Chapter 3

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The effect of elephant-modified tree canopies on sub-canopy savanna plant communities

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Abstract

Mechanisms that sustain grass-tree coexistence in savannas rely to a large extend on the longevity of mature trees. Browsing by elephants may increase tree mortality and could alter the coexistence of grasses and trees. Elephants may therefore have consequences for savanna diversity. We assessed the changes in diversity and evenness indices for grasses, woody seedlings and saplings in response to elephant-induced canopy changes. In closed woodland, elephants generated gaps in the canopy layer that favoured grass establishment and allowed woody saplings to grow into the canopy layer. Browsing by elephants and other herbivores reduced the occurrence of woody saplings but not that of seedlings. In the open woodland reduced canopy cover did not affect the presence of seedlings, but did reduced grass and woody sapling occurrence. Elephants increase the structural heterogeneity of closed woodlands, but their activities do homogenise open woodlands. This may contribute to the transformation of woodlands into grasslands.

Key Words: diversity, grasses, heterogeneity, saplings, seedlings, Tembe Elephant Park.

Introduction

Savannas are characterised by the coexistence of grasses and trees (Belsky 1990, Scholes & Archer 1997). Mechanisms sustaining this coexistence include the storage effect (Higgins *et al*. 2000), disturbance dynamics (van Langevelde *et al*. 2003) and localised heterogeneities (Jeltsch *et al*. 1998). The long-term existence of trees is vital for both the spatial (Jeltsch *et al*. 1998) and temporal (Higgins *et al*. 2000) models explaining this coexistence. Under certain conditions African elephants *Loxodonta africana* Blumenbach, can significantly increase the mortality rate of mature trees and potentially influence the coexistence of trees and grasses (Western & Maitumo 2004, Skarpe *et al*. 2004). Identifying the effect elephants may have for their environment is important for conservation management (Whyte *et al*. 2003) since disturbances such as fire, drought, trampling and herbivory can add to the impact of elephants on savannas (Ben-Shahar 1996, 1998, Dublin *et al*. 1990, Trollope *et al*. 1998).

Across African savannas, intact tree canopies provide microhabitats for shade tolerant plant species (Belsky & Canham 1994; Caylor *et al*. 2005). Shading by canopies reduces direct solar radiation and soil temperatures, and increase soil nutrients (Belsky *et al*. 1993; Ludwig *et al*. 2004) and water retention (Davis *et al*. 1998; but see Ludwig *et al*. 2004). Elephants may change these canopies by breaking branches and uprooting trees (e.g. Barnes 1982, Jachmann & Croes 1991, Lewis 1986). These changes may influence the species composition of the sub-canopy vegetation (Huntley 1991, Belsky & Canham 1994).

We examine how elephant-induced changes in the canopies of trees influence sub-canopy vegetation. Elephants are not the only agents that may influence some of the response variables. Other browsers and fire, may also affect plant species in the Park, but elephants dominate the browsing guild. We therefore often refer to the “park effect". We do however limit our study to tree species preferred by elephants and the associated community variables of grasses, woody seedlings and saplings. The study is based on the premise that intact tree canopies create microhabitats suitable for the establishment of shade tolerant grass and woody species. We hypothesised that the values will be smaller for community indices of grass, woody seedling and sapling assemblages associated with broken tree canopies than those associated with intact tree canopies.

Methods

Study area

The study area in northern KwaZulu-Natal, South Africa, includes the 300 km^2 Tembe Elephant Park (27°01'S 32°24'E) and some 200 km^2 of adjacent communal land (27°00'S 32°18'E) where few people live. Here the climate is sub-tropical with hot summers and cool to warm winters (Schulze 1982). From 1959 to 2002, the study area received a mean (±SD) annual precipitation of 748 ± 388 mm, as measured at the Park's head office. The landscape consists of undulating sand ridges with the highest point at 129m and the lowest at 50m a.s.l. (Matthews *et al*. 2001). Soil type and structure are similar both outside and inside the Park and are developed from relatively homogeneous, grey, siliceous, aeolian sands (Soil Classification Working Group 1991).

Recent elephant population estimates for the Park yield a crude density of 0.5 – 0.8 individuals per km^2 and a yearly rate of increase of 4.6 ± 0.06% (Morley 2005). The fencing of the Park, following its proclamation in 1983, excluded elephants from the adjacent communal land for 19 years before our study. The study site in the communal land experienced little resource extraction and no subsistence agriculture.

We focussed our study on the mixed woodlands. Broadleaved trees such as *Terminalia sericea* Burch. Ex DC, *Euclea natalensis* A.D.C., *Strychnos spinosa* Lam., *S. madagascariensis* Poir, *Combretum molle* R.Br. ex G.Don and *Afzelia quanzensis* Welw. are prevalent in these mixed woodlands. Based on tree and shrub density we divided the mixed woodlands into closed (mean ± SE distance between trees higher than 4m = 13 ± 0.2 m) and open woodland types (21 ± 0.4 m). The closed woodland consists of dense stands of shrubs and undergrowth with a closed and layered canopy. A grass layer and sparsely spaced mature trees dominate the open woodland. Fire is prevalent both inside and outside the Park. Park management opts for scheduled burning at the end of the dry season while fires outside the Park may occur year round. The sampling sites selected for the present study did not burn before or during the study but the fire history of the sampling sites is unknown.

Experimental design

We followed a stratified random sampling design (Krebs 1999). We distinguished between a trial area inside the Park where elephants live and a control area within the communal land where no elephants occur and where few people live. Strata were based on the two woodland types. Sampling was conducted from January to May 2002 at 19 sites, with nine sites in the closed woodland (five sites inside and four sites outside the Park) and ten sites in the open woodland (five sites both inside and outside the Park). We selected sites based on a classified satellite image for the Park and its immediate surroundings (Harris, van Aarde & Pimm, unpublished data, using a cloud free partial scene ID 167-79 of 30 August 1999). Our visit to sites outside the Park confirmed no human and/ or signs of livestock present at the selected sites.

A single line transect was randomly placed at each site, the length of which varied between two to five kilometres depending on the distance between the sampled trees. We generated random numbers (between 10 and 20) with a spreadsheet, to select the fifteen mature trees (tree samples) with a maximum canopy height > 4 meters along each transect. Selected trees were chosen from amongst the group of 15 species that were high in elephant dietary preference within Maputaland (de Boer *et al*. 2000, Klingelhoefer 1987; Appendix 3.1). Each tree was visually assessed and assigned to one of five classes depending on percentage canopy removed by elephants (1 = < 10%, 2 = 10–24%, 3 = 25–74%, 4 = 75–99%, and 5 = canopy entirely removed). Four sub-samples (using a one m^{-2} sample grid) were located at a distance of two meters from the main stem(s) of the sampled tree in the four orthogonal compass directions. Live standing woody elements within each of these were identified, separated into seedling (< 0.5 m) and sapling (0.5–2 m) classes and counted. Grasses were identified and cover-abundance values (adapted from Werger 1974) assigned as; 1 = single individual, 2 = present with < 1% cover, 3 = numerous and cover 1–5%, 4 = very numerous and cover 1–5%, 5 = cover 5–12%, 6 = cover 13–25%, 7 = cover 26–50%, 8 = cover 51–75%, 9 = cover 75–99%, 10 = single species dominance. Another four sub-sample quadrats were placed at a distance of 20 m from the sampled tree stems, perpendicular to the line transect and the sampling of grasses, woody seedlings and saplings were repeated at these locations. These served as local controls to each tree sample and represent woodland specific characteristics (shaped by ecological events other than elephants alone i.e. different fire regimes, the presence or absence of herbivory, etc.) both inside and outside the Park.

Data analysis

Elephant impact on the canopies of pre-selected trees was determined using a one-tailed G-test (Sokal & Rohlf 1995) that tested for differences in the frequency distribution of trees in canopy removal classes inside and outside the Park. Abundance values for grasses, woody seedlings and saplings were totalled separately over the four sub-samples for each tree and the associated local control. We calculated Margalef's (d) index for species richness, the reciprocal of Simpson's (λ) for diversity and the Pielou's evenness (J') as an evenness index, using PRIMER-E statistical software (Clarke & Warwick 2001). We 4th-root transformed indices values (Clarke & Warwick 2001). We used a 2 X 2 factorial analysis of variance (Sokal & Rohlf 1995) to test for significant differences between inside/ outside the Park and tree samples/ local controls for each woodland type.

Results

There were significantly more trees within the higher reduced canopy classes inside than outside the Park (closed woodland: $G = 114.4$, $df = 4$, $P < 0.0001$; open woodland: $G = 122.8$, $df = 4$, $P < 0.0001$; Fig. 3.1). This was especially the case in the open woodlands where more tree canopies were damaged than in the closed woodlands. In open woodlands almost 50% of the sampled trees had more than half of their canopies removed. Less than 10% of the trees sampled within the closed woodlands lost most of their canopies (Fig. 3.1).

Within closed woodlands, we found no significant interaction between factors (the Park and tree canopies) for indices of the sub-canopy plant assemblages (Table 3.1, Fig. 3.2). For some indices the canopy and Park effects differed. For instance, underneath tree canopies, all indices for grass assemblages were significantly lower than those for the local controls. However, for sapling and seedling assemblages these indices were higher (apart from seedling evenness) than those for the local controls. Inside the Park, indices for grasses were higher than outside the Park, while those for saplings were lower inside the Park than outside. For seedlings, there were no significant differences in the indices inside and outside the Park (Table 3.1, Fig. 3.2).

The situation within the open woodlands differed from those in the closed woodlands. For instance, for the grass and sapling indices we recorded a significant interaction between factors (the Park and tree canopies). This was not the case for the seedlings indices (Table 3.1, Fig. 3.2). Grass species richness and evenness were lower, but diversity higher underneath tree canopies than local controls. All seedling and sapling (except for sapling diversity) indices underneath tree canopies were significantly higher than local controls. Inside the Park, all grass indices were higher, but sapling indices were lower than outside the Park.

Discussion

We aimed to identify the influence of elephants for vegetation in an African savanna. To achieve this we searched for changes in sub-canopy vegetation with changes in canopy shapes induced by elephants. We distinguished between open and closed woodlands as differences in their structures and tree densities may influence the response of sub-canopy vegetation to disturbances. At our study site, like elsewhere, elephants changed tree canopies (Barnes 1982, Jachmann & Croes 1991, Lewis 1986), thereby affecting the microhabitat (Belsky *et al.* 1993, Belsky & Canham 1994). We compared sub-canopy community variables of areas exposed to elephants (inside the Tembe Elephant Park) with those of areas protected from elephants (local communal lands adjoining the Park). We recognised that browsers and grazers other than

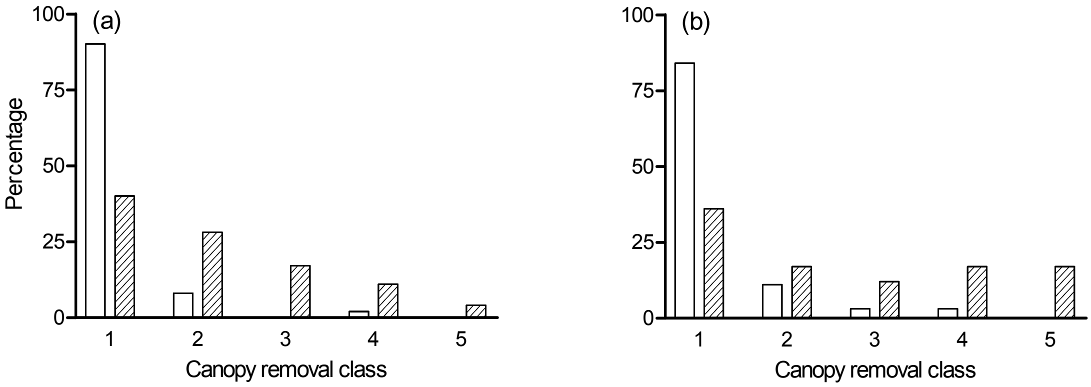

Figure 3.1. Frequency distributions of percentage of sampled trees within each canopy removal class for (a) the closed and (b) open woodland outside (clear bars) and inside (diagonal lines) the Tembe Elephant Park.

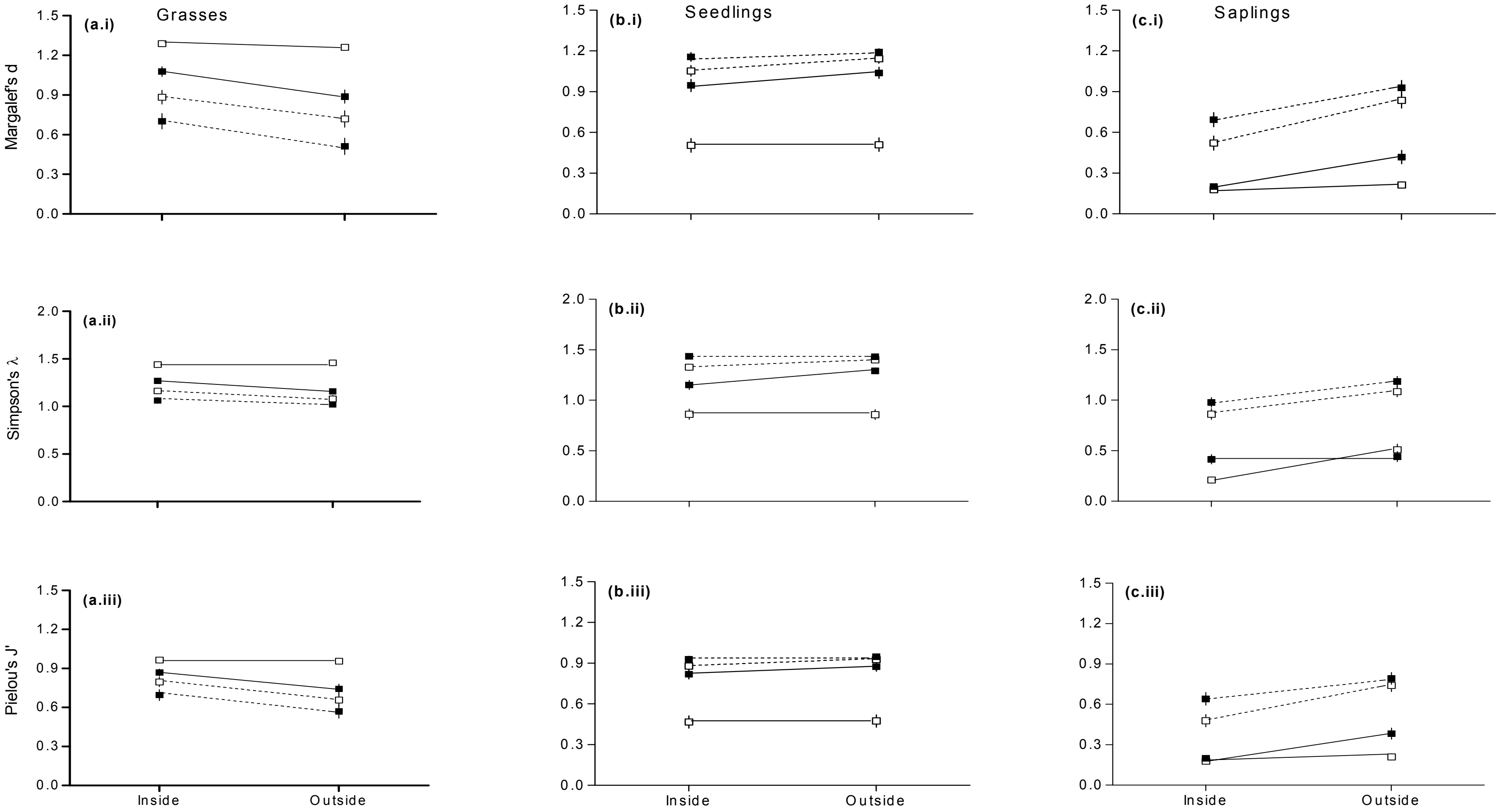

Figure 3.2. Mean (±SE) species richness (i), diversity (ii) and evenness (iii) for grasses (a), woody seedlings (b) and saplings (c) within the closed (dotted lines) and open woodlands (solid lines) inside and outside the Tembe Elephant Park. The solid squares represent tree samples and the open squares the local controls.

Table 3.1. F–values using a 2X2 factorial ANOVA for grass, woody seedling and sapling indices within the closed (n = 135) and open woodlands (n = 150). Canopy represents the difference between the sampled tree and the associated local control, Park denote differences between inside and outside the Park and Canopy*Park reflect on the interaction between the two factors. Arrows indicate direction of change from the sampled tree to the associated control, and inside to outside the Park. (P < 0.05*, P < 0.01**, P < 0.001***, NS non-significant).

		Closed woodland			Open woodland		
		Richness	Diversity	Evenness	Richness	Diversity	Evenness
Grass	Canopy	↓ 10.88**	↓ 7.92**	↓ 4.51*	↓ 75.03***	↑ 142.56***	↓ 43.53***
	Park	↑ 9.06*	↑ 4.90*	↑ 8.87**	↑ 10.45**	↑ 5.26*	↑ 8.31**
	Canopy*Park	NS	NS	NS	5.73*	10.72**	6.14*
Seedlings	Canopy	↑ 5.12*	↑ 6.90**	NS	↑ 106.02***	↑ 65.43***	↑ 89.19***
	Park	NS	NS	NS	NS	NS	NS
	Canopy*Park	NS	NS	NS	NS	NS	NS
Saplings	Canopy	↑ 5.76*	↑ 4.27*	↑ 5.17*	↑ 17.32***	NS	↑ 16.76***
	Park	↓ 25.16***	↓ 17.03***	↓ 19.73***	↓ 21.23***	↓ 13.34***	↓ 20.76***
	Canopy*Park	NS	NS	NS	11.06***	9.44*	10.14**

elephants living inside the Park may influence the responses we recorded. These responses thus may be considered as a "park effect" rather than an "elephant effect".

Nearly 60% of the trees in closed and open woodlands inside the Park had altered canopies, whereas the canopies of most trees (80%) on communal lands were intact. The altered canopies outside the Park may be ascribed to natural tree mortality, or remnants of elephant browsing before the Park were fenced. Independent of canopy shape and woodland type indices for grasses were lower at trees than at controls. The opposite was true for seedlings and saplings. In open woodlands, trees within intact canopies were associated with more seedlings and saplings than control sites. Here the perennial grass species *Panicum maximum* Jacq. dominated while controlled sites supported a variety of pioneer grass species (Ludwig *et al*. 2004).

Grass and woody sub-canopy species in closed woodlands did not respond to the small changes (<10% totally removed) in tree canopies. As elsewhere, (e.g. Favier *et al*. 2004) gaps that developed in response to elephant feeding in closed woodlands may favour grass growth (Norton-Griffiths 1979). This could result from variability and increase in sunlight (Naumburg & de Wald 1999; Ludwig *et al*. 2004).

The relatively low community indices for saplings inside the Tembe elephant Park may not only be ascribed to elephants, but also to browsing by species such as kudu *Tragelaphus strepsiceros* Pallas, nyala *Tragelaphus angasii* Gray, impala *Aepyceros melampus* Lichtenstein, red duiker *Cephalophus natalensis* A. Smith and suni *Neotragus moschatus* von Dueben). The decrease in the sapling evenness may be result from selective browsing that reduces dominant species (exploiter-mediated coexistence; Begon, Harper & Townsend 1996). Furthermore, elephants may have facilitated (*sensu* Connell & Slatyer 1977; van de Koppel & Prins 1998) the growth of saplings by reducing the inhibitory effect of shading by canopies. This may also hold for open woodlands.

In the open woodlands of Tembe, elephants reduced tree canopies. This and frequent hot fires may have reduced the grasses and woody saplings. Fire is unselective (Bond *et al*. 2005) and may reduced dominant grasses, thus explaining inducing increased species richness and evenness (see Pimm 1991). This and changes in tree canopies may have generated similar recruitment and establishment conditions for grasses at both our treatment and control sites. Grasses accordingly increased in diversity and evenness. Browsing and fire may keep woody elements within the flame zone, and stop saplings from further development. This situation may be similar to the fire-mediated recruitment bottleneck referred to by Higgins *et al.* (2000).

In our study area seedlings, on the other hand, were not influenced by canopy changes. This differs from other studies (e.g. Barnes 2001; Jachmann & Croes 1991) where elephants destroy seedlings. Canopies may provide microhabitat conditions for the establishment of seedlings (e.g. through establishing fertility patches; Anderson *et al*. 2001), but changes in the canopy clearly have little consequence for seedlings once they have been established (see Caylor *et al*. 2005).

To summarise, our study suggests that elephants enhance the structural heterogeneity of closed woodlands but homogenise that of woodlands. This is supported by the significant interactive term between the overall “park effect” and reduced canopy structures for grass and saplings indices in the open woodland (see Table 3.1). Inside the Park, there is a higher similarity in the respective grass and saplings indices between tree samples (with their canopies modified by elephants) and their local controls.

The coexistence of trees and grass in African savannas rely on the long-term survival of trees (e.g. Higgins *et al.* 2000, Jeltsch *et al.* 1998, van Langevelde *et al*. 2003). Elephants can remove trees or change their canopies and therefore affect tree/ grass ratios. With this and the interactive effects of herbivory and fire (Dublin *et al*. 1990) may result in a gradual shift from a mosaic of closed and open woodland types to an open grassland state.

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Appendix 3.1

Tree species (listed alphabetically) selected for this study are based on those most preferred by elephants in the Maputaland region (extracted from de Boer *et al.* 2000 and Klingelhoefer 1987). Species names follow Arnold & de Wet (1993).

Species name	Common name
Acacia burkei Benth.	Black Monkey Thorn
Acacia karroo Hayne	Sweet Thorn
Afzelia quanzensis Welw.	Pod Mahogany
Albizia adianthifolia (Schumach.) W.F.Wight	Flat-crown
Albizia versicolor Welw. ex Oliv.	Large-leaved False-thorn
Combretum molle R. Br. ex G. Don	Velvet Bushwillow
Dialium schlechteri Harms	Sherbet Tree
Garcinia livingstonei T.Anders	African Mangosteen
Manilkara discolor (Sond.) J.H. Hemsl.	Forest Milkberry
Sapium integerrimum (Hochst.) J. Leonard	Duikerberry
Sclerocarya birrea (A.Rich.) Hochst.	Marula
Spirostachys africana Sond.	Tamboti
Strychnos madagascariensis Poir.	Black Monkey Orange
Terminalia sericea Burch. ex DC.	Silver Cluster-leaf
Trichilia emetica Vahl.	Natal Mahogany