) behaviours – for example, elephants may damage trees by scratching on them, pushing past them, in play or as part of a display. Direct observations, or dung analysis, are required to assess these relationships further and to determine which species contribute to feeding. In this sense, our study is about patterns of stem damage – not about feeding *per se*.

Our study differs from the past assessment, in that we set out to evaluate and describe tree selection by elephants, and how location and tree characteristics influence tree damage. Babaasa (2000) had previously considered the time elephants spent in each vegetation type and had sought to identify the principal food plants. Our results and those of Babaasa (2000) agree that the elephants in Bwindi are selective based on where they range and how

Table 3 The best logistic models explaining tree toppling, branch breaking and bark stripping

	Estimate	Error	Probability
Tree toppling			
Model 1: P(toppling$_i$) = constant + β_1DBH$_i$ + as.factor (site$_i$) + as.factor (species$_i$) + e_i, AIC = 810.7			
Intercept	2.10317	1.02819	0.0408
DBH	−0.19131	0.02543	5.36×10^{-14}
Selected species with *P* value <0.01			
Neoboutonia macrocalyx	−2.80611	0.97042	0.0038
Model 2: P(toppling$_i$) = constant + β_1DBH$_i$ + as.factor (species$_i$) + e_i, AIC = 812.36			
Intercept	2.16415	0.94882	0.0226
DBH	−0.19301	0.02543	3.19×10^{-14}
Selected species with *P* values <0.01			
Neoboutonia macrocalyx	−3.12688	0.95664	0.0011
Drypetes gerrardii	−4.06248	1.39418	0.0036
Teclea nobilis	−3.13552	1.12575	0.0054
Model 3:P(toppling$_i$) = constant + β_1DBH$_i$ + β_2(species abundance) + as.factor(species$_i$) + e_i, AIC = 814.36			
Intercept	6.40	2350	0.9978
DBH	−0.193	0.0254	3.19×10^{-14}
Abundance	−0.639	354	0.9986
Selected species with *P* values <0.1			
Pauridiantha callicarpoides	−2.50	1.47	0.0883
Branch breaking			
Best model: P(breaking$_i$) = constant + β_1DBH$_i$ + as.factor (site$_i$) + as.factor (species$_i$) + e_i, AIC = 723.59			
Intercept	−0.447	1.19	0.7073
DBH	−0.0836	0.0162	2.34×10^{-07}
Selected site and species with *P* values <0.05			
BMUB (site)	−1.08	0.43	0.012
Myrianthus holstii	2.51	1.24	0.043
Bark stripping			
Model 1. P(stripping$_i$) = constant + β_1DBH$_i$ + β_2(Dperm) + as.factor (site$_i$) + e_i, AIC = 167.41			
Intercept	−1.71	0.706	0.0154
DBH	0.0346	0.00898	0.0001
Dperm	−0.00144	0.000829	0.0819
BMUB (i.e. site)	−1.21	0.518	0.0198
Nshongi (i.e. site)	−2.58	0.706	0.0003
Model 2. P(stripping$_i$) = constant + β_1DBH$_i$ + β_2(slope) + as.factor (site$_i$) + e_i, AIC = 167.68			
Intercept	−2.09448	0.57207	0.0003
DBH	0.033893	0.009141	0.0002
Slope	−0.02623	0.016455	0.1109
Model 3. P(stripping$_i$) = constant + β_1DBH$_i$ + β_2(Dwater) + as.factor (site$_i$) + e_i, AIC = 168.32			
Intercept	−3.38346	0.623242	5.67×10^{-08}
DBH	0.037224	0.009065	4.02×10^{-05}
Dwater	0.003385	0.002243	0.1313

Where i = 1,…, 897, P(toppling$_i$) is the likelihood of stem i to be toppled, P(breaking$_i$) is the likelihood of branches of stem i to be broken, P(stripping$_i$) is the likelihood of stem i to be bark stripped, Dperm is the nearest distance to permanent water surface, Dwater is the nearest distance to any water surface, and e_i is noise.

Table 4 Small trees selected or neglected by elephants across studies in Kibale and Bwindi forests

Species	Kibale author		Bwindi author	
	Kasenene, 1980, 1984[a]	Lwanga (1994)[b]	Babaasa (1994)[c]	This study[d]
Newtonia buchananii (Baker) Gilb. & Bout.	1.77	5.75	0.54	2.05
Chrysophyllum sp.	1.559	5.75	NS	1.91
Strombosia scheffleri Engl.	1.31	5.75	NS	1.45
Psychotria sp.	NS	0	NS	0.90
Teclea nobilis Del.	0.36	0	0.66	0.41
Cassipourea sp.	1.363	0	NS	0.60
Myrianthus sp.	NS	0	NS	2.05
Symphonia globulifera L. f.	0.938	NS	NS	1.31
Macaranga kilimandscharica Pax	NS	NS	0.95	1.75
Alangium chinense (Lour.) Harms.	NS	NS	1.69	2.09

NS, none in sample.

[a]0.5 m tall to ≤ 12.7 cm DBH.

[b]≥ 1.0 to <14 cm DBH.

[c]≥ 2.0 cm DBH.

[d]2.0 to <10 cm DBH.

they cause damage to trees as they move and feed. But in contrast to Babaasa (2000) who found only 17.0% damage (71 of 417 stems with DBH ≥ 2 cm, i.e., *Newtonia buchananii, Macaranga kilimandscharica, Strombosia scheffleri, Maesa lanceolata, Galiniera (coffeoides) saxifraga, Polyscias fulva* and *Alangium chinense*), we found 61.4% damage (127 of 207 stems with DBH ≥ 2 cm). This can be attributed in part to our more elephant trail focused approach. Babaasa used 20 × 10m plots located along elephant trails and transects independently of elephant tracks. We used narrower 20 × 4 m plots with the long axis following the direction of elephant trails. Despite using narrower sample plots, our data gave a calculated value of 24.6% damage for 20 × 10 m plots (after correcting for differences in plot width and assuming if there is no damage in the additional width), which is still slightly higher than that of Babaasa. Thus, our results may indicate that the intensity of elephant damage has increased.

We believe that the main reason for the increase in damage can be attributed to the increasing population of elephants and their propensity to focus their activities in a limited part of the forest. If their population continues to grow, we predict that elephants will have an increasing influence on the vegetation and thus on the habitats of the other forest's animals. By opening the forest and maintaining thick undergrowth, elephants may be creating a habitat favoured by several species of conservation interest that favour open areas and young secondary regrowth; these species include the Mountain gorilla *Gorilla gorilla beringei* (Nkurunungi *et al.*, 2004), Golden cat *Profelis aurata* (Kingdon, 1997) and the Stripe-breasted Tit *Parus fasciiventer* (Shaw & Shewry, 2001). On the other hand, an increasing population of elephants implies greater competition for finite food resources. For instance, elephants appear to target fruit trees like *Myrianthus holstii, Chrysophyllum albidum* and *Alangium chinense* (Table 4) and may thus deplete food for other fruit-eating animals including Mountain gorilla, chimpanzee and hornbills. Thus, elephants may influence other animals in a complex manner.

Our approach is conceptually simple and has, despite some limitations, indicated that Bwindi's elephants cause significant damage to trees and that this damage can be understood, at least to some degree, as selective. We had no difficulty in detecting and following elephant trails in the dense understorey vegetation – this is in contrast to researchers elsewhere that have not always been able to follow animals in more open vegetation. We were able to observe where individual animals had trampled the herbaceous vegetation and thus to follow their movements in detail. This allowed us to identify trees that the animals had been close to and examine them for any signs of

associated damage. A number of caveats should be high-lighted with respect to these data and their interpretation. As mentioned earlier, our data are records of recent damage – and although we suspect feeding behaviour as the primary cause, we do not know how or why these trees were damaged. Nor can we know for certain why these animals are in one part of the forest and not another, and how the intensity of damage may result from chance factors such as the idiosyncratic behaviour of a specific group of animals. Most of our tracking efforts involved following larger multi-animal groups. It may be that solitary animals, such as old bulls, behave differently and have distinct damage implications. Our study was carried out in the wet season, whereas elephant damage is likely to vary with season due to variation in availability of key foods such as fruits and bamboo shoots (see Babaasa, 2000). Thus, we consider our results provisional – they show the potential of our approach but need to be viewed as tentative and subjected to fuller investigation.

In spite of the low stem counts, our analyses produced significant and apparently meaningful logistic models explaining the likelihood that a stem will be damaged by elephants. This underscores the statistical power of GLM to clarify relationships offering a considerable improvement over conventional selection indices (Sheil & Salim, 2004). It should be highlighted nonetheless that disentangling patterns still requires good data and a careful appraisal of biases and confounding factors – for example, in our study, the influence of distance to various sources of water remains uncertain and would require further work to look specifically at these variables.

Further work on elephants and ecosystem dynamics in Bwindi is needed. Such work should ensure a full year of observations, should include additional data collections to clarify group sizes, animal numbers, animal sizes, ranging patterns and relationship to feeding and drinking behaviours (direct observations would be valuable – camera traps may make this practical). In addition monitoring, to understand tree dynamics and the relative influence of elephant damage, is needed.

Conclusions

Bwindi's elephants are selective concerning where, how and what trees they damage. Small trees were more likely to be pushed over or have their branches broken, whereas larger trees were more likely to be stripped of their bark. In general, the trees most likely to be damaged on a per-stem-basis appeared to be mid-successional species including *Newtonia buchananii*, *Myrianthus holstii* and *Chrysophyllum albidum*, which may be vulnerable to increasing elephant numbers. Elephants appear to be promoting vigorous pioneer tree species and open areas that likely benefit a number of other species including mountain gorillas.

We recommend monitoring of vegetation in areas frequented by elephants to evaluate their effects on the growth and survival of trees and other vegetation. As elephant populations appear to be growing, further clarification of how elephants contribute to or subtract from other conservation values in Bwindi Impenetrable National Park is needed to guide management decisions.

Acknowledgements

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