Emergent trees in *Colophospermum mopane* woodland: influence of elephant density on persistence versus attrition (#92659)

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Emergent trees in *Colophospermum mopane* woodland: influence of elephant density on persistence versus attrition

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Colophospermum mopane (mopane) forms mono-dominant woodlands covering extensive areas of southern Africa. Mopane provides a staple foodstuff for elephants, who hedge woodland by reducing trees to shrubs, leaving emergent trees which are too large to be pollarded. Emergent trees are important for supporting faunal biodiversity, but they can be killed by ringbarking. This study examined the influence of elephant density on woodland transformation and the height distribution of canopy volume, and whether canopy volume is maintained, and tall emergent trees too large to be broken can persist, under chronic elephant utilisation. Three regimes of 0.23, 0.59 and 2.75 elephants km^{-2} differed in vegetation structure and the height structure of trees. Areas under the highest elephant density supported the lowest total canopy volume owing to less canopy for plants >3 m in height, shorter trees, loss of most trees 6-10 m in height, but trees >10 m in height (>45 cm stem diameter) persisted. Under eight years of chronic utilisation by elephants, transformed mopane woodland maintained its plant density and canopy volume. Plant density was greatest for the 0-1 m height class, whereas the 3.1-6 m height class provided the bulk of canopy volume, and the 1.1-3 m height layer contained the most canopy volume. Emergent trees (>10 m in height) suffered a loss of 1.4% per annum as a result of debarking. Canopy dieback of emergent trees increased conspicuously when more than 50% of a stem was debarked, and such trees could be toppled by windthrow before being ringbarked. Thus relict emergent trees will slowly be eliminated but will not be replaced whilst smaller trees are being maintained in a pollarded state. Woodland transformation has not reduced canopy volume available to elephants, but the slow attrition of emergent trees may affect supported biota, especially cavity-dependent vertebrate species, making use of these trees.

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Abstract

Colophospermum mopane (mopane) forms mono-dominant woodlands covering extensive areas of southern Africa. Mopane provides a staple foodstuff for elephants, who hedge woodland by reducing trees to shrubs, leaving emergent trees which are too large to be pollarded. Emergent trees are important for supporting faunal biodiversity, but they can be killed by ringbarking. This study examined the influence of elephant density on woodland transformation and the height distribution of canopy volume, and whether canopy volume is maintained, and tall emergent trees too large to be broken can persist, under chronic elephant utilisation. Three regimes of 0.23, 0.59 and 2.75 elephants km^{-2} differed in vegetation structure and the height structure of trees. Areas under the highest elephant density supported the lowest total canopy volume owing to less canopy for plants >3 m in height, shorter trees, loss of most trees 6-10 m in height, but trees >10 m in height (>45 cm stem diameter) persisted. Under eight years of chronic utilisation by elephants, transformed mopane woodland maintained its plant density and canopy volume. Plant density was greatest for the 0-1 m height class, whereas the 3.1-6 m height class provided the bulk of canopy volume, and the 1.1-3 m height layer contained the most canopy volume. Emergent trees (>10 m in height) suffered a loss of 1.4% per annum as a result of debarking. Canopy dieback of emergent trees increased conspicuously when more than 50% of a stem was debarked, and such trees could be toppled by windthrow before being ringbarked. Thus relict emergent trees will slowly be eliminated but will not be replaced whilst smaller trees are being maintained in a pollarded state. Woodland transformation has not reduced canopy volume available to elephants, but the slow attrition of emergent trees may affect supported biota, especially cavity-dependent vertebrate species, making use of these trees.

Keywords. African savanna, canopy volume, Gonarezhou, hedging, Malilangwe, plant-herbivore relations, ringbarking, vegetation transformation

Introduction

The global biodiversity crisis demands astute custodianship of the remaining areas supporting significant natural biodiversity, of which protected areas should form the core. However, many protected areas constitute a small portion of the ecosystems they purportedly protect, such that certain natural processes may become perturbed and thereby pose a challenge for meeting the aims of protected areas. The ‘elephant problem’ is one such example for many African protected areas, in which increasing elephant densities resulting from compression of elephants into a protected area from outside areas, or accelerated rates of population growth because of improved protection, has caused dramatic changes in habitat that affects other species and ecosystem functioning (Laws et al. 1975; Lewis 1986; Owen-Smith 1992).

Savanna elephants are capable of transforming savanna woodlands and forest to shrubland and grassland (Laws et al. 1975; Chamaillé-Jammes et al. 2007; Guldemond and van Aarde 2008) that may cause the local extirpation of some selected species (O'Connor et al. 2007), thereby threatening the biodiversity dependent on woodland structure or on certain woody species (Cumming et al. 1997; Herremans 2005; Nasseri et al. 2010). The negative impact of elephants on tall trees has attracted close attention owing, in part, to the aesthetic appeal of such trees and their disproportionate value as nesting or resting sites for many animal species (Shannon et al. 2008; Chafota and Owen-Smith 2009). When the challenges posed by elephants first emerged in the 1960s, a common response intended to restore or maintain woodland was reduction of the size of an elephant population (Wing and Buss 1970; Laws et al. 1975). Implicit in such decisions was that elephants could be reduced to a density that would be appropriate for maintaining affected tree populations. However, the relation between elephant density and woodland structure is not well understood.

Recovery of elephant-impacted woodlands, following a change in elephant density, depends on regrowth of surviving individuals and on recruitment of new individuals. Both regrowth and recruitment are subject to ongoing impact from elephants but also additional influences including those of precipitation patterns, fire, and the impact of other herbivores (Dublin et al. 1990; van der Vijver et al. 1999; Mosugelo et al. 2002; de Beer et al. 2006). Thus, a reduction in elephant density does not necessarily ensure that recovery will occur (Laws et al. 1975). African savanna vegetation is highly diverse (White 1983), different woody species are not accorded the same attention by elephants nor do they necessarily respond in the same way (O'Connor et al. 2007). Species-specific study of the impact on and response of individual key woody species by elephants therefore offers a sound means of improving understanding of woodland-elephant relations.

Colophospermum mopane Kirk ex Benth. (hereafter mopane) woodlands are widely distributed across the semi-arid regions of southern Africa, often forming mono-dominant woodlands (Timberlake 1995), and falling within the previous geographic range of elephants (Coppens et al. 1978). Tall mopane woodlands may develop on well-watered, deep alluvial soils, whereas shallow, heavy-textured soils often support only a mopane shrubland (Timberlake 1995). Mopane forms a staple of the diet of elephants where they co-occur (Guy 1976; Villiers and Kok 1988; Viljoen 1989; Lewis 1991; Ben-Shahar 1996; Clegg 2010). Forms of utilisation of mopane by elephants includes stripping of leaves, breaking of small branches, pollarding (snapping) or toppling main stems in order to access foliage, uprooting, and debarking (Clegg 2010). However, mopane is well adapted to heavy utilisation by elephants owing to its strength of resprouting (coppicing) (Mushove and Makoni 1993), with stands of trees that have been reduced in height through pollarding termed 'hedged' mopane woodland (Styles and Skinner 2001). By reducing the height of tall trees, thereby also reducing mean canopy height, hedging increases leaf density close to the ground that increases browse availability for elephants and for other species (Martin 1974; Guy 1981; Smit and Rethman 1998; Smallie and O'Connor 2000; Rutina et al. 2005). Some tall trees may persist within hedged vegetation because their stem is too large to be pollarded or pushed over, but remaining large trees remain vulnerable to being killed through ringbarking by elephants. An unresolved question is whether increased browse availability resulting from hedging can mitigate against pollarding or debarking of remaining large trees. This is an expected outcome because pollarding and debarking of large trees is five-fold more energetically demanding for elephants than stripping of (easily accessible) leaves and twigs (Clegg and O'Connor 2016).

An alternate prediction emerges from consideration of the foraging behaviour of elephants and the seasonal phenological cycle of mopane. Elephants, especially bulls, are preferentially grazers of soft, green grasses but consume an increasing proportion of woody material as grasses become less available during the course of the dry season (Clegg 2010; Pretorius et al. 2011). Bulls rather than cows are responsible for most of the extreme damage to mopane trees in the form of pollarding, uprooting or debarking (Clegg 2010). Mopane woodlands occur in environments experiencing seasonal rainfall, with a dry season of up to seven months (Timberlake 1995). Mopane is a facultatively deciduous species, such that little mopane leaf is available to elephants at the height of the dry season (Dekker and Smit 1998). Bulls resort to increasing their use of bark during this period despite the energetic demands of this feeding pattern (Clegg 2010; Clegg and O'Connor 2016) that may result in partial or complete ringbarking of trees. Partial debarking can disrupt the transport mechanisms of the tree and cause canopy dieback, whereas ringbarking will result in death or top-kill of the stem (Lewis 1991). Although coppicing may occur at the base of a dead tall stem (Bromwich 1972), this tall stem becomes unavailable for the many animal species which use it. Thus, remaining tall trees in a hedged woodland may continue to be impacted because the increased availability of browse through hedging is not available at the height of the dry season.

The first aim of this paper was to examine the nature and extent of impact, and patterns of utilisation, under different densities of elephant on the structure of mopane woodland. Specific questions addressed were whether an increase in elephant density resulted in (i) a decrease in the density or canopy volume of shrubs or trees, or of total canopy volume, (ii) an increase in the total amount, or proportion of the total amount, of canopy volume at a height accessible to elephants, (iii) a difference in the pattern of utilisation in terms of volume removed per plant, and degree of debarking, (iv) a trend toward elimination of tall trees, and to confirm that (v) elephants were the responsible agent for any observed differences. The second aim of this study was to determine whether, under chronic utilisation by elephants sustained over years, (i) hedged mopane woodland could maintain the amount and vertical distribution of canopy volume, (ii) tall remaining trees were spared by elephants ostensibly on account of an increased volume of available browse, or (iii) tall trees were subject to ongoing attrition from debarking, (iv) the size limit of trees that elephants can topple or pollard, and that (v) recruitment into the population should ensure population persistence.

Methods

Study area

The study was conducted in south-eastern Zimbabwe within Gonarezhou National Park (GNP) and the adjacent Malilangwe Wildlife Reserve (MWR) (Figure 1). MWR is 394 km^2 in area, and is fenced. GNP has an area of 5053 km^2 and is partly fenced. The environment and vegetation of MWR has been described in Clegg and O’Connor (2012), and of GNP in Cunliffe et al. (2012). Each study area experiences a similar seasonal climate of hot, wet summers and warm dry winters. Mean annual rainfall is approximately 550 mm, and daily maximum temperatures may exceed 30°C during every month of the year. The Chiredzi River, joined by the Nyamasikana River, flows through MWR to join the Runde River, which flows west to east across northern GNP until it enters Moçambique. Woodlands in which mopane is dominant or conspicuous cover large parts of both MWR (Clegg and O’Connor 2012) and GNP (Cunliffe et al. 2012). This study focussed on mopane woodland on alluvium, described as the Mopane Woodland on Alluvium (vegetation type 4.9) in GNP (Cunliffe et al. 2012) and as *Colophospermum mopane-Courbonia glauca* shrub open tall woodland in MWR (Clegg and O'Connor 2012). This woodland type has low species richness, is dominated by mopane, and usually supports tall, emergent trees of this species.

Data collection

2001 and 2014. The study design sought to compare this woodland type under different elephant densities, using a combination of temporal changes on fixed plots and a 'space-for-time' substitution. Eight plots were randomly selected using GIS along the Nyamasikana and Chiredzi Rivers in MWR, and sampled in 2000/2001 (Clegg and O'Connor 2012). The eight plots were relocated using a GPS in 2014, and resampled (Ferguson 2014). Elephant density in MWR was 0.23 and 0.59 elephants km^{-2} in 2000/2001 and 2014, respectively (Dunham et al. 2013), designated as 'low' and 'intermediate' density for this study. The elephant population in GNP grew exponentially from 1992 (Dunham 2012) to attain a density of 2.75 elephants km^{-2} in 2013 (Dunham et al. 2013), designated as 'high' density for this study. Seven plots were randomly selected in GNP using GIS, measured in 2014 (Ferguson 2014), and remeasured in 2022, during which time elephant density had remained high (Dunham et al. 2021). Error of relocating a plot from GPS points was <5 m. Any plot within MWR or GNP was >500 m from any other plot in order to ensure spatial independence.

Different sizes of woody plants in a plot were sampled in a nested fashion (Walker 1976). A plant <3 m in height was defined as a shrub; a multi-stemmed species (e.g., *Capparis* spp.) was considered a shrub irrespective of its height, and otherwise a plant > 3 m in height was defined as a tree. We used a belt transect of 50 m length and of sufficient width to sample at least 15 individuals of the most common shrub species; belt width was then increased in order to increase the sample size of less common shrub species, and increased again to ensure more than 15 individuals of the most common tree species (mopane) were sampled. The sample size of tall, emergent mopane trees was then increased by measuring additional individual trees around a plot, and recording their GPS positions.

Live plants were measured if more than half the individual plant was included within the plot. The following were measured (to 0.1 m) or recorded for each live shrub or tree: (i) height, measured using a graduated rod up to 6.5 m, and estimated using the yard-stick method in increments of 0.5 m for heights >6.5 m; (ii) longest canopy diameter; (iii) canopy diameter perpendicular to the longest; (iv) canopy depth, and (v) shape of the canopy according to seven basic shapes (Melville et al. 1999). For trees, the following additional measurements or estimates were taken of each stem: (i) stem circumference (cm) above the basal swelling; (ii) damage experienced by a stem, as branches lost, stem broken off, stem broken or pushed over but still attached, or stem uprooted; (iii) whether elephants or an unknown agent were responsible for damage; (iv) the volume of canopy lost, estimated using an eight-point scale (Walker 1976); and (v) occurrence of coppicing. For shrubs, only the volume of canopy lost to elephants or to other agents was estimated. Age of utilisation of woody material was defined as ‘old’ and ‘new’. New utilisation was identified by exposed wood being yellow or white, not grey, and without black splodges of algal growth, or, for bark, by seepage of gum, and had been determined to be <8 months of age. Old utilisation (>8 months) was further distinguished by coppice growth or healing of wounds. Dead stems were recorded and dead plants were defined as those with dead stems and no coppicing. Recruitment was defined as stems of the smallest size class that were not coppice shoots.

GNP: 2014 to 2022. The plots in GNP were resampled in 2022, for which data collection was streamlined in order to address the main foci of (i) change in canopy volume and its height distribution, and (ii) persistence and state of large emergent trees. Measures of canopy dimensions were taken as in 2014. Repeated defoliation of a plant renders reconstruction of canopy volume unreliable. Consequently, each tree stem was scored for whether branches had been taken, the stem broken or pushed over, and, if so, whether it had continued to grow, the agent responsible, and the age of utilisation. Emergent trees were measured for the circumference and length of stem debarked, separately for old and new debarking, and their combined total was expressed as a percentage of stem circumference. The percent of canopy volume of emergent trees lost to crown dieback, easily scored because dead branches remained in the canopy, was estimated for a subset of trees. Shrubs were scored for whether canopy volume had been lost to elephants or to other agents.

Plant nomenclature follows the Flora of Zimbabwe (2022).

Data analysis

All analyses were conducted using R (R Core Team 2022).

2001 and 2014. The influence of elephant density (low, intermediate, high) on vegetation structure was examined for the set of variables canopy volume of shrubs, trees and total; density of shrubs, live trees, live standing trees, live prostrate trees, live trees < 10 m height, live trees > 10 m height, pollarded main stems, and dead trees; mean tree height; and species density of shrubs and species richness of trees. The extent of vegetation utilisation in relation to elephant density was examined for old or new utilisation of shrubs or trees by elephants or by unknown agents. Pseudo-replication and serial correlation were unavoidable features of this landscape-level study. Accordingly, each density was tested separately against the others (i.e., low versus intermediate, low versus high, intermediate versus high). Low versus intermediate density was tested with a paired *t*-test, whereas a Welch's *t*-test was used for the other two comparisons. The question of whether the height distribution of trees differed across the three elephant densities was examined with a chi-squared contingency test, using bin sizes of 3.1-6, 6.1-10. 10.1-14, and >14.0 m height. Canopy volume is emphasised because it represents potentially available food for elephants. Canopy volume was calculated for each height layer according to Melville et al. (1999). Canopy volume was $\log_{10}$-transformed for analysis. The influence of elephant density on the distribution of canopy volume across height layers was examined using a two-way analysis of variance, for which the interaction term was of primary interest.

Estimates of damage by elephants, fire, or unknown agents were derived for individual plants, height layer, and plot. A rank for damage to a plant was first converted to the class mid-point (Walker 1976). Loss of tree canopy biomass was weighted by the cross-sectional area of a stem, and bark damage was weighted by stem circumference. New shrub damage was weighted by the measured canopy volume of a shrub, and old shrub damage by the reconstructed canopy volume (V_R) prior to change calculated as: $V_R = V_M$ (100/(100-% damage)), where V_M is the measured (current) volume. (Different transect sizes were accommodated when obtaining a sum of the percentage damage for each species.) An estimate of percent damage for a plot was derived by summing these values. The influence of elephant density on the scale of damage for each damage category was examined in a pair-wise fashion, as described above.

GNP: 2014 to 2022. The following changes in density and canopy volume between 2014 and 2022 (*n*=7) were examined. Changes in total density and total canopy volume were examined with a paired *t*-test. For changes in density or canopy volume per height class or height layer, an analysis of variance was undertaken, with the main effects of year (2014, 2022) and height class or layer (0-1.0, 1.1-3.0, 3.1-6.0, 6.1-10.0, >10.0); degrees of freedom were too few to permit an interaction term. These analyses were carried out in the 'car' (Fox and Weisberg 2019) and 'emmeans' (Lenth 2022) packages in Rstudio, respectively. Changes in individual height classes or layers were examined with a paired *t*-test. The Benjamini Hochberg correction was used to account for an increased Type 1 error rate (Benjamini and Hochberg 1995). Canopy volume and density data were, respectively, $\log_{10}$- and $\log_e$-transformed for analysis. The influence of stem size on whether a stem was pollarded was examined using logistic regression, excluding stems <20 cm circumference and large stems which had been pushed over. The impact of the extent of debarking on canopy dieback of non-pollarded emergent trees was examined using logistic regression.

Results

Effect of elephant density: 2014

Vegetation structure. Elephant density had a marked influence on vegetation structure (Table 1). Under a sustained high elephant density in GNP, compared with low or intermediate density in MWR, tree canopy volume and total canopy volume were approximately halved; shrub canopy volume was unaffected; mean tree height was 3 m lower; the density of trees >10 m in height was more than halved, with a corresponding approximately six-fold increase in the density of pollarded stems, although the density of trees <10 m in height, and of live standing trees, were unaffected (live prostrate trees were almost absent); dead trees were two thirds less; and four and two species of shrubs and trees, respectively, had been lost. Effects of an increase from low to intermediate elephant density on Malilangwe Reserve over 14 years were apparent as a 21% loss of live standing trees, a 38% loss of trees <10 m in height, a corresponding four-fold increase in the density of pollarded main stems, a 29% reduction in shrub density, and a marginal loss of tree and shrub species.

Elephant density further influenced canopy volume per height layer (Figure 2; Table S1). The least canopy volume occurred in the 0-1.0 m layer ($P<0.05$), whilst the other three height layers did not differ among themselves ($P>0.05$). The smallest canopy volume under the highest elephant density shown in table 1 was apparent only for the two height layers >3.0 m, but not for those <3.0 m in height (i.e., interaction effect). Elephant density further influenced the height structure of the tree population (Figure 3; $\chi^2 = 336.3$; df = 6; $P = 2.2e-16$). Smaller trees (3.1-6.0 m in height) were well represented under all three levels of elephant density; trees from 7.1 to 11.0 m in height had been, respectively, markedly reduced or completely eliminated under an intermediate or high elephant density. There was a lower density of trees 6.1 to 14.0 m in height under a high elephant density, although a proportion of trees >14.1 m in height had persisted.

Utilisation. Consistent with an increase in elephant density was an approximately ten- and hundred-fold increase in old and new elephant damage, respectively, for trees (Table 1). Trees had lost about 25% or 60% of canopy volume to old and new elephant utilisation combined under intermediate or high elephant density, respectively, compared with 5% for the area under low elephant density. By contrast, old and new elephant damage on shrubs was considerably higher for intermediate or high elephant density than for low elephant density. Damage by unknown agents was minor, accounting for five to 14% of canopy volume, and fire damage was so slight it could be disregarded.

Areas under different elephant densities differed in terms of old or new bark damage inflicted by elephants, and for old bark damage by unknown agents, that depended on tree height (Figure 4; Table S2). Only trees > 7 m in height were debarked to any meaningful degree. Areas under high elephant density showed a 30-fold greater level of old debarking by elephants than areas under low elephant density, but that of areas under intermediate density did not differ ($P>0.05$) from either (Figure 4a). Areas under different elephant densities differed only marginally in terms of new bark damage by elephants (Table S2), attributed to the near absence of new debarking in areas under low density (Figure 4b). Old debarking by unknown agents was higher under an intermediate than under a low or high elephant density (Figure 4c; Table S2).

Influence of chronic elephant utilisation in GNP: 2014-2022

Mopane contributed more than the other 26 shrub species combined to either average shrub density or average shrub canopy volume (Figure S1), and almost all trees were mopane. The combined value of all species was therefore used for analyses. For trees and shrubs combined, no change was evident between 2014 and 2022 for either total density ($t = 0.51$; df = 11.81; $P = 0.6208$) or for total canopy volume ($t = 0.8632$; df = 9.8475; $P = 0.4086$). For the analysis of variance, there was no main effect of year (2014 to 2022) on changes in density by height class, or changes in canopy volume by height class or by height layer (Table S3). Nor were there any changes in density or canopy volume of individual height classes, or canopy volume of individual height layers ($P > 0.05$ for all paired *t*-tests) between 2014 and 2022 (Figure 5). Although plants <1 m in height constituted most, and plants >6 m in height constituted very little of population number in either year (Figure 5a), the bulk of canopy volume was provided by plants between 3.1 and 6.0 m in height (Figure 5b), whereas the 1.1 to 3.0 m height layer contained the greatest amount of canopy volume (Figure 5c). The abundance of mopane in the smallest size class (Figure 5a) indicates this species has recruited well. Other than some dead emergent trees, dead stems and trees were conspicuously almost absent, presumably having long since been knocked over by elephants.

Mopane trees had been severely utilised by 2022 (Table 2). In terms of old elephant damage, two thirds of the tree stem population had been pollarded and about 11% had escaped attention, whereas removal of branches was the main recent impact because very few stems remained to be pollarded or pushed over. The height at which a stem was pollarded was from close to ground level up to 3 m. Shrubs received less attention; only 23.4% of shrubs <1 m in height, and 80.2% of shrubs 1.1-3 m in height, had been used. The main stem of a tree was unlikely to be pollarded by elephants if it was approximately >45 cm in diameter (Figure 6), which is the size of the emergent canopy trees >10 m in height (Figure S2)).

In summary, canopy volume was effectively maintained over an eight-year period despite chronic utilisation by elephants.

Emergent trees ($n = 89$) experienced attrition between 2014 and 2022, with 73% surviving intact, 15.8% having lost one or more of the main stems (>90 cm circumference), and 11.2% of trees having been lost completely. Twelve of the 15 trees with two main stems had lost the smaller stem, and two of the six trees with more than two stems had lost at least one stem.

Expressing this as a stem population (*n*=127) of these trees in 2022, 71.7% of the stems remained standing, and 28.3 % had been lost as large stems owing to being pollarded (18.1%), falling over (8.7 %), or other causes (1.6 %). Percent of circumference debarked of an emergent standing tree increased on average by 25% between 2014 and 2022 (Figure S3). The proportion of canopy volume of an emergent tree lost to dieback in relation to the extent of debarking was described by a logistic relationship (Figure 7). Taken together, collapse of tall stems was primarily attributed to windthrow of a stem preconditioned by advanced canopy dieback once debarking exceeded 50% of stem circumference (Figure 7). One exception was probable collapse directly from windthrow. Thus elephants indirectly caused the toppling of emergent trees and stems through canopy dieback resulting from debarking; complete ringbarking was not necessarily required.

Discussion

Elephant-mopane relations

Conversion of mopane woodland to shrubland by elephant utilisation has been widely reported, including in northern Botswana (Ben-Shahar 1996), Tuli Block, Botswana (Styles and Skinner 1997, 2000), Luangwa Valley, Zambia (Caughley 1975; Lewis 1991), Kruger National Park and Limpopo Valley, South Africa (Trollope et al. 1998; Smallie and O'Connor 2000), and, in Zimbabwe, in Sengwa Wildlife Research Area (Anderson and Walker 1974), Hwange National Park (Boughey 1963), and Gonarezhou National Park (Bromwich 1972; Tafangenyasha 1997; this study). In this study, conversion of riverine mopane woodland to shrubland depended on elephant density. In MWR, conversion of riverine mopane woodland had been initiated between 2001 and 2014 when elephant density rose from 0.23 to 0.59 elephants km^{-2}, as evidenced by an increase in the density of pollarded stems and a loss of canopy volume (Table 1). However, the tallest height classes were maintained (Figure 3). By contrast, riverine mopane woodlands in GNP had been converted to shrubland by 2014 through the loss of all trees between 6.1 m to 10 m in height, with a low density of relict tall trees too large to be pollarded (Figure 6) remaining. Prior to the 1991/92 drought, elephant density in GNP was mostly maintained below 1.0 individual km^{-2} through population reduction, and was reduced to 0.8 individuals km^{-2} by this drought, but thereafter the population grew exponentially at 6.2% per annum to attain a density of >2 elephants km^{-2} in 2013 (Dunham et al. 2013). Riverine mopane woodland apparently was converted during this 23-year period. The responses observed in this study are consistent with woodland conversion becoming apparent at an elephant density of about 0.5 individuals km^{-2} (Cumming et al. 1997). Ground observations emphasised the role bulls play in woodland conversion, with the changes on MWR between 2001 and 2014 strongly influenced by an influx of about 70 bulls from GNP before 2014 (BW Clegg, unpublished data).

Conversion of tall woodland to a hedged shrubland in GNP by 2014 had not decreased the amount of browse available to elephants (Figure 2), nor has it decreased under eight years of chronic use by elephants (Figures 5b, c). Furthermore, coppicing of mopane increases the availability and palatability of foliage (leaf, twig, or twig bark) (Smallie and O'Connor 2000; Smit and Rethman 1998; Styles and Skinner 1997, 2000; Hrabar et al. 2009) that should improve the foraging efficiency of elephants. Mopane leaf is the staple foodstuff of female elephants in south-eastern Zimbabwe (Clegg 2010). We therefore propose that the increased availability of this foodstuff through hedging is an important influence on maintaining a high density (~2 km^{-2}) of elephants in a semi-arid environment.

Conversion of mopane woodland to shrubland has not threatened persistence of the mopane population. Elephants have transformed the growth form of an individual plant and, thereby collectively, of the vegetation structure of a woodland, but complete mortality (i.e., no coppicing) of mopane recorded in this study was relatively slight. Mortality of large trees as a result of ringbarking observed in this study is an expected result (Lewis 1991). Reports of apparently high mortality of mopane in GNP as a consequence of toppling or pollarding by elephants (Tafangenyasha 1997) are equivocal because trees may appear dead based on a once-off visual assessment of tree loss, but subsequent monitoring of toppled mopane trees in GNP has revealed that most affected trees coppice from the base months after impact (Bromwich 1972). Lewis (1991) found that complete mortality of mopane trees toppled or pollarded by elephants in the Luangwa Valley, Zambia, depended on edaphic characteristics, and was precipitated by drought. Elsewhere in semi-arid, non-riparian mopane woodlands, a single drought event has caused the loss of between 4.5 % and 6.9 % of mopane individuals, usually smaller plants (Scholes 1985; O'Connor 1999), and the loss of patches of adult mopane trees on degraded habitats where water retention had been compromised (McGregor and O'Connor

1997). Fire does not cause conspicuous mortality of mopane because of its coppicing ability (Timberlake 1995) and, in any event, riverine mopane woodland in Gonarezhou National Park rarely carries sufficient fuel for a burn.

Caughley (1976) proposed, based on his studies of mopane woodland and baobabs in the Luangwa Valley, Zambia, that elephant-woodland relations may follow a stable limit cycle, with a periodicity of about 200 years in the Luangwa Valley. His proposal questioned the prevailing assumption of management of that period that a stable equilibrium point exists between elephants and woodland. Putting aside theoretical and empirical challenges to his proposal (e.g., Cumming 1982; Lewis 1986, 1991; Duffy et al. 1999; Baxter and Getz 2005), we do not consider a stable-limit cycle to be an appropriate conceptual model for elephant-mopane woodland relations in south-eastern Zimbabwe. This model requires a close coupling between elephants and mopane, which apparently exists in south-eastern Zimbabwe where mopane provides the bulk of the food intake of cows (Clegg 2010). However, this study showed that the abundance of mopane did not materially diminish even after a few decades of chronic utilisation by elephants. Furthermore, elephants show a catholic use of food species using more than 100 species in south-eastern Zimbabwe (Clegg 2010) and comparable numbers in other systems where mopane does (Williamson 1975; Guy 1976) or does not occur (De Boer et al. 2000). Elephants therefore have many options for foodstuffs should mopane decline; there is no convincing evidence that elephants have a close coupling with any individual plant species.

Can relict emergent trees survive?

An hypothesis put forward for this study was that an increased availability of forage as a result of hedging would decrease use of remaining emergent trees, provided that elephant density did not continue to rise. The condition of elephant density remaining approximately stable was met (Dunham et al. 2021). The elephant population remained at approximately 9000-10000 individuals (~ 2 individuals km^{-2}) from 2014 to 2021. The conditions were also met that hedging would not result in a decreased availability of mopane for elephants (Figure 2), and that the amount of mopane canopy volume would be maintained under chronic elephant utilisation (Figure 5b, c). However, the hypothesis was rejected on the basis of ongoing attrition of emergent trees through debarking, at a slow rate of 1.4% per annum lost over eight years. On

MWR, elephants make greater use of debarking toward the end of the dry season when the availability of other foodstuffs has declined (Clegg 2010). Debarking is interpreted as a foraging action of necessity rather than a preferred action because elephants require about 18 hours a day to meet their foraging needs, with an adult male consuming 1-1.2 % of its body weight per day (Owen-Smith 1992), and debarking of large stems is an energetically costly process, taking about five times longer to harvest and chew a mouthful of bark from the main stem than a mouthful of leaves (Clegg and O’Connor 2016). The time required for debarking mopane trees may be less because large sections of bark can be relatively quickly stripped off a large mopane stem once an incision has been made, compared with some tree species (e.g., *Sclerocarya birrea*) for which small fragments have to be tediously chiselled off (Clegg 2010). However, bark off large mopane stems is conspicuously fibrous. Bark therefore seems less than ideal for meeting foraging needs, unless it perhaps offers an essential constituent (cf. Anderson and Walker 1974), which has not yet been identified.

Emergent mopane trees in riverine mopane woodland, GNP, appear set to experience an ongoing slow decline in density if conditions remain similar to those recorded over the eight years of study – a high elephant density and a lack of foraging alternatives at the height of the dry season. Bulls are primarily responsible for debarking mopane, but they are preferentially grazers of green grass (Clegg 2010, and references therein). Clegg (2010) proposed that the impact of bulls on woody vegetation would be considerably less if they had access to suitable grasslands, especially floodplain or riverine grasslands (e.g., Lewis 1986), wetlands and reedbeds, during the dry season, which, he proposed, was the historical norm before unbridled human expansion. The far-reaching ranging patterns of elephant bulls, for which travel in the order of 50-100 km is not uncommon (summary in Dolmia et al. 2007) should enable them to access winter foraging grounds of such a nature both within and outside of GNP. Options within GNP are limited. Extensive reedbeds have occurred along portions of the Runde River within GNP that have been stripped by large floods and then regrown. For example, the flood resulting from Cyclone Eline in 2000 denuded a four kilometre stretch of reedbeds, which then recovered within about a decade, but was again stripped by Cyclone Dineo’s flood in 2017, and has not yet re-established (TG O’Connor, unpublished data). Options outside of GNP should be substantial with the creation of the 89000 km^2 Greater Limpopo Transfrontier Conservation Area in 2002 (Ferreira 2004) that potentially offers extensive wetlands or riverine grasslands within the

Banhine and Zinave National Parks, and along the Save River, in Moçambique. To date, bull elephants have begun to explore the habitat available in Moçambique, but not in numbers or for a duration that would make a material difference to their impact within GNP (Gonarezhou Conservation Trust, unpublished data). Their subdued use of Moçambique is attributed, in part, to the hunting pressure they encounter along the border between GNP and Moçambique (Dunham et al. 2021), compounded by an increase in human settlement along the Save River and its tributaries. If these constraints change, then Moçambique may become an important foraging area for, at least, bull elephants that should diminish impact on emergent mopane trees.

Implications of structural transformation for supported biodiversity

Although an abundant mopane population has persisted in GNP in the face of chronic elephant utilisation, the potential consequences of dramatic transformation of vegetation structure for supported biota need to be considered because an aim for protected areas is to conserve all elements of indigenous biodiversity. Herremans (1995) showed an effect of elephant-transformed vegetation on avifaunal composition of comparable mopane woodland in northern Botswana, but this topic is essentially unstudied for mopane woodland. By contrast, structural change of miombo woodland in Zimbabwe by elephants had a pronounced negative effect on the richness of other plant species, birds, and some invertebrate taxa (Cumming al. 1997). The purpose of this section is to collate selected facets of indirect evidence to propose that such biodiversity impacts are also considerable in mopane woodland, in support of further study.

Tall mopane trees possess stem cavities as a consequence of their heartwood disappearing with age (heart rot; Timberlake 1995) which are used by a large number of vertebrate species for nesting or as a home. Many species of birds use these cavities for nesting, including hornbills, barbets, and chats (Hockey et al. 2005). Tree squirrels *Paraxerus cepapi* are sometimes termed mopane squirrels because of their penchant for using this species as a home and place for breeding; in addition, the large seeds of mopane are an important constituent of their diet in mopane woodland (Skinner and Chimamba 2005). On account of seed production of mopane being related to tree height (Timberlake 1995), availability of mopane seed in hedged riverine mopane woodlands in GNP was low because only the relict emergent mopane trees, which occurred at a low density (Figure 5), produced seed, pollarded trees did not (pers. obs.), although hedged mopane woodland produced seeds, albeit at a reduced amount, in Tuli Block, Botswana (Styles and Skinner 2001). Emergent trees were also the only source of cavities, but there was a slow attrition of emergent trees primarily through debarking. The potential value of the mopane woodlands we studied for squirrels appears to have been compromised by a dramatic reduction in mopane seeds and a loss of breeding sites that is expected to impact on their numbers and on the numbers of the many predators which prey upon them. Use of tree cavities by reptiles is not as conspicuous as by birds, but some snake, skink, and agama species, as well as the rock monitor *Varanus albigularis*, do so (Alexander and Marais 2007).

Caterpillars of the lepidopteran *Imbrasia belina* (Saturniidae; mopane worm) may exceed the biomass of elephants in semi-arid savannas during periods of irruption that affects ecosystem functioning and vegetation structure (Duffy et al. 2017; de Swardt et al. 2021). However, chronic utilisation of mopane by elephants, among other factors, has been implicated in reducing their abundance or even their disappearance (Styles and Skinner 1996; Hrabar and du Toit 2014), in part because of the disappearance of tall trees which are their preferred sites for laying eggs (Hrabar et al. 2009). Mopane worms are consumed by a suite of bird species that changes in composition as instars develop (Gaston et al. 1997) – reduction in the availability of mopane worms therefore has obvious ramifications for trophic patterns.

In summary, conversion of mopane woodland to shrubland is expected to have had far-reaching effects on the biodiversity supported by these woodlands through disruption of trophic and non-trophic linkages of mopane with faunal elements.

Conclusions

Mopane is the most resilient woody plant in the face of sustained elephant utilisation of which we are aware, on account of its resprouting ability following damage, and its levels of seedling regeneration. Despite a decade of chronic use of riverine mopane woodland in GNP by elephants, this woody species continues to support a high plant biomass that provides a relatively stable supply of a staple elephant foodstuff. Thus there is no apparent threat to this woody species persisting, but for tall mopane trees that became relicts, only those too large to be toppled remained. We propose that relict tall trees are of disproportionate importance for maintaining faunal diversity, such that the slow erosion of their numbers over time through debarking should be contained, if possible. The conversion of mopane woodland to shrubland being related to increases in elephant density suggests that an adjustment of elephant density might achieve this aim. However, a traditional approach of instituting population reduction is not the only means whereby density can be adjusted; rather, ensuring access to potentially available foraging habitats, especially wetlands in which bulls can forage during the dry season, should form part of the solution.

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Figure 1

Map of the study area and sampling locations.

The location of sampling plots (red dots) within Malilangwe Wildlife Reserve (*n* = 8) and Gonarezhou National Park (*n* = 7), Zimbabwe.

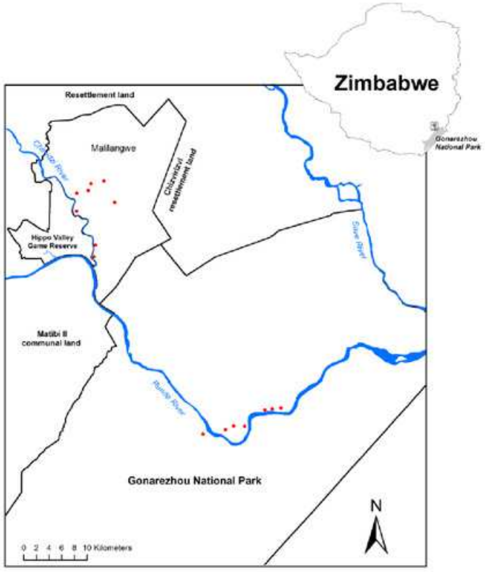
Zimbabwe
Gonarezhou National Park
Resettlement land
Mallangwe
Chiredzi River
Chizvirizvi resettlement land
Save River
Hippo Valley Game Reserve
Matibi II communal land
Runde River
Gonarezhou National Park
N
0 2 4 6 8 10 Kilometers

Figure 2

Influence of elephant density on canopy volume.

Comparison of the average canopy volume (± SE) per site (ha^{-1}) under three different elephant densities (low, solid; intermediate, dotted; high, hatched) and four height layers. Refer to the study area section for context on the three density regimes. Refer to Table S1 for the results of the analysis.

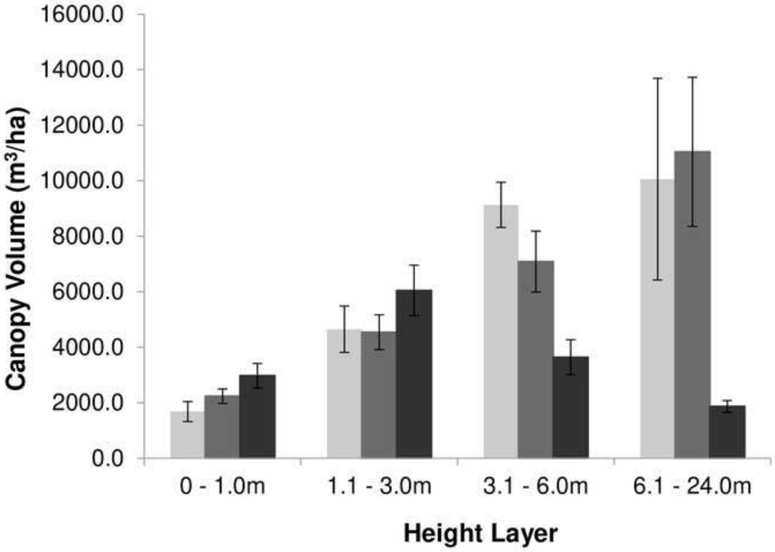
16000.0
14000.0
12000.0
10000.0
8000.0
6000.0
4000.0
2000.0
0.0
Canopy Volume (m³/ha)
0 - 1.0m
1.1 - 3.0m
3.1 - 6.0m
6.1 - 24.0m
Height Layer

Figure 3

The height distribution of *Colophospermum mopane* trees across three elephant densities.

Frequency distribution of tree height for a) low, b) intermediate, and c) high elephant density in *Colophospermum mopane* woodland on alluvium in south-east Zimbabwe. Refer to the Study Area section for context on the three density regimes.

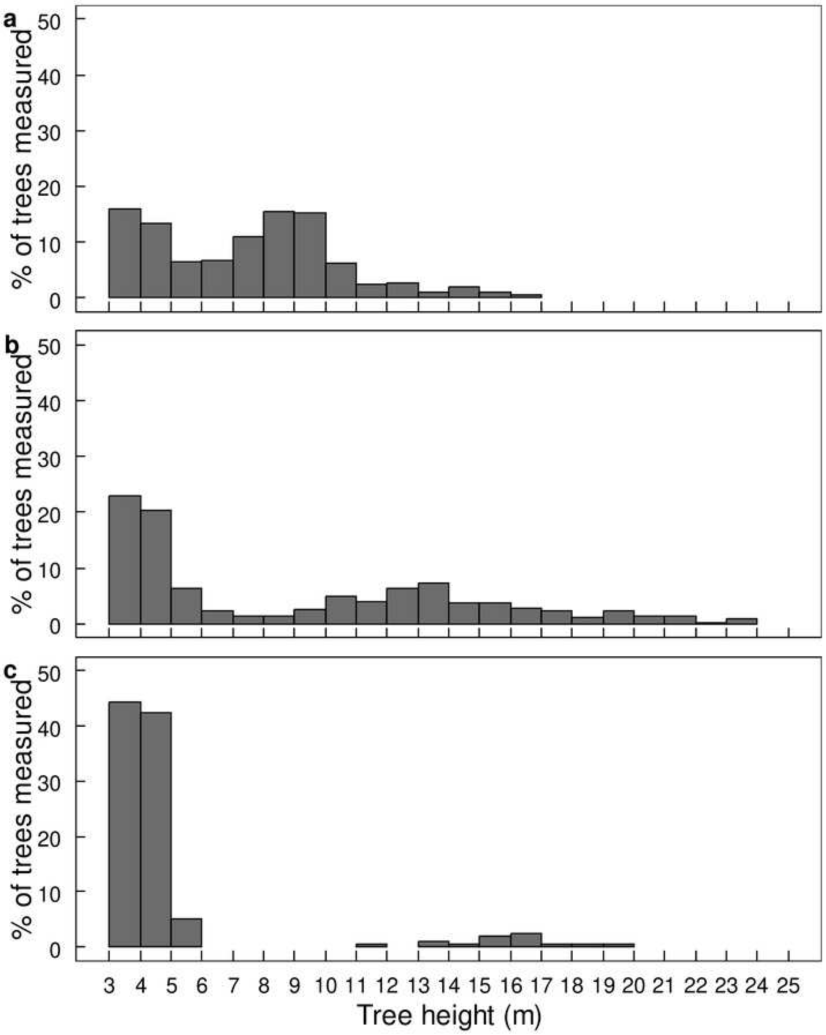
a
b
c
% of trees measured
0
10
20
30
40
50
3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Tree height (m)

Figure 4

Old and new bark damage to *Colophospermum mopane* by elephants or unknown agents.

Differences in the percentage bark damage for trees ≤ 7 m, or > 7 m in height, across areas supporting high (diamond), intermediate (square), or low (solid circle) elephant density for (a) old elephant debarking (OBE), (b) new elephant debarking (NBE), and (c) old unknown debarking (OBU). Note the different scale of the y-axes. Refer to Table S2 for results of the analyses.

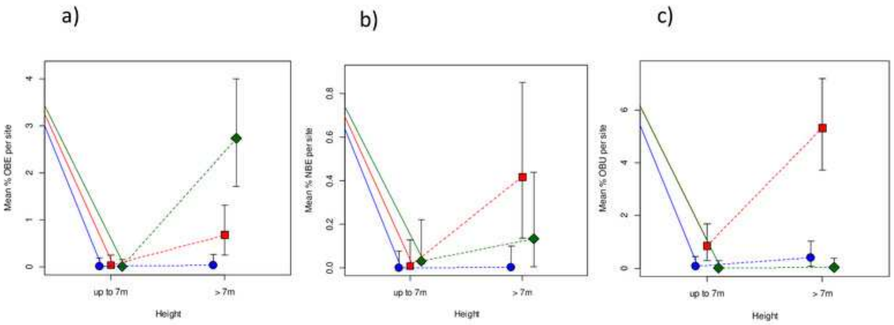
a)
b)
c)
Mean % OBE per site
0
1
2
3
4
Mean % NBE per site
0.0
0.2
0.4
0.6
0.8
Mean % OBU per site
0
2
4
6
up to 7m
> 7m
Height

Figure 5

Changes in the density and canopy volume of *Colophospermum mopane* in Gonarezhou National Park between 2014 and 2022.

Changes of Riverine Mopane Woodland, GNP, between 2014 and 2022 (n = 7) of (a) density (ha^{-1}) by height class, and canopy volume (m^3 ha^{-1}) by (b) height class, and (c) by height layer. Refer to Table S3 for analysis of variance tables. Superscripts indicate differences among height classes or height layers. In no case was any significant change ($P<0.05$) shown for height class or height layer as tested by individual t-tests per height class or layer ($\log_e$ transformed data used for density; $\log_{10}$ transformed data used for canopy volume).

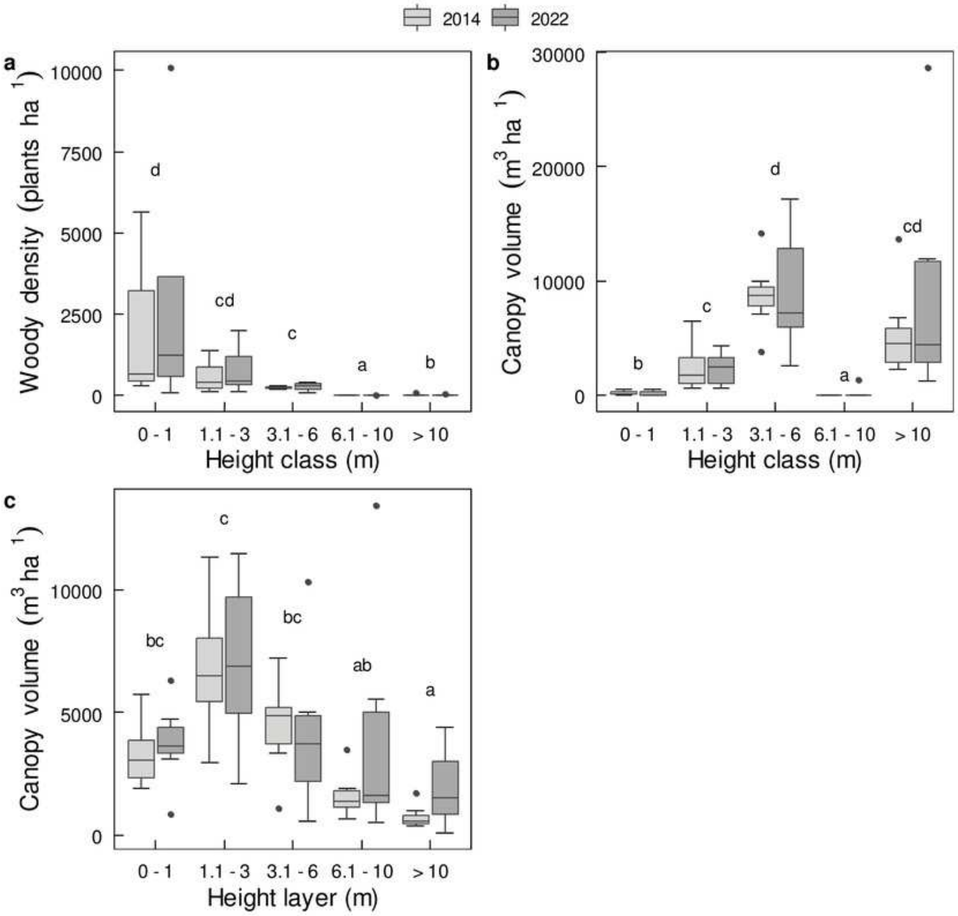
2014
2022
a
Woody density (plants ha⁻¹)
10000
7500
5000
2500
0
d
cd
c
a
b
0 - 1
1.1 - 3
3.1 - 6
6.1 - 10
> 10
Height class (m)
b
Canopy volume (m³ ha⁻¹)
30000
20000
10000
0
b
c
d
a
cd
0 - 1
1.1 - 3
3.1 - 6
6.1 - 10
> 10
Height class (m)
c
Canopy volume (m³ ha⁻¹)
10000
5000
0
bc
c
bc
ab
a
0 - 1
1.1 - 3
3.1 - 6
6.1 - 10
> 10
Height layer (m)

Figure 6

Relationship between stem size of *Colophospermum mopane* and pollarding.

Pollarding of large stems (>20 cm circumference) of mopane in relation to stem diameter was described by the linear logistic relationship logit(p) = 4.5596 -10.0834x (both intercept and slope: P <2e-16).

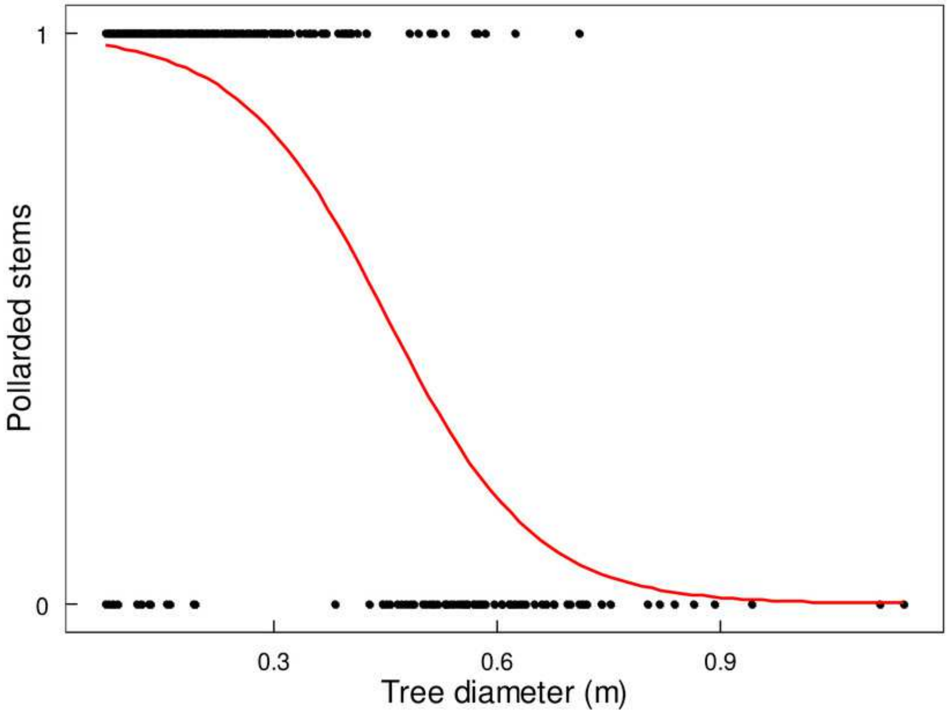
1
0
Pollarded stems
0.3
0.6
0.9
Tree diameter (m)

Figure 7

The relationship between canopy dieback and the extent of debarking for *Colophospermum mopane.*

The relationship between the amount of canopy volume lost to canopy dieback and the percentage of stem circumference debarked is described by the logistic function y = 0.63541 / (1 + exp (-0.57294 * (x – 0.034))), (adjusted R^2= 0.5970). (The two points in the bottom right were excluded.)

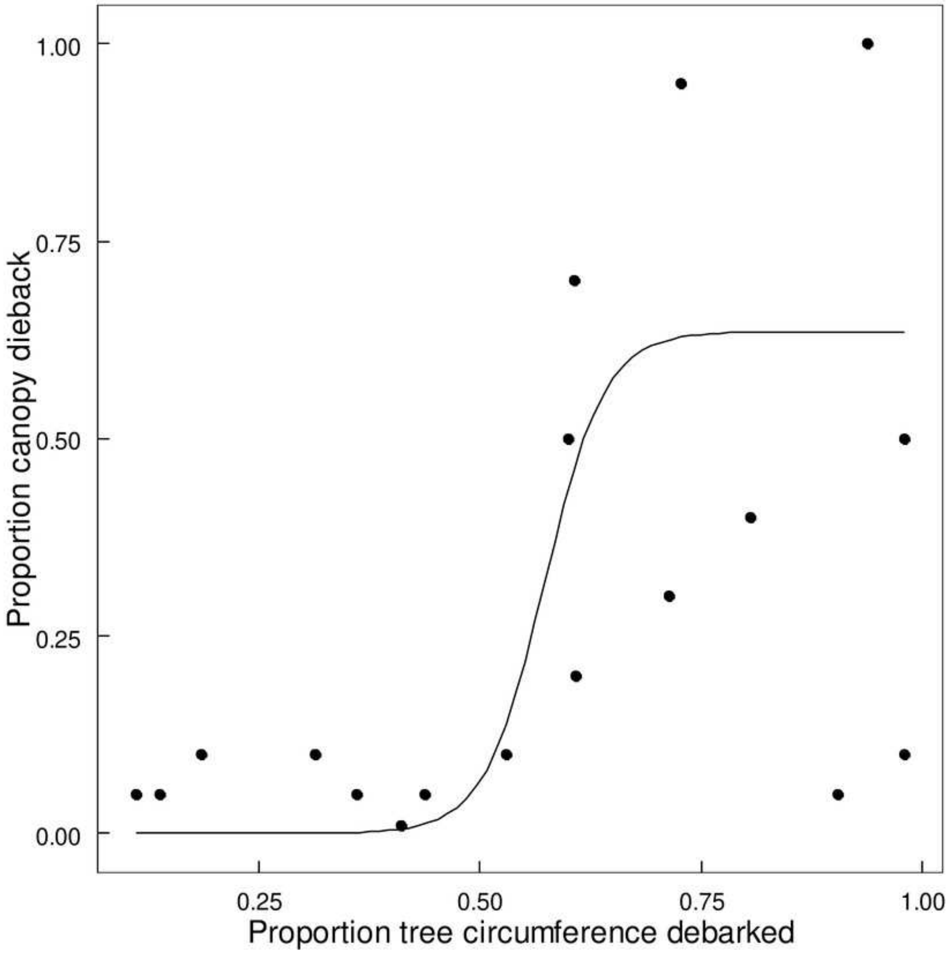
1.00
0.75
0.50
0.25
0.00
Proportion canopy dieback
0.25
0.50
0.75
1.00
Proportion tree circumference debarked

Table 1(on next page)

Structure and extent of use of *Colophospermum mopane* woodland under three elephant densities

Differences in vegetation structure and woody species richness across *Colophospermum mopane* woodland areas in south-east Zimbabwe experiencing low, intermediate and high elephant density. Cell values denote mean ± SE (na denotes not applicable)

Elephant density	Low (L) (n=8)	Intermediate (I) (n=8)	High (H) (n=7)	L v I	L v H	I v H
Total shrub canopy volume (m^3 ha^{-1})	4716 ± 2402.7	2420 ± 380.7	3715 ± 1025.0	t=1.0263; P=0.3389	t=0.3793; P=0.7126	t=1.1162; P=0.2991
Total tree canopy volume (m^3 ha^{-1})	23194 ± 3942.0	25838 ± 5765.0	11404 ± 1619.0	t=0.5366; P=0.6082	t=2.7386; P=0.0217	t=2.3980; P=0.0424
Total canopy volume (m^3 ha^{-1})	27911 ± 4286.5	28258 ± 5451.7	15119 ± 1918.7	t=0.0563; P=0.9567	t=2.6919; P=0.0227	t=2.2558; P=0.0508
Shrub density (ha^{-1})	1406 ± 246.0	1004 ± 269.1	2100 ± 811.3	t=3.3788; P=0.0118	t=0.7699; P=0.4667	t=1.2404; P=0.2580
Density of dead trees (ha^{-1})	32 ± 6.0	24 ± 3.6	9 ± 3.5	t=1.3517; P=0.2185	t=3.3899; P=0.0057	t=2.9285; P=0.0119
Density live trees (ha^{-1})	259 ± 59.3	205 ± 48.0	193 ± 24.1	na	na	na
Density of standing live trees (LS) (ha^{-1})	258.8 ± 10	205 ± 48.0	193 ± 24.1	t=2.3526; P=0.0509	t=1.0194; P=0.3333	t=0.229; P=0.8235
Density of live prostrate trees (ha^{-1})	0.5 ± 0.5	0	0	na	na	na
Density of trees <10 m height (ha^{-1})	220 ± 67.9	136 ± 46.7	178 ± 23.9	t=2.7931; P=0.0268	t=0.5734; P=0.5805	t=0.7898; P=0.4468
Density of trees >10 m height (ha^{-1})	40 ± 10.8	69 ± 13.4	14 ± 2.3	t=1.7408; P=0.1320	t=2.2929; P=0.0522	t=3.9998; P=0.0046
Density of pollarded main stems (ha^{-1})	28 ± 8.6	120 ± 23.9	191 ± 27.6	t=5.5654; P=0.0008	t=5.3064; P=0.0011	t=1.8751; P=0.0853
Mean tree height (m)	7.9 ± 0.81	9.4 ± 1.47	5.1 ± 0.28	t=1.8235; P=0.1110	t=3.1826; P=0.0113	t=2.8499; P=0.0227
Species richness of shrubs	11.5 ± 3.2	9.3 ± 3.5	7.4 ± 2.1	t=2.1223; P=0.0715	t=2.7357; P=0.0224	t=2.2280; P=0.0448
Species	3.4 ±	2.4 ± 0.5	1.1 ±	t=1.9296;	t=5.5624;	t=4.0909;

richness of trees	1.3		0.4	P=0.0950	P=0.0004	P=0.0027
Trees: Old damage by elephants (%)	5.3 ± 1.0	21.3 ± 3.0	50.1 ± 4.3	t=6.4378; P=0.0004	t=9.4453; P=4.7e-05	t=5.2335; P=0.0003
Trees: Old damage by unknown agents (%)	9.7 ± 1.7	14.3 ± 2.2	5.2 ± 2.3	t=1.5402; P=0.1674	t=1.4833; P=0.1658	t=2.7430; P=0.0171
Trees: New damage by elephants (%)	0.1 ± 0.0	2.4 ± 1.1	11.3 ± 0.9	t=2.1572; P=0.0679	t=11.921; P=2.06e-05	t=6.3255; P=2.65e-05
Trees: New damage by unknown agents	0	0	0	na	na	na
Shrubs: Old damage by elephants (%)	4.2 ± 2.1	36 ± 4.7	28.8 ± 3.6	t=7.3440; P=0.0002	t=5.5755; P=0.0003	t=1.1864; P=0.2570
Shrubs: Old damage by unknown agents (%)	3.6 ± 1.1	4.8 ± 1.8	1.3 ± 0.5	t=0,5591; P=0.5935	t=1.8806; P=0.08917	t=1.8841; P=0.0951
Shrubs: New damage by elephants (%)	0.1 ± 0.0	6.1 ± 1.7	6.6 ± 0.9	t=3.6176; P=0.0085	t=6.5194; P=0.0006	t=0.2681; P=0.7935
Shrubs: New damage by unknown agents (%)	0	1.6 ± 1.4	0	na	na	na

Table 2(on next page)

Elephant damage to *Colophospermum mopane* trees in Gonarezhou National Park in 2022.

The percentage of the entire tree stem population ($n = 312$) affected by different forms of elephant damage inflicted recently (new, < 8 months) or prior to that (old) in Gonarezhou National Park, recorded in 2022 ($n = 7$)

Elephant damage score	Percent old	Percent new
No impact	10.9	34.9
Branches taken	16.3	64.7
Main stem broken	65.7	0.32
Main stem pushed over	7.1	0