



The composition and complexity of the woody and succulent components of Albany thicket with and without elephants



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ABSTRACT

African elephants (*Loxodonta africana*) are capable of visibly altering the structure of vegetation through their browsing habits, and such alteration of habitat may be magnified when the broader movements of elephants are restricted by fences. I assessed the structure and composition of the woody and succulent components of Albany thicket vegetation at 10 fenced sites in the Eastern Cape Province, South Africa – five with elephants present, paired with five where elephants were absent. Contrary to expectations, woody and succulent thicket vegetation was structurally similar across the 10 sites, despite the vegetation at the non-elephant sites being slightly taller, denser and more complex than the sites with elephants. Woody plant community composition was also similar across the 10 sites and elephant-induced damage to woody and succulent plants was generally low. Combined, these findings support the idea that at least the woody component of thicket vegetation is generally resilient to the browsing effects of indigenous browsers such as elephants. However, it is also possible that Albany thicket vegetation at the five elephant sites may not have been exposed to elephants for long enough for elephant browsing effects to manifest. Thus, I recommend continued monitoring of elephant browsing in fenced reserves within the Thicket Biome to establish how overall vegetation structure and composition may change over time, and with increases in elephant densities.

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1. Introduction

The pattern of land use in the Eastern Cape Province of South Africa has and continues to change rapidly from agriculture and livestock farming to wildlife ranching and eco-tourism (Langholz and Kerley, 2006). This change in land use has undoubtedly promoted the conservation of some plant and animal species in the region (Sims-Castley et al., 2004; Langholz and Kerley, 2006; Sigwela et al., 2006). However, in many instances, even relatively small areas (from 10 km²) have been fenced and elephants (*Loxodonta africana*) have been re-introduced in order to attract tourists. Thus, although wildlife ranches and eco-tourism destinations may contribute towards the conservation of the biodiversity of the region by releasing the land from the degradation pressure of domestic herbivores in the short-term (Aucamp and Tainton, 1984; Sigwela et al., 2006), the long-term effects of re-introducing elephants to these enclosed areas have not been quantified.

Albany thicket vegetation, which forms a major part of the Thicket Biome, is restricted to the Eastern Cape Province (Lubke et al., 1986; Mucina and Rutherford, 2006). Albany thicket is a transitional vegetation type between subtropical forest, Afromontane forest, fynbos,

Karoo and grassland vegetation (Kerley et al., 1995). In general, thicket vegetation is low (2–3 m), dense, spinescent, succulent, evergreen and not fire-prone (Lubke et al., 1986; Hoffman, 1989; Moolman and Cowling, 1994). The Thicket Biome is also a major centre of endemism for several succulent and geophytic plant species (Moolman and Cowling, 1994) and contains a high number of threatened plant species (Lubke et al., 1986). Significantly, published studies have demonstrated that elephants are capable of visibly altering the structure of vegetation through their browsing across their range (e.g. Ben-Shahar, 1993; Moolman and Cowling, 1994; Cumming et al., 1997; Kerley and Landman, 2006). In the Thicket Biome, elephants can reduce the available biomass and cover of woody species and decrease the abundance of some plant species (Cowling and Kerley, 2002). This is particularly relevant when it is considered that herbivory is one of the most important factors influencing the distribution of the Thicket Biome (Kerley et al., 1999; Vlok and Euston-Brown, 2002). However, thicket vegetation, in general, appears to be relatively resilient to the browsing effects of indigenous browsers (Sigwela et al., 2009). This resilience is believed to be due to thicket vegetation co-evolving with megaherbivores such as elephants and black rhinoceroses (*Diceros bicornis*) (Kerley et al., 1999).

Elephants are notoriously messy foragers (O'Conner et al., 2007) and can therefore promote coppicing when breaking the branches of woody

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species in the thicket (Kerley et al., 1995). In addition, as large, hind-gut fermenters, elephants also promote seed dispersal in the Thicket Biome (Kerley et al., 1995). Thus, elephant foraging, even at high densities, may in fact increase woody plant densities in thicket (Stuart-Hill and Danckwerts, 1988; Stuart-Hill and Aucamp, 1993; Kerley et al., 1995). However, several important woody species in the Thicket Biome require closed canopies for their recruitment, presumably to protect them from herbivory (Sigwela et al., 2009). Closed canopy/untransformed thicket also has significantly higher litter levels than transformed thicket which also likely promotes seedling growth (Lechmere-Oertel et al., 2008). Given that elephants are important browsers and patch creation agents in the Thicket Biome (Stuart-Hill and Danckwerts, 1988; Stuart-Hill and Aucamp, 1993; Kerley et al., 1995), and that they would have historically been migratory in the Eastern Cape Province (Kerley et al., 1995), enclosed reserves may experience persistent and sustained elephant browsing pressure, ultimately resulting in decreased woody biomass (Kerley et al., 1995).

In this study, I compare the structure (height, density and basal cover), complexity (vertical biomass) and community composition (species richness and diversity) of the woody and succulent components of Albany thicket vegetation at fenced sites with and without elephants in the Eastern Cape Province, South Africa. I also assess the extent of elephant browsing (loss in biomass or mortality) at the same sites.

2. Materials and methods

2.1. Study sites and experimental design

The study was conducted at five sites with elephants, where elephants had been present for a minimum of one year prior to the study (range: 1–13 years) and were at similar densities (between 0.1–0.5 elephants/km²) in the Eastern Cape Province, South Africa (Table 1). I considered the absence of elephants on game reserves or commercial farmland adjacent to sites with elephants as regional controls for the study. Consequently, five paired sites without elephants, located adjacent to each elephant site, were also used (Table 1). The five non-elephant sites were selected based on their proximity (<2 km) to each elephant site so as to mirror all other conditions (i.e. vegetation, rainfall, geology, aspect, past land-use and the presence/absence of other ungulates) as closely as possible and to account for the range of inherent spatial and temporal variability across non-elephant sites (Fig. 1; Table 1). The elephant sites were: Amakhala Game Reserve (hereon referred to as Amakhala; 33°31'S, 26°06'E); Kariega Game Reserve (Kariega; 33°35'S, 26°37'E); Kwandwe Private Game Reserve (Kwandwe; 33°09'S, 26°37'E); Pumba Private Game Reserve (Pumba; 33°25'S, 26°21'E); and Shamwari Private Game Reserve (Shamwari;

33°20'S, 26°01'E) (Fig. 1). In four cases, the paired non-elephant site was an adjacent game reserve but without elephants. In the remaining case, this was not possible, and the non-elephant site was an adjacent livestock farm (Table 1). The climate for the region is classified as semi-arid but with rainfall in all seasons (Stone et al., 1998). Mean annual rainfall is approximately 680 mm with bimodal peaks in spring and autumn at all sites (Stone et al., 1998). The dominant vegetation type across all sites was Albany thicket (Mucina and Rutherford, 2006). According to Vlok et al. (2003), Albany thicket can be further categorised into 112 more specific thicket vegetation units. Eight of these individual thicket types were sampled across the study sites (Table 1).

A stratified sampling design, with thicket vegetation as the stratum, was used in the study (Cohen and Holliday, 2001). This approach has been employed in numerous studies that have assessed the impacts of elephants in Africa (Hatton and Smart, 1984; Cumming et al., 1997; Musgrave and Compton, 1997; Fenton et al., 1998; Botes et al., 2006; Guldemond and Van Aarde, 2007; Bonnington et al., 2007). Accordingly, the data were analysed at a regional scale. It is recognised that the local distribution and abundance of plant species (the main stratum in the analysis) at each site is likely strongly influenced by bottom-up factors such as rainfall and soil. Indeed, the fact that eight individual thicket types were sampled during the study supports this contention. However, these effects were likely ameliorated by utilising non-elephant sites in proximity to the elephant sites (Fig. 1).

2.2. Vegetation sampling

The field sampling of thicket vegetation took place between October and December 2006. Three sampling stations were sampled at each elephant ($n = 5$) and paired non-elephant site ($n = 5$). Sampling stations at each site were selected by using digitised vegetation maps of each area and ensuring that they were all located in apparently homogeneous (~4 Ha) patches of Albany thicket (Mucina and Rutherford, 2006) and far enough apart (all at least >500 m) to ensure independence of the data.

A sampling effort of three sampling stations per site was considered adequate given the practical difficulties of sampling within this vegetation type and a preliminary sampling efficiency assessment at each site (see Parker, 2008). At each sampling station, the vegetation was characterised using the point-centred-quarter (PCQ) method (Cottam and Curtis, 1956) with modifications as suggested by Dahdouh-Guebas and Koedam (2006). A transect of 28 points (separated by 10 m intervals) was conducted in a predetermined cardinal direction. All transects were completed on North facing slopes of similar gradient at each site. The GPS positions of the starting points for each transect were also recorded using a handheld GPS.

Table 1
The details of the sites used in the current study, including the density of elephants present (/km²) at the with-elephant sites (= elephant density), the current land-use of each of the sites (= land-use), the length of time (in years) that each site had been under its present land use (= years) (this value also corresponds to the duration that elephants had been present at the with-elephant sites at the time of the study), the historical land-use of each site (= past), and whether other indigenous browsers were present (= herbivores). The specific thicket vegetation unit present at each site, according to Vlok et al. (2003), is also shown. Conservation = An enclosed reserve used for conservation; Farm = Commercial farmland.

Location	Treatment	Elephant density	Land-use	Years	Past	Herbivores	Thicket type
Amakhala	With	0.2	Conservation	2	Livestock	Yes	Paterson Savana Thicket; Salem Karroid Thicket; Alicedale Fynbos Thicket
	Without	–	Farm	–	–	Yes ^a	Albany Valley Thicket; Albany Spekboomveld Thicket
Kariega	With	0.5	Conservation	1	Livestock and crops	Yes	Albany Thicket; Albany Spekboomveld Thicket
	Without	–	Conservation	15	Livestock and crops	Yes	Albany Thicket; Albany Spekboomveld Thicket
Kwandwe	With	0.2	Conservation	4	Livestock	Yes	Fish Noorsveld; Fish Spekboomveld
	Without	–	Conservation	32	Livestock	Yes ^b	Fish Noorsveld; Fish Spekboomveld
Pumba	With	0.2	Conservation	1	Livestock and crops	Yes	Albany Spekboomveld Thicket
	Without	–	Conservation	7	Livestock and crops	Yes	Albany Spekboomveld Thicket
Shamwari	With	0.3	Conservation	13	Livestock	Yes	Paterson Savana Thicket; Salem Karroid Thicket; Alicedale Fynbos Thicket
	Without	–	Conservation	10	Livestock	Yes	Paterson Savana Thicket; Salem Karroid Thicket; Alicedale Fynbos Thicket

^a Other indigenous browsers were present but in lower numbers at this site and included: Greater kudu (*Tragelaphus strepsiceros*), Common duiker (*Sylvicapra grimmia*), Cape grysbok (*Raphicerus melanotis*) and bushbuck (*Tragelaphus scriptus*);

^b This was the only non-elephant site that had black rhinoceroses (*Diceros bicornis*) present.

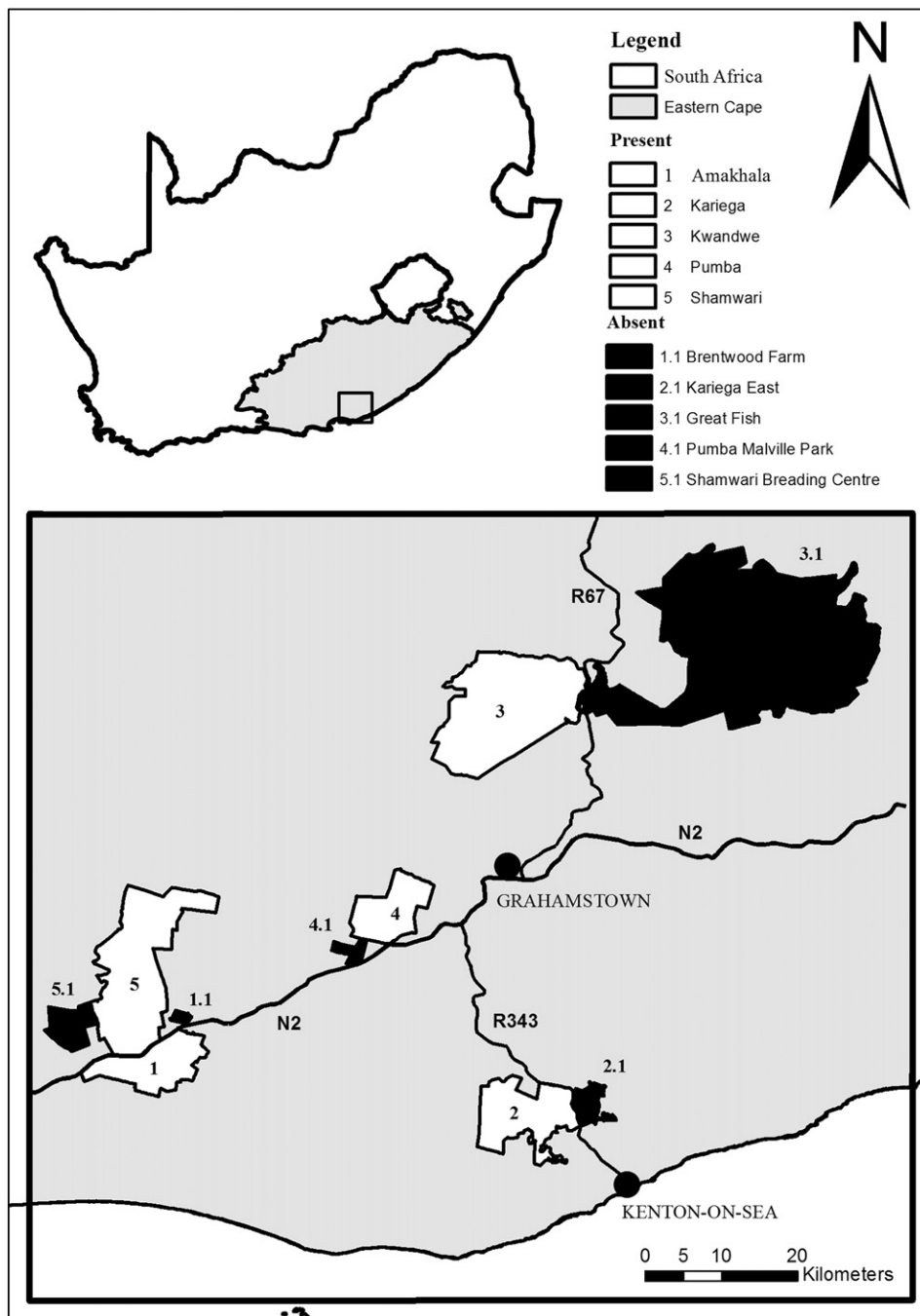


Fig. 1. A map of South Africa, highlighting the Eastern Cape Province (grey) and the study sites used for the current study (enlarged inset). All sites with elephants present are numbered in white (whole numbers) and all paired sites with elephants absent are numbered in black (corresponding decimal numbers). Full details of the study sites can be found in the text.

At each individual point, a cross was laid down, to represent four quarters and the nearest individual plant (>1.3 m in height) in each quarter identified (Guy, 1976; Jachmann and Bell, 1985; Dahdouh-Guebas and Koedam, 2006). The 1.3 m height threshold was chosen as it is similar to the preferred foraging height of elephants (Guy, 1976; Jachmann and Bell, 1985; O'Conner et al., 2007) and because it improves the accuracy of the basal area estimates calculated by the modified PCQ method (Dahdouh-Guebas and Koedam, 2006). Plants >10 m from the sampling point were excluded from the analysis to ensure that no one plant was considered more than once (Dahdouh-Guebas and Koedam, 2006). The distance (m) from the sampling point to the centre of the plant was measured using a tape measure; the height (m) measured using a calibrated pole, and the stem girth (cm) at 1.3 m above ground level, measured using a tape measure. For multi-stemmed plants, the

stem girth of the central stem(s) was recorded instead of the nearest stem (Dahdouh-Guebas and Koedam, 2006). In addition, a damage rating (0–7 scale) and the type of damage (elephant or other) for each plant were recorded (Anderson and Walker, 1974; Walker, 1976; Conybeare, 1991). Damage was defined as a loss of vegetative biomass or as mortality (Anderson and Walker, 1974; Conybeare, 1991). The categories of damage were: 0 = no damage; 1 = 1–10% loss; 2 = 11–25% loss; 3 = 26–50% loss; 4 = 51–75% loss; 5 = 76–90% loss; 6 = 91–99% loss; 7 = 100% loss or dead individual (Walker, 1976; Conybeare, 1991). In order to arrive at a particular rank, a series of value judgements were made for each plant sampled i.e. is it more or less than half? Is it less than a quarter?. Damage was classed as either being due to elephants or some other factor. Elephant damage was relatively easy to identify, and included uprooted trees, evidence of

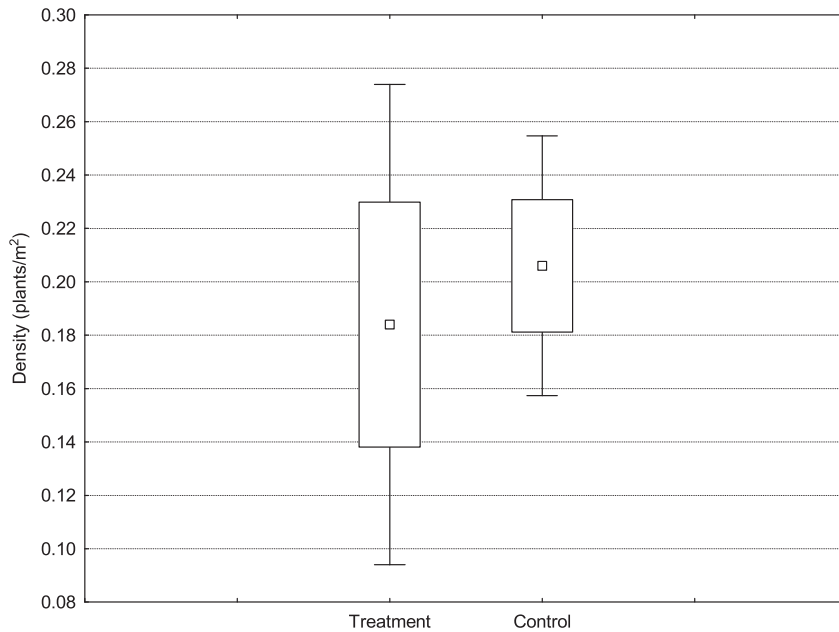


Fig. 2. The density (plants/m²) of thicket vegetation at elephant (treatment) and non-elephant (control) sites. Data are means, boxes are means \pm SE and whiskers are means \pm 1.96*SE.

bark stripping and characteristically browsed branches. Other damage included any visible signs of browsing by other ungulates, frost damage, insect damage or disease (Anderson and Walker, 1974; Conybeare, 1991). From these data, the stem density (trees/m²), basal area (m²/0.1 Ha) and average height (m) were calculated for each site using published spreadsheets (Dahdouh-Guebas and Koedam, 2006). In addition, an importance value for each species was calculated (Dahdouh-Guebas and Koedam, 2006). The importance value was calculated for each species at each site by adding the density (trees/m²), dominance (basal area per species/total basal area, expressed as a percentage) and frequency (number of trees of a species/total number of trees, expressed as a percentage) estimates for each species (see Dahdouh-Guebas and Koedam, 2006).

An assessment of vegetation complexity was also made using a modified checkerboard method (MacArthur and MacArthur, 1961). Vegetation complexity was assessed at 1.5 m above the ground and 25 m along each transect. The method involved recording the proportion (%) of the checkerboard (90 cm \times 60 cm and consisting of 10 cm \times 10 cm red and white blocks) obscured by vegetation 10 m away from the central point. Open vegetation had a lower percentage of the checkerboard obscured, while more complex vegetation had a higher percentage of the checkerboard obscured. The procedure was conducted four times, once in each cardinal direction, at each sampling station. The mean complexity (%) for treatment and control sites was calculated using these data.

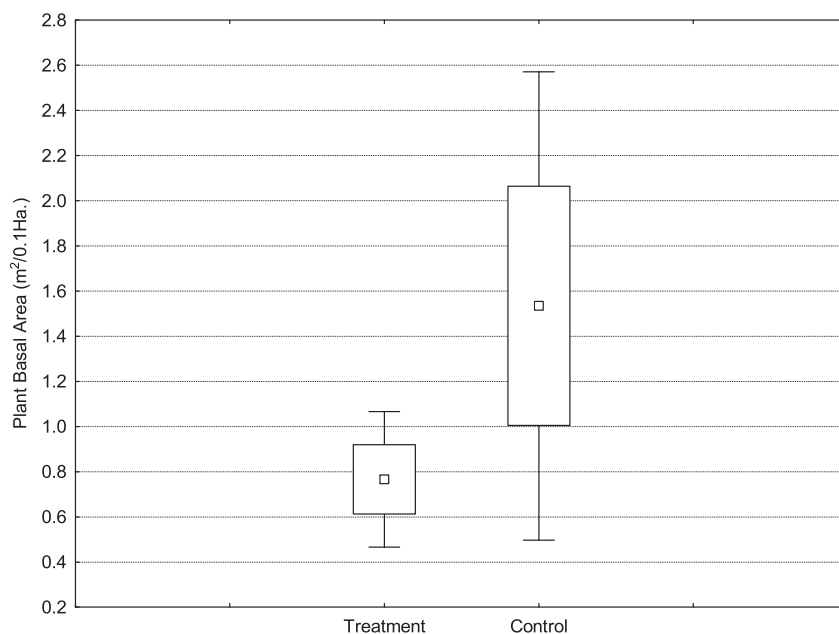


Fig. 3. The basal area covered by thicket plants (m²/0.1 Ha.) at elephant (treatment) and non-elephant (control) sites. Data are means, boxes are means \pm SE and whiskers are means \pm 1.96*SE.

2.3. Data analysis

The shared species, unique species, Morista-Horn index, overall species richness and diversity (Shannon Wiener H') statistics were all calculated using EstimateS (Colwell, 2005). Differences between the mean height, plant density, basal area, complexity and percentage damage at elephant and non-elephant sites were all tested using paired t-tests (Statistica, Statsoft, version 7.0). Significant variation in the species richness, diversity and relative abundance (importance values) of plant species, and percentage damage attributed to elephants compared to other species were tested in the same way. Chi-Square tests

were used to test for differences in the overall species composition of plants at elephant and non-elephant sites (Cohen and Holliday, 2001). The non-elephant site values were used as the expected values.

3. Results

Although non-elephant sites had slightly higher woody and succulent plant densities compared to the sites with elephants (Fig. 2), there was no significant difference between the two (Fig. 2; $P = 0.43$, $t_{14} = -0.82$). The basal area occupied by woody and succulent plants followed a similar trend, with plants at non-elephant sites covering a

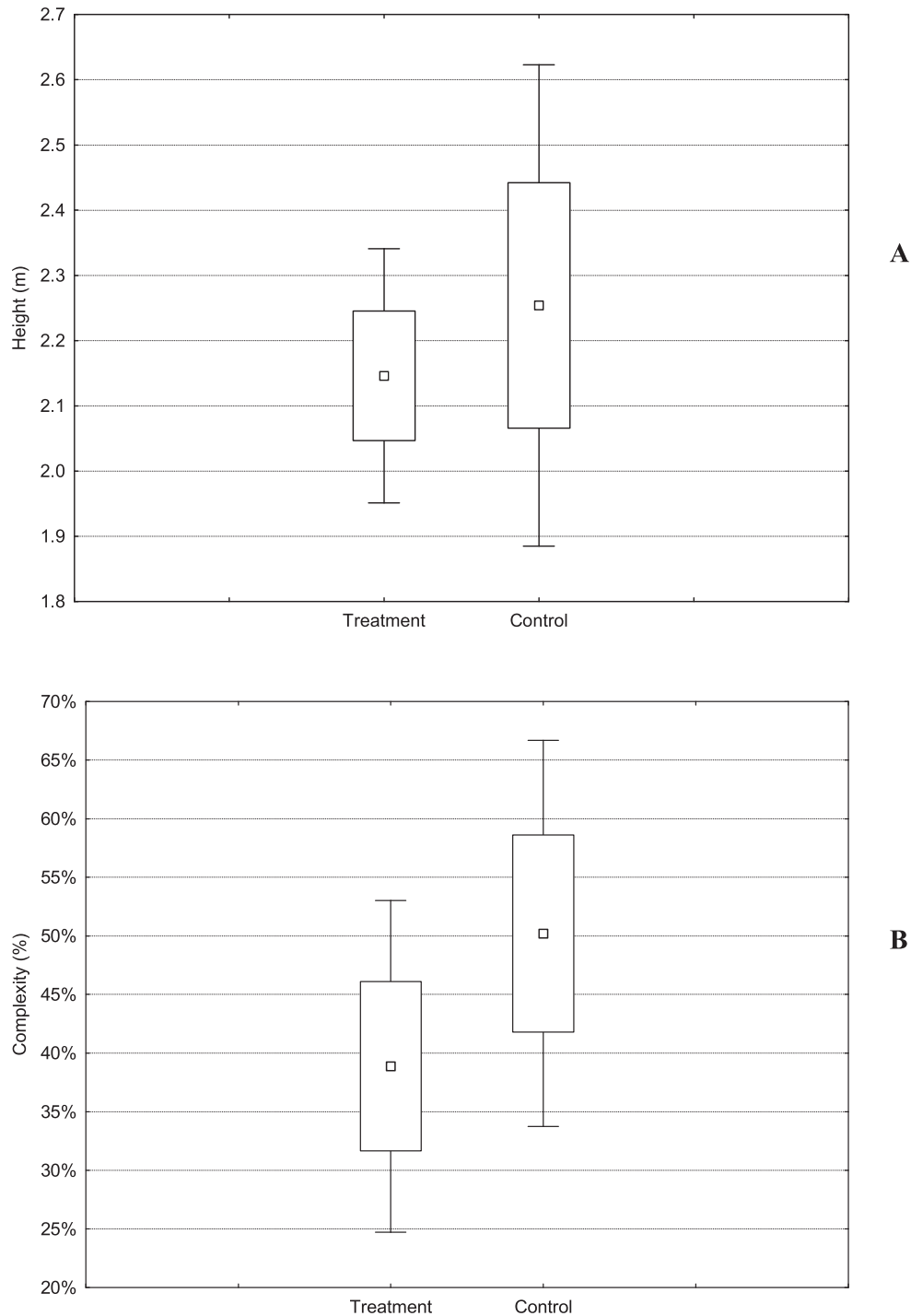


Fig. 4. The height (A) and complexity (B) of thicket vegetation at elephant (treatment) and non-elephant (control) sites. Data are means, boxes are means \pm SE and whiskers are means \pm 1.96*SE.

Table 2

The mean importance values for thicket plant species at the elephant (Ele) and non-elephant (Non-E) sites. SD = standard deviations.

Family	Species	Ele	SD	Non-E	SD
Fabaceae	<i>Acacia karroo</i> Hayne	6.73	15.37	4.70	9.90
Asphodelaceae	<i>Aloe africana</i> Mill.	10.19	32.32	1.45	3.42
Asphodelaceae	<i>Aloe bainesii</i> Dyer	–	–	0.51	1.99
Asphodelaceae	<i>Aloe ferox</i> Mill.	15.12	33.81	19.62	32.81
Salvadoraceae	<i>Azima tetraacantha</i> Lam.	8.45	10.08	16.49	13.07
Asteraceae	<i>Brachylaena huillensis</i> Hiern	2.37	6.35	–	–
Asteraceae	<i>Brachylaena ilicifolia</i> Lam.	1.31	2.45	8.87	16.21
Buddlejaceae	<i>Buddleja saligna</i> Willd.	5.20	14.43	1.51	5.86
Rubiaceae	<i>Canthium inerme</i> Kuntze	0.70	2.81	–	–
Capparaceae	<i>Capparis sepiaria</i> Wall.	6.03	9.99	4.65	5.56
Apocynaceae	<i>Carissa bispinosa</i> Desf.	2.28	4.49	1.81	3.65
Rubiaceae	<i>Coddia rudis</i> Verdc.	2.16	4.74	0.47	1.28
Crassulaceae	<i>Crassula ovata</i> Druce	7.25	19.42	–	–
Crassulaceae	<i>Crassula</i> sp.	0.62	1.07	–	–
Araliaceae	<i>Cussonia spicata</i> Thunb.	1.65	3.55	1.93	5.21
Ebenaceae	<i>Diospyros lycioides</i> Desf.	2.17	4.94	1.45	3.03
Ebenaceae	<i>Diospyros</i> sp.	0.15	0.59	–	–
Boraginaceae	<i>Ehretia rigida</i> Druce	6.31	6.65	5.54	9.10
Ebenaceae	<i>Euclea natalensis</i> A.DC.	0.29	1.14	–	–
Ebenaceae	<i>Euclea undulata</i> Thunb.	41.85	29.92	32.64	23.46
Euphorbiaceae	<i>Euphorbia bothae</i> Lottsy & Goddijn	0.16	0.62	–	–
Euphorbiaceae	<i>Euphorbia tetragona</i> Haw	–	–	0.57	2.19
Euphorbiaceae	<i>Euphorbia triangularis</i> Desf.	2.53	6.67	10.23	32.08
Euphorbiaceae	<i>Flueggea verrucosa</i> Thunb.	4.07	9.59	0.45	0.94
Tiliaceae	<i>Grewia occidentalis</i> L.	1.55	2.43	1.61	4.01
Tiliaceae	<i>Grewia robusta</i> Burch.	2.63	5.06	9.85	14.99
Celastraceae	<i>Gymnosporia buxifolia</i> Szyszyl.	1.43	2.37	3.15	5.76
Celastraceae	<i>Gymnosporia capitata</i> Marais	5.60	8.80	6.56	13.11
Celastraceae	<i>Gymnosporia polyacantha</i> Szyszyl.	6.54	10.90	11.97	18.23
Sapindaceae	<i>Hippobromus alata</i> Eckl. & Zeyh.	0.15	0.59	0.21	0.80
Solanaceae	<i>Lycium</i> sp.	0.53	1.12	1.45	2.27
Celastraceae	<i>Mystroxydon aethiopicum</i> Thunb.	11.81	16.87	3.46	4.04
Loganiaceae	<i>Nuxia congesta</i> R.Br.	–	–	0.14	0.54
Oleaceae	<i>Olea africana</i> Mill.	1.21	2.30	0.78	2.02
Cactaceae	<i>Opuntia ficus-indica</i> Mill.	7.99	19.43	10.69	16.55
Anacardiaceae	<i>Ozoroa mucronata</i> R.Fern. & A.Fern.	2.51	4.81	1.20	2.30
Sapindaceae	<i>Pappea capensis</i> Eckl. & Zeyh.	12.33	19.83	10.13	15.80
Plumbaginaceae	<i>Plumbago auriculata</i> Lam.	2.49	3.79	1.31	3.25
Polygalaceae	<i>Polygala myrtifolia</i> L.	0.77	2.97	–	–
Portulacaceae	<i>Portulacaria afra</i> Jacq.	49.45	56.55	47.51	53.94
Ptaeroxylaceae	<i>Ptaeroxylon obliquum</i> Radlk.	4.02	13.69	0.88	2.38
Celastraceae	<i>Putterlickia pyracantha</i> Endl.	3.98	6.79	0.75	2.04
Rhizophoraceae	<i>Rhigozum obovatum</i> Burch.	5.73	12.96	7.53	18.37
Fabaceae	<i>Schotia afra</i> Thunb.	16.55	16.10	34.51	27.25
Fabaceae	<i>Schotia latifolia</i> Jacq.	2.65	7.08	0.27	1.06
Flacourtiaceae	<i>Scolopia zeyheri</i> Warb.	1.57	3.37	0.65	1.49
Rhamnaceae	<i>Scutia myrtina</i> Merr.	6.48	10.45	10.99	16.81
Anacardiaceae	<i>Searsia crenata</i> Rydb.	6.61	9.32	5.81	7.80
Anacardiaceae	<i>Searsia longispina</i> Eckl. & Zeyh.	7.50	11.53	2.75	3.16
Anacardiaceae	<i>Searsia pallens</i> Eckl. & Zeyh.	3.19	6.49	3.65	8.12
Anacardiaceae	<i>Searsia</i> sp.	0.55	1.15	–	–
Asteraceae	<i>Senecio linifolius</i> Goldblatt & J.C. Manning	0.51	1.99	0.00	0.00
Sapotaceae	<i>Sideroxylon inerme</i> Krauss ex A.DC.	3.21	7.66	6.32	10.58
Rutaceae	<i>Zanthoxylum capense</i> Harv.	0.68	2.63	0.13	0.52

Grewia robusta, *Gymnosporia polyacantha*, and *Schotia afra*, were all substantially more important at non-elephant sites than at the sites with elephants (Table 2).

Damage (or percentage biomass removal) to woody and succulent plants was low and not significantly different at elephant and non-elephant sites (Fig. 6A; $P = 0.55$, $t_4 = 0.65$). In addition, damage caused exclusively by elephants to woody and succulent species was lower at elephant sites than the damage caused by other herbivores and natural causes (Fig. 6B; $P = 0.47$, $t_4 = 0.79$).

4. Discussion

While not significant, woody and succulent vegetation at elephant sites was somewhat less dense, covered a slightly smaller basal area, and was generally shorter and less complex compared to non-

elephant sites. In terms of habitat structure and complexity, examples of dramatic alteration to woody plant populations, reportedly caused by elephants, abound in the scientific literature (Van Wyk and Fairall, 1969; Croze, 1974; Penzhorn et al., 1974; Guy, 1981; Barnes, 1985; Stuart-Hill, 1992; Lock, 1993; Barnes et al., 1994; Cumming et al., 1997; Trollope et al., 1998; Skarpe et al., 2004). In addition, these examples are widespread and cover broad spatial and temporal scales on the African continent. However, very few of these studies have incorporated adequate spatial and temporal controls (Penzhorn et al., 1974; Stuart-Hill, 1992; Cumming et al., 1997; Trollope et al., 1998; Skarpe et al., 2004). All of these authors reported substantially (sometimes significantly) lower tree cover, density or biomass along with an associated increase in shrub cover, at sites with elephants compared to those where elephants were absent. Importantly, those studies conducted within the nearby Addo Elephant National Park of South Africa found that elephant exposed plots had 45% less woody biomass than control plots (Penzhorn et al., 1974), and that canopy cover was significantly lower in the presence of elephants (Stuart-Hill, 1992). In addition, overall woody plant density was higher where elephants were absent compared to plots sampled within the national park (Stuart-Hill, 1992). The results from the Addo Elephant National Park are more dramatic than those from the present study and it is likely that this reflects the longer exposure (>50 years) to elephants at a high density, and the provision of artificial water points, which concentrate the effects of elephants (Penzhorn et al., 1974; Stuart-Hill, 1992; Ben-Shahar, 1993).

At the woody and succulent plant community level, my results show that the species composition of elephant and non-elephant sites was similar. However, the importance values of some woody and succulent plants were significantly different between the sites, with some species being more important at elephant sites than non-elephant sites and vice versa. Guldmond and Van Aarde (2007) reported analogous results when assessing the impact of elephants on plant communities in Maputaland, South Africa. Although there were statistically significant differences between habitats inside and outside of areas with elephants, some plant species were either abundant or rare in the park (with elephants present) compared with sites outside and vice versa (Guldmond and Van Aarde, 2007). In addition, Richardson-Kageler (2004) assessed changes to plant communities that had been exposed to herbivores (including elephants) for 10 years using fence-line contrasts in Zimbabwe, and demonstrated that the total species richness and the number of species with different functional attributes (e.g. seed dispersal mechanisms) were similar across seven fence-line contrasts. However, Smart et al. (1985) demonstrated that the long-term (14 years) exclusion of elephants and other large herbivores in Uganda enhanced the species diversity of woodlands. Moreover, Moolman and Cowling (1994) assessing the influence of elephants on endemic thicket plants in the Addo Elephant National Park showed that the total number of endemic thicket species was consistently lower within the park compared to a botanical reserve that had excluded elephants and all other large herbivores for a period of approximately 38 years.

It has been suggested that plant species compositional patterns (losses or gains) are not as sensitive to disturbance (such as browsing) as are the relative abundances of the same species in the short (<10 years) term (Richardson-Kageler, 2004). The findings of Smart et al. (1985) and Moolman and Cowling (1994) support this suggestion. However, in both of these publications elephant-induced changes were compared to a “total” control where all large herbivores were excluded (Smart et al., 1985; Moolman and Cowling, 1994), which represents an unnatural situation in terms of the evolution of plant diversity (Cowling and Kerley, 2002). Thus, a more elaborate exclusion/inclusion study, similar to those employed by Goheen et al. (2007) in Kenya, is required in the Thicket Biome to disentangle the role of elephants in structuring the functional components (richness and diversity) of the woody and succulent plant community.

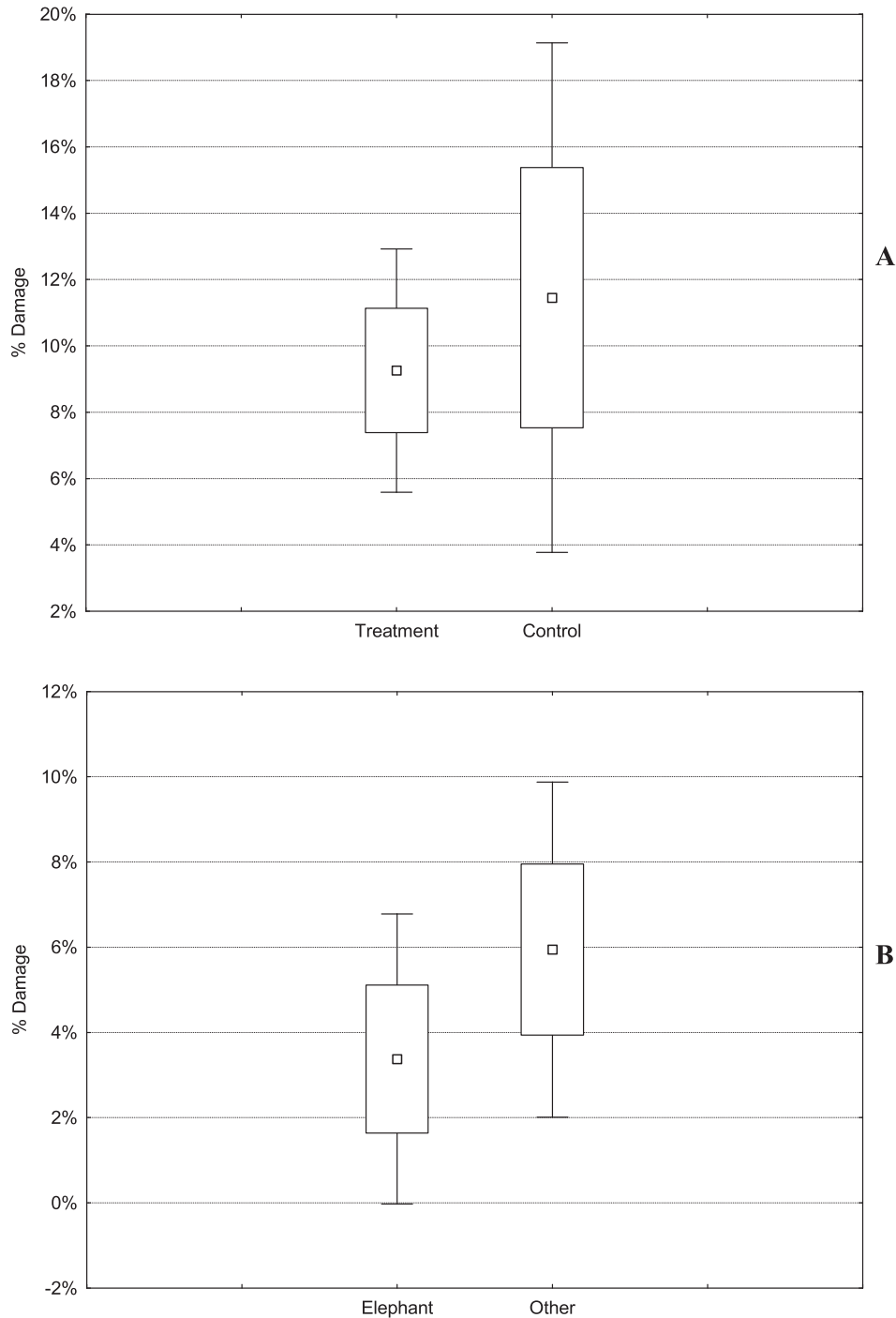


Fig. 6. The overall percentage damage (biomass removed) to thicket vegetation at elephant (treatment) and non-elephant (control sites) (A) and the percentage damage caused by elephants and other factors for elephant sites only (B). Data are means, boxes are means \pm SE and whiskers are means \pm 1.96*SE.

Aloes (*Aloe africana* and *A. ferox* in particular) are important indicator species within thicket vegetation (Parker and Bernard, 2009). Interestingly, *A. africana* was more prevalent at the elephant sites than the non-elephant sites, but *A. ferox* showed no difference. Such a result could suggest that there may be localised differences in the habitats across the sites (e.g. at the individual thicket unit level based on Vlok et al.'s (2003) classification) which is driving woody and succulent plant distribution in thicket, rather than elephant browsing. Alternatively, the slightly more open or patchy habitat created by elephants at elephant sites may promote the recruitment of *A. africana*, whereas it is shaded out in the more dense vegetation at the non-elephant sites

(see Kerley et al., 1995). *Aloe ferox* does not show the same trend as it is likely able to grow above the somewhat denser thicket at non-elephant sites (see Parker and Bernard, 2008, 2009). By contrast, *Euphorbia triangularis* and *Grewia robusta* were more important at non-elephant sites than elephant sites and this may suggest that elephant browsing has reduced their abundance at the elephant sites. *Euphorbia triangularis* tends to be associated with tall, dense, and generally "closed" thicket (Mucina and Rutherford, 2006) which is the kind of thicket that develops if elephants are absent (this study; Kerley et al., 1995). Sigwela et al. (2009) also demonstrated that *G. robusta* was more prevalent in intact compared to degraded thicket vegetation.

Thus, while some woody and succulent plant species in thicket potentially benefit from elephant browsing (e.g. *A. africana*), others (e.g. *E. triangularis* and *G. robusta*) do not and require closed canopies for their recruitment (Sigwela et al., 2009).

When interpreting the effects of elephant browsing, it is also important to recognise the effects of historical overgrazing (past land-use) in the region as a whole as it will have had a profound influence on the vegetation prior to the re-introduction of elephants. The majority of the large, indigenous herbivores (including elephants) which co-evolved with thicket were all but extirpated from the Eastern Cape when the first European pastoralists arrived in the early 19th century and they were replaced with domestic stock (Kerley et al., 1999). Significantly, thicket vegetation is extremely sensitive to utilisation by domestic stock (Stuart-Hill and Aucamp, 1993; Lechmere-Oertel et al., 2008; Sigwela et al., 2009). Consequently, a significant proportion of the thicket vegetation in the province had been permanently transformed under pastoralism before the re-introduction of elephants (Stuart-Hill, 1992; Kerley et al., 1999), making the spontaneous regeneration of woody canopy trees near impossible (Sigwela et al., 2009). While the overall change in land-use from pastoralism to conservation may have released the land from the degradation pressure of domestic herbivores (Aucamp and Tainton, 1984; Sigwela et al., 2006), it is plausible that historical browsing pressure transformed modern thicket into a highly resilient vegetation type with only the hardiest species remaining. Thus, it is not necessarily surprising that elephants did not have a significant impact on the taller woody and succulent components of thicket in my study. In fact, such a trend may persist with elephants present, but other growth forms which were not part of this study (e.g. geophytes) could very well show more dramatic (negative) effects of elephant browsing over time (sensu Moolman and Cowling, 1994).

I have shown that at relatively low (<0.5 elephants/km²) elephant densities and after a short period of re-exposure (<13 years) to elephant browsing, there is little evidence of significant damage to woody and succulent vegetation in the Albany thicket. In addition, there was no significant difference in the woody and succulent plant communities at elephant and non-elephant sites, even though the sites with elephants had slightly higher species richness, diversity and more unique species than the sites without. These findings suggest that at current densities, elephants either 1) do not disrupt the compositional make-up of woody and succulent plants (Guldemond and Van Aarde, 2007), 2) that woody and succulent plants in thicket are resilient to elephant browsing (Stuart-Hill, 1992; Guldemond and Van Aarde, 2007; Sigwela et al., 2009) or 3) that the elephant sites have not been exposed to elephants for long enough for their browsing effects to manifest. My results for elephant damage to the woody and succulent plants corroborate the latter. Biomass removal attributed exclusively to elephants was lower than damage caused by any other factor at all sites with elephants. However, my results also reinforce the notion that thicket vegetation appears to be resilient to the browsing effects of indigenous megaherbivores such as elephants (Sigwela et al., 2009). While it is tempting to interpret my findings as being an example of an overall positive effect of elephants on woody and succulent plants within enclosed reserves, this should be resisted. The short occupation time and relatively low densities of elephants at the study sites during my study precludes such a conclusion. Thus, I recommend the continued monitoring of this aspect of elephant ecology to establish if the trends observed here continue over an extended time-period, and with increases in elephant densities on the full range of thicket growth forms.

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