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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.

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 km^2) 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/km^2) 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 homogenous (~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 (/km^2) 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.