Elephant impacts on woody vegetation around artificial waterholes in Zambezi National Park, Zimbabwe

Luke Wilson

Supervisors:

Professor Timm Hoffman, Professor David Cumming and Angela Ferguson

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Percy FitzPatrick Institute of African Ornithology

University of Cape Town

Rondebosch, 7701

Cape Town, South Africa

e-mail: wlsluk001@myuct.ac.za

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ABSTRACT

Elephant are renowned for their ability to substantially alter vegetation. However, as they need to drink regularly, surface water exerts a strong influence over the distribution and magnitude of elephant impacts on vegetation. This study was conducted in Zambezi National Park, a 560 km^2 unfenced protected area in northwest Zimbabwe. It aimed to investigate the impacts of elephant on woody vegetation, particularly in relation to artificial waterholes. Sampling plots were located at different distances from four pumped waterholes in teak *(Baikiaea)* and *Terminalia* woodlands, the two main woody vegetation types recognised in the study area. Plots were set at 200, 500, 1000, 2000 and 4000 m from waterholes in the teak woodland. Due to the close proximity of waterholes, a lower maximum distance of 2500 or 3000 m from waterholes had to be used in the *Terminalia* woodland, but sampling intervals from 200-2000 m were otherwise the same. Assessment of elephant browsing and a series of measurements were performed on trees and shrubs within these plots, with plants assigned to one of three height classes (0.2 - <1 m; 1 - <3 m and ≥3 m). Elephant dung counts were also conducted in these plots, to provide a measure of elephant occupancy.

A clear decline in elephant browsing with distance from waterholes was evident in both the teak and *Terminalia* woodlands. However, elephant browsing was consistently higher in the latter woodland type. Averaged across all plant height classes, elephant had removed 30-45% of plant canopies in most *Terminalia* woodland plots. More moderate canopy removal of 10-30% was found in most teak woodland plots. Plants ≥3 m were particularly highly browsed in the *Terminalia* woodland, with over 50% of their canopy volume removed in most plots. Elephant browsing impacts were also considered at the species level, which revealed clear differences in browsing levels among species. Some uncommon and highly browsed species were flagged as being potentially vulnerable to disappearance from the area, even in the teak woodland where overall elephant browsing was lower.

The effects of elephant browsing on vegetation structure at different distances from artificial waterholes were also investigated. Little change was apparent in the teak woodland, where the only noted impact was a reduction in the density and canopy volume of plants 1 - <3 m tall, limited to within 1 km of waterholes. More pronounced structural impacts were evident in the *Terminalia* woodland. Substantial declines in the basal area and canopy volume of trees (i.e. plants ≥3 m) occurred closer to waterholes, with widespread conversion of woodland to shrubland evident. Reductions in both tree and shrub canopy volumes closer to waterholes also suggested a reduction in browse availability in the *Terminalia* woodland.

Finally, elephant dung declined with distance to waterholes, confirming that elephant were found in higher densities closer to waterholes. However, dung counts did not reveal different levels of elephant occupancy between the two vegetation types, despite higher browsing in the *Terminalia* woodland. This finding suggests elephant might be using the teak woodland for purposes other than just browsing, such as for shade.

The study thus provided evidence that waterholes have had a significant impact on vegetation in the area, particularly on the favoured *Terminalia* woodland. Acknowledging the tourism value of retaining waterholes in the area, it is suggested that distances between waterholes should be increased, through only continuing pumping at waterholes with viewing platforms. This could result in a more heterogeneous elephant browsing regime across the highly impacted *Terminalia* woodland in particular, and lessen further homogenisation of this vegetation type towards a shrubland.

1. INTRODUCTION

African elephant (*Loxodonta africana)* are renowned as a keystone species, capable of having a substantial impact on vegetation in areas where they occur (Laws, 1970a). While in decline over much of Africa, elephant populations in southern Africa are generally stable or increasing, although escalating poaching may be reversing this trend in some areas (Thouless et al., 2016). At the same time, ongoing human population growth and habitat conversion have severely restricted elephant ranges, resulting in high elephant densities in many protected areas in the southern African region (Cumming et al., 1997). Given their ability to substantially alter vegetation, high elephant densities in protected areas have generated concern for some time. Laws (1970a), for example, cited it as one of the major conservation problems in Africa.

1.1. Elephant impacts on woody vegetation

The transformation of habitats by elephant has been widely documented. The general effect of high elephant densities has been a decline in woody vegetation, and shifts in the structure of woodland towards shrubland and wooded grassland (Conybeare, 2004). Early dramatic examples include the large-scale conversion of wooded areas to grassland in Murchison Falls National Park (Beuchner & Dawkins, 1961) and Tsavo National Park (Laws, 1970b). General declines in tree densities, and conversion of woodland to shrubland, have been noted in a number of studies from the southern African subregion (Anderson & Walker, 1974; Guy, 1989; Conybeare, 1991; Ben-Shahar, 1998; Mosugelo et al., 2002; Skarpe et al., 2004; Sianga et al., 2017; van Staden et al., 2017). A synergistic effect between elephant and fire has been suggested, in which elephant facilitate grass growth through canopy removal, which in turn leads to more intense and frequent fires (Van Wyk & Fairall, 1969; Laws, 1970a; Guy, 1989; Holdo, 2007). This altered fire regime can then contribute to maintaining former woodland vegetation in a more open grassy or shrubby state. The relative importance of elephant and fire in driving changes in savannah structure is not always obvious, with some studies finding a strong effect of fire, but no clear relationship with elephant densities (Ben-Shahar, 1998; Fox, Vandewalle & Alexander, 2017; Staver, Botha & Hedin, 2017). Elephant also often select for certain plant species (Anderson & Walker, 1974; Jachmann & Bell, 1985; Holdo, 2003; Owen-Smith & Chafota, 2012), potentially resulting in declines or local extirpations of favoured species, and altered community composition (Guy, 1981; Guy, 1989; Skarpe et al., 2004; O'Connor, Goodman and Clegg, 2007; Boundja and Midgley, 2009). Similarly, elephant tend to prefer certain vegetation types for browsing (Anderson & Walker 1974; Conybeare, 1991; Ben-Shahar, 1998; Boundja and Midgley, 2009; Staub, Binford & Stevens, 2013). Some vegetation types in an area might thus undergo little change despite high elephant densities, while substantial alteration of preferred vegetation types may occur, making identification and monitoring of vulnerable vegetation types important.

1.2. The influence of surface water over elephant distributions and vegetation impacts

The distribution of surface water in an area can have a substantial influence on the effects of elephant on vegetation. Surface water exerts a strong constraint on elephant distributions (Chamaillé-Jammes, Fritz & Murindagomo 2007; Harris et al., 2008), with distance to water cited as the most important factor determining where spatial refugia from elephant browsing can exist (O'Connor et al., 2007). This stems from the need for elephant to drink almost daily, mostly limiting foraging to within 15 km of water (Loarie, Van Aarde & Pimm, 2007), though family herds tend to remain much closer to water sources where foraging resources allow this (Stokke and du Toit, 2002). Plants located further than 15 km from water may thus have a near total refuge from elephant foraging, while plants close to the potential foraging range limit have a partial refuge, due to the greater travelling distances required (O'Connor et al., 2007). Given their need for regular access to water, elephant and a number of other herbivores tend to be found in higher densities closer to water sources (Redfern et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007). Increased browsing and trampling from concentrations of herbivores around water sources can result in a gradient of vegetation utilisation pressure, which increases closer to water points (Thrash & Derry, 1999). This phenomenon has been termed the piosphere effect (Lange, 1969). Piosphere effects around water sources have been reported from a number of areas where elephant occur (Van Wyk & Fairall, 1969; Anderson & Walker, 1974; Thrash et al., 1991; Ben-Shahar, 1993, Brits et al., 2002; Chamaillé-Jammes, Fritz & Madzikanda, 2009; Gaugris & Van Rooyen, 2010; Landman et al., 2012; Mukwashi, Gandiwa & Kativu, 2012; Staub et al., 2013; Sianga et al., 2017; Davies, Gaylard & Asner, 2018). Impacts noted in these studies include higher elephant browsing closer to water points, changes to vegetation structure (e.g. changes in plant density or canopy volume) and alteration of the species composition of plant communities.

The addition of artificial water sources can thus have a substantial effect on elephant movements and impacts on vegetation, through the development of piospheres. Natural perennial water sources are scarce over much of southern Africa. Hence, elephant and other large herbivores are adapted to making irregular movements between available water and foraging resources (Walker, 1979; Skarpe et al., 2004). Vegetation over much of the region would be subject to only seasonal browsing when ephemeral water sources are present, allowing for a recovery period from elephant impacts (Owen-Smith, 1996). However, the addition of artificial permanent water sources has eroded vegetation refugia (O'Connor et al., 2007). Adding artificial water sources can decrease travel distances to foraging resources, leading to higher utilisation of vegetation which might previously have been beyond or near the upper range limits of elephant travel distances from water. Elephant can become increasingly sedentary where artificial water points are added to areas which previously lacked permanent water, facilitating year-round browsing where only seasonal or no elephant browsing was possible before (Thrash & Derry, 1999; Chamaillé-Jammes, Fritz & Murindagomo, 2007; Loarie et al., 2009). When artificial waterholes are numerous and closely spaced, vegetation across most or all of a protected area may be subject to heavy, year-round browsing, potentially leading to a coalescing of piospheres, and a loss of ecosystem heterogeneity (Owen-Smith, 1996; Gaylard, Owen-Smith & Redfern, 2003; Sianga et al., 2017). On the other hand, artificial water sources may increase ecosystem heterogeneity if spacing between them is large enough to allow for areas with low to no elephant browsing, with higher elephant browsing closer to water points (Gaylard et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007). However, the close spacing of artificial water sources in many conservation areas does not allow for zones where little to no elephant impacts occur (Owen-Smith, 1996).

Despite their drawbacks, artificial water sources are a common feature of wildlife areas in southern Africa. On the positive side, they can increase the economic viability and attractiveness of protected areas, by enhancing game viewing opportunities and creating focal points for tourists (Owen-Smith, 1996; Shannon et al., 2009). They may also be seen as a way of reducing pressure on vegetation around other water sources, through providing alternative areas for elephant to disperse to in the dry season. Given their influence over the spatial distribution of elephant feeding, the addition or closure of artificial waterholes is regarded as one of the key management options for modifying elephant distributions in protected areas (Owen-Smith, 1996; Gaylard et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007; Shannon et al., 2009).

1.3. Study rationale

The southern portion of Zambezi National Park presents a relevant area to study the effects of elephant on vegetation, particularly in relation to artificial water sources. A number of previously pumped waterholes have been re-opened in the park from 2013-2016, following a period of disrepair. Additionally, some new waterholes have been added. These provide the only permanent water sources in the southern part of the park, permitting year-round foraging by elephant in the area. This has prompted concerns about the impact that reopening and adding waterholes may have on vegetation in the area, especially given the close spacing of these waterholes, and the fact that elephant densities in the park are thought to be high (Muphoshi et al., 2016). Considering the potential travel distance of elephant, a minimum spacing of 15 km between perennial water points to maintain adequate wet season 'dispersal range', in which little dry season pressure on vegetation occurs, has been suggested (Owen-Smith, 1996; Sianga et al., 2017). At about 5 km on average, waterholes in the study area are much more closely spaced than this (Figure 1). This suggests that large areas of the park may be exposed to heavy year-round elephant browsing, and raises the possibility that areas of vegetation degradation may coalesce through a merging of piospheres (Owen-Smith, 1996; Gaylard et al., 2003).

Although elephant impact studies have been conducted in a number of areas, this study provides the first assessment of elephant impacts on vegetation in Zambezi National Park. By focusing on elephant impacts in relation to artificial waterholes, it also responds to an active management issue in the park. Fullman and Child (2012) note that a number of piosphere studies focused on the supposed results of elephant browsing, for example changes in plant density or canopy cover, rather than directly evaluating elephant utilisation levels. This study of Zambezi National Park set out to include both approaches, by considering both direct measures of utilisation, the potential effects of elephant browsing on vegetation structure. To directly assess utilisation levels, elephant browsing at different distances from waterholes was estimated. As other studies have found selectivity by elephant for certain plant species, sometimes resulting in declines or disappearances of these, species-specific browsing levels were also investigated. This could improve the understanding of elephant feeding preferences in the area, and highlight plant species which are potentially threatened by high elephant browsing. Finally, trends in vegetation structure (e.g. canopy cover, basal area) in relation to distance to waterholes were also investigated, as any patterns here could be the result of increased elephant browsing closer to waterholes. In addition to these measures of vegetation, elephant dung counts were conducted, to provide an estimate of elephant occupancy in relation to distance from waterholes, and their impact on vegetation.

1.4. Aim

To conduct a first assessment of elephant impacts on woody vegetation in southern Zambezi National Park, particularly in relation to artificial waterholes.

1.5. Objectives

1. To assess elephant browsing levels in relation to distance from artificial waterholes.

2. To compare elephant browsing levels across different vegetation types in the study area.

3. To compare elephant browsing levels across individual plant species found in the study area.

4. To assess changes in vegetation structure resulting from elephant browsing, in relation to distance from artificial waterholes.

5. To discuss management implications for the park’s surface water regime, based on evidence found in the study.

2. METHODS

2.1. Study area

This study was conducted in Zambezi National Park, which is located in the north-western corner of Zimbabwe, just west of Victoria Falls. The park is an unfenced protected area about 560 km^2 in extent, and forms part of the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), which extends across Botswana, Namibia, Zambia and Angola (Muposhi et al., 2016). The KAZA TFCA is the biggest remaining stronghold for elephant on the continent, holding 75% of southern Africa’s regional elephant population (Thouless et al., 2016). Terrain in the park is gently undulating, ranging from 600 m above sea level along the Zambezi River at the northern boundary of the park, to 1200 m further south (Mandinyenya et al., 2018). Mean annual rainfall is around 650 mm and is strongly seasonal, falling almost exclusively from October to April.

The Zambezi River provides a perennial source of water in the northern part of the park, while pumped waterholes provide the only permanent water sources to the south. At the time of the study, seven pumped waterholes were in operation. Five were located along the Chamabondo Vlei, and two in the Kalisosa region in the far south of the park. These waterholes have value for enhancing wildlife-viewing opportunities in the area, and for providing focal points for tourist activity, especially the three waterholes with game-viewing platforms. Pumping began recently at the two easternmost Chamabondo waterholes, where pumps were first installed in 2014 and 2015 (Trevor Lane, personal communication, 2019 July 17). The other five waterholes have a longer, albeit sporadic, pumping history. Intermittent pumping at these waterholes commenced in the 1970s (Vernon Booth, personal communication, 2020 January 24). However, pumping ceased during the 2000s, as confirmed through historical satellite imagery. Following at least a decade of inactivity, new solar pumps were installed at all these originally pumped waterholes from 2010-2013 (Trevor Lane, personal communication, 2019 July 17).

Vegetation in the park has not been described in great detail, but can be broadly differentiated according to the two main soil types. The majority of the park is covered by Kalahari sands. These are associated with teak woodland, which covers most of the southern and central parts of the park (Mandinyenya et al., 2018), including the southwestern region where sampling was conducted. This vegetation type is named after *Baikiaea plurijuga* (common name Zambezi teak), the dominant large tree species, which is often found in association with *Guibortia coleosperma*. *Bauhinia petersiana* and *Baphia massaiensis* are the dominant shrub species. The next most sizeable vegetation type is found on basalt soils, and is variably dominated by *Colophospermum mopane* and *Combretum* species. This vegetation type, referred to simply as 'mixed' vegetation by Mandinyenya et al. (2018), is mostly found in the north of the park, as well as in the extreme southeast.

Four of the waterholes with a longer pumping history were chosen for sampling, namely Chamabondo 1, 2 and 3, and Kalisosa 2 (Figure 1). All were located in the southwestern part of the park. In addition to having comparable pumping histories, these particular waterholes were selected to maximise similarity of vegetation, as they are all located on Kalahari sands with teak woodland the dominant vegetation type. The waterholes themselves are all located in lower lying grassy drainage lines, which become moist during the rainy season. These seasonally wet grasslands are known locally as vleis or dambos. The largest of these drainage lines is the Chamabondo Vlei, in which three of the study waterholes are located (Chamabondo 1, 2 and 3). The vlei was once much wetter, however the hydrology of the downstream watercourse changed in the 1960s, altering the drainage line to its current status as a seasonally wet grassland (Vernon Booth, personal communication, 2020 January 24). The fourth waterhole (Kalisosa 2) is located in a narrower grassy drainage line in the far south of the park, but surrounding woody vegetation is similar to the other waterholes. A belt of *Terminalia* woodland is often found at the margin of these grassland areas, which gives way to teak woodland further upslope, away from the grassland. In addition to having comparable vegetation, selected waterholes were also topographically similar. Terrain rises steadily into the woodland away from the lower lying grassy drainage lines, flattening out after about 1 km.

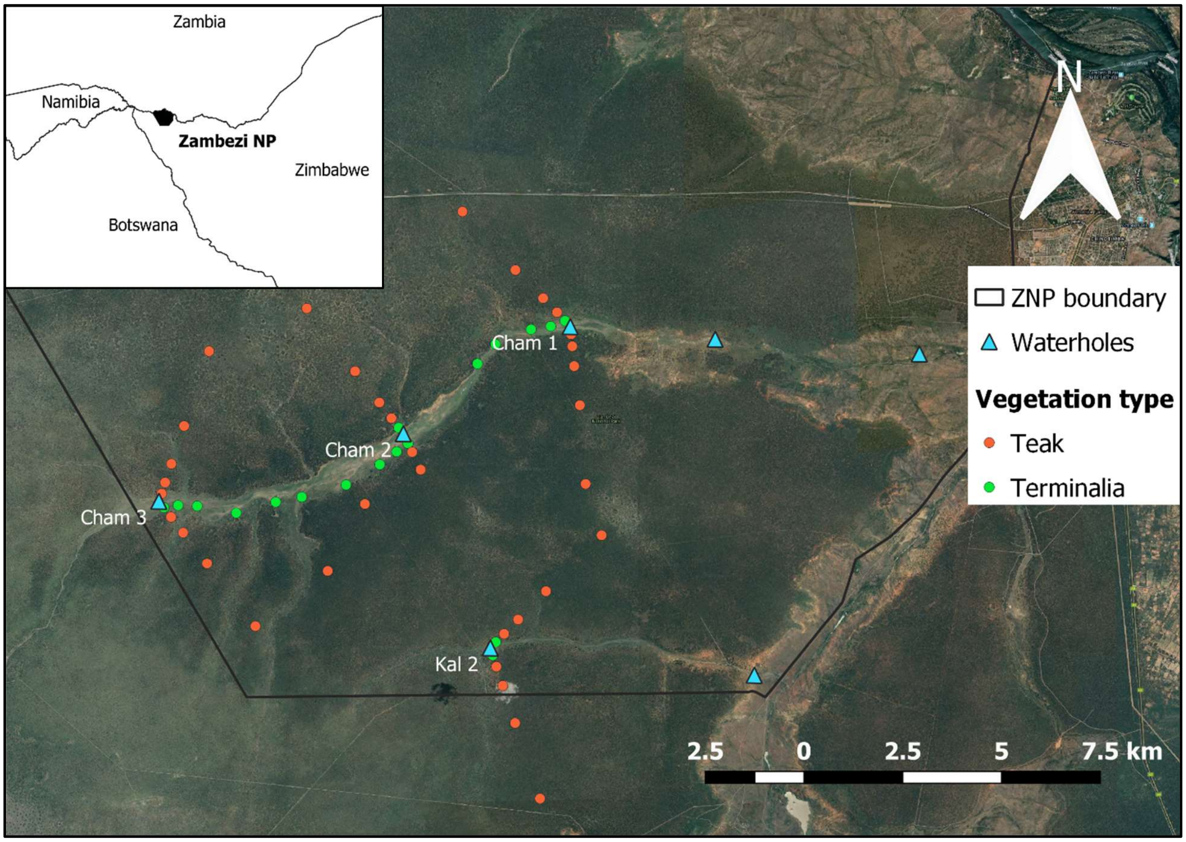

Figure 1: Satellite image of southern Zambezi National Park (ZNP) and surrounding areas, with inset showing location of the park shaded in black. Locations of waterholes are shown, with names included for waterholes around which sampling occurred (Cham = Chamabondo and Kal = Kalisosa). Locations of sampling plots are colour coded by vegetation type (Teak = teak woodland, *Terminalia* = *Terminalia* woodland).

2.2. Plot selection

At each of the four selected waterholes, two 4 km line transects were extended into the woodland on either side of the grassy drainage lines, one in a roughly northerly direction and the other in a southerly one (Figure 1). Along these, sampling plots were located at intervals of 200, 500, 1000, 2000 and 4000 m from each waterhole. Selection of transect direction was done on a semi-random basis, informed by the spatial distribution of waterholes in the study area. Due to the proximity of waterholes, care had to be taken to avoid setting transects which would move away from one waterhole but towards neighbouring ones. This was especially necessary for plots at 4 km, which might be 4 km from the waterhole the transect originated from, but significantly closer to neighbouring waterholes. To avoid this, 4 km and 5 km buffer circles were created around each of the waterholes in Google Earth. Each transect was then assigned an arc of possible bearings which avoided the 4 and, where possible, 5 km buffer circles around neighbouring waterholes. A random number generator was used to select the bearing for each transect from the range of possible ones. Lines along these selected bearings were then plotted in Google Earth. Finally, place markers were set at the aforementioned 200, 500, 1000, 2000 and 4000 m distance intervals along these transect lines, with distances from the waterhole again measured in Google Earth. These place markers provided coordinates for centre points of the sampling plots, which were entered into a GPS for subsequent location in the field. Setting plot coordinates in advance helped avoid bias in plot selection in the field.

The plots south of Chamabondo 2 waterhole were the only case where not all teak woodland plots were located along a single straight line (Figure 1). The grassland south of Chamabondo 2 waterhole is particularly wide, and a relatively oblique transect bearing was required to ensure plots at 2000 and 4000 m avoided neighbouring waterholes. However, if all plots were located along this bearing, then the plot at 200 m would still be in the grassland where no woody vegetation was present, while plots at 500 and 1000 m would be just inside the woodland margin. To improve comparability with other waterholes, where 200 m plots were inside the woodland margin, and plots from 500 m onwards were well within the woodland, plots from 200-1000 m were located on a line perpendicular to the grassland band. Plots at 2000 and 4000 m were then located along the originally chosen transect bearing. Plots at 2000 and 4000 m south of Kalisosa 2 waterhole were set in the adjacent Panda Masuie Forest Reserve (Figure 1). This was unavoidable given the location of the waterhole near the park's southern boundary. Vegetation was similar in the forest reserve, and the lack of a fence meant elephant could move freely between it and the national park. Setting these plots outside the park boundary thus did not raise any comparability concerns.

In addition to plots set along north/south transects extending away from the grassland band, further plots were located near the grassland/woodland margin between waterholes (Figure 1). This was done to increase coverage of the *Terminalia* woodland band found along much of the grassland/woodland interface, which was only captured in plots at 200 m from waterholes on the north/south transects. These plots also addressed the potential criticism that a decline in elephant impacts with distance from waterholes along the north/south transects could simply be due to elephant preferring to move along the drainage lines, rather than the effect of distance to water *per se*. Setting plots at a fixed distance from the grassland margin responded to this, by allowing for investigation of whether elephant impacts declined with distance from waterholes, while keeping the position of plots in relation to the grassland and catena constant. The close spacing of waterholes meant it was impossible to set plots in the *Terminalia* band at 4000 m from waterholes. Hence a distance of 3000 m was used instead where possible, while a maximum distance of only 2500 m was possible between Chamabondo 1 and 2 waterholes. Apart from this, the same distance intervals were used. Unfortunately, time limitations prevented further sampling along the grassland/woodland margin at the fourth waterhole, though the two plots at 200 m along the north/south transects did fall within the *Terminalia* woodland. Plot centres were situated 50 m beyond the grassland/woodland margin, ensuring a similar position relative to the grassland/woodland margin in all cases. The fairly low distance of 50 m from the woodland margin was selected to ensure all plots would fall within the *Terminalia* woodland band, especially in areas where it was particularly narrow.

2.3. Determination of plot sizes

Once located, the centre point of each plot was marked. An initial plot width of 5 m was then set by placing pegs 2.5 m either side of the centre point, along the bearing of the line transect from the waterhole. Plot length was then measured perpendicular to the initial 5 m line. The length of plots varied from 12.5 to 50 m, depending on the density of plants. To ensure adequate representation of different size classes of plant, three height classes were recognised, with varying plot sizes for each of these. Target sample sizes for each height class were 50 each for plants 0.20-0.99 m and 1.00-2.99 m tall, and 25 for plants 3 m or more in height. This was informed by time considerations, and the minimum sample sizes for obtaining adequate plot-level damage estimates suggested by Walker (1976). These three height classes will be referred to hereafter as <1 m, 1 - <3 m and ≥3 m respectively. Plot size was increased from the 12.5 x 5 m starting point, until the target sample size for a particular height class was reached. In some cases, plot width was also increased beyond 5 m, where an adequate sample of plants was not captured in a 50 x 5 m plot. The smallest plot sizes occurred where plants <1 m occurred in high densities, where a plot size of 12.5 x 5 m was sufficient to capture the 50 plant target number. In areas where plants were sparse, plot sizes ranged up to 50 x 50 m. In some areas where high elephant impacts resulted in very low densities of plants ≥3 m, the target of 25 individuals in this height class could not be reached as very large plots would have been required. However, the high number of "converted trees" (i.e. plants with a stem diameter ≥6 cm but which had been reduced in height to less than 3 m (see next section)) in such areas increased the sample size for estimating browsing levels, as is explained in the next section. To account for varying plot sizes, all measurements were reported on a per hectare basis.

2.4. Sampling procedures

Sampling procedures largely followed the methodology described in Walker (1976), which has been widely used in the region for studying the impacts of elephant on vegetation. Each plant was firstly identified to species level wherever possible. This could be achieved in the majority of cases. In a few instances, plants could only be identified to genus level, while some individual plants in the <1 m height class could not be identified to genus level either. For the group of species belonging to the genus *Terminalia,* a decision was made to identify individuals to genus level only. One reason was that separating similar species of *Terminalia* when the trees were not in leaf would be difficult and likely unreliable, as bark and other characteristics can be very similar. The difficulty is compounded by the fact that certain *Terminalia* species in the study area may hybridise, e.g. *T. sericea* and *T. brachystemma* (Palgrave, 2003). Lastly, plants appeared to be subject to similar browsing levels regardless of the species of *Terminalia* they were thought to belong to, suggesting differentiating to species level would not result in significant differences in browsing between species in the genus.

2.4.1. Plant measurements

A range of measurements was taken for each plant. Heights of all plants were measured. For plants ≥1 m, maximum canopy diameter and canopy diameter at right angles to this were measured, as well as height of the lowest canopy branches. Canopies of plants <1 m tall were not thought to be worth measuring, as the very small canopies of these plants would make a negligible contribution to overall canopy volume. Canopies were also assigned to one of the seven shapes indicated in Melville, Cauldwell and Bothma (1999), to improve the accuracy of canopy volume estimation (see Appendix 1 for canopy shapes, and Appendix 2 for the equations used in calculating canopy volumes for the different shapes). While many plant species might have a characteristic canopy growth form, this was often modified by elephant browsing, meaning that different individuals from the same species could be assigned a variety of canopy shapes. For all plants with a basal diameter ≥6 cm, stem circumference immediately above the buttress swelling was recorded. Plants ≥3 m tall with basal diameters ≥6 cm were classed as standing trees. Plants with a basal diameter ≥6 cm, but reduced by browsing to less than 3 m in height, were recorded as converted trees. Dead stems ≥6 cm in diameter were also measured. These differentiations allowed the basal areas of standing, converted and dead trees to be estimated and compared across plots.

2.4.2. Assessment of elephant browsing levels

Assessment of elephant browsing levels involved estimating what proportion of a plant's canopy volume had been removed by elephant (Walker, 1976). Canopy losses due to fire and other/unknown causes were also noted in separate categories. Only canopy removal which could be conclusively attributed to elephant was included in the elephant category. However, it is likely that a substantial portion of canopy removal placed in the other/unknown category was also due to elephant. Within each category (elephant, fire and unknown/other), canopy removal was further split into old and new (since the previous rainy season). Scars from browsing or other damage take on a greyish colour once wet by rain, allowing browsing from before and after the end of the previous rainy season to be distinguished. Levels of canopy removal were assigned to each plant according to the eight-point scale suggested by Walker (1976). Ranges of canopy removal estimates at each point of this scale were as follows: 0 = 0%, 1 = 1-10%, 2 = 11-25%, 3 = 26–50 %, 4 = 51–75 %, 5 = 76–90%, 6 = 91-99%, 7 = 100%). A plant was assigned a 7 (100% canopy removal) if it had been completely killed by elephant, fire or other/unknown causes. Unbrowsed plants were assigned a canopy removal score of zero. Individuals which had been very lightly browsed, presumably by other browsing species like giraffe, kudu and impala, were also assigned a canopy removal score of zero. For plants which were neither dead nor unbrowsed by elephant, the estimation procedure involved first asking whether more or less than half of the plant canopy had been removed. If less, then one would ask whether more or less than a quarter had been removed and so on, until the final rating for canopy loss to elephant and/or other causes was obtained (Anderson & Walker, 1974). The class midpoint of each point on the eight-point scale was then used to give each plant a percentage canopy loss estimate for the different forms of browsing/damage (e.g. 18.5% for a canopy removal rating of 2). The process was aided by the presence of an experienced field botanist on the research team, who had used the same estimation procedure extensively.

Converted trees (stem diameter ≥6 cm but reduced to <3 m in height) presented a special case for estimating browsing impacts. Any browsing of coppice growth subsequent to reduction of the plant below 3 m in height was counted as browsing of the 1-3 m or <1 m height class, depending on the current height of the plant. However, browsing of the original main stem and/or branches, which would have reduced the plant to below 3 m in height, was counted as canopy removal in the ≥3 m height class, as the plant would have been above 3 m at the time. Hence, a number of converted trees had some browsing included in the ≥3 m size class and other browsing included in the 1-3 m or <1 m height class.

2.4.3. Elephant dung counts

In addition to the various plant assessments, a count of elephant dung was done at each plot. The purpose of this measurement was to provide an estimate of relative elephant occupancy at different distances from waterholes. Four 30 x 5 m transects were walked, radiating out from the centre point of each plot. The aim was to count the number of dung piles rather than dung balls, with each pile representing an excretion event by one elephant. Colour, age and texture of dung were used to decide whether dung came from a single elephant at a single point in time, and thus should be counted as one pile.

2.5. Data Analysis

2.5.1. Descriptive statistics for browsing levels and measures of vegetation structure

All field data was initially entered into Microsoft Excel, and plot averages for each of the measures of browsing and vegetation structure were calculated. Estimates of browsing for the two height classes of plants below 3 m was obtained by averaging the scores for percentage canopy removal by elephant of all plants in the height class. Due to large differences in plant sizes in the ≥3 m size class, canopy removal estimates were weighted by the basal area of the plant. By giving more weight to browsing of larger trees, this method provides a more accurate representation of the levels of biomass lost (Walker, 1976). However, Walker (1976) further recommends weighting browsing by the natural logarithm of the basal area, as very large trees, which may be largely unaffected by elephant browsing, can have basal areas more than an order of magnitude greater than smaller ones. The presence or absence of a few very large trees in a plot can thus substantially alter the damage estimates when weighting by the untransformed basal area, reducing comparability across plots with different numbers of large trees present. Weighting damage by the natural logarithm of the basal area is suggested as the best solution, as it avoids giving very large trees disproportionate influence over browsing estimates, while still allowing for an effect of tree size in determining the average canopy removal in a plot. Elephant browsing levels for plants ≥3 m were thus calculated as follows:

Weighted canopy removal (individual plant) = ln(Basal area) x % canopy removal.

A plot level estimate of % canopy removal was then obtained as follows:

Weighted canopy removal (plot level) = Σ{weighted canopy removal of each plant / ln(basal area)},

where Σ = the sum of all individual plants ≥3 m in the plot. An alternative or additional approach to control for the influence of very large trees would have been to consider these individuals separately. However, as such a separation was not performed in the field, it would have been difficult to retrospectively adjudicate browse availability on the basis of a measure like tree height or stem diameter, given the variation in canopy growth forms across and within species. Furthermore, there were cases of very large trees which had been killed due to debarking by elephant. These may have been excluded from damage estimates if very large trees had been separated out.

In addition to plot-level estimates of elephant browsing, species-level estimates of browsing were calculated to investigate impacts of elephant browsing on different plant species in the study area. Due to the differences in composition and browsing levels between the teak and *Terminalia* woodland, species-specific browsing scores were calculated and analysed separately for the two vegetation types. For the two smaller height classes, browsing estimates were obtained by averaging the percentage canopy removal estimates for all individuals of a given species within the vegetation type. For the ≥3 m size class, estimates were again weighted by the natural logarithm of the plant's basal area, with species-level browsing estimates obtained as follows:

Weighted canopy removal (per species) = Σ{(weighted canopy removal of each plant / ln(basal area)},

where Σ = the sum of all individual plants ≥3 m of the particular species in the vegetation type.

A number of measures of vegetation structure were also calculated for each plot. Density estimates for each of the smaller height classes were obtained by dividing the number of individual plants in the plot by the plot area to obtain density/ha. Due to substantial differences in plant size in the ≥3 m height class, basal area (m^2/ha) was used instead of number of individuals per hectare. Basal area in m^2 was calculated from each tree's basal diameter using the formula $\pi^*\{\text{basal diameter (cm)}/200\}^2$. Long and short canopy dimensions, and canopy depths, were used to calculate canopy volume, according to the canopy shape each plant had been assigned. Formulae for this were obtained from the geometric equations described in Melville et al. (1999). As with other measures, canopy volumes of individual plants were summed for each plot and divided by the plot area to obtain an estimate of canopy volume/ha for each plot. In addition to the basal area/hectare of standing trees (≥3 m high and basal diameter ≥6 cm), basal areas of converted trees (basal diameter ≥6 cm but reduced to <3 m tall) were summed for each plot, allowing the relative proportions of standing and converted trees to be calculated. While a more comprehensive analysis of vegetation structure may have incorporated further measures such as stem diameter size class distribution graphs, it was felt this would require removing other analyses to avoid an overly complex and figure-heavy results and discussion section.

2.5.2. Nonmetric multidimensional scaling (NMDS) analysis of plot composition data

Ordination analysis of species composition data was undertaken to test the hypothesis that the area comprised two distinct vegetation types, and to differentiate sampling plots accordingly. To do this, a relative abundance score for each species in each plot was calculated. The first step involved dividing the number of plants of a species in a particular height class by the total number of plants in that height class. This was repeated for each of the three height classes. The relative abundance scores for each species in each of the three height classes were then averaged to give overall relative abundance for the species within the plot. The approach of first working out relative abundances within each height class was used to ensure adequate weight was given to trees in differentiating between vegetation types. As fewer trees were sampled than shrubs in each plot (target sample size of 25 for trees versus 100 for the two smaller height classes), simply dividing the total number of individuals of a species by the total number of plants in the plot would have biased the ordination towards plants found in the smaller height classes. Species lists and abundances of all plants that could be identified to species level are included in the appendices (Appendix 3 for teak woodland and Appendix 4 for *Terminalia* woodland).

Relative abundance data for each species in each plot where then used to calculate a distance matrix using the Bray-Curtis method in R (R Core Team, 2019). The vegan package (Oksanen et al., 2019) was used to do so. Nonmetric multidimensional scaling (NMDS) was then carried out using this distance matrix. The NMDS was run repeatedly with increasing numbers of dimensions, starting from one up to five. Stress values were obtained in each case. The chosen number of dimensions was three, reflecting a balance between reducing stress and avoiding unnecessary dimensions, which would only have a small impact on stress while reducing interpretability of the results. The low stress value of 7.6 suggested a three-dimensional NMDS handled the data well. All analyses were undertaken in R (R Core Team, 2019).

2.5.3. Regression analysis of elephant browsing levels

Once the correct differentiation of plots into the two main vegetation types had been obtained, regression analysis was undertaken in R (R Core Team, 2019). For evaluating the predictors of elephant browsing levels, the full models were specified with the following fixed effects: i) distance to nearest waterhole, ii) vegetation type and iii) waterhole ID, as well as a distance to nearest waterhole:vegetation type interaction term. Distance to nearest waterhole was included to test the piosphere hypothesis that elephant browsing would decline with distance to waterholes. Vegetation type was included to evaluate differences in elephant browsing between teak woodland and *Terminalia* woodland. Waterhole ID was used to account for possible differences in the amount of elephant browsing at different waterholes. Finally, the distance to nearest waterhole:vegetation type interaction term was included to allow for a different relationship between distance to water and browsing levels for the two vegetation types.

Residuals of all models were checked for normality and homogeneity of variance using graphical tools in R. In a number of cases, plots of residuals against fitted values showed increasing variance at higher values of the response variable. To combat this, generalised linear models (GLIMs) with a gamma or inverse gaussian error distribution were used for some response variables. In certain cases, a gamma error structure and/or log link function appeared to be appropriate for the data, but could not be used initially due to the presence of zero values in the response variable. A small nonzero constant was added to every value in such cases. Where curvature was evident in a response variable that was not adequately captured by GLMs or GLIMs, generalised additive models (GAMs) were used. The mgcv package (Wood, 2017) was used for GAMs, with a thin plate regression spline smoother applied to the distance to waterholes covariate, as well as to the distance to nearest waterhole:vegetation type interaction term.

Using the car package (Fox & Weisberg, 2019), Type II analysis of deviance using the F-test statistic was used to evaluate the significance of predictors. Backward stepwise elimination was carried out to remove the least significant predictor from the full statistical models, until only predictors with significance level of $p < 0.1$ were retained in the final model. Finally, predicted values were extracted from all models. Fitted regression lines from these predicted values were then plotted against observed values using the package ggplot2 (Wickham, 2016). These plots were used to evaluate model fit, as well as to provide a visual representation of model outputs to aid interpretation, and have been included in the results section.

2.5.4. Regression analysis of vegetation structure

The regression analysis of changes in vegetation structure with distance to the nearest waterhole differed in being done separately for the two vegetation types. Field impressions suggested a clear difference in vegetation structure between teak and *Terminalia* dominated plots, making it of little scientific interest to test for this. This was confirmed during data exploration, which indicated that measures of vegetation structure differed substantially between the two vegetation types. These large differences in structure *between* vegetation types would potentially obscure any changes in vegetation structure *within* each vegetation type as distance to the nearest waterhole varied. Given the aim of the study was to assess elephant impacts on vegetation in relation to artificial waterholes, analysing vegetation structure separately for the two vegetation types appeared to be more appropriate. As a result, only waterhole ID and distance to the nearest waterhole were used as predictors in the models of vegetation structure. The analysis otherwise followed the same steps as those used in the analysing of levels of elephant browsing, with a mixture of GLMs, GLIMs and GAMs used. Outliers in the response variables were evident in some cases for the measures of vegetation structure. Once it had been confirmed that these did not reflect errors in measurement or data entry, analyses were performed with and without outlier plots included, to see how they affected the strength and direction of relationships between the given measure of vegetation structure and distance to waterholes. The analysis of vegetation structure for *Terminalia* woodland was confined to plots along the Chamabondo Vlei woodland margin, due to differences in the structure of the *Terminalia* woodland on the Kalisosa side of the park, where the grassland band was much narrower. The two *Terminalia* plots at 200 m from Kalisosa 2 waterhole were thus excluded from the analysis of vegetation structure to improve comparability.

2.5.5. Regression analysis of elephant dung counts

Finally, regression analysis of elephant dung counts was also performed. Similar to the analysis of elephant browsing levels, distance to the nearest waterhole, vegetation type and waterhole ID were included in the full model, with backward elimination performed to remove predictors that were not significant at the $p < 0.1$ level from the model.

3. RESULTS

3.1. Ordination analysis

The results of the NMDS analysis were in line with field impressions of the differentiation of vegetation types within the study area. Two main clusters of points along the first axis of the NMDS analysis can be seen (Figure 2), with a few plots at intermediate positions along the NMDS 1 axis. Most plots at 200 m from waterholes on the north/south transects, and all plots located near the grassland/woodland margin, clustered towards the right-hand side of the first NMDS axis. Most plots at 500-4000 m from waterholes on the northerly and southerly transects were found on the opposite end of the first NMDS axis. A few plots from the northerly and southerly transects occupied an intermediate position along the first axis (around 0-0.1 on NMDS 1). Inspection of the species composition data of these plots indicated that although there was some commonality with *Terminalia* woodland plots, they were more similar to the teak woodland plots. They were thus assigned to the teak woodland group for the subsequent regression analysis, as they were not different enough to be placed in their own vegetation type. Furthermore, the separation of a third vegetation type containing only these intermediate plots would have a very small sample size. The differentiation of plots into the two vegetation types as depicted in Figure 2 was used throughout the subsequent analyses. The final split consisted of 34 plots in the teak woodland and 18 plots in the *Terminalia* woodland. As most plots at 200 m from waterholes were still within the *Terminalia* woodland band, the teak woodland group only contained two plots from this distance interval. The *Terminalia* woodland group had more plots at 200 m than at any another distance interval. This is because the two plots at 200 m along the north/south transects from Kalisosa 2 waterhole were included, while time constraints meant additional *Terminalia* plots at other distances were not sampled at this waterhole.

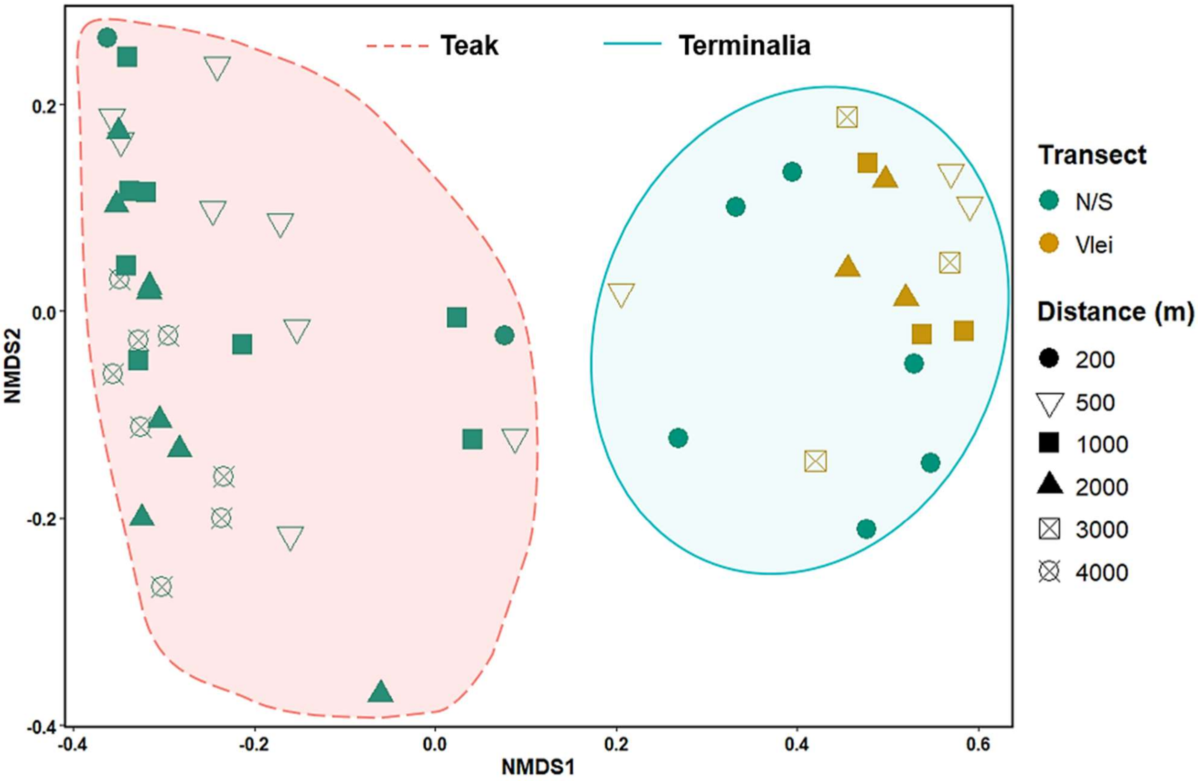

Figure 2: Nonmetric multidimensional scaling (NMDS) of all sampling plots. Each point represents the position of a sampling plot in NMDS coordinate space. Points representing plots along north/south transects are shown in green, while plots from transects along the vlei margin are shown in yellow-brown. Point shapes indicate the distance of the plot from the nearest waterhole. Plots within the red shaded area were classed as teak woodland, while those in the blue shaded area were classed as *Terminalia* woodland.

3.2. Elephant browsing in relation to distance to waterholes and vegetation type

Throughout this section, elephant browsing levels refers to the average percentage canopy removal attributed to elephant, as this was the measure of elephant browsing used in the study. Neither Waterhole ID nor the distance to nearest waterhole:vegetation type interaction term were significant at the $p < 0.1$ level in any of the full statistical models (Table 1), and were thus dropped in the process of backward elimination. This left vegetation type and distance to the nearest waterhole as predictors of elephant browsing in the final models.

Table 1: Results of the full statistical models of elephant browsing of the different plant height classes, as measured by % canopy removal. Factors in bold remained in the final model.

Response variable	Model type	Predictors	F Test	*p*
% canopy removal (all height classes)	Gaussian GLM (identify link)	**Dist to water**	**$F_{1,45}$ = 23.87**	**<0.001**
		Veg type	**$F_{1,45}$ = 85.22**	**<0.001**
		Waterhole ID	$F_{3,45}$ = 0.70	0.558
		Dist*veg type	$F_{1,45}$ = 0.09	0.768
% canopy removal (≥3 m)	Gaussian GLM (identity link)	**Dist to water**	**$F_{1,45}$ = 10.03**	**0.003**
		Veg type	**$F_{1,45}$ = 144.45**	**<0.001**
		Waterhole ID	$F_{3,45}$ = 0.55	0.649
		Dist*veg type	$F_{1,45}$ = 0.02	0.890
% canopy removal (1- <3 m)	Gaussian GLM (identity link)	**Dist to water**	**$F_{1,45}$ = 10.87**	**0.002**
		Veg type	**$F_{1,45}$ = 12.08**	**0.001**
		Waterhole ID	$F_{3,45}$ = 0.51	0.676
		Dist*veg type	$F_{1,45}$ = 0.18	0.670
% canopy removal (<1 m)	Gamma GLIM (log link)	**Dist to water**	**$F_{1,45}$ = 12.36**	**0.001**
		Veg type	**$F_{1,45}$ = 4.07**	**0.050**
		Waterhole ID	$F_{3,45}$ = 1.29	0.291
		Dist*veg type	$F_{1,45}$ = 3.43	0.070

Elephant browsing levels consistently showed a negative relationship with distance to water in both vegetation types (Figures 3-6). Elephant browsing levels were also significantly higher in the *Terminalia* woodland than in the teak woodland in most cases, indicating a preference for browsing in the former vegetation type. Despite the difference in browsing levels, the non-significance of the distance to nearest waterhole:vegetation type interaction term indicates elephant browsing declined with distance to waterholes at similar rates in both vegetation types.

3.2.1. All size classes combined

Total elephant browsing averaged across all height classes (Figure 3) declined with distance to waterholes (estimate ± SE = -3.07 ± 0.61, $F_{1,49}$ = 25.30, $p < 0.001$), and was significantly higher in the *Terminalia* woodland (estimate ± SE = 15.52 ± 1.64, $F_{1,49}$ = 89.20, $p < 0.001$). Average canopy removal was generally moderate in the teak woodland, where canopy removal in most plots was around 10-30%. By 4 km from waterholes, browsing was generally low, with most plots below 20% and a few with less than 10% canopy removal. Browsing was substantially higher in the *Terminalia* woodland, with canopy removal over 40% in most plots at 200 and 500 m from waterholes. Despite declining with distance, elephant browsing was still high in the *Terminalia* woodland at 2-3 km from waterholes, with 30-40% canopy removal across most plots in this distance range.

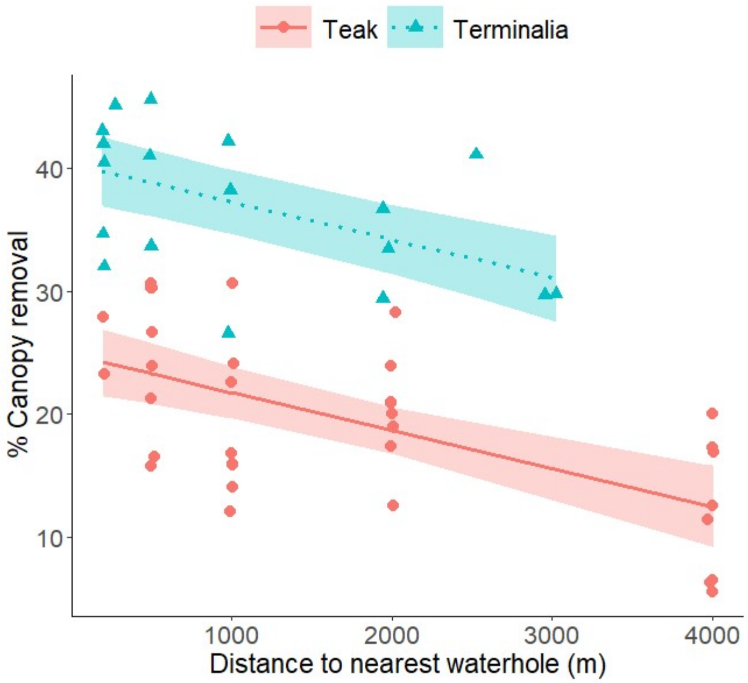

Figure 3: Plot averages for canopy removal by elephant, averaged across all height classes. Blue triangles and red circles indicate the canopy removal scores for *Terminalia* woodland and teak woodland plots respectively. The blue dotted line shows the predicted relationship between canopy removal and distance to the nearest waterhole for *Terminalia* woodland from the regression model, while the red solid line indicates the regression relationship for teak woodland. For both vegetation types, the shaded area indicates the 95% confidence limits of the predicted relationship from the regression model. The symbols used here are also used in Figures 4-6.

3.2.2. Plants ≥3 m high

Canopy removal by elephant in the ≥3 m height class (Figure 4) showed a negative relationship with distance to waterholes (estimate ± SE = -3.27 ± 0.10, $F_{1,49} = 10.67$, $p = 0.002$). There was a particularly large difference between vegetation types, with substantially higher elephant browsing in the *Terminalia* woodland (estimate ± SE = 33.36 ± 2.70, $F_{1,49} = 153.0$, $p < 0.001$). Browsing of the ≥3 m was moderate to low in the teak woodland, with average canopy removal below 50% in all but one plot, and around 10-30% in most plots. Only one teak woodland plot had a higher canopy removal score than any of the *Terminalia* woodland plots, indicating the clear difference in browsing levels between the two vegetation types for this height class. By 4 km from the nearest waterhole, elephant browsing was generally low in the teak, with average canopy removal values below 20% for most plots. In contrast, elephant browsing levels in the *Terminalia* woodland were consistently high for the ≥3 m height class, with most plots having average canopy removal estimates above 50%. Even at 3 km from the nearest waterhole, plots in the *Terminalia* woodland had canopy removal scores around 50%.

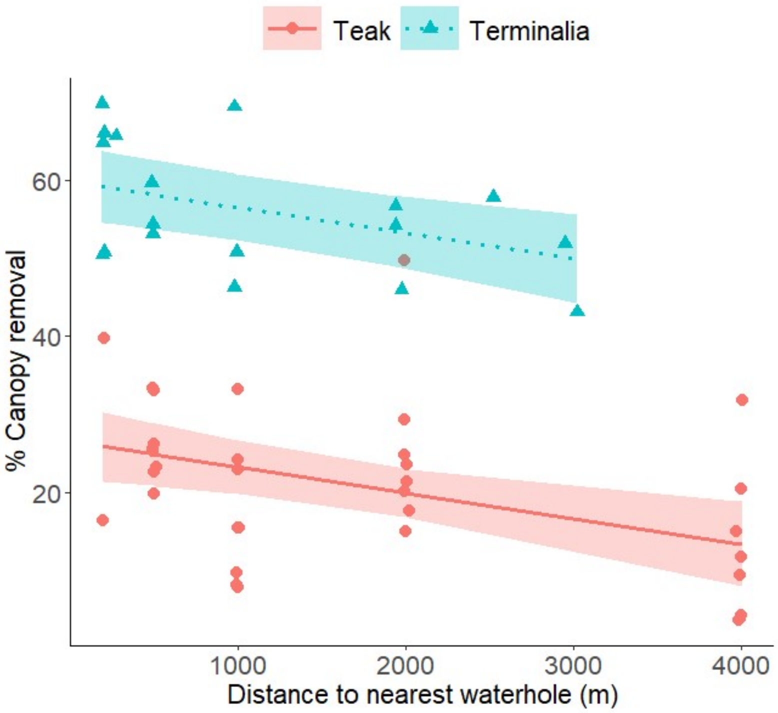

Figure 4: Plot averages for canopy removal by elephant for the ≥3 m height class (including browsing events which reduced trees to less than 3 m). See Figure 3 for full explanation of the symbols used.

3.2.3. Plants 1 - <3 m high

More variation in browsing levels within distance intervals was evident for the 1 - <3 m height class (Figure 5), though a negative relationship with distance to water and browsing was still evident (estimate ± SE = -3.07 ± 0.90, $F_{1,49} = 11.67$, $p = 0.001$). Though not as pronounced as in the ≥3 m size class, the difference in elephant browsing levels between vegetation types was still strongly significant (estimate ± SE = 8.53 ± 2.42, $F_{2,49} = 12.44$, $p < 0.001$), again with higher browsing in the *Terminalia* woodland. Plots in the teak woodland again had mostly low average canopy removal estimates by 4 km from the nearest waterhole (below 20%), although two plots still had relatively high canopy removal scores of around 30%. Canopy removal levels in the *Terminalia* woodland were generally lower than they were in the ≥3 m height class, and closer to the browsing levels seen in the teak woodland. Nevertheless, most *Terminalia* woodland plots had moderately high canopy removal estimates of 30-40%, with one outlier plot at 1 km from the nearest waterhole having an unusually high canopy removal score of close to 60%.

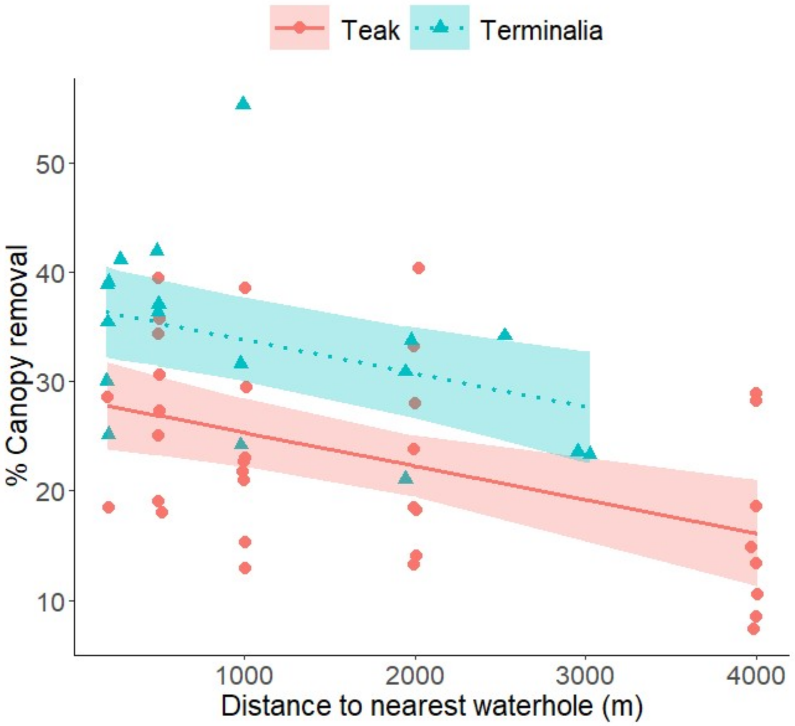

Figure 5: Plot averages for canopy removal by elephant in the 1 - <3 m height class. See Figure 3 for full explanation of the symbols used.

3.2.4. Plants <1 m high

As in the 1 - <3 m height class, considerable variation in browsing levels within distance intervals was evident for plants <1 m tall (Figure 6). However, the overall effect of distance to waterholes was again significant ($F_{1,49} = 12.32$, $p = 0.001$). The difference between the vegetation types was marginally non-significant ($F_{1,49} = 3.92$, $p = 0.053$), although estimated browsing levels once more appeared to be higher in the *Terminalia* woodland. Despite the high variability elsewhere, browsing levels for this height class were low in all cases in the teak woodland by 4 km from waterholes, with canopy removal ranging from around 5-15% in all plots at this distance.

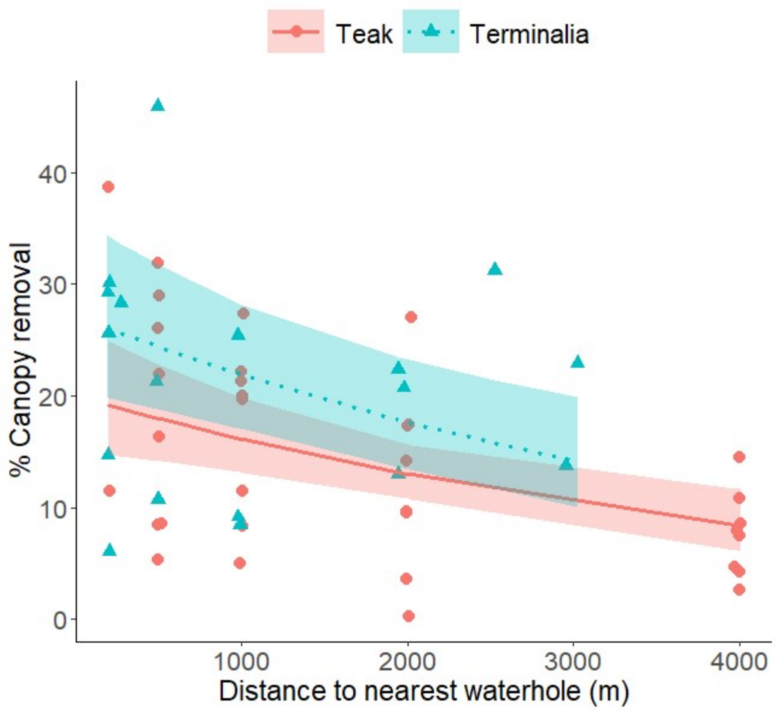

Figure 6: Plot averages for canopy removal by elephant in the <1 m height class. See Figure 3 for full explanation of the symbols used.

3.3. Elephant browsing of selected plant species

3.3.1. Elephant browsing of selected species in teak woodland

Average canopy removal scores for the more common plant species in teak woodland are shown in Figure 7 (see Appendix 5 for the breakdown of canopy removal into new and old browsing). *Baikiaea plurijuga,* the most abundant species in the ≥3 m height class in the teak woodland (Appendix 3), exhibited very low browsing levels, with an average score for canopy removal by elephant of just 2.6%. The second most abundant species in the ≥3 m height class, *Bauhinia petersiana,* was substantially more browsed (25.3%). *Baphia massaiensis* was the third most abundant species in the height class, and had one of the highest scores for average canopy removal (42.7%). Of the less abundant species, the three *Combretum* species and *Guibortia coleosperma* were moderately browsed (ranging from 23.0-31.2%), while *Croton gratissimus* and *Friesoldesia obovata* had low browsing levels (9.7% and 11.4% respectively). *Terminalia* spp. trees in the teak were heavily browsed (54.6%), which was the highest average canopy removal score of any of the more widespread species in the height class.

In the 1-3 m height class, *Bauhinia petersiana* and *Baphia massaiensis* were the most abundant species (Appendix 3). Both had moderately high browsing levels: 24.0% canopy removal for *B. petersiana* and 27.6% canopy removal for *B. massaiensis* (Figure 7). As in the ≥3 m height class, *Baikiaea plurijuga* had very low browsing levels (5.0% canopy removal). Of the less abundant species, *Grewia monticola* was the most highly browsed of any species in the height class (50.1% canopy removal), while *Grewia flavescens* was also relatively highly browsed (29.6% canopy removal). Other plants with above average canopy removal for this height class included *Guibortia coleosperma* (32.7%)*, Pseudolachnostylis maprouneifolia* (24.9%) and *Croton gratissimus* (36.7%). The three *Combretums, F. obovata, Burkea africana, Psydrax livida* all had moderately low browsing scores (ranging from 13.5% to 22.7% canopy removal), as did *Terminalia* spp. (16.6% removal), despite being the most highly browsed in the ≥3 m height class. *Ochna pulchra* was the least browsed species in this height class, with an average canopy removal of just 1.3%.

In the <1 m height class, *Baphia massaiensis* and *Bauhinia petersiana* were again the dominant species (Appendix 3). Browsing scores were fairly low for these species in this height class, with 18% average canopy removal for *B. massaiensis* and 12.1% for *B. petersiana* (Figure 7). As in the other height classes, browsing of *Baikiaea plurijuga* was low (4.4% canopy removal). Other species of note were *Grewia monticola,* which again had the highest browsing score for the height class (56.5% canopy removal), though the sample size was low. *Combretum collinum* was relatively highly browsed (25.9% canopy removal), whilst the other *Combretum* species were not (both around 5% canopy removal). *Psydrax livida* and *Pavetta schumanniana* are two species which had particularly high abundance in this height class relative to their occurrence in other height classes. *P. livida* was lightly browsed (15.5% canopy removal), while *P. schumanniana* were virtually untouched (1.8% canopy removal). Again in contrast to the ≥3 m height class, *Terminalia* spp. <1 m were lightly browsed (9.2% canopy removal). Finally, *Ochna pulchra* had a very low score for average canopy removal (2.5%).

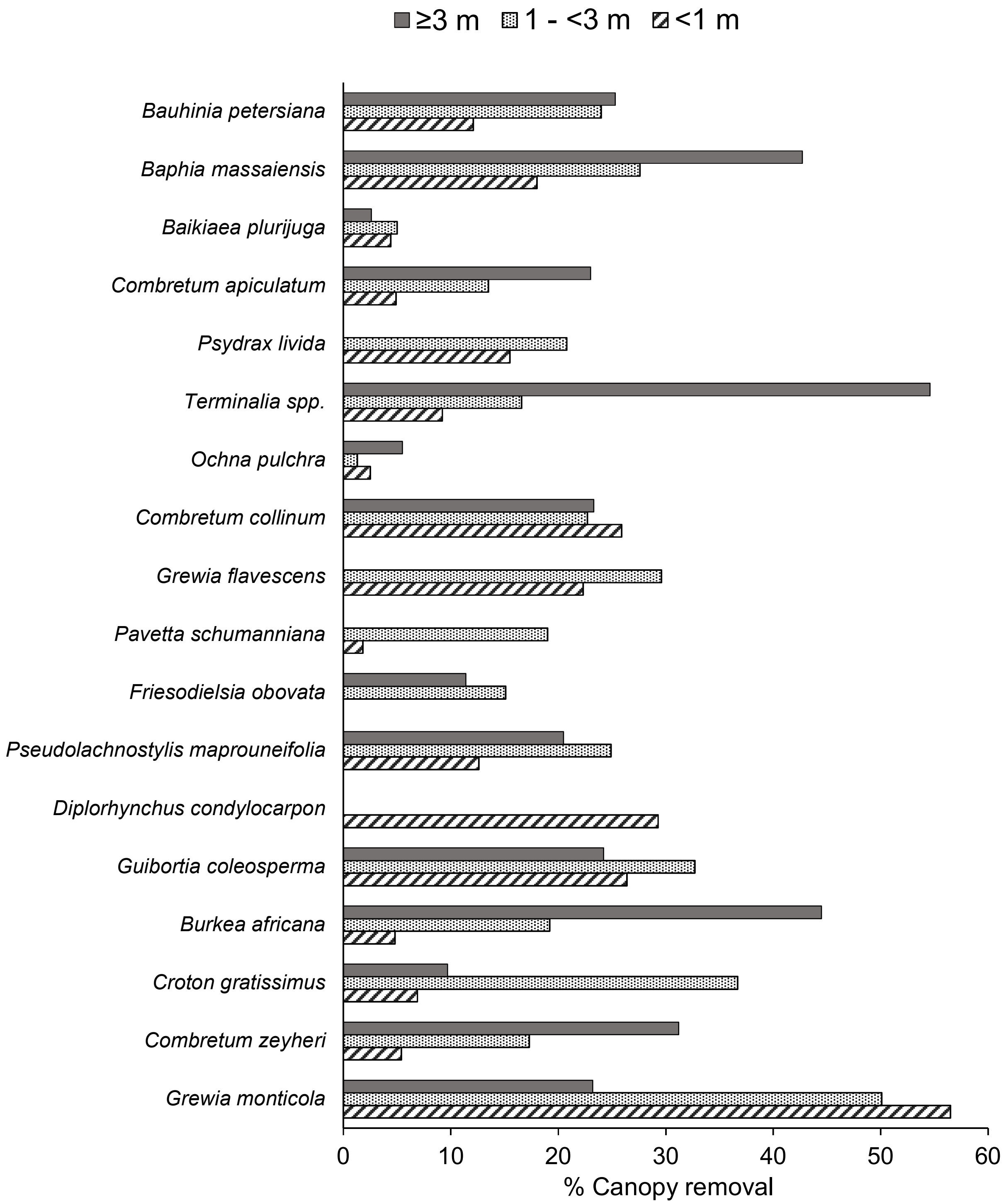

Figure 7: Average % canopy removal by elephant for selected species in teak woodland, with bars patterned according to height class. Species are arranged in order of abundance, and only species with 20 or more individuals in at least one height class are shown. Missing bars indicate where no individuals of a particular species were found in the height class.

3.3.2. Elephant browsing of selected species in Terminalia woodland

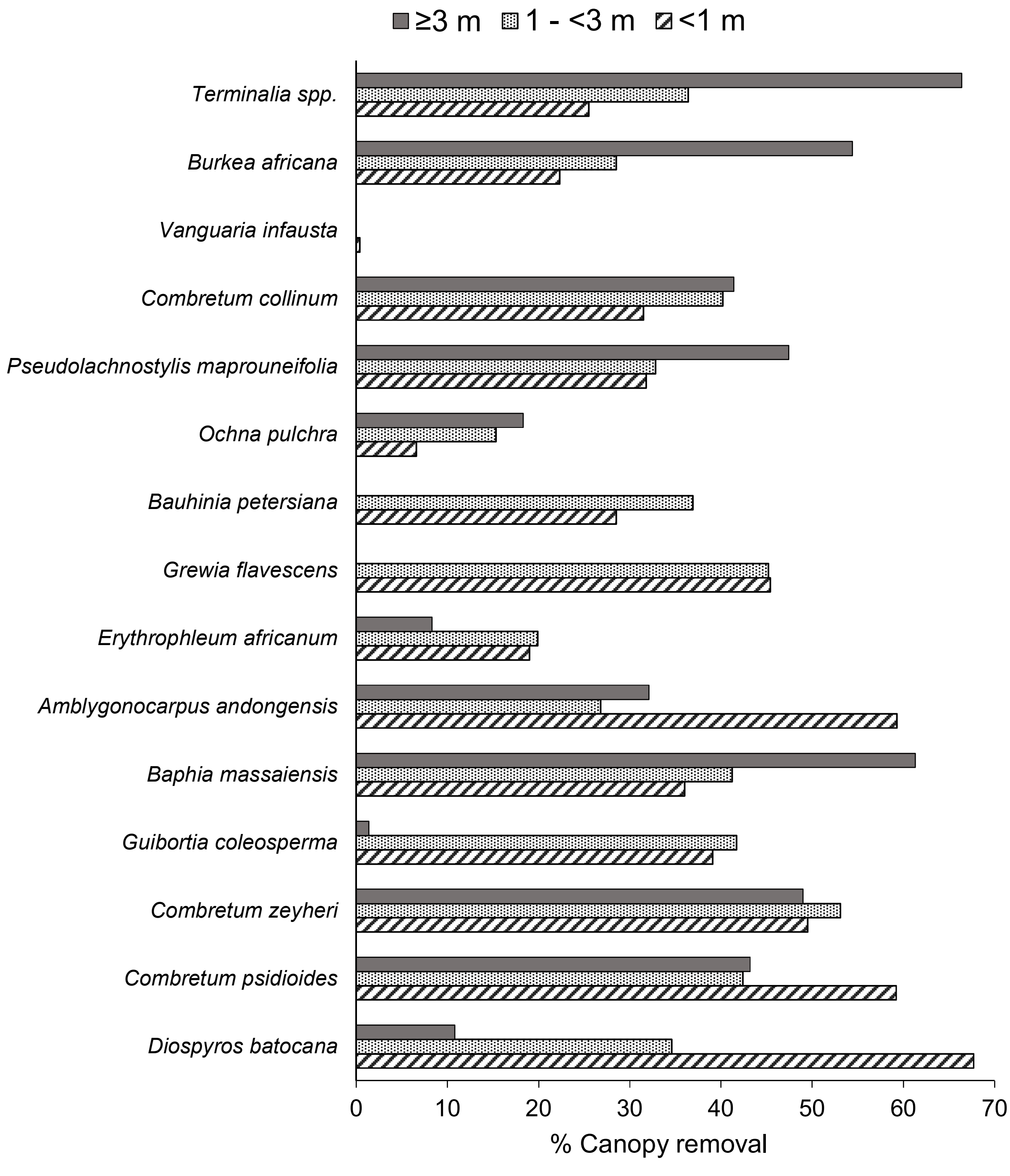

Figure 8: Average % canopy removal by elephant for selected species in *Terminalia* woodland, with bars patterned according to height class. Species are arranged in order of abundance, and only species with ≥20 individuals in at least one height class are shown. Missing bars indicate where no individuals of a particular species were found in the height class.

Average canopy removal scores for the more common plant species in *Terminalia* woodland are shown in Figure 8 (see Appendix 6 for the breakdown of canopy removal into new and old browsing). In the ≥3 m height class, *Terminalia* spp. were dominant in this vegetation type (Appendix 4), and were also the most highly impacted by elephant, with an average canopy removal score of 66.4% (Figure 8). This estimate includes a large number of converted trees. *Burkea africana,* the next most abundant tree species when including converted trees, also had a high average canopy removal score of 54.4%. The three *Combretum* species were likewise relatively highly browsed (41.4% - 54.4% canopy removal), while *Amblygonocarpus andongensis* was less highly impacted (32.1%). *Erythrophleum africanum* was lightly browsed relative to most other species in the height class (8.3% canopy removal). Sample sizes for all other species in this height class were small and browsing scores should thus be interpreted with caution, though of note is the particularly high browsing score for *Baphia massaiensis* (61.3% canopy removal), and relatively low browsing of *Ochna pulchra* (18.3%).

Terminalia spp. were again the most abundant plants in the 1- <3 m height class (Appendix 4), with a substantially lower but still slightly moderately high average canopy removal estimate of 36.4% (Figure 8). Species subject to heavier browsing in this height class included *Grewia flavescens* (45.2% canopy removal)*, Baphia massaiensis* (41.2% canopy removal) and all three *Combretum* species. *C. zeyheri* had the highest average canopy removal score in the height class (53.1%), while *C. collinum* and *C. psidioides* were also highly browsed (40.2% and 42.4% canopy removal respectively). *B. petersiana* (36.9% canopy removal) and *Pseudolachnostylis maprouneifolia* (32.8% canopy removal) were browsed at a similar level to *Terminalia* spp. Species which exhibited relatively low browsing levels in this height class included *Amblygonocarpus andongensis* and *Burkea africana* (26.8% and 28.5% canopy removal respectively). The latter species was also the second most abundant species in the height class. Finally, *Erythrophleum africanum* and *Ochna pulchra* were the two least browsed species (19.9% and 15.3% canopy removal respectively).

In the <1 m height class, *Burkea africana* was the most abundant species (Appendix 4), with a moderate browsing score of 22.3% average canopy removal (Figure 8). *Vangueria infausta* was the next most abundant species, and was virtually untouched by elephant (0.4% canopy removal). Highly browsed species with an adequate sample size in this height class were *Grewia flavescens* (45.4% canopy removal)*, Guibortia coleosperma* (39.1% canopy removal) and *Baphia massaeiensis* (36.0% canopy removal). *Diospyros batocana* (67.7% canopy removal)*, Amblygonocarpus andongensis* (59.3% canopy removal) and *Combretum psidioides* (59.2% canopy removal) were the most highly browsed species in the height class, although sample sizes of all three were low. *Pseudolachnostylis maprouneifolia* (31.8% canopy removal), *Combretum collinum* (31.5% canopy removal) and *Terminalia* spp. (25.5% canopy removal) were more moderately browsed. Finally, *Erythrophleum africanum* (19.0% canopy removal) and *Ochna pulchra* (6.6% canopy removal) again had low browsing levels, especially the latter species.

3.4. Vegetation structure in relation to distance from waterholes

3.4.1. Teak woodland

Table 2: Results of the full statistical models of measures of vegetation structure in relation to distance from waterholes, in teak woodland. Factors in bold remained in the final model. Models with no bold factors indicate where neither predictor was significant at the $p < 0.1$ level.

Response variable	Model type	Predictors	F Test	*p*
Standing basal area/ha	Gamma GLIM	log(Dist to water)	$F_{1,29} = 1.11$	0.301
	(log link)	Waterhole ID	$F_{3,29} = 1.14$	0.351
Standing basal area/ha	Gamma GLIM	Dist to water	$F_{1,28} = 0.01$	0.936
(outlier removed)	(log link)	**Waterhole ID**	**$F_{3,28} = 3.03$**	**0.046**
Converted/standing basal area	Gamma GLIM	Dist to water	$F_{1,29} = 0.765$	0.389
	(log link)	Waterhole ID	$F_{3,29} = 0.306$	0.821
Canopy volume/ha (≥3 m)	Gamma GLIM	**Dist to water**	**$F_{1,29} = 3.77$**	**0.062**
	(log link)	Waterhole ID	$F_{3,29} = 0.17$	0.914
Canopy volume/ha (≥3 m)	Gamma GAM	s(Dist to water)	$F_{2.9,26.1} = 0.97$	0.364
(outlier removed)	(log link)	Waterhole ID	$F_{3,26.1} = 0.91$	0.448
Canopy volume/ha (1-<3m)	Gamma GAM	**s(Dist to water)**	**$F_{3.7,26.3} = 7.24$**	**<0.001**
	(log link)	Waterhole ID	$F_{3,26.3} = 0.77$	0.523
No. of plants/ha (1 - <3 m)	Inv. Gaussian	**s{log(Dist to water)}**	**$F_{2.8,27.2} = 9.27$**	**<0.001**
	GAM (log link)	Waterhole ID	$F_{3,27.2} = 2.23$	0.107

Once more, waterhole ID was not significant at the $p < 0.1$ level in the full models (Table 2), and was thus removed in the process of backward elimination. In the ≥3 m height class, one plot at 4 km from waterholes had an unusually high number of very large teak trees, and as a result had canopy volume/ha and basal area/ha figures several times higher than any other plot. To control for the influence of this data point, analysis was run with and without it included. The effect of distance to waterholes did not significantly explain canopy volume/ha or basal area/ha in either case, though both of these were relatively low in the two plots at 200 m from waterholes. Distance to waterholes also did not significantly explain the ratio of converted to standing tree basal area. Overall, canopy volume/ha, basal area/ha and the ratio of converted to standing tree basal area showed much variation within distance intervals for the ≥3 m height class, with no clear influence of distance to waterholes.

In the 1- <3m height class, canopy volume/ha was significantly related to distance to the nearest waterhole ($F_{3.6,29.4} = 7.06$, $p < 0.001$), increasing over 200 and 500 m to more or less plateau from 1000 m onwards (Figure 9a). Density of plants in the 1 - <3 m height class showed a similar trend (Figure 9b), though the relationship with distance to the nearest water was slightly less strong ($F_{2.4,30.6} = 6.06$, $p = 0.004$).

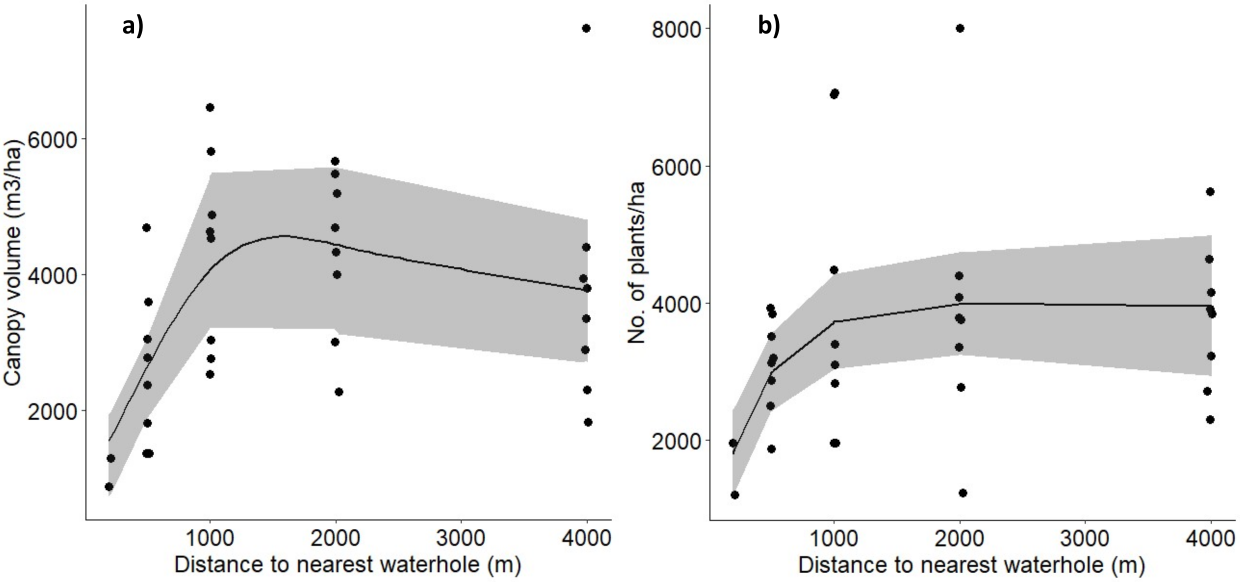

Figure 9: Canopy volume/ha (a) and density (b) (number of plants/ha) of plants in the 1-3 m height class in teak woodland. Black line indicates the predicted relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

3.4.2. Terminalia woodland

As in the teak woodland, waterhole ID was not significant at the $p < 0.1$ level in the full models (Table 2), and was thus removed in the process of backward elimination. In the ≥3 m height class, standing basal area was not significantly related to distance from waterholes when all plots were considered (Figure 10a). However, one plot at 200 m had an anomalously high number of large, mature trees, resulting in an unusually high basal area/ha value. When analysis was performed with this plot excluded (Figure 10b), the positive relationship between the basal area/ha of standing trees (≥3 m high and basal diameter ≥6 cm) and distance to the nearest waterhole was significant ($F_{2.4,11.6} = 9.15$, $p = 0.002$). Apart from the anomalous plot at 200 m, standing tree basal area/ha showed a curved relationship with distance to the nearest waterhole. Standing tree basal area/ha was low but gradually increasing from 200-1000 m, with more substantial increases up to 3000 m. Excluding the anomalous plot at 200 m, standing tree basal area/ha was several times greater at 2500-3000 m from the nearest waterhole than at 200-500 m.

Table 3: Results of the full statistical models of measures of vegetation structure in *Terminalia* woodland. Factors in bold remained in the final model. Models with no bold factors indicate where neither predictor was significant at the $p < 0.1$ level.

Response variable	Model type	Predictors	*F* Test	*p*
Standing basal area/ha	Gamma GLIM (log link)	**Dist to water**	**$F_{1,12} = 5.30$**	**0.040**
		Waterhole ID	$F_{2,12} = 0.81$	0.467
Standing basal area/ha (outlier removed)	Gamma GLIM (log link)	**Dist to water)**	**$F_{1,11} = 30.81$**	**<0.001**
		Waterhole ID	$F_{2,11} = 0.18$	0.841
Combined basal area/ha	Gaussian GLM (log link)	Dist to water	$F_{1,12} = 1.27$	0.281
		Waterhole ID	$F_{2,12} = 0.10$	0.903
Combined basal area/ha (outlier removed)	Inv. Gaussian GLIM (log link)	**Dist to water**	**$F_{1,11} = 16.13$**	**0.002**
		Waterhole ID	$F_{2,11} = 0.86$	0.451
Converted/standing basal area	Gamma GLM (log link)	**Dist to water**	**$F_{1,12} = 6.74$**	**0.023**
		Waterhole ID	$F_{2,12} = 1.32$	0.304
Converted/standing basal area (outlier removed)	Gamma GAM (log link)	**s(Dist to water)**	**$F_{2.3,8.7} = 7.59$**	**0.007**
		Waterhole ID	$F_{2,8.7} = 0.04$	0.962
Canopy volume/ha (≥3 m)	Gaussian GLM (log link)	**Dist to water**	**$F_{1,12} = 9.77$**	**0.009**
		Waterhole ID	$F_{2,12} = 0.03$	0.968
Canopy volume/ha (≥3 m) (outlier removed)	Gaussian GAM (identity link)	**s(Dist to water)**	**$F_{2,10} = 76.5$**	**<0.001**
		Waterhole ID	$F_{2,10} = 0.42$	0.668
Canopy volume/ha (1-<3m)	Gaussian GLM (identity link)	**Dist to water**	**$F_{1,12} = 6.15$**	**0.029**
		Waterhole ID	$F_{2,12} = 0.55$	0.590
No. of plants/ha (1 - <3 m)	Gaussian GLM (identity link)	Dist to water	$F_{1,12} = 1.15$	0.304
		Waterhole ID	$F_{2,12} = 0.46$	0.642

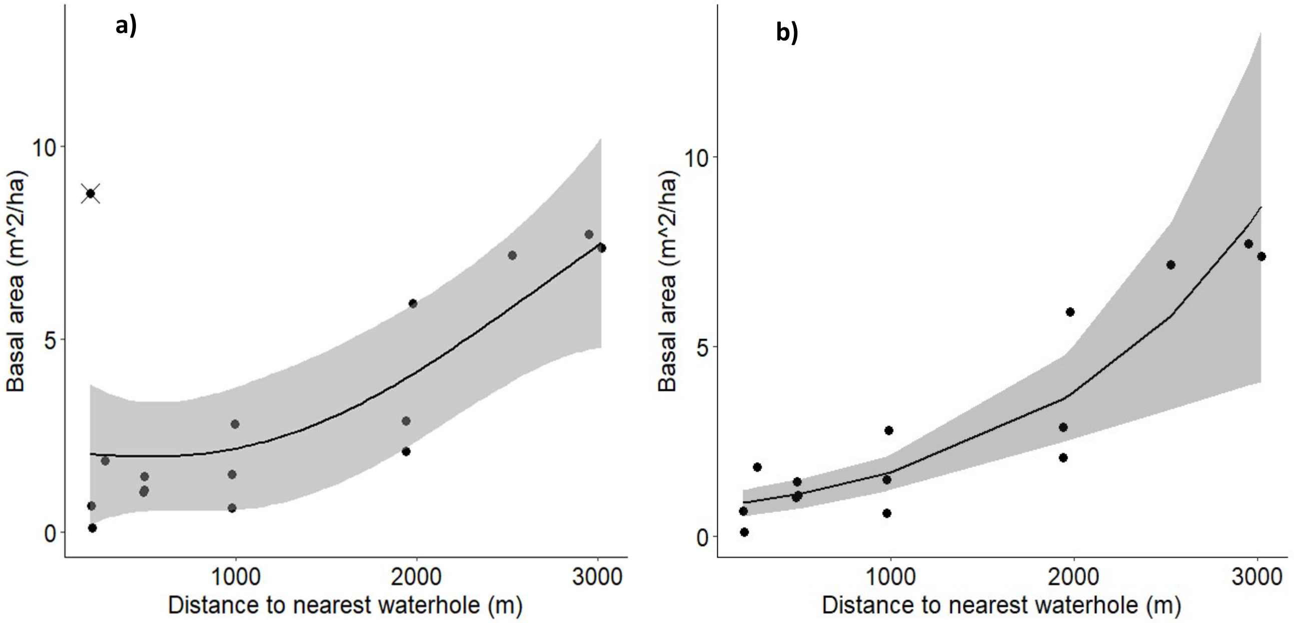

Figure 10: Basal area/ha of standing trees (≥3 m high and basal diameter ≥6 cm) in *Terminalia* woodland, with outlier plot included (a) and excluded (b). The black line indicates the predicted relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

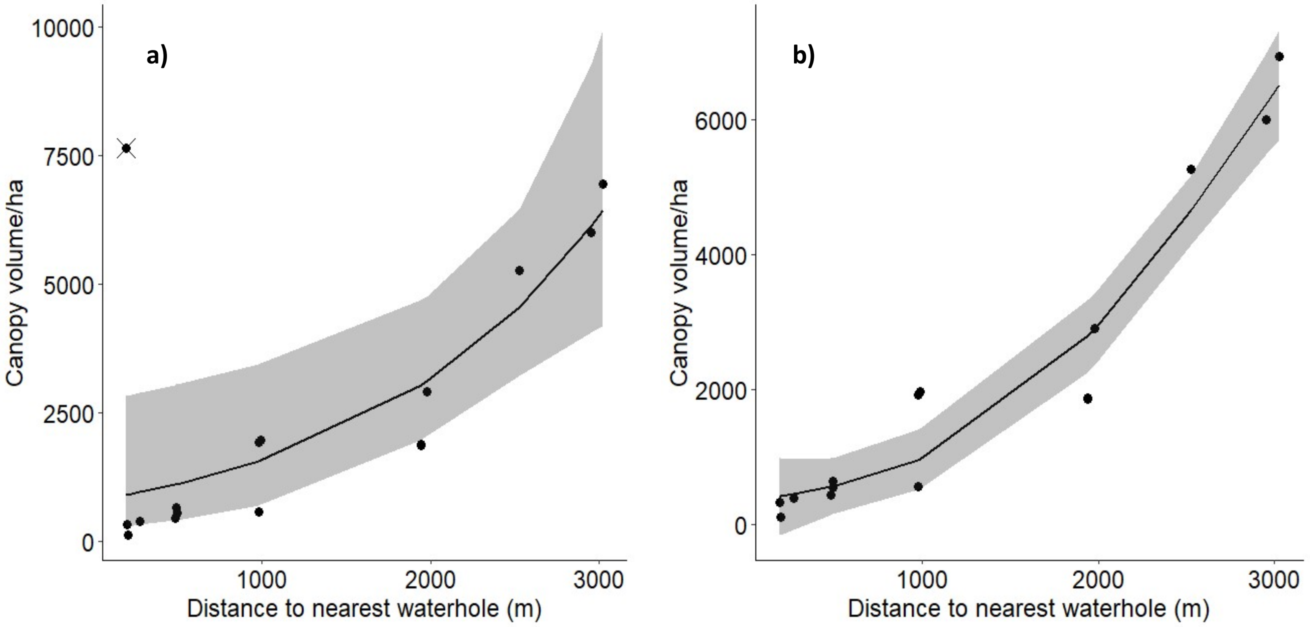

Figure 11: Canopy volume/ha for plants ≥3 m in *Terminalia* woodland with (a) and without (b) outlier plot (indicated by crossed circle) included. The black line indicates the predicted

relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

Canopy volume showed a similar curved relationship with distance to the nearest waterhole, remaining low from 200-1000 m before increasing over 2000-3000 m. Again, the plot at 200 m with an unusually high number of mature trees deviated from the general trend. However, the relationship between canopy volume and distance to the nearest waterhole was significant even with this plot included ($F_{1,14} = 11.99$, $p = 0.004$) (Figure 11a), though the effect of distance became substantially stronger when it was excluded ($F_{2,12} = 83.52$, $p < 0.001$) (Figure 11b). As with standing basal area/ha, canopy volume/ha was several times greater by 2500-3000 m from the nearest waterhole than at 200-500 m, except for the anomalous 200 m plot.

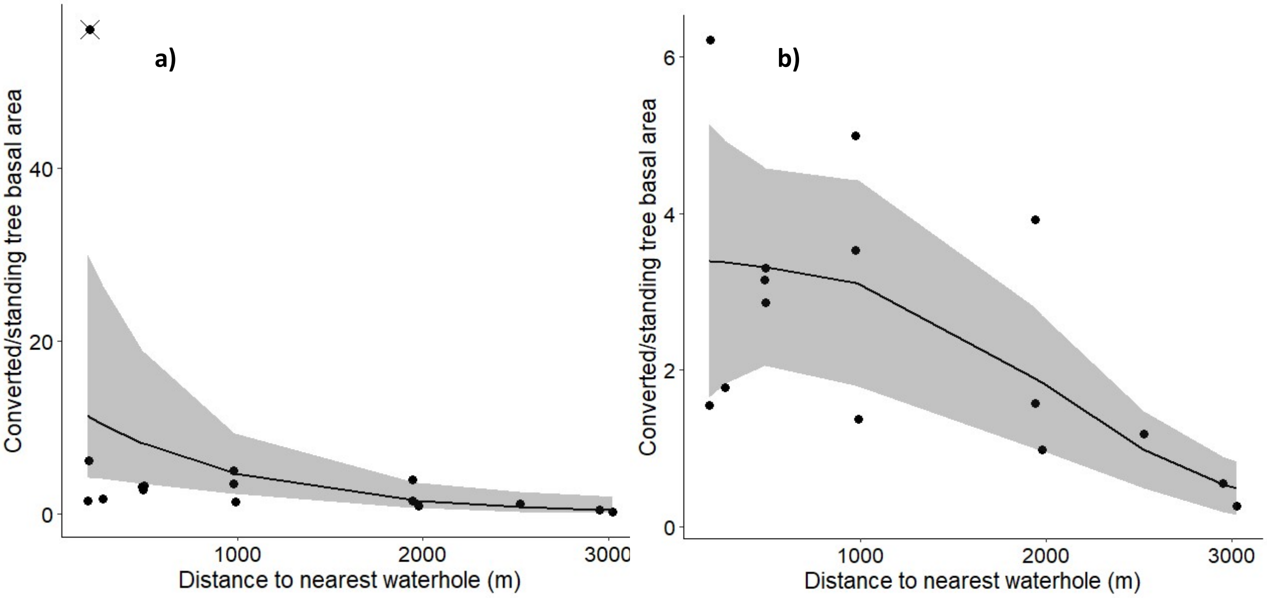

Figure 12: Ratio of converted to standing tree basal areas in *Terminalia* woodland with (a) and without (b) outlier plot (indicated by crossed circle) included. The black line indicates the predicted relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

The ratio of converted to standing tree basal areas was generally high in the *Terminalia* woodland, exceeding one for most plots. This indicates that converted trees (basal diameter ≥6 cm but reduced to <3 m in height) are dominant over unconverted trees across much of the vegetation type. A clear outlier existed at 200 m from Chamabondo 3 waterhole, with a converted to standing tree basal area ratio of 56. This resulted from the near total lack of standing trees close to this waterhole. With this plot included (Figure 12a), the ratio of converted to standing tree basal area declined with distance to the nearest waterhole ($F_{1,14} = 28.23$, $p < 0.001$). Given the severity of this outlier, models were also run with it excluded (Figure 12b). Distance to the nearest waterhole remained significant with the outlier plot excluded ($F_{2.4,11.6} = 9.15$, $p = 0.002$). Despite the significance of the relationship with distance to the nearest waterhole, the ratio of converted to standing tree basal areas was quite variable within distance intervals, especially at 200 m where multiple plots had relatively low values. Nevertheless, a general decline in the dominance of converted trees 2000-3000 m from waterholes was evident.

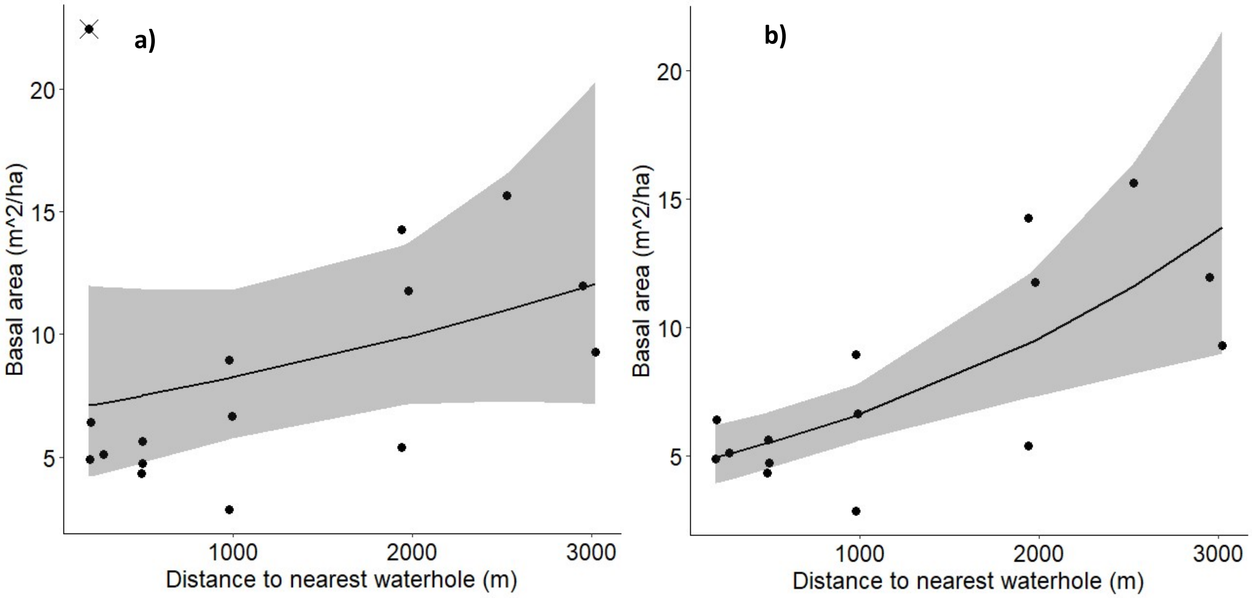

Figure 13: Combined basal area/ha of standing and converted trees in *Terminalia* woodland, with (a) and without (b) outlier plot included. The black line indicates the predicted relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

Given the high numbers of converted trees in the *Terminalia* woodland, I also investigated whether basal area/ha declined when both converted and standing trees were considered together. Hence, the response variable was basal area/ha of all plants with stem diameters ≥6 cm. The plot at 200 m was an even stronger outlier here, due to a high number of large standing and converted trees. With this plot included (Figure 13a), distance to the nearest waterhole did not significantly explain combined standing and converted tree basal area, while a positive relationship emerged when it was removed from the analysis ($F_{1,13} = 18.35$, $p < 0.001$) (Figure 13b). Aside from the anomalous plot at 200 m, combined basal area was low at 200-500m from the nearest waterhole, with generally increasing but highly variable values from 1000 m onwards.

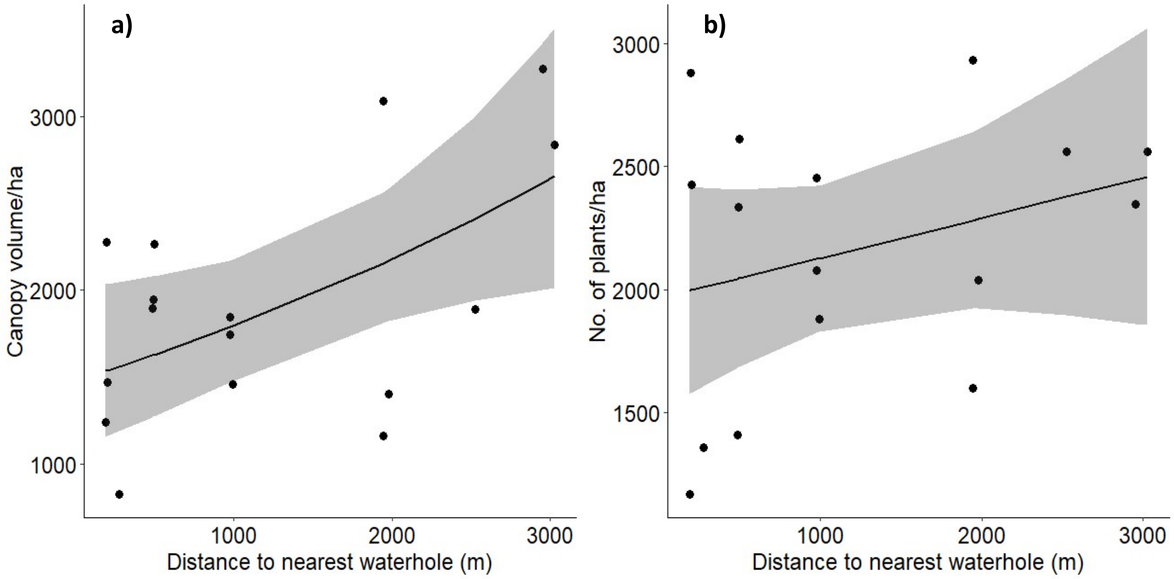

Figure 14: Canopy volume/ha (a) and density (b) (number of plants/ha) of plants in the 1-3 m height class in *Terminalia* woodland, in relation to distance to waterholes. The black line indicates the predicted relationship from the regression model, while shaded areas indicate 95% confidence intervals of the regression relationship.

In the 1 - <3 m height class, canopy volume was significantly related to distance to the nearest waterhole ($F_{1,14} = 6.06$, $p = 0.027$) (Figure 14a), but plant density was not ($F_{1,14} = 1.41$, $p = 0.255$) (Figure 14b). While canopy volume/ha estimates of plants 1 - <3 m tall showed much variation within distance intervals, the general pattern was an increase in canopy volume with distance from the nearest waterhole.

3.5. Elephant dung counts in relation to distance from waterholes

Amounts of elephant dung were not significantly related to vegetation type in the full statistical model (Table 4), thus vegetation type was removed from the final model. Hence, a single regression line for dung counts across both vegetation types is shown in Figure 15a. The amount of dung showed a curved relationship with distance to the nearest waterhole ($F_{4.1,44.9} = 9.62$, $p <$

0.001), declining from 200-2000 m. At 2000 m it levelled out, with similar amounts of dung at 2000 and 4000 m. Unlike in the models of the vegetation response variables, waterhole ID was a significant predictor of amounts of dung counted ($F_{3,43.9} = 4.02$, $p = 0.013$). Dung counts appeared to be higher at Chamabondo 3 and Kalisosa 1 waterholes than at Chamabondo 2 and 3 (figure 15b). However, when a Tukey posthoc test was conducted, no waterhole was significantly different from the others at the $p < 0.05$ level, despite the overall significance of waterhole ID as a predictor of dung counts.

Table 4: Results of the full statistical model of elephant dung counts. Factors in bold remained in the final model.

Model type	Predictors	F test	*p*
Gamma GAM (log link)	**Distance to water**	$\boldsymbol{F_{3.8,44.2} = 8.58}$	**<0.001**
	Veg type	$F_{1,44.2} = 0.28$	0.600
	Waterhole ID	$\boldsymbol{F_{3,44.2} = 3.98}$	**0.014**

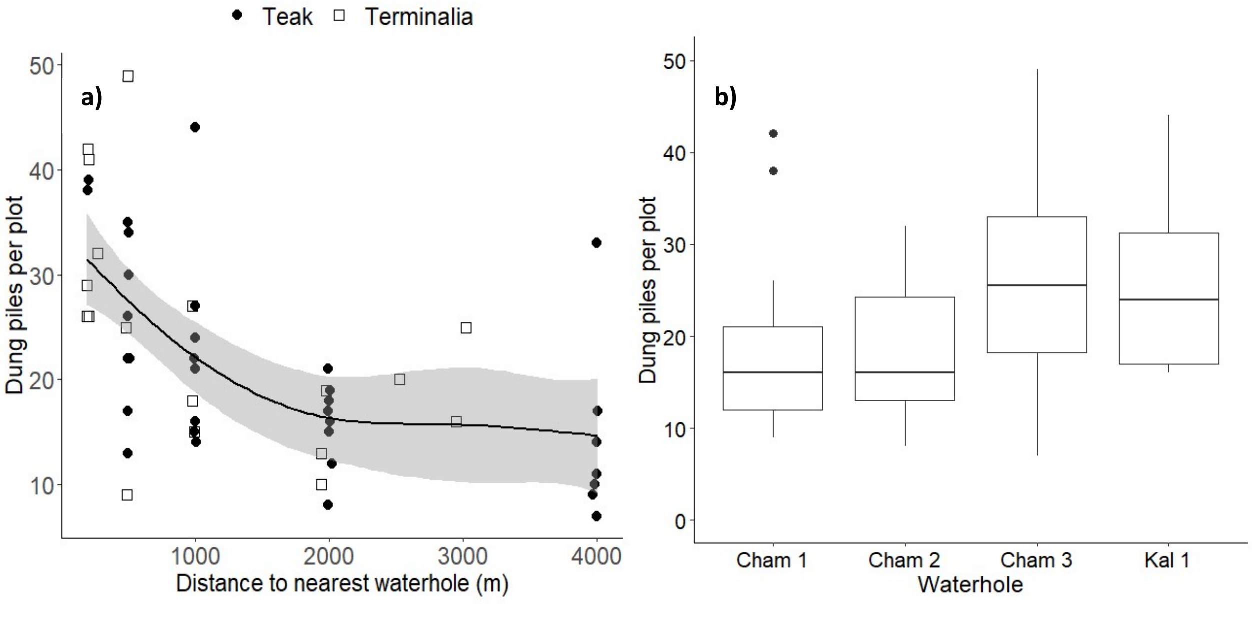

Figure 15: Number of elephant dung piles counted per sampling plot in relation to distance from waterholes (a), with circles for teak woodland plots and squares for *Terminalia* woodland plots. Boxplot (b) shows dung counts by waterhole.

4. DISCUSSION

Given the breadth of content covered, the following discussion is broken down into similar categories to those used in the results section. It begins with a discussion of elephant browsing levels in relation to distance to waterholes and vegetation type. The main finding here were declines in elephant browsing moving away from waterholes in both vegetation types, but with browsing consistently higher in the *Terminalia* woodland. This is followed by a discussion of elephant browsing impacts on selected plant species in the two woody vegetation types of the study area. Structural impacts of elephant browsing on vegetation at different distances from waterholes are then discussed for the two vegetation types. As structural impacts on the *Terminalia* woodland were much more marked than they were in the teak woodland, this section focuses on the former vegetation type. Finally, elephant occupancy in relation to distance to waterholes and impacts on vegetation is discussed, using elephant dung counts as the proxy for occupancy.

4.1. Elephant browsing in relation to distance to waterholes and vegetation type

For all height classes, the piosphere prediction of increased elephant browsing closer to waterholes was upheld, concurring with the findings of a number of other studies (Van Wyk & Fairall, 1969; Laws, 1970; Anderson & Walker, 1974; Thrash et al., 1991; Ben-Shahar, 1993; Gaugris and Van Rooyen, 2010; Mukwashi et al., 2012; Davies et al., 2018). This negative relationship between browsing and distance to water was found in both vegetation types. As elephant browsing declined with distance to waterholes in the *Terminalia* woodland along the vlei margin, this indicates that waterholes *per se*, rather than the vlei, were responsible for the piosphere effect. Vegetation type was also an important predictor of browsing levels, again matching the findings of other studies which have compared elephant impacts across vegetation types (Anderson & Walker, 1974; Guy, 1981; Conybeare, 1991; Ben-Shahar, 1998; Staub et al., 2013). Elephant browsing was consistently higher in the *Terminalia* woodland than in the teak woodland, indicating a preference for the former vegetation type. This would be expected, as teak woodland is generally not favoured for elephant browsing (Conybeare, 1991; Ben-Shahar, 1998; Holdo, 2006).

In the ≥3 m size class, mostly moderate levels of elephant browsing were evident in the teak woodland, particularly further away from waterholes. New browsing levels in particular were especially low at 4 km from the nearest waterhole, with canopy removal estimates below 2% in all plots. This indicates little dry season browsing by elephant in the teak woodland beyond 2 km from waterholes. Despite the general trend of moderate browsing declining away from waterholes, a few plots were outliers. Anomalously high browsing levels in one plot at 2 km from waterholes can be attributed to a high number of *Combretum psidioides* and *C. collinum* trees, many of which had been recently heavily browsed. One of the plots at 4 km also showed unexpectedly high browsing levels, which can be linked to an unusually high number of *Julbernardia globiflora* trees. This species was not frequently encountered in the study area, but was often highly browsed, as was the case in this plot. These examples highlight how certain favoured species in the teak woodland are still prone to high browsing further away from waterholes. Concerns are thus raised for the persistence of such species in the study area, where much of the vegetation is within 4 km of waterholes. Given the potential for elephant to travel distances of 15 km or more from water (Loarie et al., 2009), favoured species at 4 km from waterholes would still be within relatively easy reach.

Despite declining with distance from waterholes, elephant browsing levels in the *Terminalia* woodland were consistently high for the ≥3 m size class, even at 3 km from waterholes. As no part of the *Terminalia* woodland is much more than 3 km from waterholes, this shows that the tree layer across the entirety of the vegetation type is subject to heavy elephant browsing. Current management thinking argues that the aim of water supplementation schemes should be to develop a range of elephant browsing levels across protected areas, thus promoting ecosystem heterogeneity (Gaylard et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007). However, the present distribution of waterholes instead appears to be facilitating heavy elephant browsing of the ≥3 m size class throughout the *Terminalia* woodland. Closer to waterholes, where browsing levels were highest, marked reductions in basal area and canopy volume of plants ≥3 m have resulted.

In the 1 - <3 m height class, the piosphere prediction of a decline in browsing levels with distance from waterholes was again upheld. Despite a fairly high degree of variability within distance intervals, relatively low elephant use of vegetation was generally evident by 4 km from waterholes in the teak woodland, although some plots were again exceptions. In the *Terminalia* woodland, canopy removal estimates still suggest fairly intense elephant browsing particularly close to waterholes, although utilisation was not as heavy as in the ≥3 m size class. However, of note were the particularly high values for new elephant browsing in the *Terminalia* woodland, with average canopy removal estimates of 20% or more for new browsing in a number of plots. This indicates intense browsing pressure over the 2019 dry season, which might be the result of low rainfall in the 2018-2019 rainy season. If seasonal water sources dried up earlier than usual, then increased and more prolonged concentration of elephant around waterholes would be expected. As the *Terminalia* woodland provides a favoured foraging resource with water in close proximity, more prolonged, intensive browsing may have resulted. Lower rainfall could have also meant reduced graze availability, which would have increased elephant reliance on woody vegetation compared to wetter years. This is supported by studies reporting a preference of elephant for grazing when available, resulting in heavier consumption of woody vegetation during the dry season (Guy, 1976; Barnes, 1982; Owen-Smith et al., 2019), and during drier years in general (Van Wyk & Fairall, 1969; Conybeare, 1991; Owen-Smith, 1998; Smallie & O'Connor, 2000; Chafota, 2007). As it appears to be favoured for elephant browsing, the *Terminalia* woodland would be expected to bear the brunt of an increased reliance on woody vegetation over the 2019 dry season.

The highest variability in browsing levels with distance to waterholes was evident in the <1 m height class, although browsing was still significantly related to distance to the nearest waterhole. A confounding factor in certain plots in this height class was the presence of species like *Vangueria infausta* and *Psydrax livida.* In some plots, young specimens of these were found growing in particularly high densities, but were generally not browsed. The presence of high numbers of these species appears to underly the particularly low browsing levels (< 10% canopy removal) observed in certain plots from 200 to 2000 m from waterholes. Despite the high variability elsewhere, browsing levels in the teak by 4 km from waterholes were all moderate to low, again providing evidence of lower browsing pressure by this distance from waterholes.

4.2. Elephant browsing by selected plant species

4.2.1. Teak woodland

In the teak woodland, the dominant tree species, *Baikiaea plurijuga,* was not browsed much by elephant in any height class. This matches a number of other studies which have reported that *B. plurijuga* is not palatable to elephant (Conybeare, 1991; Ben-Shahar, 1998; Holdo, 2006). Higher browsing levels were found for *Bauhinia petersiana* and *Baphia massaiensis,* the dominant shrub species. These species formed the bulk of elephant browsing in similar Kalahari sandveld woodland of Chobe (Chafota, 2007; Owen-Smith & Chafota, 2012). Given the importance of these two species in elephant diets, their high numbers across the height classes despite moderate browsing suggest food availability for elephant was not being compromised in the teak woodland.

Terminalia spp. were heavily browsed in the teak woodland, although canopy removal levels were not quite as high as they were in the *Terminalia* woodland. This shows clear selection for *Terminalia* spp. trees by elephant, subjecting them to heavy browsing even in the teak woodland where they are more sparsely distributed. Comparable browsing of *Terminalia* spp. was found in Sengwa, where biomass loss to elephant was estimated to be around 50% (Anderson & Walker, 1974), while *Terminalia* spp. were also favoured by elephant in Chobe (Owen-Smith & Chafota, 2012). However, younger *Terminalia* spp. plants were not so heavily browsed, indicating a preference of elephant for mature individuals, and suggesting recruitment into at least the smaller size classes is not being inhibited. Owen-Smith and Chafota (2012) similarly found that tree saplings of *Terminalia* spp. were less favoured.

Similar to what Chafota (2007) recorded in Chobe, *Grewia monticola* was also heavily browsed by elephant, with the highest browsing scores in both of the smaller height classes. All *Grewia* species, including *G. monticola,* were also reported to be favoured by elephant in Kruger (Van Wyk & Fairall, 1969). Given the species is not common in the study area, this again suggests a high degree of selectivity by elephant. Heavy elephant pressure also raises concerns around persistence of the species, especially as digging for roots and/or uprooting of some individuals was noted. Indeed, its relative rarity might already be the result of high elephant browsing pressures removing individuals.

Certain plant species had unexpectedly low numbers of mature individuals. *Burkea africana* was one such species. Only one standing *B. africana* above 3 m was found, despite much greater numbers of individuals in the smaller height classes. Although the sample size is small, the presence of several highly browsed converted trees suggests the lack of large individuals may be the result of prolonged heavy elephant browsing of mature individuals. This is supported by Chafota (2007), who found that *B. africana* individuals in the 11-20 cm stem diameter size class were the focus of severe elephant impacts, while Owen-Smith and Chafota (2012) found that young *B. africana* were not favoured by elephant. If heavy browsing of older *B. africana* has occurred over time, it may explain the notable lack of large specimens.

Similarly, *Diplorhynchus condylocarpon* was almost exclusively limited to the <1 m height class. The relatively high average canopy removal score for the species again suggests elephant may be preventing recruitment into larger height classes. Furthermore, elephant browsing was likely underestimated, as most individuals were coppicing plants growing from stems broken down to ground level. The age of damage and near total removal of the original larger plant often made it difficult to conclusively identify elephant as the agent, though elephant were likely responsible in some if not all cases. The suggestion that elephant browsing is preventing the recruitment of *D. condylocarpon* into larger height classes is supported by it being a favoured plant species by elephant in Chobe (Chafota, 2007; Owen-Smith & Chafota, 2012), Kruger (Van Wyk & Fairall, 1969) and Sengwa (Anderson & Walker, 1974; Guy, 1989). Guy (1981) noted that most remaining *D. condylocarpon* in Sengwa had been reduced to spindly shrubs coppicing from elephant damaged trees, which was the growth form most often encountered in the current study.

Several rare but highly browsed species are also highlighted here, as these are potentially at risk of disappearing from the study area. *Brachystegia spiciformis* trees were particularly heavily browsed by elephant. This may explain the rarity of the species, especially considering smaller individuals were also browsed, potentially impeding recruitment. This contrasts with what was found in Sengwa, where *B. spiciformis* was only lightly utilised (Anderson & Walker, 1974; Guy, 1981). However, it was a preferred species in Malawi's Kasungu National Park (Jachmann & Bell, 1985), and adjacent to Hwange National Park (Holdo, 2006), with vegetation in the latter study similar to the current study area. *Julbernardia globiflora* trees were also scarce and generally highly browsed, though the few smaller individuals encountered were not, suggesting a better chance of recruitment of young plants.

Pericopsis angolensis and *Pterocarpus angolensis* were both rarer than would be expected, especially as mature specimens of these species were noted in areas of the park further away from waterholes, where soil conditions and vegetation communities are similar. The few *Pericopsis angolensis* encountered in the study area were fairly heavily browsed, suggesting elephant may be responsible for the rarity of this species. The absence of individuals <1 m also potentially raises concerns about its persistence in the area. Browsing estimates for the few small *Pterocarpus angolensis* individuals encountered were not particularly high. However, this was another species where most plants exhibited old damage down to ground level, with elephant the probable but not definite cause. Declines in *Pterocarpus angolensis* have resulted from elephant feeding elsewhere, suggesting elephant may be the cause of the species' rarity in the study area. For example, it was the most heavily impacted species in a study of important timber species conducted south of Zambezi National Park, with a number of individuals killed by elephant (Campbell et al., 1996). Mortality was also reported following reintroduction of elephant to Songimvelo Game Reserve in South Africa (Steyn & Stalmans, 2001), and along the Chobe River frontage (Owen-Smith, 1988).

4.2.2. Terminalia woodland

As in the teak woodland, *Terminalia* spp. trees were heavily browsed in the *Terminalia* woodland. Elephant browsing was again highest for larger individuals (≥3 m), matching what Owen-Smith and Chafota (2012) found in Chobe. Given that *Terminalia* spp. are the dominant trees in the vegetation type, heavy impacts on *Terminalia* spp. account in large part for the particularly high canopy removal scores for the ≥3 m size class in this vegetation type. However, *Terminalia* spp. appear to have some resilience to heavy browsing, given that they remain numerous, with high numbers of coppicing plants. Nevertheless, a number of *Terminalia* spp. trees were also found to be killed by elephant, indicating that they can be vulnerable to heavy elephant impacts. The potential vulnerability of *Terminalia* spp. was indicated in Sengwa, where heavy browsing of *T. sericea* eventually reduced their dominance in a similar vegetation type (Anderson & Walker, 1974) as well as in *Terminalia-Combretum* bushland in Hwange National Park (Conybeare, 1991), where the unpalatable *Ochna pulchra* eventually became the most abundant tree (Conybeare, 2004). A similar decline in the dominance of *Terminalia* spp. in the study area under prolonged high elephant browsing thus cannot be ruled out. However, the high numbers of individuals sampled in the less favoured smaller height classes does suggest recruitment into sapling stages is occurring.

While abundant in the smaller height classes, relatively few *Burkea africana* above 3 m were encountered, with converted trees much more numerous than standing ones. Furthermore, no large trees of the species were encountered. Given the high canopy removal found for *B. africana* in the ≥3 m height class, and the severe impacts on large individuals of the species reported elsewhere (Conybeare, 1991; Chafota, 2007), high elephant impacts may have historically eliminated large individuals while currently limiting recruitment into larger size classes. Declining densities of *B. africana* under heavy elephant browsing in Hwange National Park (Conybeare, 1991) support this suggestion. A similar suggestion was made to explain the lack of large *B. africana* in the teak woodland. As Owen-Smith and Chafota (2012) found that saplings were less favoured by elephant than mature individuals in Chobe, the much higher abundances of *B. africana* found in the smaller height classes might be expected. This suggests the species may remain common in the smaller height classes, despite little recruitment to tree size.

Pseudolachnostylis maprouneifolia exhibited a similar pattern to *B. africana,* with few large *P. maprouneifolia* individuals found. Furthermore, only converted trees were encountered, with no plants ≥3 m tall remaining. Canopy removal levels for *P. maprouneifolia* were not particularly high. However, this was another species with many plants coppicing after being broken down to ground level, making determining the agent of damage difficult. If elephant are the cause of this kind of damage, they could be contributing to the lack of recruitment of the species into larger height classes. Heavy browsing of tree forms of *P. maprouneifolia* in Kruger (Van Wyk & Fairall, 1969) supports this suggestion.

The three *Combretum* species were relatively highly browsed, particularly in the smaller height classes. Like *Terminalia* spp., these species showed an ability to coppice following heavy browsing. However, some uprooted plants were also encountered, as well as a number of trees that were unlikely to survive due to heavy elephant damage. High levels of elephant browsing may thus explain the relatively small numbers of these species found in the vegetation type. This is supported by high browsing and elephant-induced mortality of *Combretum* spp. around waterholes in Hwange National Park, reducing densities of these species over time (Conybeare, 1991).

After *Terminalia* spp*., Erythrophleum africanum* was the only other species in the *Terminalia* woodland where large trees were encountered with some regularity. It was also one of the few species which had low browsing across all height classes, along with *Ochna pulchra.* This aligns with other studies, which have found that both species are avoided by elephant (Conybeare 1991; Holdo, 2007; Owen-Smith & Chafota, 2012). With *Terminalia* spp. trees heavily impacted by elephant, *E. africanum* may increasingly become the only large tree species in the vegetation type, particularly closer to waterholes where browsing levels were highest. This is supported by the declining dominance of *Terminalia* spp. under elephant pressure in similar plant communities (Anderson & Walker, 1974; Conybeare, 1991; Conybeare, 2004).

The uncommon but highly browsed category in the *Terminalia* woodland shared a number of species with the teak woodland. With only single, highly damaged converted trees and no young specimens encountered for both *Brachystegia spiciformis* and *Commiphora mollis,* these two species appear to be at risk of disappearing from the *Terminalia* woodland. *Julbernardia globiflora* was also rare, although unlike the first two species, a few young individuals were encountered. *Peltophorum africanum* was only encountered in the *Terminalia* woodland*,* with all trees highly browsed. However, individuals generally showed an ability to coppice extensively. As found in the teak woodland, a lack of recruitment into larger height classes was apparent for *Pericopsis angolensis* and *Pterocarpus angolensis,* with a few small individuals but no standing trees of either species encountered.

4.3. Vegetation structure in relation to distance from waterholes

4.3.1. Teak woodland

Significant relationships between distance to waterholes and both plant density and canopy volume/ha were found in the teak woodland for the 1 - <3 m height class, suggesting elevated browsing around waterholes may have removed plants in this height class. Similar declines in shrub density around waterholes have been reported from Kruger National Park (Brits et al., 2002). However, declines in plants 1 - <3 m tall appeared to be limited to within 1 km of waterholes. The spatial extent of these reductions in canopy volume and plant density, in relation to the size of the vegetation type in the park, suggest a minimal effect on carrying capacity. Hence, significant concerns around browse availability were not raised. However, given high elephant densities in the area and the relatively recent re-opening of the waterholes, there is a possibility that discernible reductions in canopy volume and plant density in the teak woodland may extend beyond 1 km from waterholes in the future.

In contrast, no significant relationships between distance to water and basal area or canopy volume/ha were found for the ≥3 m height class. As Owen-Smith and Chafota (2012) suggest, impacts of elephant browsing in this vegetation type are most likely limited to changes in woodland composition due to selective feeding on certain plant species, rather than structural transformation of the woodland to more open shrubland or grassland. Given low elephant browsing of the dominant tree species of the woodland (*B. plurijuga),* marked structural impacts on the ≥3 m size class would not be expected. Overall, marked variation in woody cover in the teak woodland, with little to no clear effect of distance to waterholes, concurs with Chamaillé-Jammes et al.'s (2009) study of woody cover around waterholes in Hwange National Park, where remote sensing revealed much heterogeneity within piospheres and a weak effect of distance to waterholes.

4.3.2. Terminalia woodland

Unlike in the teak woodland, there was clear evidence for changes in vegetation structure with distance to waterholes in the ≥3 m height class in the *Terminalia* woodland. However, in some cases, the significance of the relationship with distance to the nearest waterhole depended on whether or not the anomalous plot at 200 m was included. Trees in this plot appeared to be larger and more mature than in other parts of the *Terminalia* woodland. Vegetation in this plot might thus be a relic of older riverine woodland, while the *Terminalia* woodland sampled in all other plots appeared to be of a younger age, mostly developing after the drying out of the Chamabondo Vlei in the 1960s (Vernon Booth, personal communication, 2020 January 24). Both with and without the outlier plot included, canopy volume/ha of plants ≥3 m high increased substantially with distance to the nearest waterhole, particularly from 1 km onwards. This suggests intense browsing has substantially reduced tree canopy volumes around waterholes, as might be expected given the high canopy removal found in the ≥3 m size class. Furthermore, given elephant browsing levels were still high 2-3 km from waterholes, canopy volumes further away from waterholes may undergo similar substantial reductions in future years, under the current waterhole regime and with high elephant densities. Similar to canopy volume, basal area/ha of standing trees (≥3 m tall and ≥6 cm basal diameter) increased substantially with distance to the nearest waterhole, particularly from 1 km onwards. This suggests that high browsing pressures closer to waterholes have reduced the number of standing trees. This finding concurs with what Conybeare (1991) found in a comparable plant community in Hwange National Park, where high elephant densities reduced tree density and tree height over time, with greater declines in tree density closer to waterholes.

A converse negative relationship was found between distance to waterholes and the ratio of converted to standing tree basal areas, again aligning with Conybeare (1991). As elephant are largely responsible for conversion of these trees to shrubs, the greater dominance of converted trees over standing ones closer to waterholes can be seen as another result of heavier elephant browsing. Converted trees exceeded the basal area of standing trees in most plots, providing a further illustration of the substantial impact that elephant have had on the structure of the *Terminalia* woodland. The generally lower combined basal area of converted and standing trees also shows that while there are many surviving converted trees, a number of trees appear to have been lost completely closer to waterholes. Furthermore, Conybeare (1991) found that converted trees were more prone to other causes of mortality apart from elephant, suggesting that additional plant losses might be expected given the dominance of converted trees over much of the *Terminalia* woodland.

Together, the low standing tree basal areas and high proportion of converted, coppicing trees suggest that conversion of woodland to shrubland has occurred, particularly closer to waterholes. This matches what has been reported elsewhere in areas with high elephant densities (Beuchner and Dawkins, 1961; Laws, 1970a; Anderson & Walker, 1974; Guy, 1989; Sianga et al., 2017; Dzinotizei, Murwira & Masocha, 2019), and more specifically, what Conybeare (1991) found in a similar vegetation type in Hwange National Park. While increased canopy volume and basal area of plants ≥3 m high indicated that more trees remained at 2-3 km from waterholes, continued heavy elephant browsing may result in conversion or removal of these too. This would signify increased homogenisation of the *Terminalia* woodland, which is already dominated by converted trees with few remaining 'true' trees.

In the 1 - <3 m height class, impacts of elephant browsing appeared to be less pronounced. Canopy volume/ha also increased with distance from waterholes in this height class, which could again be the result of higher browsing pressure closer to waterholes. However, the increase was not as pronounced as it was in the ≥3 m height class, which might be expected given the higher levels of elephant browsing found in the ≥3 m size class. Hence, elephant browsing appears to have had a greater impact on the tree layer of the *Terminalia* woodland. Unlike canopy volume/ha, plant density in the 1 - <3 m height class was not significantly related to distance from waterholes. An explanation might be that high levels of elephant browsing reduce the canopy volume of plants without necessarily killing them. If plants are not killed by elephant browsing, then density would remain unchanged.

Overall, these results indicate notable reductions in plant biomass in the *Terminalia* woodland closer to waterholes, particularly for plants ≥3 m. In some cases, coppice regrowth following the breaking down of large trees by elephant has been found to enhance browsing for smaller species. This results from the increased availability of forage at lower heights, where it is more accessible to smaller browsing species (Guy, 1981; Jachmann & Bell, 1985; Rutina, Moe & Swenson, 2005; Makhabu, Skarpe & Hytteborn, 2006; Valeix et al., 2011). However, heavy elephant browsing around waterholes does not appear to be enhancing browsing for other species in the *Terminalia* woodland of the study area. Instead, lower canopy volume closer to waterholes in both the ≥3 m and 1 - <3 m height classes suggest reduced browse availability at both upper and lower browsing levels. Indeed, it has been argued that the lowering of browse height by elephant is only beneficial to other species where elephant rebrowsing is not so intense that it depletes all new shoots (Makhabu et al., 2006; Valeix et al., 2011). Both the high canopy removal by elephant, and resultant declines in canopy volume, thus suggest heavy elephant browsing around waterholes has reduced browse availability in the *Terminalia* woodland.

Reductions in browse availability in the *Terminalia* woodland would be of particular concern for more selective feeders like greater kudu *(Tragelaphus strepsiceros)* and southern giraffe *(Giraffa giraffa)*, which may be more dependent on this vegetation type than elephant are. Kudu and giraffe in Zambezi National Park have been found to avoid teak woodland, which is attributed to the denser vegetation and lower abundance of preferred nutritious plant species (Mandinyenya et al., 2019). In contrast, elephant in the current study were found to browse a wide range of species in both the teak and *Terminalia* woodlands, albeit with a preference for browsing in the latter vegetation type. Furthermore, the similar elephant dung counts for these two vegetation types suggest elephant do not avoid the teak woodland in the same way that other herbivore species have been reported to do. Declines in the availability of browse in the *Terminalia* woodland would thus appear to be of less concern for elephant.

4.5. Elephant occupancy in relation to distance to waterholes

Elephant dung counts declined with distance to the nearest waterhole, providing evidence that elephant in the park are found in higher densities closer to waterholes. This matches the piosphere prediction of higher animal activity closer to water sources (Lange, 1969; Thrash & Derry, 1999), as would be expected especially for a water dependent species like elephant. Declining elephant dung counts with distance to waterholes are in line with the declines in elephant browsing away from waterholes found in the study. In the case of dung, a clear plateau was seen between 2 and 4 km from waterholes. This concurs with what Conybeare (1991) reported in Hwange National Park, where elephant occupancy could be very high in close proximity to water, but dropped to a more uniform level for some kilometres beyond this. The plateau in dung counts also suggests that although capable of travelling further, elephant preferred to stay within 2 km or less of waterholes, at least during the dry season when sampling was conducted. With the high number of waterholes in the area placing large areas of the woodlands in easy reach of water, it may be that elephant had little need to range beyond 2 km from waterholes to obtain adequate forage. This suggestion is supported by the analysis of elephant telemetry date by Harris et al. (2008), where elephant travelled less than a few kilometres per day when essential food and water resources occur locally.

Despite the finding of generally higher elephant browsing in the *Terminalia* woodland, elephant dung counts did not differ significantly between vegetation types, suggesting similar levels of elephant occupancy. Relatively high elephant occupancy in teak woodland despite lower browsing has been found in other studies (Anderson & Walker 1974; Ben-Shahar 1998). These authors suggested elephant may be using teak woodland for purposes other than just browsing, for example for shade and moving between water sources. As large trees have mostly been removed from the *Terminalia* woodland, shade does provide a possible explanation for the unexpectedly high dung counts in the teak woodland, which has more large trees and a generally more closed canopy.

Unlike for any of the other variables measured in the study, waterhole ID was a significant predictor of elephant dung counts, suggesting varying levels of elephant occupancy around different waterholes. However, a Tukey posthoc test did not reveal significant differences between any of the waterholes at the $p < 0.05$ level. Dung counts did appear to be generally higher at Chamabondo 3 and Kalisosa 2 waterholes. This might be explained by the greater isolation of these two waterholes compared to Chamabondo 1 and 2. Chamabondo 1 and 2 are located in the middle of the band of five waterholes in the Chamabondo Vlei, with waterholes in close proximity to the east and west. Chamabondo 3 and Kalisosa 2 are both located in the far west of the park, and are comparatively more isolated from other waterholes in the park. Hence, elephant could be said to have more waterholes to choose from in the vicinity of Chamabondo 1 and 2, potentially reducing their reliance on any one particular waterhole.

4.6. Study Limitations

The study could have benefitted from having some plots at greater distances from waterholes than the 4 km limit used. This could have revealed whether the trend of declining elephant browsing continued beyond 4 km from waterholes. Any evidence for a plateau in elephant impacts at 4 km or further from waterholes could indicate where the “natural” level of vegetation utilisation was reached, thus signifying the spatial extent of the piosphere effect around the waterholes. In any case, the proximity of the Chamabondo and Kalisosa waterholes meant that it was not possible to set plots at more than 4 km from waterholes between the Chamabondo and Kalisosa drainage lines. Hence, setting plots at over 4 km from waterholes would only have been possible in the teak woodland to the north of the Chamabondo waterholes.

The unfenced nature of the park and lack of exclusion plots precluded having control sites where elephant impacts were lacking. Control sites could have provided a point of comparison for vegetation structure in the absence of elephant, thus enriching the analysis of the impacts of elephant browsing on vegetation structure. Comparing abundances of plant species in comparable plant communities with and without elephant would also have enriched the analysis of elephant impacts at the plant species level. While it was suggested that certain uncommon, highly browsed species may have declined in abundance due to elephant, more support would have been provided for this hypothesis if highly browsed species were more common in control sites.

On a similar note, the lack of previous elephant impact studies meant it was not possible to determine the extent to which the observed impacts are the result of the recent reinvigoration of waterholes. Given the intermittent pumping history of the waterholes, one can expect that at least some of the impacts observed pre-date the most recent resumption of pumping in the area. In this regard, the application of remote sensing methods and/or analysis of aerial photography could be helpful for enhancing the temporal understanding of changes to vegetation in the study area.

5. MANAGEMENT IMPLICATIONS

The distribution of surface water in protected areas is one of the main management interventions available for modifying elephant distributions and impacts on vegetation (Owen-Smith, 1996; Gaylard et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007; Harris et al., 2008; Shannon et al., 2009). Effects on tourism should also be considered when evaluating whether to change the surface water regime in a protected area (Shannon et al., 2009). Wildlife sightings in the study area would likely diminish if all artificial waterholes were removed, especially in the dry season when natural water sources are lacking. The waterholes themselves also provide focal points for wildlife activity. They thus increase the attractiveness of the southern part of the park for tourists. Furthermore, investment has been made in facilities for game-viewing and camping at some of the waterholes. While acknowledging these tourism benefits, it must also be noted that the spacing of the waterholes in the study area is significantly closer than the minimum of 15 km suggested by Owen-Smith (1996). My study provides some evidence that this has had a significant effect on vegetation, particularly the *Terminalia* woodland. Except for a few potentially vulnerable species, the waterholes appear to be of less concern for vegetation in the teak woodland, given the more moderate browsing and lack of evidence for extensive changes to vegetation structure here. Hence, the following management recommendations largely respond to the high browsing and clear declines in plant biomass found in the *Terminalia* woodland.

With most of the *Terminalia* woodland in the study area found within 3 km of waterholes, the entirety of the woodland is placed within relatively easy reach of elephant, eroding refugia and allowing year-round browsing across this favoured vegetation type. The high elephant browsing levels, and substantial reductions in canopy volume found in this study, suggest notable reductions in browse availability have occurred in the *Terminalia* woodland around waterholes. It was argued that this could be of particular concern for browsing species which avoid the teak woodland. By facilitating moderate to high browsing across the *Terminalia* woodland, the current distribution of waterholes does not promote heterogeneous elephant browsing levels across the vegetation type, particularly in the highly impacted ≥3 m size class. This is contrary to current management thinking, in which ecosystem heterogeneity is increasingly aimed for (Gaylard et al., 2003; Chamaillé-Jammes, Valeix & Fritz, 2007). The increase in taller vegetation at 2-3 km from waterholes indicates some structural heterogeneity remains in the woodland. However, trees may decline here too, given ongoing high elephant browsing of the ≥3 m size class across the woodland. Indeed Sianga et al. (2017) found that favoured tree species occurred primarily as immature, pollarded populations up to 5 km from permanent water sources in the Okavango and Linyanti Swamps. Hence, there is a clear potential for further homogenisation of the entire vegetation type towards shrubland, with the current close spacing of waterholes placing most of the vegetation type within 3 km from permanent water.

Acknowledging the need to balance impacts on vegetation and tourism objectives (Shannon et al., 2009), continued pumping at some or all of the waterholes where viewing platforms have been built might produce the best balance of ecological and tourism concerns. It would ensure wildlife-viewing opportunities are not affected at the sites which have the best infrastructure for this. The waterholes with platforms are also quite widely spaced, which would be beneficial from an ecological perspective. Of the waterholes in the Chamabondo region, Chamabondo 3 in the far west of the park, and Timot's Pan to the east (not included in the study) have platforms. If pumping is continued at just these two waterholes (Appendix 8a), the minimum waterhole spacing suggested by Owen-Smith (1996) and Sianga et al. (2017) would just be achieved, as the straight-line distance between them is about 15 km. While the potential foraging range of elephant means *Terminalia* woodland between these two waterholes is unlikely to have an absolute refuge from dry season elephant browsing (O'Connor, Goodman & Clegg, 2007), increased travel distances should result in a reduction in dry season browsing in *Terminalia* woodland around the midpoint of these waterholes. This is supported by the declines in elephant browsing with distance to waterholes found in my study, suggesting that further reductions in browsing might be expected if distances between waterholes are increased. This might also improve the chances of retaining the higher numbers of trees currently found in the *Terminalia* woodland at around 2-3 km from the present waterholes, thus lessening further homogenisation of the *Terminalia* woodland towards a shrubland. The findings of Sianga et al. (2017) support this suggestion, as they reported an increase in mature, tall populations of favoured tree species at 10-15 km from permanent water sources.

If pumping is also continued at Kalisosa 2 (the third waterhole with a platform) (Appendix 8b), then distances between waterholes would decrease to 9-10 km, somewhat less than the suggested 15 km minimum spacing (Owen-Smith, 1996; Sianga et al., 2017). Reductions in distances to water over areas of the teak woodland between the Chamabondo and Kalisosa drainage lines would occur, potentially with negative consequences for preferred species of elephant in this vegetation type. Heavy browsing of the *Terminalia* woodland along the Kalisosa drainage line would also be expected. However, distances to waterholes across much of the highly impacted *Terminalia* woodland along the Chamabondo Vlei would be increased relative to the current surface water regime. Thus, while pumping at just Timot's and Chamabondo 3 waterholes might be preferable ecologically, maintaining Kalisosa 2 as a third pumped waterhole would still be an improvement over the current distribution of waterholes (Appendix 7).

While beyond the geographic scope of this study, the situation is complicated by surface water regimes in Matetsi Safari Area to the west, and Panda Masuie Forest Reserve to the south. As in Zambezi National Park, management appeared to favour increasing surface water availability in these areas, with addition of a number of new pumps ongoing at the time of the study (Bruce Grobler, personal communication, 2019 October 26). Exploration of satellite imagery revealed that some of these pumped waterholes are within relatively close proximity (6-8 km) of pumped waterholes in the national park. Hence, even if the spacing between waterholes is increased in Zambezi National Park, close spacing with waterholes in neighbouring areas will persist if waterhole closures in these surrounding areas do not occur. As has been argued in relation to the close spacing of waterholes in the park, this could mean continued erosion of vegetation refugia and ecosystem heterogeneity, especially in favoured vegetation types, as was found in the *Terminalia* woodland of the study area.

6. CONCLUSION

This study set out to investigate elephant impacts on woody vegetation in southern Zambezi National Park, with a particular focus on artificial waterholes. The piosphere prediction of higher elephant impacts on vegetation closer to waterholes was generally upheld, indicating that pumped waterholes do have a significant influence over elephant browsing and associated impacts on vegetation in the area. Declines in elephant browsing with distance to waterholes were evident in both the teak and *Terminalia* woodlands, although elephant browsing was consistently higher in the latter vegetation type. This was especially so for plants ≥3 m tall, which were subject to particularly high elephant browsing across the entirety of the *Terminalia* woodland. Investigation of elephant browsing across individual plant species indicated elephant impacts were not even at the species-level. This analysis showed that favoured plant species in the teak woodland could still be subject to high elephant browsing, despite the lower overall browsing levels found for the vegetation type. Some uncommon and highly browsed species in both woodland types were highlighted as potentially vulnerable to declining and even disappearing from the area.

Effects of elephant browsing on vegetation structure at different distances from waterholes were also assessed. Only minor structural impacts were found in the teak woodland. However, elevated elephant browsing around waterholes appeared to have had a substantial impact on vegetation structure in the *Terminalia* woodland, particularly on the highly browsed tree (≥3 m tall) layer. Conversion of woodland to a shrubland with few trees remaining was evident across most of this vegetation type, especially closer to waterholes. Reductions in canopy volumes also suggested declines in browse availability closer to waterholes had occurred in the *Terminalia* woodland. This raises concerns for browsing species which generally avoid the teak woodland, for example, giraffe and kudu.

Finally, elephant dung counts were conducted to give a measure of elephant occupancy in relation to distance to waterholes and vegetation type. Declines in elephant dung with distance to waterholes were found. This confirmed elephant were found in higher densities closer to waterholes, aligning well with the increased elephant browsing and greater impacts on vegetation structure found closer to waterholes. Despite the greater elephant impacts found in the *Terminalia* woodland, dung counts suggested similar elephant occupancy in the two woodland types. This finding suggests elephant used the teak woodland for purposes other than just browsing, such as for shade.

Management implications arising from the main findings of the study were discussed. Given the less severe elephant impacts on the teak woodland, these largely responded to the greater impacts found in the *Terminalia* woodland. It was argued that the close spacing of waterholes facilitated moderate to high browsing across the entire *Terminalia* woodland, most of which was located within 3 km of pumped waterholes. Recognising the touristic value of retaining some waterholes in the area, it was suggested that pumping should only continue at waterholes where viewing platforms have been built. This would potentially result in a more heterogenous elephant browsing regime across the *Terminalia* woodland. If so, chances of retaining the higher numbers of trees remaining in the *Terminalia* woodland further away from waterholes might be improved, thus lessening further homogenisation of the vegetation type towards a shrubland.

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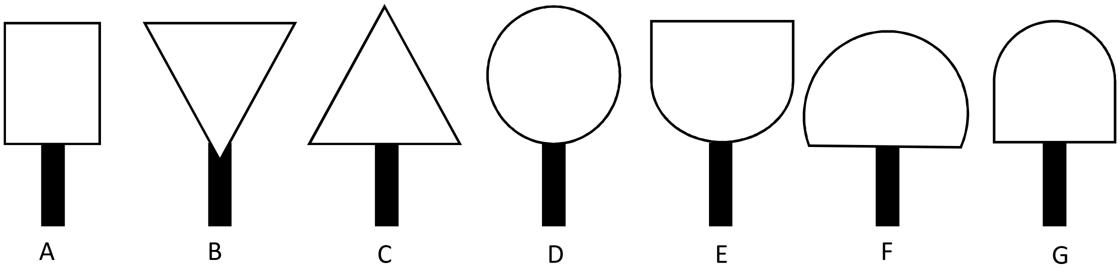
APPENDICES



Appendix 1: The seven canopy shapes plants were assigned for calculating canopy volume

Appendix 2: Equations for canopy volume calculation

For canopy shapes A to C as well as G, canopy diameter (2R) was calculated from the long (D_1) and short (D_2) canopy diameters using the equation: (D1+D2)/2.

For shapes D-F, plant height (X) was used in the calculation of R as follows:

- Shape D: $2R = (X+D_1+D_2)/3$
- Shape E and F: $2R = (2X+D_1+D_2)/3$

Canopy volumes were then obtained using the following equations, where R = 0.5*canopy diameter from previous step, X = plant height and Y = height of the lowest leaves.

- Shape A: Volume = $\pi R^2 * (X-Y)$
- Shape B: Volume = $0.333\pi R^2 * (X-Y)^3 * (X-Y)^{-2}$
- Shape C: Volume = $0.333\pi R^2 * (X-Y)$
- Shape D: Volume = $0.333\pi * 4R^3$
- Shape E: Volume = $0.333\pi * 2R^3$
- Shape F: Volume = $0.333\pi * 2R^3$
- Shape G: Volume = $\pi R^2(X-R-Y) + 0.333\pi(2R^3)$

Appendix 3: Plants identified to species level in teak woodland, arranged in order of abundance. Number of individuals across all teak woodland plots in each height class shown, as well as total number of individuals across height classes.

Species	≥3 m	1 - ≤3 m	<1 m	Total
Bauhinia petersiana	206	831	421	1458
Baphia massaiensis	101	465	570	1136
Baikiaea plurijuga	265	130	69	464
Combretum apiculatum	52	53	96	201
Terminalia spp.	38	58	34	130
Psydrax livida	-	20	99	119
Combretum collinum	6	33	71	110
Ochna pulchra	5	36	61	102
Grewia flavescens	-	37	45	82
Pavetta schumanniana	-	2	69	71
Guibortia coleosperma	10	47	8	65
Friesoldesia obovata	19	23	18	60
Pseudolachnostylis maprouneifolia	2	38	16	56
Burkea africana	1	25	21	47
Diplorhynchus condylocarpon	-	1	41	42
Combretum zeyheri	6	27	7	40
Croton gratissimus	20	12	6	38
Grewia monticola	1	24	11	36
Allophylus africanus	-	1	21	22
Erythrophleum africanum	13	6	3	22
Vangueria infausta	3	5	10	18
Julbernardia globiflora	9	7	1	17
Combretum psidioides	3	7	4	14
Commiphora mollis	-	1	12	13
Brachystegia spiciformis	5	5	2	12
Peltophorum africanum	-	6	6	12
Amblygonocarpus andongensis	5	3	2	10
Artabotrys brachypetalus	-	9	-	9
Erythroxylum zambesiacum	5	2	-	7
Schrebera trichoclada	5	2	-	7
Pericopsis angolensis	1	4	-	5
Strychnos pungens	-	-	3	3
Markhamia zanzibarica	-	1	1	2

Senegalia ataxacantha	1	1	-	2
Peltophorum africanum	-	2	-	2
Pterocarpus rotundifolius	-	-	2	2
Strychnos cocculoides	-	-	1	1
Commiphora africana	-	-	1	1
Euphorbia espinosa	-	-	1	1
Diospyros batocana	-	-	1	1
Ximenia caffra	-	1	-	1

Appendix 4: Plants identified to species level in *Terminalia* woodland, arranged in order of abundance. Number of individuals across all teak woodland plots in each height class shown, as well as total number of individuals across height classes.

Species	≥3 m	1 - ≤3 m	<1 m	Total
Terminalia spp.	180	469	95	744
Burkea africana	18	245	245	508
Vangueria infausta	-	-	118	118
Combretum collinum	7	38	37	82
Pseudolachnostylis maprouneifolia	-	53	26	79
Ochna pulchra	2	41	34	77
Bauhinia petersiana	-	33	42	75
Grewia flavescens	-	30	40	70
Amblygonocarpus andongensis	9	54	3	66
Erythrophleum africanum	26	29	10	65
Baphia massaiensis	1	26	26	53
Combretum zeyheri	7	27	2	36
Guibortia coleosperma	1	10	24	35
Combretum psidioides	2	19	13	34
Diospyros batocana	-	19	5	24
Vangeriopsis lanciflora	-	1	21	22
Combretum apiculatum	1	12	6	19
Strychnos pungens	-	-	8	8
Pericopsis angolensis	-	3	4	7
Catunaregam taylorii	-	-	7	7
Peltophorum africanum	3	-	3	6
Diplorhynchus condylocarpon	-	-	6	6

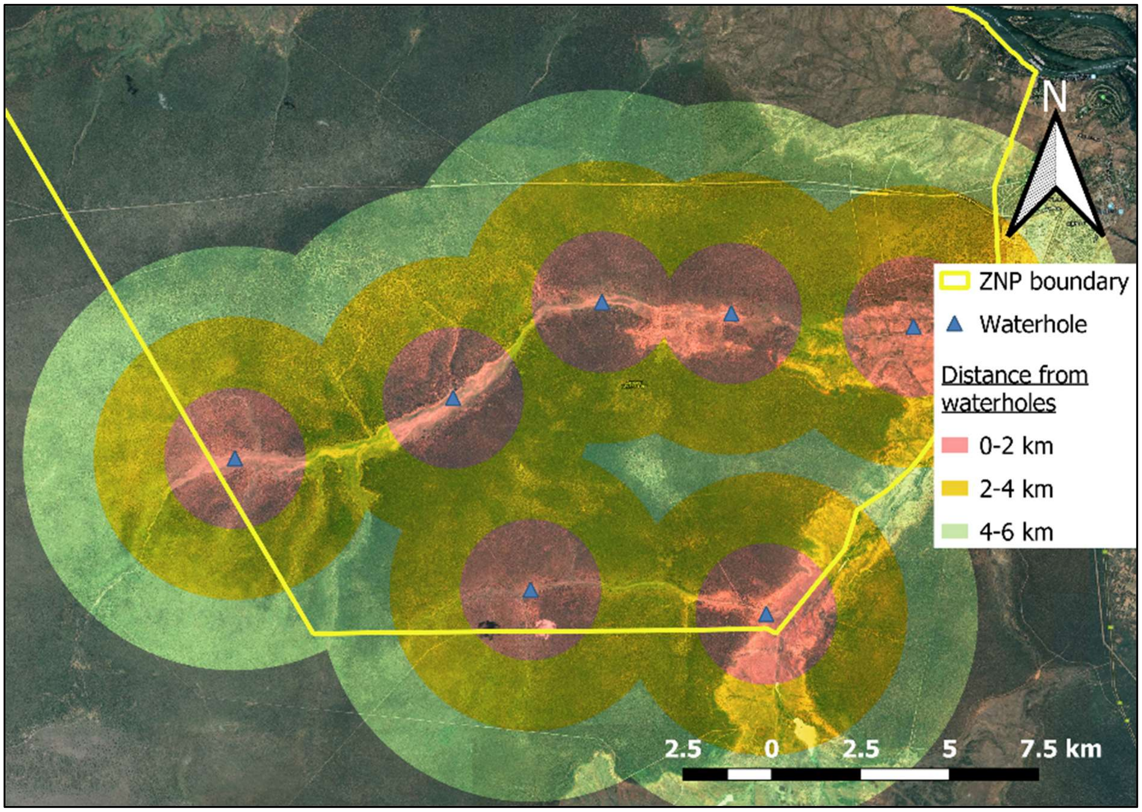
Friesoldesia obovata	-	2	2	4
Julbernardia globiflora	1	2	1	4
Grewia monticola	-	-	3	3
Baikiaea plurijuga	2	-	1	3
Pterocarpus angolensis	-	1	2	3
Dichrostachys cinerea	-	3	-	3
Diospyros mespiliformis	-	2	-	2
Allophylus africanus	-	-	2	2
Strychnos cocculoides	-	-	2	2
Paropsia brazzeana	-	-	1	1
Commiphora mollis	-	1	-	1
Erythroxylum zambesiacum	-	1	-	1
Commiphora mollis	-	-	1	1
Strychnos madagascariensis	-	-	1	1
Vitex mombassae	-	1	-	1
Securidaca longepedunculata	-	-	1	1
Pavetta schumanniana	-	-	1	1
Euclea natalensis	-	1	-	1

Appendix 5: Average % canopy removal by elephant (± standard error) across plant species in teak woodland. Only species with at least 20 sampled individuals within one or more height class are shown. Standard error estimates could not be obtained for plants ≥3 m tall due to the way canopy removal scores were calculated for this height class.

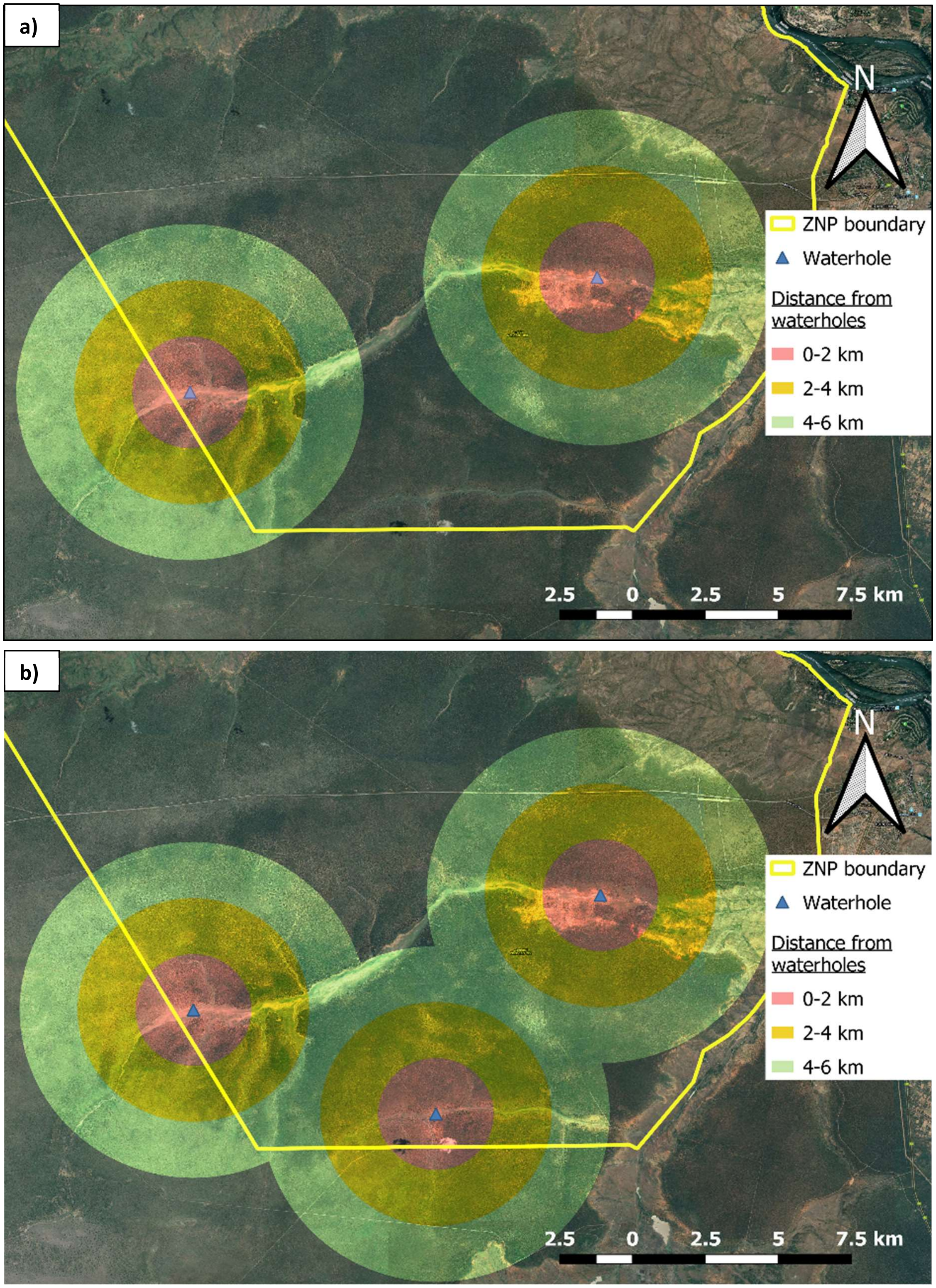
Species	**≥3 m**		**1-3 m**		**<1 m**	
	%OED	**%NED**	**%OED**	**%NED**	**%OED**	**%NED**
Baikiaea plurijuga	2.4	0.2	4.7±(1.6)	0.3±(0.3)	4.4±(2.4)	0
Baphia massaiensis	36.7	6.0	19.8±(1.2)	7.8±(0.7)	11.5±(1)	6.5±(0.7)
Bauhinia petersiana	22.3	3.0	20.0±(0.8)	4±(0.3)	9.3±(1.1)	2.8±(0.5)
Burkea africana	39.7	4.8	5.7±(2.3)	13.5±(4.5)	4.8±(4.5)	0
Combretum apiculatum	19.1	3.9	10.2±(2.6)	3.3±(1.1)	3.3±(1.5)	1.6±(0.7)
*Combretum collinum **	19.6	3.7	15.3±(4.8)	7.5±(2.6)	11.6±(3.1)	14.3±(3.2)
Combretum zeyheri	28.6	2.6	11.2±(4.2)	6.1±(3)	0	5.4±(5.4)
Croton gratissiums	7.0	2.8	18.4±(6.1)	18.3±(7.5)	3.0±(3.0)	3.9±(3)
Diplorynchus condylocarpon	-	-	-	-	14.8±(4.8)	14.5±(4.2)
Friesoldesia obovata	11.3	0.1	14.6±(3.4)	0.5±(0.3)	0	0
Grewia flavescens	-	-	28.5±(5.4)	1.1±(0.5)	18.9±(4.6)	3.4±(1.7)
Grewia monticola	16.7	6.6	39.2±(6.7)	10.9±(4.7)	46.5±(12.3)	10±(5.7)
Guibortia coleosperma	23.7	0.5	27.2±(7.1)	5.5±(2.3)	19.6±(12.4)	6.8±(4.6)
Ochna pulchra	5.5	0.0	1.3±(0.7)	0	2.2±(1.6)	0.3±(0.3)
Pavetta schumanniana	-	-	19±(19)	0	1.1±(0.6)	0.7±(0.8)
Pseudolachnostylis maprouneifolia	20.5	0.0	16.0±(5.1)	8.9±(3.7)	12.3±(7.6)	0.3±(0.3)
Psydrax livida	-	-	14.7±(2.0)	6.1±(3.2)	11.9±(2.2)	3.6±(1.2)
Terminalia spp.	47.8	6.8	11.2±(4.0)	5.4±(2.3)	8.4±(4.7)	0.9±(0.6)

Appendix 6: Average % canopy removal by elephant (± standard error) across plant species in *Terminalia* woodland. Only species with at least 20 sampled individuals within one or more height class are shown. Standard error estimates could not be obtained for plants ≥3 m tall due to the way canopy removal scores were calculated for this height class.

Species	**≥3 m**		**1 - <3 m**		**<1 m**	
	%OED	**%NED**	**%OED**	**%NED**	**%OED**	**%NED**
Amblygonocarpus andongensis	29.6	2.5	25.1±(2.3)	1.7±(0.6)	59.3±(29.9)	0
Baphia massaiensis	58.5	2.8	26.7±(4.2)	14.5±(4.2)	27.4±(6.3)	8.6±(4.3)
Bauhinia petersiana	-	-	24.6±(3.1)	12.3±(2.5)	22±(4)	6.5±(1.6)
Burkea africana	49.7	4.7	18±(1.4)	10.4±(1.1)	13±(1.5)	9.5±(1.4)
Combretum collinum	34.5	6.8	21.1±(6.2)	19.1±(4.6)	19±(4.9)	14.7±(4.1)
Combretum psidioides	29.5	13.7	20.9±(4.7)	21.5±(2.7)	38.6±(8.9)	20.5±(6.4)
Combretum zeyheri	40.2	4.8	37±(4.9)	16.1±(3.2)	40.5±(22.5)	9±(9)
Diospyros batocana	10.8	0.0	17.9±(3.8)	16.7±(3.2)	46.8±(15.7)	20.9±(11.1)
Erythrophleum africanum	8.1	0.2	15.1±(4.7)	4.9±(3.6)	9.5±(9.5)	9.5±(9.5)
Grewia flavescens	-	-	39.4±(4.7)	5.9±(2)	28.7±(5.9)	16.7±(4.5)
Guibortia coleosperma	1.4	0.0	38.4±(10.3)	3.2±(2)	26.5±(7.3)	12.6±(4.3)
Ochna pulchra	17.3	1.0	10.8±(3.5)	4.5±(2)	3.5±(2.8)	3.1±(2.1)
Pseudolachnostylis maprouneifolia	47.4	0.0	20.6±(4.3)	12.2±(3.1)	19.2±(6.6)	12.7±(5.9)
Terminalia spp.	58.5	7.9	16.5±(1.2)	19.9±(1.2)	13.9±(3)	11.6±(2.7)
Vanguaria spp.	-	-	-	-	0.2±(0.2)	0.2±(0.2)
Vangeriopsis lanciflora	-	-	0	0	10.4±(5)	0



Appendix 7: Satellite image of the southern portion of Zambezi National Park, indicating the distribution of pumped waterholes at the time of the study. Buffer circles indicate the proximity of surrounding vegetation to waterholes.



Appendix 8: Satellite image of proposed waterhole distributions if pumping is continued at only Chamabondo 3 and Timot's waterholes (a), or at Chamabondo 3, Timot's and Kalisosa 2 waterholes (b). Buffer circles indicate the proximity of surrounding vegetation to waterholes.