High elephant impact is capable of converting tall mopane woodland to shrubland in the South East Lowveld of Zimbabwe

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Abstract

African elephants are known to be important agents of structural and compositional changes in several vegetation types in southern Africa. This is of concern for biodiversity conservation and management of wildlife areas in the region. This study assesses how increasing elephant numbers have already altered and are likely to continue to modify the structure and composition of mopane woodlands in the south-eastern lowveld of Zimbabwe. Several features of vegetation structure and composition were quantified and compared across areas under three different elephant densities: low, intermediate and high. We assessed the degree, nature and patterns of damage incurred by woody plants within these woodlands to determine how elephants are both driving and responding to the changes in the vegetation. Increasing elephant densities were associated with increased losses of tall trees and the resultant development of a coppiced shrub layer. As elephant densities increased from low to intermediate levels, so did the level of damage to both shrubs and trees. However, elephants appeared to exhibit a functional response such that the increase in damage to the shrub layer was proportionately higher than to trees, probably because the coppiced shrub layer was a preferable food source. Nevertheless if elephant density increases further to high levels, damage to trees is likely to continue increasing suggesting that tree losses are likely to continue. In particular, the high level of bark damage to emergent trees is predicted to contribute greatly to further tree losses. This study provides evidence to suggest that increasing elephant impact is capable of completely converting tall mopane woodlands to shrublands. This is likely to have indirect effects on the ecosystem functioning and diversity of these areas as well as tourism, and is consequently of concern for local management. Continued monitoring of these woodlands and management of elephant abundance is advisable if a total conversion to shrubland is to be avoided.

Introduction

Protected areas such as national parks and privately owned reserves are a vital component of conservation efforts in Africa (de Beer et al. 2006). African elephants (*Loxodonta africana)* are charismatic mega-herbivores that inhabit many of these areas. In these areas they are a major attraction for tourists and a keystone species that supports important ecosystem processes such as seed dispersal and nutrient cycling (O'Connor et al. 2007; Shannon et al. 2008; Gandiwa et al. 2011). However, as a result of their large body size and energy requirements (Shannon et al. 2006), elephants can profoundly impact vegetation dynamics and ecosystem processes and are thought to be the most ecologically influential of all herbivores in savanna ecosystems (Chamaillé-Jammes et al. 2007). Particularly when they occur in high densities elephants are capable of driving significant changes to vegetation structure and composition (Rutina et al. 2005; Chamaillé-Jammes et al. 2007; O'Connor et al. 2007; Teren & Owen-Smith 2010; Dunham 2012). The fact that elephants can be both beneficial and detrimental to savanna ecosystems simultaneously necessitates and complicates their management.

Numerous studies have demonstrated that elephants modify landscapes and woodlands (Herremans 1995). Elephant impact is a major cause of the reduction of or sometimes complete loss of woodlands (Ben-Shahar 1996; Mosugelo et al. 2002), often seen as a transition to open savanna grassland (Rutina et al. 2005; O'Connor et al. 2007; van de Vijver et al. 2007; Gandiwa et al. 2011) or shrubland (Mosugelo et al. 2002; Chamaillé-Jammes et al. 2007). In addition to browsing damage, elephants increase tree mortality (van de Vijver et al. 1999), subdue recruitment and regeneration (O'Connor et al. 2007; Gandiwa et al. 2011), and in some cases cause the local extirpation of certain woody species (O'Connor et al. 2007). Often elephant impact acts together with other factors such as drought, fire and other herbivores in causing damage to vegetation (Mosugelo et al. 2002; de Beer et al. 2006; O'Connor et al. 2007).

Although elephants are primarily grazers in the wet season, in the dry season they switch to browse (Pretorius et al. 2011). Browse foraging involves leaf and branch removal, barkstripping, pollarding and uprooting trees (Midgley et al. 2005; O'Connor et al. 2007; Nasseri et al. 2010; Gandiwa et al. 2011; Pretorius et al. 2011). Mopane (*Colophospermum mopane)* are the dominant woody species in mopane woodlands and are an important as well as often preferred food source for elephants (Ben-Shahar 1996; Smallie & O'Connor 2000; Nasseri et al. 2010). Therefore this species is particularly prone to elephant incurred damage and mortality. Despite this, mopanes are relatively tolerant to elephant impacts in comparison to many other woody species. This is because they exhibit coppice growth (O'Connor et al. 2007) such that regrowth can arise from a felled adult tree or plants can recover after extreme browsing (Lewis 1991) to form a 'coppice shrub'. In light of the coppicing ability of *C. mopane* and the fact that elephants have been known to considerably modify other vegetation types, it is plausible to expect that elephant impact is an influential mechanism in shaping mopane woodlands structurally and compositionally.

Mopane woodlands in several river valleys in southern Africa are a key habitat for wildlife, especially elephants (Lewis 1991). Such mopane woodlands occur within the Malilangwe Wildlife Reserve in the south-eastern lowveld of Zimbabwe. Since the year 2000, elephant numbers in Malilangwe have almost trebled from about 115 to approximately 291 individuals in 2014 (Clegg, personal communication 2014). To a large extent this was due to immigration of bulls from neighbouring Gonarezhou National Park (Clegg, personal communication 2014). Consequently the degree of elephant impact has markedly increased and this study assesses to what extent this has modified the structure of mopane woodlands on alluvium associated with the Chiredzi and Nyamasikana Rivers (Clegg & O'Connor 2012).

Initially these woodlands were largely composed of tall mopane trees (Clegg, personal communication 2014). However the gradual increase in elephant impact over the past fourteen years as a result of increasing elephant numbers in Malilangwe is thought to have caused several structural and compositional changes. Whilst the tree layer has been particularly targeted, a shrub layer has begun to develop in response due to the coppicing ability of mopane. Therefore it is possible that these woodlands have been altered to some extent, from tall open mopane woodlands to dense shrublands.

The newly developed shrub layer in Malilangwe is likely to be superior to the tree layer for supplying the elephants' foraging needs, both qualitatively and quantitatively. A study by Smallie & O'Connor (2000) showed that elephants selectively utilized mopane plants whose stems had previously been broken and had coppiced as a result. This is probably because coppice shrubs have a greater number of branches of the preferred range of diameter (Smallie & O'Connor 2000) and because coppice growth has a much higher density of leaf per unit canopy volume than non-coppice growth (Smit & Rethman 1998). These both contribute to increased browse availability, making it very profitable for elephants to forage from coppiced plants. Furthermore, numerous studies have shown that an elephant's preferred feeding height is below 2 m (Smallie & O'Connor 2000), the height at which much of the shrub canopy occurs. If the developing shrub layer in Malilangwe does provide sufficient and preferable browse for elephants, then it is reasonable to suggest that eventually a point will be reached where it is no longer necessary for them to fell the tall trees.

Tall trees serve a number of important roles. Not only are they aesthetically valuable (van de Vijver et al. 1999), they are also ecologically valuable, offering food and shelter for many animals and contributing to nutrient cycling (Shannon et al. 2008). Vegetation structure can have a profound influence on both faunal diversity and species composition. Areas with a more layered structure consisting of tall trees, lower shrubs and herbs often have a higher species richness of birds and insects than open woodlands with no layering. This has been found in miombo woodlands where the tree layer has been removed by elephants (Cumming et al. 1997). Additionally, the height of mopane trees is critical for their seed production, as has been shown with trees in the Luangwa Valley in Zambia that begin fruiting at heights > 5 m (Lewis 1991). Therefore although mopane trees are relatively robust to elephant damage in the short-term, tree losses in the long-term are likely to be detrimental for regeneration and recruitment and ultimately the local persistence of this species (Smallie & O'Connor 2000).

Large trees are clearly valuable for maintaining ecosystem function (Shannon et al. 2008). Therefore it would be desirable for the elephants in Malilangwe forage proportionately more from the developing mopane shrub layer rather than continue to fell the tall trees at such high rates. Tree losses should therefore decline and thus a complete conversion from woodland to shrubland would be avoided.

This study investigated the likelihood of this scenario. To do this we conducted a long-term assessment of the woody component of mopane woodlands in Zimbabwe under various levels of elephant density. Woody species can be seen as ‘ecological indicators’ and monitoring them is useful for understanding the effects of elephants on woodland dynamics (van de Vijver et al. 1999; Chira & Kinyamario 2009). Additionally, long-term studies are preferable because they provide a more accurate indication of long-term trends (van de Vijver et al. 1999) and changes in vegetation cover (Mosugelo et al. 2002).

According to Walker (1976) proper management of areas subject to elephant herbivory requires that a number of considerations be made: the structure and composition of the vegetation, the nature of utilization by elephants as well as any changes occurring or likely to occur in the vegetation and its utilization.

In making these considerations for mopane woodlands we predicted that:

1) The shrub layer in the Malilangwe Wildlife Reserve had developed as a consequence of the increase in elephant numbers.

2) The elephants are exhibiting a functional response to this change in vegetation structure by increasing their utilization of the shrub layer proportionately more than of the tree layer.

3) As elephant density increases further, elephant utilization of shrubs is likely to level off. Additionally utilization of trees is likely to either level off or decline such that tree losses will decrease and tree densities may eventually reach equilibrium.

To test these predictions, we assessed the structural and compositional differences between areas of mopane woodlands on alluvium under low, intermediate and high densities of elephants. Additionally we investigated the degree, nature and patterns of damage incurred to woody plants within these woodlands and assessed how these vary with increasing elephant density.

Methods

Study site and plot locations

The current study was conducted in two areas of tall mopane woodland on alluvium; one within the Malilangwe Wildlife Reserve (Zimbabwe) and the other in the Gonarezhou National Park (Zimbabwe). Located in south-eastern lowveld of Zimbabwe, the Malilangwe Wildlife Reserve (20°58′–21°15′ S, 31°47′–32°01′ E), is an extremely diverse protected area. A wide variety of plants and animals, including elephants, inhabit its highly heterogeneous landscape. The reserve is 39 378 ha in size and consists of 38 vegetation types with a total of 468 recorded plant species (Clegg & O'Connor 2012). A data set already existed for 8 plots within Malilangwe in the mopane woodlands close to the Chiredzi and Nyamasikana Rivers

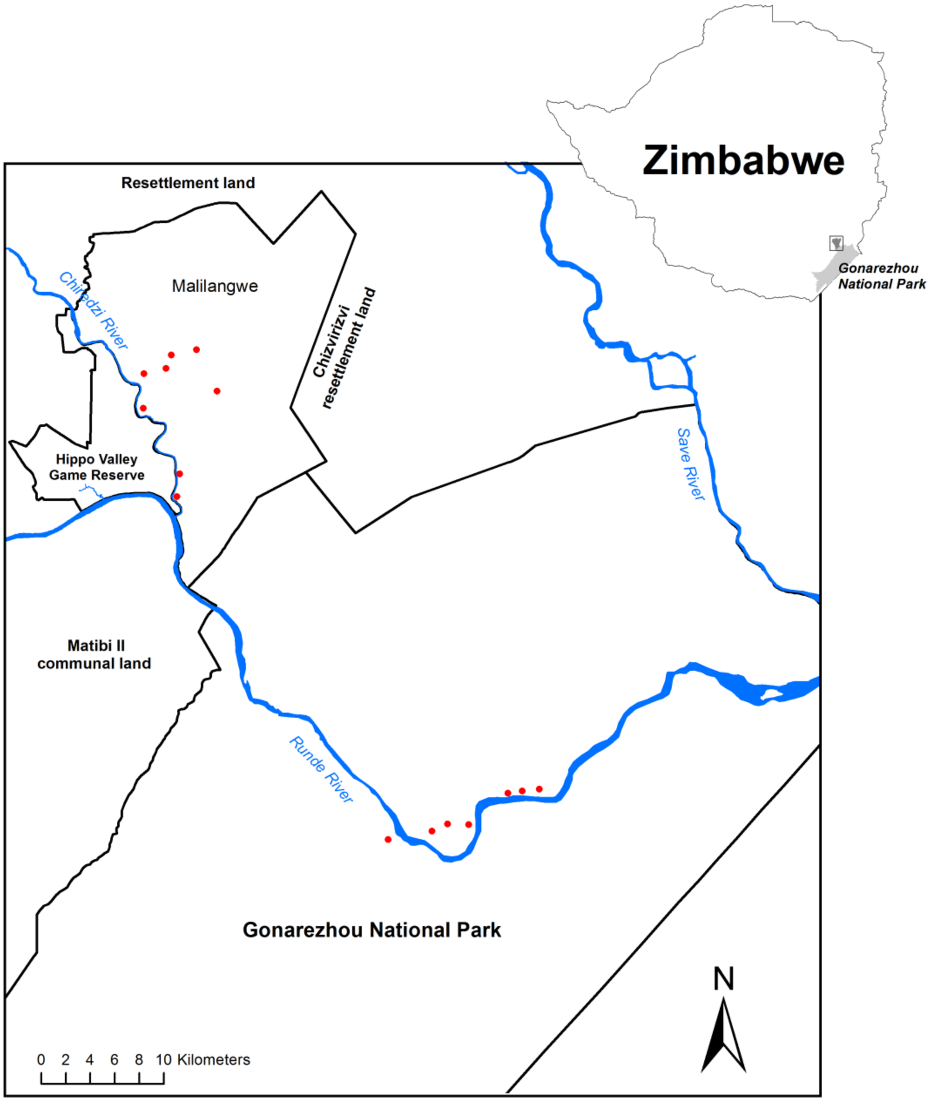


Figure 1: The location of sampling sites (red dots) in tall mopane woodlands on alluvium within the Malilangwe Wildlife Reserve (n = 8) and Gonarezhou National Park (n = 7).

(Figure 1). The woody component in these plots were initially sampled by Clegg (Clegg & O'Connor 2012) using similar techniques to those outlined below in the description of the Gonarezhou sampling effort. The initial sampling took place during the dry season (July, August and September) in 2000 and 2001, a time frame when elephant density was relatively low, just 0.23 elephants/km^2 (Dunham et al. 2013). To assess changes in structure and composition as well as elephant utilisation in this vegetation type since elephant numbers have increased, we resampled the original 8 plots within Malilangwe in August 2014 after elephant density had increased to an intermediate level of 0.59 elephants/km^2 (Dunham et al. 2013).

Plots were relocated and mapped out using GPS coordinates and transect diagrams from the original sampling effort. Due to GPS error, the re-sampled plots and transects within them were only accurate to between 1 and 5 m, however, this margin of error was inconsequential considering the broad scaled nature of the study. Each 'plot' consisted of nested 'transects' of variable sizes ranging in size from 0.005 ha to 0.25 ha for shrubs, and 0.125 ha to 0.475 ha for trees where transect size was dependent on the density and diversity of woody species in the initial transect (Walker 1976).

A further 7 new plots were sampled in neighbouring Gonarezhou National Park which was a suitable 'space for time substitute' for Malilangwe for two reasons. Firstly, the plots were within the same vegetation community, mopane woodlands on alluvium. Secondly, Gonarezhou had been heavily impacted by a super-abundance of elephants (Dunham 2012) for a prolonged period of time and had a shrub layer which had been well established for several decades (Clegg, personal communication 2014). Elephant density there in 2013 was estimated to be 2.75 elephants/km^2 (Dunham et al. 2013) which for the purpose of this study was considered high. The vegetation composition and structure in Gonarezhou was therefore likely to be representative of Malilangwe in the future if elephant numbers continue to increase.

GPS locations for the Gonarezhou plots were randomly generated using ArcGIS software such that they were at least 500 m apart and located along suitable sections of road running through the mopane woodlands on alluvium close to the Runde River in the northern region of the park (Figure 1). As with the prior sampling in Malilangwe, the 'initial transects' were built out from a pegged GPS point 50 m East or West, and a variable width North or South to avoid crossing any roads or vegetation boundaries. Where necessary the transect width was extended to include at least 15 individuals of the more common species, a sufficient number of less common species and a total of at least 30 individuals irrespective of species from each plot. This meant that in some cases, the transect size for one species was different to that of another, with more common and less common species generally having smaller and larger transect sizes respectively. This was non-problematic firstly because the plots were largely homogenous in species composition and distribution. Secondly canopy volume estimates and damage estimates were calculated in such a way as to avoid any bias associated with differing transect size as explained in the data analysis section below.

Data collection

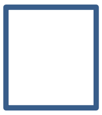
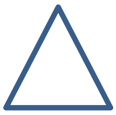
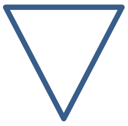
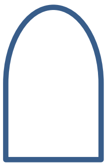
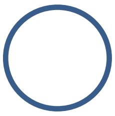
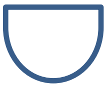
Data collection involved simple observation and taking measurements of individual plants of all woody species within plots. In each area, a two part sampling approach was used to quantify: 1) vegetation structure and composition, and 2) damage by several damage agents.

1) Vegetation structure and composition

Canopy volume estimates were calculated based on the Arbour structure method developed by Cauldwell in 1998 and described by Melville et al. (1999). This method was chosen because it allows for quick field data collection (only 3 or 4 plant dimensions are measured in the field), facilitates more user-friendly analysis (because Microsoft Excel can be used for data entry and calculations), and accommodates a variety of plant shapes.

Plants that were shorter than 3 m tall were classified as ‘shrubs’ and those 3 m tall or taller as ‘trees’. Where a plant was close to the edge of the transect, it was included only if at least half its canopy in the case of shrubs, or in the case of trees, more than half of its stems (mult-stemmed) or half its stem basal area (single-stemmed) fell within the transect. According to Cauldwell’s method, the canopy of each individual was classified as one of seven basic shapes (Table 1). A series of measurements were taken to the nearest 0.1 m and only considering live material; total plant height, the maximum canopy diameter and canopy diameter at right angles to that maximum diameter. Shrubs were recorded as true shrubs or shrubs resulting from coppice growth.

Table 1: Seven basic canopy shapes assigned to individual woody plants to assist in calculating canopy volume (Caudwell as cited in Melville et al. 1999).

A 	B 	C 	G 
D 	E 	F 	

For trees, additional measurements were taken; the height of the lowest leaves of the canopy (to the nearest 0.1 m) such that canopy depth could be calculated, the number of stems and the circumference of each individual stem (to the nearest 1 cm) just above the buttress swelling. Stems that joined below ground were treated as separate stems and their circumferences measured as such. If a tree was completely dead, whether fallen or standing, only its stem circumference was measured in order to weight its damage. If the main stem of a tree had been broken or pushed over but remained alive, its stem circumference was measured to weight its damage. If regrowth had occurred and was 3 m tall or taller, its canopy volume was included in the tree estimates. Where the regrowth was less than 3 m tall, its canopy volume was included in the shrub estimates but only if the tree was within the shrub transect.

Plant heights were measured using a 6.5 m tall Aluminium Telescopic English 'E' Staff, or for trees taller than 6.5 m, heights were estimated to the nearest 0.5 m using the simple ‘yard stick method’. A flexible tape measure was used for diameter and stem circumference measurements.

2) Damage

A method developed by Walker (1976), which was modified and used by Clegg in the 2000/ 2001 sampling effort, was used for quantifying the type and extent of damage to woody species within plots. The damage type to each individual plant was assessed based on the age of damage, plant part damaged (biomass or bark) and the agent of damage, such that 10 damage types were considered. Old damage was that which had been incurred more than one season prior to assessment. New damage was any damage that was incurred since the previous old damage (if this occurred long ago) or during the most recent season.

i) Old elephant damage (OED)
ii) New elephant damage (NED)
iii) Old unknown damage (OUD)
iv) New unknown damage (NUD)
v) Old fire damage (OFD)
vi) New fire damage (NFD)
vii) Old bark damage by elephants (OBE)
viii) New bark damage by elephants (NBE)
ix) Old bark damage by unknown agent (OBU)
x) New bark damage by unknown agent (NBU).

For each damage type a damage score was assigned. To do this, one had to imagine what the plant was like before it was damaged and then assess how much biomass had been removed or killed according to an 8 point scale (0 = 0%, 1 = 1-10%, 2 = 11-25%, 3 = 26–50 %, 4 = 51–75 %, 5 = 76–90%, 6 = 91-99%, 7 = 100). For shrubs, biomass was the plant’s canopy volume and for trees it was usually canopy branches. For trees, more detailed observations were recorded regarding the fate of each stem (1 = branches broken, 2 = main stem broken, 3 = main stem pushed over but still rooted, and 4 = tree uprooted). Additionally, it was noted if the tree had coppiced or not.

Trees were additionally assigned a bark damage score which was based on the same 8 point scale but here the percentage was based on the total circumference of the stem rather than biomass. Unlike Malilangwe, the very tall emergent trees (> 7 m) in Gonarezhou were widely dispersed, and therefore we included individual emergent trees from outside each plot to increase the sample size for a separate bark damage assessment. However, the canopy volume for these trees was not included in the canopy volume per hectare estimates.

Data analysis

The three data sets represented the three levels of elephant density: Malilangwe 2000/2001 = low elephant density, Malilangwe 2014 = intermediate elephant density, Gonarezhou 2014 = high elephant density. To allow for direct comparisons between these, the original Microsoft Excel template compiled by Clegg from the previous sampling effort was used for processing of data collected in 2014. All statistical analyses were conducted using RGui (64-bit version 3.0.2) open-source software.

1) Vegetation structure and composition

Canopy volume estimates were calculated using height measurements, canopy dimensions and geometric equations based on the assigned canopy shape. In some cases, the shape had to be adjusted if the originally assigned shape was impossible based on the measured dimensions (e.g. if shape F was originally assigned and canopy depth was greater than diameter, the shape could not have been F and would be adjusted to G). Various canopy volume estimates could then be made at various levels: per individual, per species, or per hectare. At all these levels canopy volume could be given as a total estimate or occurring within user specified height classes (m above ground level). Overall canopy volume estimates for the site needed to be calculated in a stepwise manner in order to remove biases associated with different transect sizes. Initially estimates were calculated per species based on the size of the transect in which they were measured. These estimates were then summed to give overall canopy volume (m^3/ha) estimates for each site.

To improve normality of the data, canopy volume estimates were log-transformed before analysis. A two-way ANOVA was used to test for the effect of elephant density and height class in determining canopy volume (m^3/ha) as well as if there was an interaction between these two factors. Other features of vegetation structure and composition were quantified per site and then as averages of sites grouped accorded to elephant density: total canopy volume (m^3/ha), shrub density, tree density (alive and dead, standing and fallen), mean tree height (m), mean lower level of the canopy (m), total basal area of trees (m^2) and species richness of shrubs and trees. Percentage frequency distributions of tree heights (m) and lowest level of the canopy (m) were also used to give further indications of changes in structure.

2) Damage

Damage estimates for each damage type were calculated in a stepwise manner ultimately to give estimates of percentage biomass damaged per site. According to Walker's (1976) method, damage scores were first converted to their corresponding midpoint percentages. Damage estimates were then calculated for individual shrubs and trees separately based on a weighting procedure. Tree damage was weighted against stem cross sectional area, as this could be measured more accurately than canopy volume.

Absolute tree damage was weighted against individual stem cross sectional area:

$$Weighted\ damage\ (WD) = Stem\ area\ (m^2) \times\ \%\ damage\ (midpoint\ of\ range)$$

Bark damage to tree stems was weighted against individual stem circumference:

$$Weighted\ damage\ (WD) = Stem\ circumference\ (m) \times\ \%\ damage\ (midpoint\ of\ range)$$

Stem cross sectional area is not used to weight shrubs because it would take too long to measure all the stems because shrubs are often multi-stemmed. Instead, absolute old and new shrub damage was weighted against old and new reconstructed canopy volumes respectively:

$$Weighted\ damage\ (WD) = V_R(m^2) \times\ \%\ damage\ (midpoint\ of\ range)$$

where V_R is the reconstructed volume. Volumes for use in weighting needed to be reconstructed such that they were increased according to the degree of damage, because damage reduces volume and therefore would be underestimated if it were weighted by the smaller post-damage volume (V_M). Reconstructed volumes were calculated as:

$$V_R = V_M \times \frac{100}{100 - \%\ damage}$$

where V_M is the measured volume.

Percentage damage estimates were then worked out per species. For trees:

$$\%\,damage(SpeciesA)\ =\frac{\Sigma\, WD(SpeciesA)}{\Sigma\, stem\ area\ (SpeciesA)}$$

For bark damage to trees:

$$\%\,damage(SpeciesA)\ =\frac{\Sigma\, WD(SpeciesA)}{\Sigma\, stem\ circumference\ (SpeciesA)}$$

For shrubs:

$$\%\,damage(SpeciesB)\ =\frac{\Sigma\, WD(SpeciesB)}{\Sigma\, canopy\ volume\ (SpeciesB)}$$

To remove biases associated with differing transect sizes, these estimates were then weighted against the respective species' contribution to total biomass (canopy volume for shrubs, basal area for trees, and stem circumference for bark damage). Finally these were summed to give percent damage estimates per site:

$$\%\,damage(Site) = \Sigma_{Species\ A-Z}\left(\%\,damage\ (Species)\ \times \frac{\Sigma biomass(Species)}{Total\ biomass\ (Plot)}\right)$$

Site damage estimates were square root transformed and a series of parametric ANOVAs and non-parametric Kruskal Wallis tests were run to test for significant differences in overall percent damage between sites under the three levels of elephant density. Each damage type was assessed and shrubs and trees were tested separately because damage to each of these was weighted differently.

Elephant damage was assessed at a finer scale and compared across levels of elephant density. The number of stems that incurred broken branches, were themselves broken, pushed over but still rooted, or uprooted were each expressed as a percentage of the total number of stems measured. For each damage type, the mortality of stems was calculated as a percentage of the number of stems damaged. Additionally, the number of stems that had been broken and subsequently coppiced was expressed as a percentage of the total number of stems measured. This was compared within the Malilangwe plots to assess change as elephant density has increased, as well as broadly across all three levels of elephant density.

To answer whether or not elephants are functionally responding to the changes in vegetation structure and composition, we assessed how OED and NED estimates vary with elephant density. Shrubs were compared to trees which were divided into two groups for the comparison: trees between 3 and 7 m tall, and trees taller than 7 m.

Upon observation, the bark damage to emergent trees (> 7 m) in Gonarezhou appeared to be very high in comparison with damage to lower trees (≤ 7 m) in the area and emergent trees in Malilangwe. After square root transforming the damage estimates, 4 two-way ANOVAs, one for each bark damage type, were used to test for significant effects of elephant density, tree height and the interaction between these two factors in determining the level of bark damage.

Results

1) Vegetation structure and composition

Both height class and elephant density were significant factors in determining canopy volume (Table 2). Furthermore there was a significant interaction between these two factors indicating that the trend (Figure 2) is not constant across all height classes or elephant densities. Post-hoc tests revealed that canopy volume within the height class 0 - 1.0 m was significantly different to that occurring in all three of the other height classes ($p < 0.05$ for all three comparisons) (Figure 3a). All other height classes had similar canopy volume estimates ($p > 0.05$ for all three comparisons). Sites with a high elephant density had

Table 2: Results of the two-way ANOVA showing all 3 factors considered have a significant effect in determining canopy volume (m^3/ha) at sites. (Levels of significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$).

Factor	Df	Sum Sq	Residual Df	Δ Sum Sq	Variation Explained	F	p
NULL		59.7	91				
Height Class	3	43.3	88	16	48.9%	16.8	P < 0.0001***
Elephant density	2	40.2	86	3	9.1%	4.7	0.012*
Height class : Elephant density	6	26.1	80	14	42.0%	7.2	P < 0.0001***

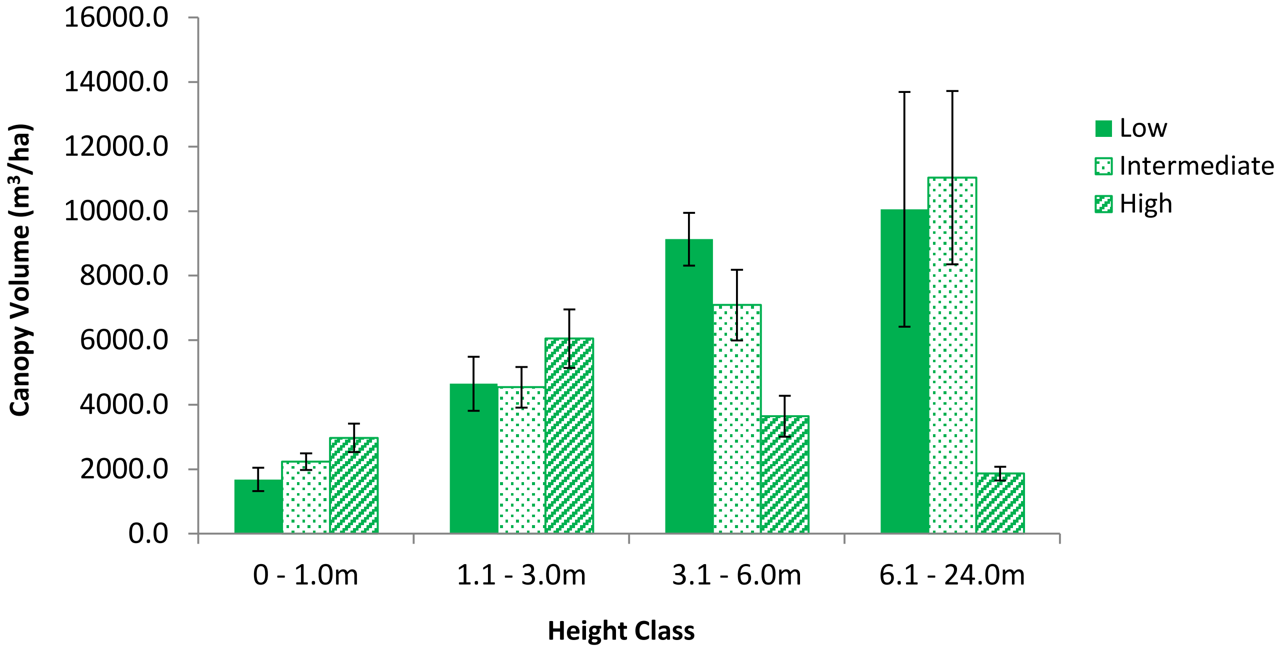


Fig 2: Differences in canopy volume per site (mean ± SE) within various height classes and under different levels of elephant density: Low n = 8 sites, Intermediate n = 8 sites, High n = 7 sites)

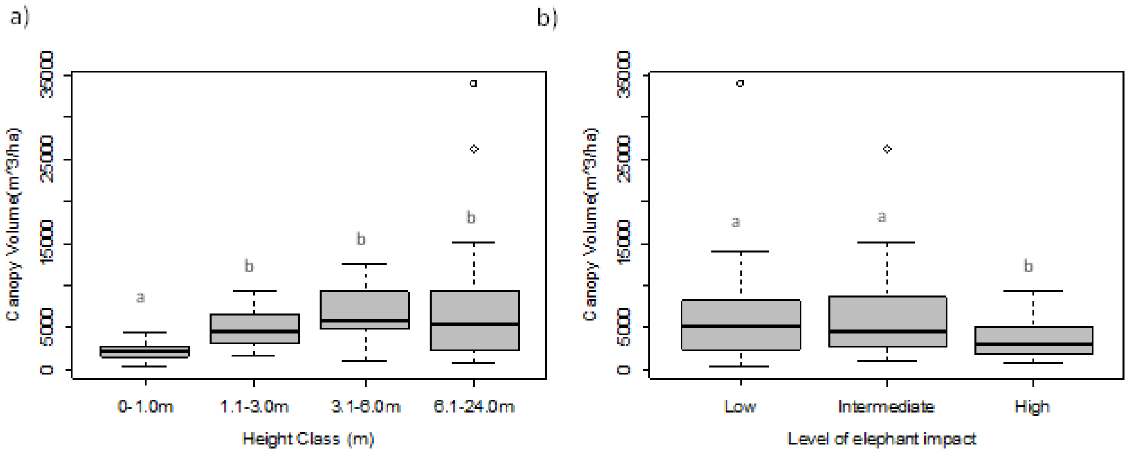


Fig 3: Differences in mean canopy volume a) within various height classes and b) between different levels of elephant density : Low n = 8 sites, Intermediate n = 8 sites, High n = 7 sites.

significantly lower canopy volume estimates compared to sites with both low and intermediate elephant density ($p < 0.05$ for both comparisons) (Figure 3b). However, sites with low elephant density had similar canopy volume estimates to those with intermediate level density.

There was a weak negative relationship between elephant density and the density of alive trees, and a negative relationship between elephant density and density of alive, standing trees (Table 3). The ratio of alive, standing trees to alive, fallen trees decreased more than three times in Malilangwe as elephant density trebled. This was attributable to both decreases in densities of standing trees as well as a five-fold increase in the density of fallen, alive trees. Although Gonarezhou had a lower density of trees than Malilangwe under intermediate elephant density, the ratio of alive, standing to alive, fallen trees varied little between the two areas. The species richness of both shrubs and trees declined with increasing elephant density.

As elephant density increased in Malilangwe, the density of trees ≤ 10 m tall decreased by about 100 trees / ha, whereas the density of emergent trees > 10 m tall more than tripled. In contrast, the densities of trees ≤ 10 m tall and > 10 m were much higher and much lower respectively in Gonarezhou than those in Malilangwe under intermediate elephant density. The trees in Malilangwe were on average taller under low compared to intermediate elephant density, whereas those in Gonarezhou under high elephant density were generally much shorter. Furthermore, the average height of the lowest level of the canopy in

Table 3: Descriptive measures of vegetation structure and composition in mopane woodlands on alluvium in the south-eastern lowveld of Zimbabwe.

Area Year sampled No. plots	Malilangwe 2000/2001 8	Malilangwe 2014 8	Gonarezhou 2014 7
Relative elephant density	Low	Intermediate	High
Total canopy volume (m^3/ha)	25519 ± 3988	24906 ± 3027	14530 ± 1868
Shrub density (no./ha)	1640 ± 254	1564 ± 155	2050 ± 932
Alive trees density (no./ha)	264 ± 61	235 ± 54	225 ± 29
Dead trees density (no./ha)	49 ± 17	27 ± 4	8 ± 3
Alive tree standing AS (no./ha)	219 ± 10	173 ± 14	112 ± 6
Alive trees fallen AF (no./ha)	6 ± 3	26 ± 5	19 ± 3
Ratio AS: AF	28.53 ± 10.80	8.72 ± 1.64	8.42 ± 3.12
Tree density ≤ 10m (no./ha)	237 ± 66	135 ± 49	177 ± 25
Tree density > 10m (no./ha)	22 ± 10	69 ± 15	14 ± 2
Mean tree height (m)	7.85 ± 0.81	9.43 ± 1.47	5.13 ± 0.29
Mean lower level of canopy (m)	1.95 ± 0.29	1.55 ± 0.28	0.42 ± 0.03
Total tree basal area (m^2 /ha)	17.05 ± 1.32	17.04 ± 1.26	17.13 ± 1.38
Species richness (shrubs)	11.5 ± 3.2	9.3 ± 3.5	7.4 ± 2.1
Species richness (trees)	3.4 ± 1.3	2.4 ± 0.5	1.1 ± 0.4

Gonarezhou was much closer to ground level than in Malilangwe both under low and intermediate elephant density.

Distributional differences existed in both tree height and height of the lowest level of the canopy under different levels of elephant density. At low elephant density 29.0 % of trees were between 3 and 5 m tall, and this had increased to 43.4 % at intermediate elephant density (Figure 4a) i). As elephant density increased, tree heights became bi-modally distributed Figure 4a) ii). This was most pronounced under high elephant density where as many as 86.7 % of trees were shorter than 5 m, trees in the 7 -11 m height class were totally absent and a notable percentage of trees > 12 m tall still persisted (8.2 %) (Figure 4a) iii).

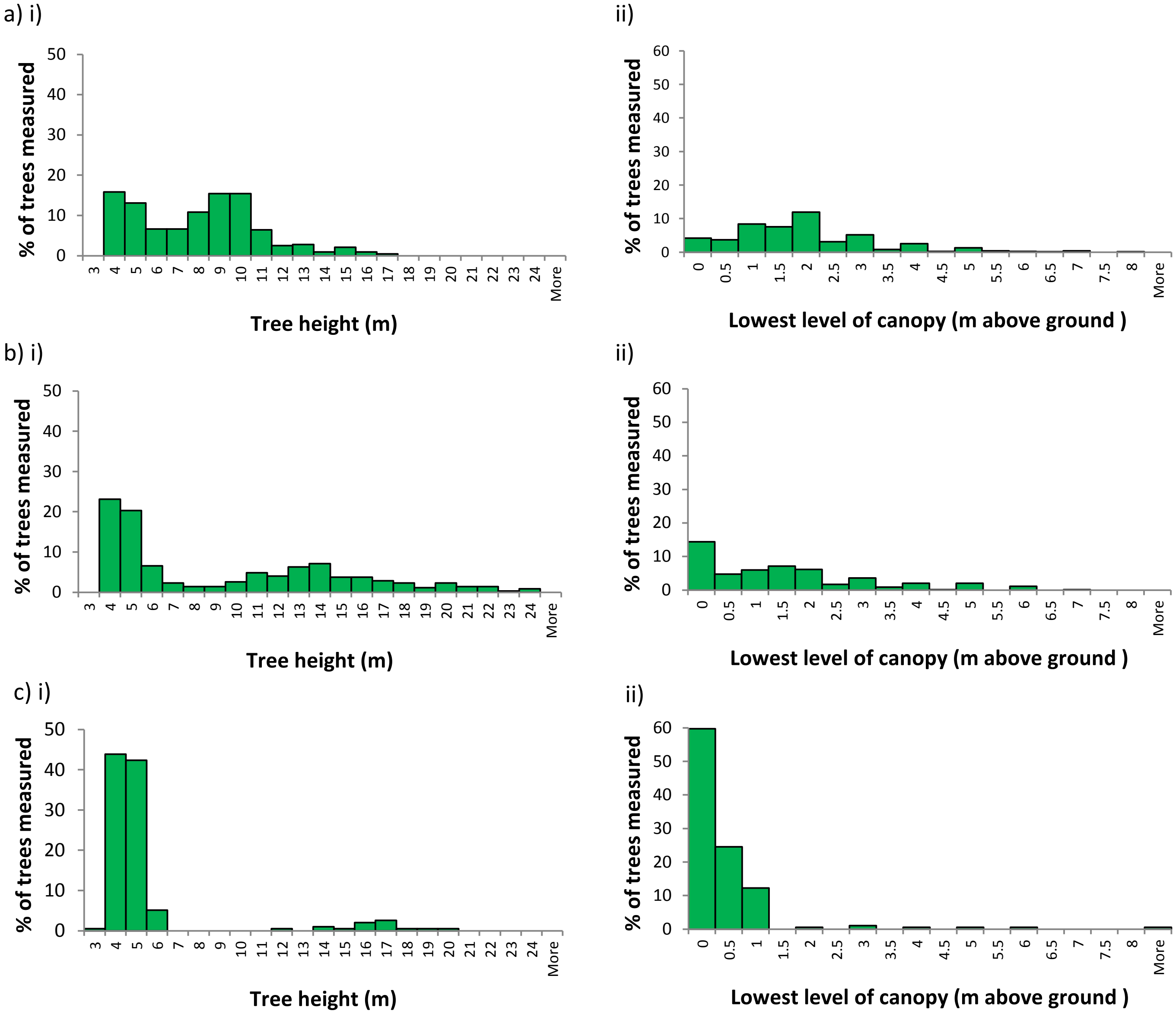


Fig 4: Percentage frequency distributions of i) tree heights and ii) lowest level of canopy of alive trees under 3 levels of elephant density: a) low (n = 435 trees); b) intermediate (n = 350 trees) and c) high (n = 196 trees).

The data clearly demonstrates that trees in the 5 – 10 m height class are being targeted by elephants; at low elephant density the majority of trees (54.9 %) were in this height class, whereas at intermediate density this decreased to 14.3 %, and under high elephant density only 5.1 % were found within this height class. In contrast, trees > 10 m high had increased by 23.6 % under intermediate compared to low elephant density, and 8.2 % still persisted with high elephant density.

The progressive lowering of tree height with increasing elephant density shifted the canopy of trees closer to the ground. At high elephant density 60 % of trees had canopies that were within 0.5 m of the ground (Figure 4b) iii), while this was only 28.9 % and as little as 8.3 % for intermediate Figure 4b) ii) and low elephant density respectively (Figure 4b) ii).

2) Damage

There were significant differences across the three levels of elephant density for both OED (Kruskal-Wallis $\chi^2 = 15.1502$, df = 2, $p < 0.001$) and NED (Kruskal-Wallis $\chi^2 = 13.5432$, df = 2, $p < 0.01$) to shrubs. Post hoc tests revealed that sites with intermediate and high elephant density had similar OED estimates and these were both significantly higher than sites with low elephant density ($p < 0.05$ for both comparisons) (Figure 5a). Sites with intermediate and high elephant density had similar NED estimates ($p > 0.05$) and both had significantly higher estimates than sites with low elephant density ($p < 0.05$ for both comparisons) (Figure 5b). There were no significant differences for any the other damage types, whose mean estimates are provided in Table 3.

Table 3: Mean shrub damage estimates (% ± SE) for sites under various levels of elephant density: low density n = 8 sites, intermediate density, n = 8 sites, high density n = 7 sites.

	Low	Intermediate	High
OED	4.49 ± 2.06	33.06 ± 4.29	28.30 ± 2.34
OUD	3.56 ± 1.06	5.02 ± 1.77	1.47 ± 0.42
NED	0.11 ± 0.06	5.61 ± 1.57	6.87 ± 0.67
NUD	0	2.17 ± 2.01	0.15 ± 0.07
NFD	0	0	0
OFD	0.89 ± 0.89	0.09 ± 0.09	0

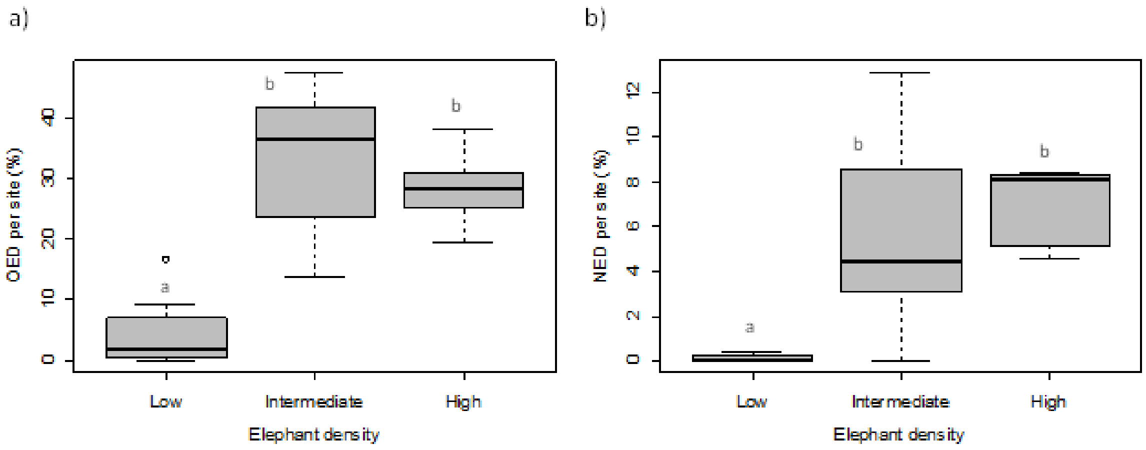


Fig 5: Differences in percent a) old (OED) and b) new (NED) elephant damage to shrubs (mean ±SE) under various levels of elephant density: low (n =8 sites), intermediate (n = 8 sites) and high (n = 7 sites). Note that y-axis ranges vary.

Significant differences also existed across the three levels of elephant density for both OED (F = 63.38, df = 2, p < 0.001) and NED (Kruskal-Wallis χ^2 = 18.8254, df = 2, p < 0.001) to trees. Post hoc tests revealed significant differences in OED damage estimates between all three levels of elephant density (p < 0.05 for all comparisons); sites under high elephant density had the highest damage estimates, followed by sites with intermediate and low elephant density respectively (Figure 6a). Post hoc tests for NED (Figure 6b) indicated that sites with intermediate and high elephant density had similar NED estimates (p > 0.05) and both have

Table 4: Mean tree damage estimates (% ± SE) for sites under various levels of elephant density: low density n = 8 sites, intermediate density, n = 8 sites,high density n = 7 sites.

	Low	Intermediate	High
OED	5.06 ± 0.95	21.83 ± 3.39	50.13 ± 4.64
OUD	9.68 ± 1.73	14.06 ± 2.27	5.23 ± 2.45
DRT	9.06 ± 3.24	0	0
NED	0.05 ± 0.03	3.43 ± 0.96	10.29 ± 0.95
NUD	0.00 ± 0.00	0.02 ± 0.02	0
NFD	0	0	0
OFD	0.01 ± 0.01	0	0
OBE	0.09 ± 0.03	1.03 ± 0.32	3.18 ± 1.06
OBU	0.58 ± 0.11	7.24 ± 1.14	0.41 ± 0.27
NBE	0.01 ± 0.01	0.88 ± 0.46	0.49 ± 0.27
NBU	0	0.09 ± 0.09	0

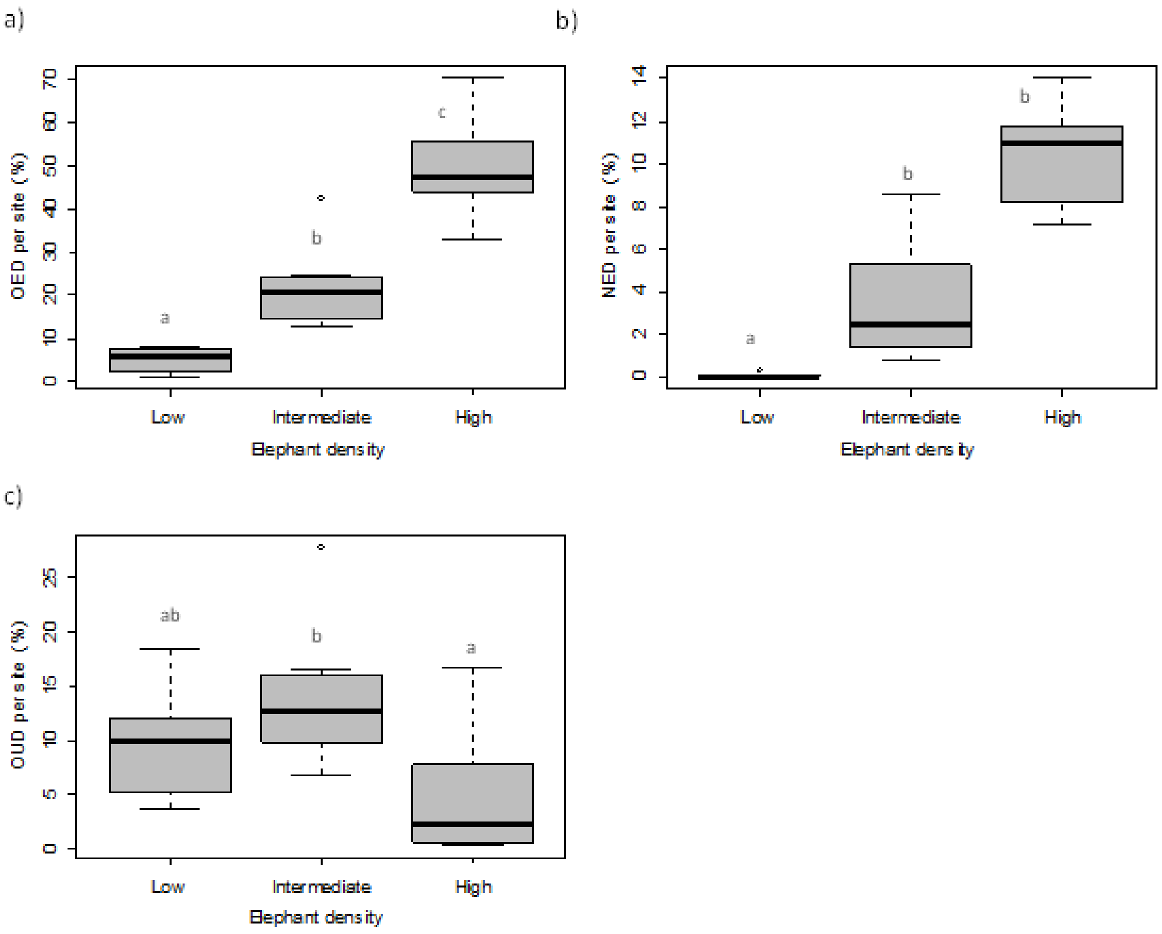


Fig 6: Differences in percent a) old elephant damage (OED), b) new (NED) elephant damage and c) old unknown damage (OUD) to trees (mean ±SE) under various levels of elephant density: low (n =8 sites), intermediate (n = 8 sites) and high (n = 7 sites). Note that y-axis ranges vary.

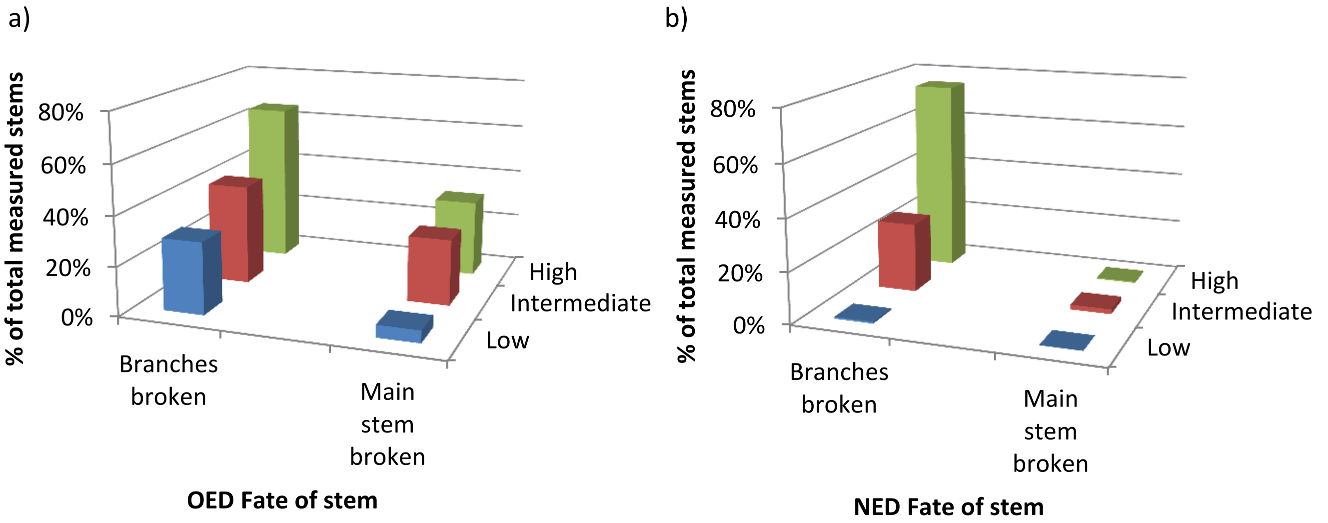


Fig 7: The relative percentage of stems that had either ‘branches broken’ or ‘main stem broken’ as a result of a) old elephant damage (OED) and b) new elephant damage (NED) under three levels of elephant density: low (n = 1023 stems), intermediate (n = 800 stems) and high (n = 635 stems).

significantly higher estimates than sites with low elephant density ($p < 0.05$ for both comparisons*)*.

There were significant differences in OUD estimates according to elephant density ($F = 5.866$, $df = 2$, $p < 0.01$) and post hoc-tests indicated that this was due to sites under intermediate elephant density (Figure 6c) which had significantly higher damage estimates than those with high elephant density ($p < 0.05$). Sites with intermediate compared to low, and high compared to intermediate elephant density had similar damage estimates. There was only one site under intermediate elephant density that showed any sign of NUD, only one site under low elephant density with OFD, no NFD was observed in either 2000/2001 or 2014 and no drought damage (DRT) was recorded in 2014 (Table 4). Therefore these damage types were excluded from the analyses.

As elephant density increased, so did both the percentage of stems that had branches broken through OED and NED (Figure 7a and b) and the percentage that were themselves broken through OED (Figure 7a). Very few stems were pushed over, either rooted (0 to 1 % per site) or uprooted (0 to 1% per site) under any level of elephant density although those that were had high mortality rates: 67 % of those that were pushed over but still rooted were dead and between 33 % and 80 % of those uprooted were dead. No stems were observed to have died from having branches broken, however, between 9 and 24 % of stems that were broken were dead.

The relative amount of coppice increased tremendously in all the Malilangwe plots as elephant density tripled (Figure 8a). The total number of stems in the Malilangwe plots had decreased by approximately 25 %. Despite this, the percentage of all stems measured that were broken and had coppiced increased in all plots, with some plots showing greater increases than others. Overall, there was also a declining curvilinear relationship between elephant density and relative amount of coppiced stems (Figure 8b). A total of 1023 stems were measured under low elephant density, 800 under intermediate density and 635 under high density.

With increasing elephant density, the shrub damage estimates increased rapidly and then plateaued for both OED (Figure 9a) and NED (Figure 9b). As elephant density increased NED estimates to trees taller than 7 m increased slightly before leveling off.There was a declining curvilinear relationship between NED to trees up to 7 m tall and elephant density as

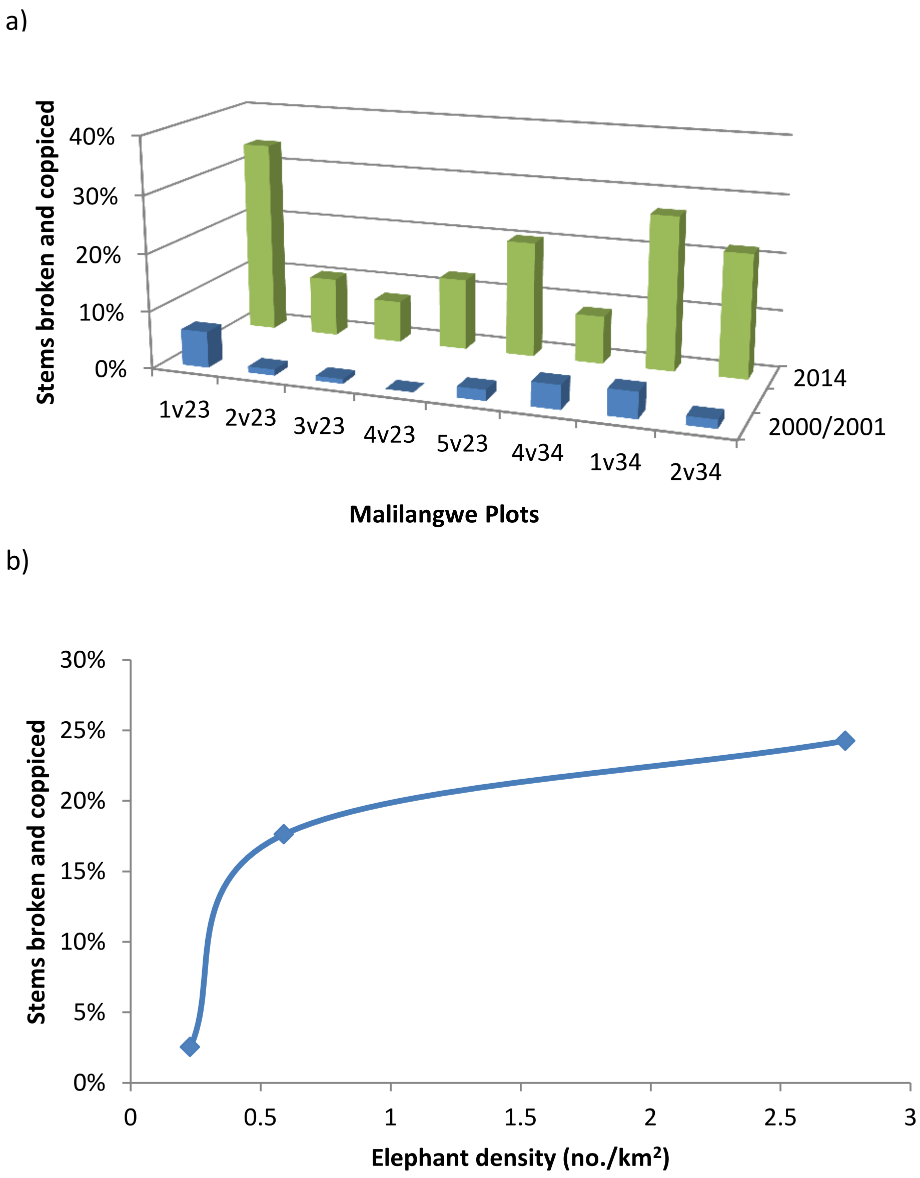


Fig 8: Changes in the relative amount of coppice expressed as the percentage of measured stems that were broken and coppiced in a) individual Malilangwe plots and b) in relation to increasing elephant density.

opposed to a simple positive linear relationship. Nevertheless, NED to these shorter trees continues to increase and eventually exceeded that for shrubs (Figure 9b).

In terms of bark damage, there were significant differences between sites under the three levels of elephant density for both OBE (Kruskal-Wallis $\chi^2 = 13.1825$, df =2, $p < 0.01$) and NBE (Kruskal-Wallis $\chi^2 = 6.9061$, df = 2, $p < 0.05$). Post hoc tests showed that sites with high elephant density had significantly higher OBE estimates than sites with low elephant density ($p < 0.05$) but not intermediate elephant density ($p > 0.05$). Sites with low and intermediate elephant density had similar damage estimates (Figure 10a). However sites under the three levels of elephant density all had similar NED estimates ($p > 0.05$ for all comparisons) (Figure 10b).

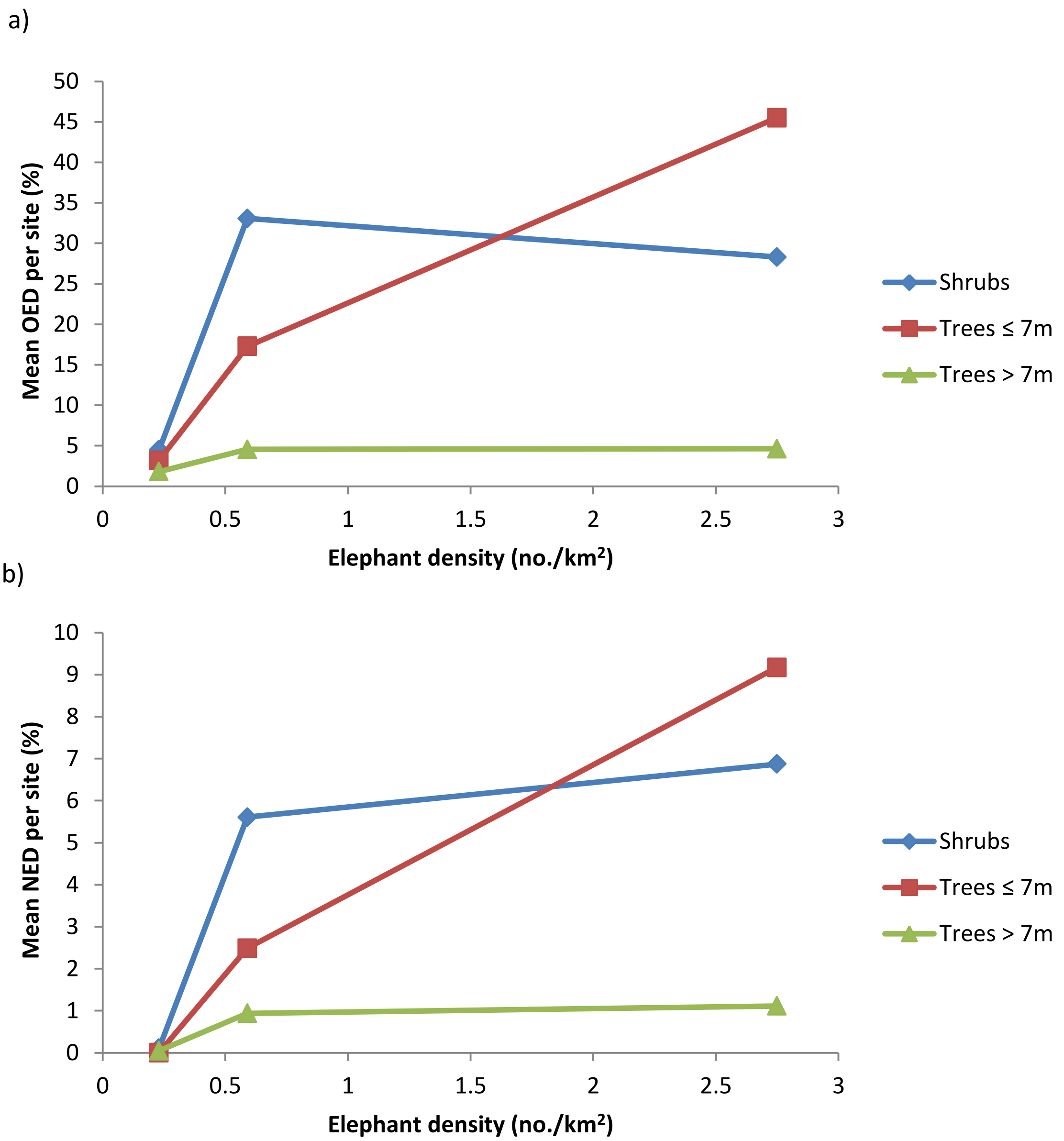


Fig 9: Differences in mean a) old (OED) and b) new (NED) elephant damage per site to shrubs, trees up to 7 m tall and taller than 7 m as elephant density increases.

For OBU, there were significant differences between sites under the different levels of elephant density (Kruskal-Wallis $\chi^2 = 15.9966$, df =2, $p < 0.001$). Post hoc tests revealed that sites under intermediate elephant density had significantly higher damage estimates than sites under both high and low elephant density (Figure 10c). Only one site with intermediate elephant density showed any sign of NBU (Table 4) and therefore this was not analysed.

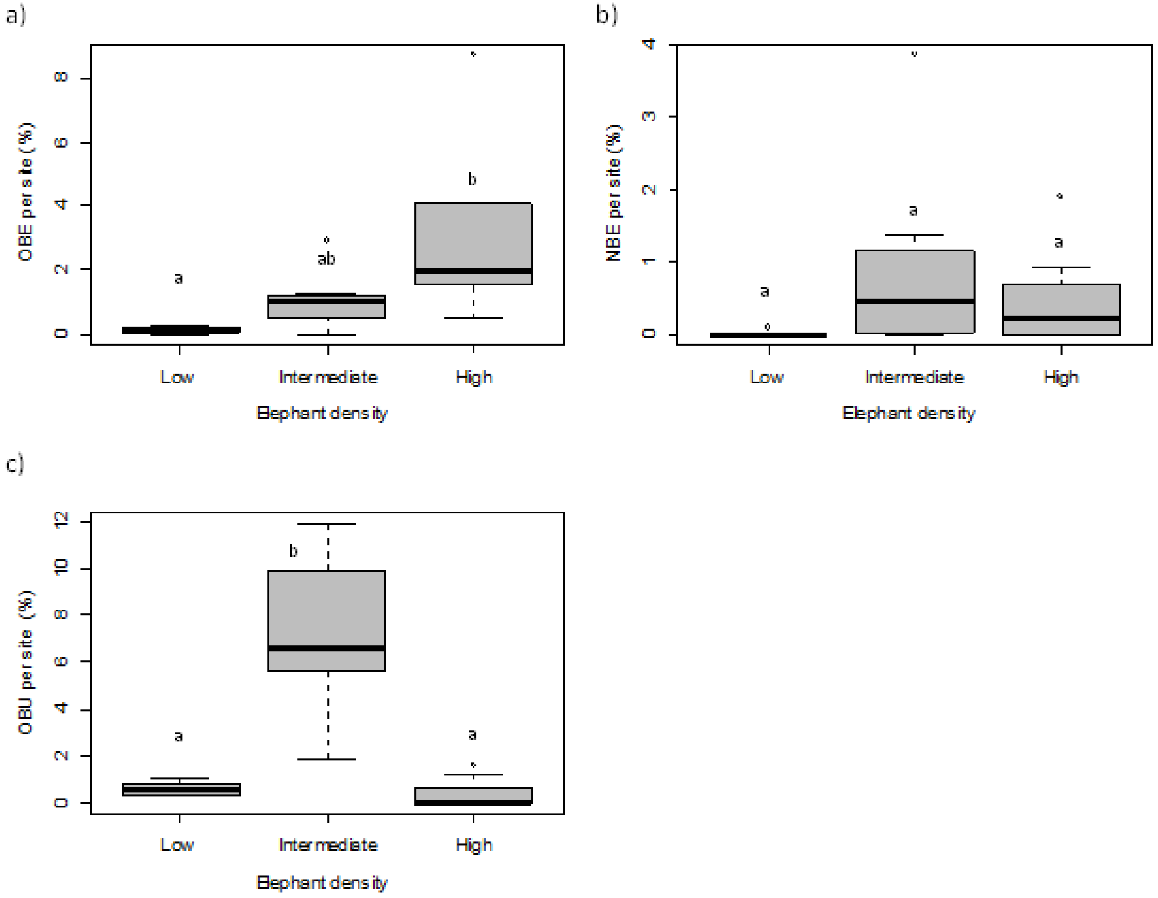


Fig 10: Differences in percent a) old (OBE) and b) new (NBE) bark damage due to elephants, and c) old unknown bark damage (OBU) to trees (mean ±SE) under various levels of elephant density: low (n = 8 sites), intermediate (n = 8 sites) and high (n = 7 sites). Note that y-axis ranges vary.

Both tree height and elephant density as well as the interaction between them had a significant effect on OBE (Table 5a) and OBU (Table 5c). Only height was significant in determining NBE (Table 5b). Post-hoc tests revealed that emergent trees taller than 7 m incurred significantly higher damage compared to those up to 7 m tall and this was true for all three types of bark damage ($p < 0.05$ in all cases).

Table 5a) Results of the two-way ANOVA showing that both factors considered as well as the interaction between them have a significant effect in determining % old bark damage due to elephants (OBE). (Levels of significance: * = p < 0.05, ** = p < 0.01, *** = p < 0.0001).

Factor	Df	SumSq	Residual Df	Δ SumSq	Variation Explained	F	p
NULL		23.1802	45				
Height	1	16.8682	44	6.312	44%	28.7847	p < 0.0001***
Elephant density	2	13.1497	42	3.7185	26%	8.4789	p < 0.0001***
Height : Elephant density	2	8.7713	40	4.3784	30%	9.9836	p < 0.0001***

b) Results of the two-way ANOVA showing that of the factors considered, only height has a significant effect in determining % new bark damage due to elephants (NBE).

Factor	Df	SumSq	Residual Df	Δ SumSq	Variation Explained	F	P
NULL		8.8446	45				
Height	1	8.0217	44	0.8229	34%	5.1257	0.029*
Elephant density	2	7.0089	42	1.0128	42%	3.1541	0.053
Height : Elephant density	2	6.4218	40	0.5871	24%	1.8286	0.174

c) Results of the two-way ANOVA showing that both factors considered as well as the interaction between them have a significant effect in determining % old bark damage due to unknown causes (OBU).

Factor	Df	SumSq	Residual Df	Δ SumSq	Variation Explained	F	P
NULL		37.829	45				
Height	1	33.351	44	4.478	17%	15.1344	p < 0.0001***
Elephant density	2	15.504	42	17.847	69%	30.1526	p < 0.0001***
Height : Elephant density	2	11.837	40	3.667	14%	6.1955	p < 0.01**

On average, OBE to emergent trees compared to shorter trees was markedly higher under high elephant density, slightly higher under intermediate elephant density but actually lower under low elephant density (Figure 11a). In the case of NBE, average damage to emergent trees compared to shorter trees was markedly higher under intermediate elephant density slightly higher under high elephant density and again actually lower under low elephant density (Figure 11b). For OBU, damage to emergent trees compared to shorter trees was markedly higher when under intermediate elephant density. However there seemed to be little difference between trees of different heights in terms of damage under both low and high elephant density (Figure 11c).

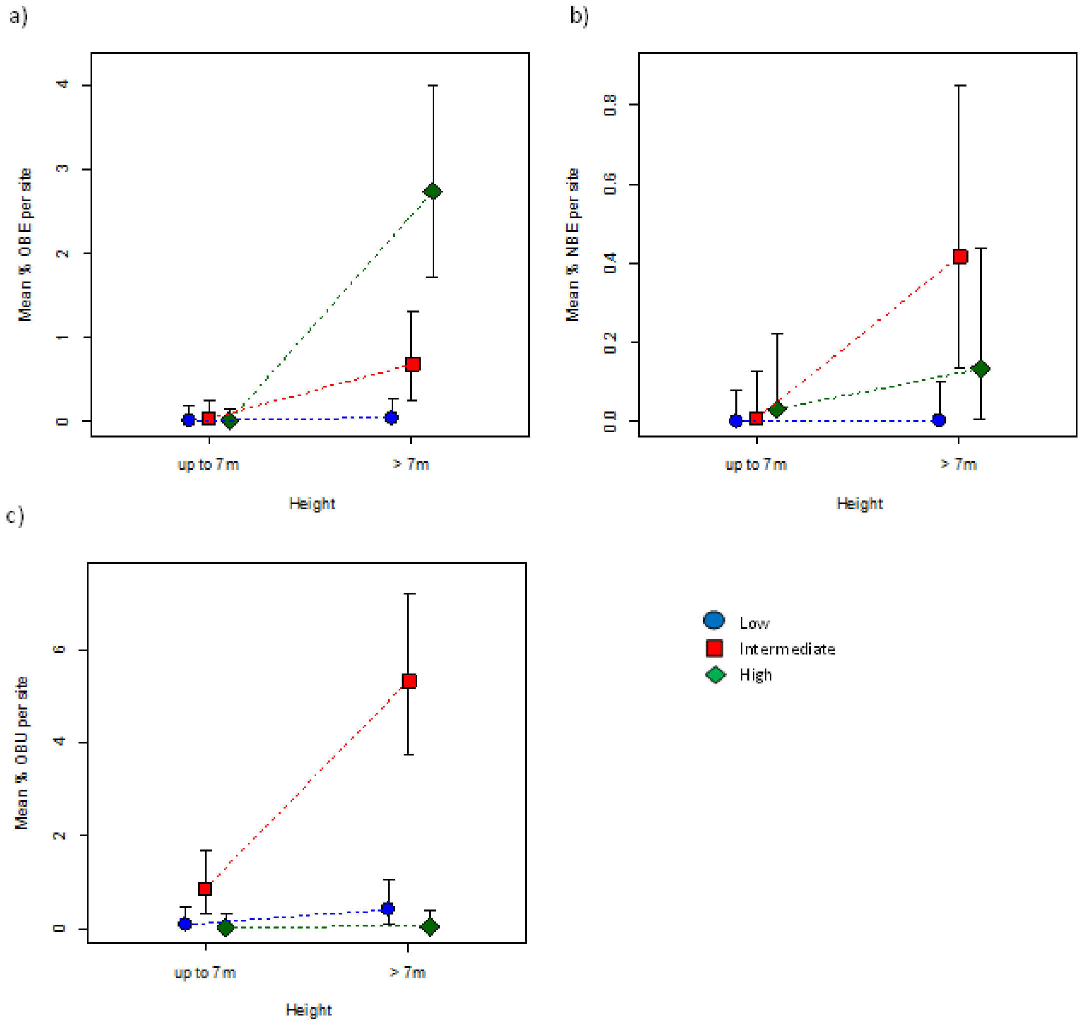


Fig 11: Differences in percent a) old bark damage due to elephants (OBE), b) new bark damage due to elephants(NBE) and c) old bark damage due to unknown causes (OUD) per site according to tree height (up to 7 m tall and taller than 7 m) and level of elephant density (low, intermediate and high).

Discussion

This study demonstrates that increasing elephant impact is a powerful mechanism in shaping the structure and composition of mopane woodlands in the south-eastern lowveld of Zimbabwe. Increased elephant density was associated with increased damage as well as differences in features of vegetation structure and composition, evidenced by the comparisons between the Malilangwe Wildife Reserve and Gonarezhou National Park.

As the number of elephants increased in Malilangwe, the impact to the mopane woodlands increased considerably; old and new elephant damage to both shrubs and trees was significantly higher under intermediate elephant density than under low elephant density. This was associated with substantial alterations to vegetation structure and composition. Although total tree density only decreased slightly with increasing elephant density, the structure of these woodlands had been altered in numerous other ways. van de Vijver et al (1999) showed that as elephant density increased in Tarangire National Park in Tanzania, total tree density varied little whereas plant size distributions varied considerably. Similarly in this study even though tree density did not change much there was a distributional shift in tree heights and progressive lowering of the canopy associated with increased elephant density.

This lowering of tree height and canopy was matched with decreases in canopy volume between 3 and 11 m above ground. This, in conjunction with the four-fold decrease in the proportion of trees between 5 and 10 m tall and the total lack of trees between 7 and 11 m tall in Gonarezhou, strongly suggests that the elephants have been targeting trees and particularly those between approximately 5 and 10 m tall. Due to the coppicing ability of mopane trees this loss of trees was associated with the development of a coppiced shrub layer.

Our results clearly demonstrated that at a broad scale the shrub layer in Malilangwe had developed; shown by increased canopy volume at the shrub layer and increased levels of coppice growth. As elephant densities increased canopy volume within the lower height classes increased, whereas at heights between 3 m and 11 m above ground level canopy volume decreased. This provided further evidence that the shrub layer was developing at the expense of the tree layer. Even though canopy volume actually increased in the 11 m - 24 m height class this was probably attributable to the increased proportion of emergent trees in Malilangwe. These trees may have outgrown the size threshold for pollarding (Teren & Owen-Smith 2010) and or are too tall for elephants to reach the canopy to forage branches and leaves. Not only are these very tall trees safe from elephant damage by pollarding, they together with the shrubs appear to be safe from fire damage.

The low fire damage estimates could indicate that fire was not an important factor in shaping the structure and composition of mopane woodlands in these areas. Although fire often influences vegetation structure (Ben-Shahar 1993) and dynamics in savanna ecosystems (Mosugelo et al. 2002), in some cases, for example in east African savannas (van de Vijver et al. 1999) it is less influential. In this study, this may be due to a lack of grass to carry fire within this vegetation type (Teren & Owen-Smith 2010) and in Malilangwe due to fire control and limited controlled burning (Kaschula 2004). With the dismissal of fire as a largely unimportant factor in this case, the high estimates of elephant damage proved that this was the dominant mechanism of change in these woodlands.

The nature and degree of old elephant damage can be viewed as a record of the conversion process. The five-fold increase in the percentage of stems that had been broken through old elephant damage in Malilangwe verifies that this was how the elephants had been converting the landscape. The immensely increased levels of coppice, expressed as the percentage of the total stems in a plot that had been broken and subsequently coppiced, provides further evidence for the development of the shrub layer. However, the coppiced hedged layer had not fully developed at all plots indicating that elephant utilization is patchily distributed. As expected the shrub layer in Gonarezhou was much more developed than that in Malilangwe, shown by its comparatively greater relative level of coppice. The fact that this difference was small (6 %), does not mean that the hedge layer in Malilangwe is almost as developed as in Gonarezhou. The comparison is based on the percentage of stems that were coppiced, but gives no indication of the absolute amount of coppice. This can be better assessed by considering the changes in canopy volume.

Not only are canopy volume estimations a more useful measure of evaluating levels of coppice, they were also vastly more useful than basal area as a measure of quantifying changes in vegetation structure. Although evident changes in canopy volume within height classes as well as differences in many other features of the vegetation reflected the occurrence of major changes in the vegetation, basal area varied little as elephant density increased. However, basal area was considered to be a relatively poor indicator of the abundance of tall trees and canopy volume due to the coppicing ability of mopane. This is because a standing tree could have the same basal area as a fallen tree that had remained alive and coppiced. The basal area of these two trees may be similar but both height and canopy volume are obviously different. This further strengthens the case for the comparison of canopy volume estimates as an extremely good way of assessing changes in vegetation structure and composition.

It does appear that the elephants in Malilangwe are exhibiting a functional response to the developing shrub layer. The increases in elephant damage in Malilangwe were more pronounced for shrubs than for trees. This suggests that the elephants were utilizing the shrub layer progressively more as it developed. New elephant damage estimates to trees under intermediate density were considerably lower than in high elephant density (Gonarezhou). Statistically they were similar, although this was probably driven by one or two very high damage estimates in Malilangwe. On closer examination, Gonarezhou had considerably higher old elephant damage estimates to trees up to 7 m tall compared to Malilangwe (intermediate elephant density), as well as a slightly higher percentage of old elephant-felled stems. These findings suggest that despite the increased use of the shrub layer in Malilangwe, tree felling is likely to continue in the near future if elephant numbers increase further.

Furthermore, although damage to shrubs levels off as elephant density increases from intermediate to high levels, damage to trees between 3 and 7 m tall continues to increase and even surpasses the level of shrub damage. At first this may seem very concerning as it leads one to think that tree losses due to pollarding are set to continue in Malilangwe. However one must consider that compared to trees in Malilangwe the majority of trees in Gonarezhou were much shorter and their lower levels of canopy also much lower. This was because most of these trees were not true trees, but rather coppice trees (Ferguson, personal observation 2014). Although they had originally been felled the coppice regrowth had sufficient time to grow to at least 3 m or taller such that they were considered as ‘standing-alive trees’ rather than ‘fallen-alive trees’. The high level of damage to trees between 3 and 7 m tall was largely through branches being broken from these coppice trees rather than through pollarding. Breaking of branches or harvesting of leaves is much less damaging to a plant than pollarding, especially if this is from a well-developed coppiced layer such as that in Gonarezhou. None of the stems were observed to have died as a result of branches being broken whereas 9 % of stems that were broken in Gonarezhou died.

It is also possible that damage may not be a good proxy for frequency of utilization. A coppiced shrub can be utilized frequently and incur relatively little damage because the constant pruning has created a structure such that leaves can be easily harvested by trunk-stripping as opposed to breaking branches. This is why the damage was expected to plateau or even decline once the coppice layer had developed. In contrast a tree can be utilized once and incur heavy damage because it needs to be pushed over or pollarded in order for an elephant to access the leaves, thus explaining the higher damage estimates for trees. Although mopane trees often survive felling due to their ability to coppice (Lewis 1991), felling is still likely to be a major cause of tree mortality (Midgley et al. 2005; O’Connor et al. 2007; Gandiwa et al. 2011). As many as 21 % and 24 % of those stems that had been felled in Malilangwe in 2000/2001 and 2014 respectively were dead.

Although felling can be a cause of mortality, if a tree survives and coppices, this is likely to provide a much more accessible and preferred food source than the taller true trees (Smallie & O’Connor 2000). This means that the trees in Gonarezhou are functionally shrubs as far as the elephants are concerned. This is supported by the fact that most of the new elephant damage in that area is occurring to the shorter trees (up to 7 m tall) through browsing only; 75 % of stems had branches broken but no newly felled or uprooted stems were observed. Despite this, considering the extreme paucity of emergent trees in Gonarezhou (Figure 10), it is possible that this highly accessible and probably preferred coppice food source was insufficient, or became available too late only after the vast majority of trees had already been felled. Another possibility is that the continued felling of tall trees despite the readily available forage is non-feeding behavior displayed by elephants. It may be a social behavior by bull elephants that are practicing for intra-sexual

Figure 12. Elephants in Gonarezhou National Park (Zimbabwe) with mopane woodlands in the background. These woodlands are characterized by an extremely well-developed shrub layer and a paucity of emergent trees. Photographed by Angela Ferguson (August 2014).

contests to assert dominance, or it may simply be a non-adaptive or deviant acquired behavior (Midgley et al. 2005).

Although the tall trees in Malilangwe may be safe from pollarding due to their large trunk sizes, other causes of trees losses are likely to become detrimental for these tall trees if elephant numbers increase further. This was highlighted by the fact that canopy volume in the 11 m - 24 m height class (tree layer) in Gonarezhou decreased and this was matched by a small relative proportion of emergent trees. This together with our findings that estimates unknown damage (Malilangwe) and bark damage (Malilangwe and Gonarezhou) is high, leads us to believe that further tree losses can be expected and tree density will most probably not reach equilibrium.

Although, not statistically different, old bark damage by elephants in Gonarezhou was higher than in Malilangwe under intermediate elephant density. This may have been because there were fewer tall trees to provide main stem bark in Gonarezhou and therefore those few available trees incurred higher individual damage. In this study old damage was a superior indicator of general bark damage than new bark damage because the latter was that which had occurred only within the last season. Elephants, bulls in particular, generally damage bark (Midgley et al. 2005; O'Connor et al. 2007) usually when they are nutritionally stressed (Pretorius et al. 2011) and it is possible that they were not nutritionally stressed in the most recent season when rainfall was above average, hence the low estimates of new bark damage by elephants.

Previous studies have found that high utilization of bark occurs during the dry season (Ihwagi et al. 2009), and is often associated with a deficiency of good quality alternative food sources and is frequently indicative of nutritional stress in elephants (Pretorius et al. 2011). In Gonarezhou the total canopy volume per hectare was much lower, and the density of elephants much higher than in Malilangwe (according to Dunham et al. (2013) estimate elephant abundance was the highest recorded since 1975). Therefore it is possible that the high bark damage in Gonarezhou is because elephants there are generally nutritionally stressed as a consequence of high competition for a limited food resource. Whatever the reason for elephants damaging bark, bark damage is extremely high in Gonarezhou and increasing in Malilangwe and might be contributing to the loss of trees.

Emergent trees are particularly prone to bark damage and thus may be more vulnerable to mortality from debarking. Elephant bark damage was noticeably higher to the emergent trees (> 7 m tall) than to smaller trees for both intermediate and high elephant densities. This is in partial agreement with findings by Smallie & O'Connor (2000) who found that bark damage accounted for most of the damage to *C. mopane* taller than 4 m and findings by Ihwagi et al. (2009) who found a positive correlation between debarking intensity and stem circumference of *Acacia*. Debarking, either directly or in combination with successive fires and insect damage (Jacobs & Biggs 2002; Midgley et al. 2005), is a common cause of death of large trees (Lewis 1991; Teren & Owen-Smith 2010). The difference in bark damage between short and emergent trees was particularly extreme in Gonarezhou. Thus the high bark damage is predicted to cause the death of the few remaining emergent trees in Gonarezhou. Even though comparatively the bark damage in Malilangwe was lower than in Gonarezhou, it was still high. It is worth noting that the combination of bark and damage caused by unknown agents could pose a threat to the future survival of trees in Malilangwe.

Malilangwe under an intermediate density of elephant had notably high estimates of old unknown damage to trees, both to general biomass as well as to bark. This could simply be old elephant damage that was too old to be deciphered as such because it was incurred before and or soon after the 2000/2001 sampling effort. It is also possible that this damage is caused by other agents such as other herbivores, insects, parasites, disease, wind or frost (Guldemond & Van Aarde 2008; Chafota & Owen-Smith 2009; Teren & Owen-Smith 2010). As the estimates were so high, it may be advisable to investigate these further as they may contribute to future tree losses in Malilangwe.

The changes in vegetation structure with increasing elephant densities demonstrated in this study are largely in agreement with Lewis' (1991) predictions for soils that promote coppicing. As elephant densities and felling rates increased, adult tree density decreased and these trees were replaced by an abundance of coppiced trees with an associated increase in canopy volume at preferred browsing height, as well as a notable scarcity of tall trees. Despite the severe lack of tall trees in Gonarezhou, substantial seedling recruitment was observed although this was patchily distributed (Ferguson, personal observation 2014). Although this was not assessed in this study, it may be in accordance with Lewis' predictions that recruitment by tall trees may be sustained if the nutrient status of the soil is high.

Lewis (1991) goes on to make further predictions which imply that the current status of Gonarezhou's woodlands may not be an end point. He suggests that even if coppice-promoting soils are nutrient rich enough to support long-term survival of coppiced trees and recruitment by adult trees, continued increases in browsing pressure could result in decreased recruitment rates, lowered tolerance of coppiced trees to stem damage and eventually lead to large scale die-offs in coppiced tree numbers. Additionally, although the very tall trees present in Gonarezhou now are probably not at risk of being felled; bark damage appears to be an eminent threat. In consideration of this, we expect that all the tall trees will disappear from these woodlands. If this happens, these woodlands would have undergone a complete conversion from tall mopane woodland to shrubland.

Gonarezhou is representative of a possible, but extreme, future state for mopane woodlands in Malilangwe if elephant numbers are allowed to increase to comparable levels. The comparison between Malilangwe and Gonarezhou is useful but not completely robust in its predictive power. Although as many variables as possible were controlled for, some ecological variables that were not assessed in this study may have unavoidably differed between areas. Possible variables include depth of the water table, proximity to water sources (Ben-Shahar 1993; Mosugelo et al. 2002;Nellemann et al. 2002; Chamaillé-Jammes et al. 2007), terrain (Nellemann et al. 2002), soil characteristics (van de Vijver et al. 1999; Vanak et al. 2012), other herbivores (van de Vijver et al. 1999; Wiseman et al. 2004), and availability, suitability and nearness of other vegetation types for forage (Clegg, personal communication 2014). It is possible that some of these factors also have an influence on and or interact with elephant herbivory to influence vegetation structure and composition, in this case, the extent of coppicing, woodland structure and the long-term survival of mopane (Lewis 1991).

Results of this study are important for the management and conservation of the mopane woodlands in the Malilangwe Wildlife Reserve particularly as well as potentially in Gonarezhou National Park and elsewhere in the region. Many past studies in Gonarezhou National Park have identified elephants as major influencers of change in woodlands (Gandiwa et al. 2011). A recent study by Zisadza-Gandiwa et al. (2013) found that disturbances such as herbivory are significantly impacting the woody vegetation in riparian zones along the three major rivers that run through the park, one of which is the Runde River which is where our Gonarezhou plots were located. In light of these changes in the vegetation, the authors identified the need to continuously monitor the riparian vegetation. Our study highlights the need to do precisely this. Specific consideration of the high levels of bark damage being incurred by trees is recommended as this may lead to the total loss of trees. It may also be indicative that elephant numbers are too high and elephants are nutritionally stressed.

Whilst the likelihood of these tall woodlands in Malilangwe becoming totally converted to shrubland is low under current elephant densities, if elephant numbers are allowed to reach sufficiently high levels a conversion is certainly possible. It is worth noting that the Malilangwe Wildlife Reserve is a much smaller and privately owned and fenced reserve compared to the larger Gonarezhou National Park. This makes it easier to manage the various factors that influence these woodlands, of which the most influential seems to be elephant densities. A partial or complete conversion to shrubland is likely to have repercussions for the biodiversity and aesthetic value of the park and these must be taken into consideration when deciding how to manage the problem. It is recommended that the management of the Malilangwe Wildlife Reserve continues with its conservation mandate to scientifically monitor the changes in the reserve (www.themalilangwetrust.org), in this case the mopane woodlands and elephant abundance. Although management of elephant abundance is extremely complex and methods such as culling, sterilization and translocation are often ineffective and/or expensive(van Aarde & Jackson 2007), these should be considered if management wishes to control elephant numbers.

Conclusion

This study demonstrates the strong development of the resprouting shrub layer in the mopane woodlands on alluvium within Malilangwe Wildlife Reserve in response to increasing elephant impact on tall trees. This was associated with a functional response from the elephants which seem to have increased their utilisation of shrubs proportionately more than trees. As elephant numbers increase this trend is likely to change, and the gradual attrition of the tree layer is expected to continue. The study also showed that the mopane woodlands in Gonarezhou National Park have a very prominent shrub layer with a paucity of tall trees relative to Malilangwe. In light of the fact that tree damage and particularly bark damage to the few remaining emergent trees in Gonarezhou is so high, all the very tall trees in these woodlands are likely to be lost over time. This suggests that increasing elephant impact will ultimately lead to a total loss of tall trees rather than to equilibrium of trees. This prediction is particularly relevant for the managers of the Malilangwe Wildlife Reserve. If elephant numbers are left to increase, tree losses are predicted to increase despite the growing shrub layer and therefore a total conversion from tall mopane woodland to shrubland is possible. If this conversion is to be avoided, it is advisable that management continues to monitor changes in these woodlands and if necessary implements strategies to control elephant abundance.

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