

---

# The impact of elephants on plants and their community variables in South Africa's Maputaland

Robert Guldemond and Rudi van Aarde\*

*Conservation Ecology Research Unit, Department of Zoology & Entomology, University of Pretoria, Hatfield 0082, South Africa*

## Abstract

Elephants confined to protected areas could affect co-occurring species. We expected measurable deviations in the density, species number, turnover and composition, abundance-incidence and rank-abundance patterns of woody plant communities where elephants browse. We examined these variables in the presence (inside South Africa's Tembe Elephant Park) and absence (uninhabited communal land adjacent to the park) of elephants for sand forests, closed and open woodlands. Woodland type influenced the apparent effect of elephants on tree densities and number of species. In sand forests, the presence of elephants was not associated with lowered tree densities but this did not hold for mixed woodlands. The rates of species turnover in the park were consistently higher than on communal land for all three woodland types. Species composition also differed significantly between these areas, as did the number of favoured food trees of elephants. Elephants had a clear influence on vegetation at the species level. However, at the community level they had no apparent effect on woodland-specific abundance-incidences and rank-abundance relationships. Elephants were confined to Tembe for only some 20 years before this study and still occur at relatively low densities. This may explain why we could not detect an impact on the bivariate relationships.

*Key words:* abundance, composition, density, incidence, rank, turnover

## Résumé

Les éléphants confinés dans des aires protégées pourraient avoir un impact sur les autres espèces qui s'y trouvent. Nous nous attendions à des déviations mesurables de la densité, du nombre, du turnover et de la composition des

espèces, et aussi des patterns d'abondance et de la classification par ordre d'abondance des communautés de plantes ligneuses là où les éléphants se nourrissent. Nous avons examiné les valeurs de ces variables en présence (dans le *Tembe Elephant Parc* en Afrique du Sud) et en l'absence d'éléphants (dans le terrain communal inhabité voisin du parc) pour des forêts sableuses et des forêts ouvertes et fermées. Le type forestier influençait l'effet apparent des éléphants sur la densité des arbres et le nombre d'espèces. Dans les forêts sableuses, la présence des éléphants n'était pas associée à une densité plus faible des arbres, mais il n'en était pas de même dans les forêts mixtes. Le rythme du turnover des espèces dans le parc était constamment plus élevé que dans le terrain communal pour les trois types de forêt. La composition des espèces différait aussi significativement entre ces zones, ainsi que le nombre d'arbres appréciés par les éléphants. Les éléphants avaient une nette influence sur la végétation au niveau des espèces. Cependant, au niveau de la communauté végétale, ils n'avaient pas d'effet apparent sur l'incidence de l'abondance spécifique du milieu forestier et sur les relations rang/abondance. Les éléphants étaient confinés à Tembe depuis seulement 20 ans au moment de cette étude, et leur densité était encore relativement faible. Ceci pourrait expliquer pourquoi nous n'avons pas pu déceler d'impact sur les relations bivariées.

---

## Introduction

Ecological assemblages often include many rare species and a few that are dominant (Sugihara, 1980; Tokeshi, 1993; Gaston, 1994; Lennon *et al.*, 2004). Several models have been developed to predict and describe this pattern (e.g. Magurran & Henderson, 2003; Ulrich & Ollik, 2004). Assemblages across different scales (Guo, Brown & Valone, 2000) and disturbance regimes (Gaston & Warren, 1997) also show positive abundance-incidence

---

\*Correspondence: Tel.: (+27) 12 420 2753; Fax: (+27) 12 420 4523; E-mail: rjvaarde@zoology.up.ac.za

relationships (Hanski, 1982; Brown, 1984; Gotelli & Simberloff, 1987; Collins & Glenn, 1990; Maurer, 1990; Hanski & Gyllenberg, 1993; also see Gaston & Lawton, 1990; Gaston, 1996). This could be explained by meta-population dynamics (Hanski & Gyllenberg, 1993; Van Rensburg *et al.*, 2000), resource partitioning (Brown, 1984; Guo *et al.*, 2000), the resource availability hypothesis (see Hanski, Kouki & Halkka, 1993; Gaston, 1994) and neutral models (Hubbell, 2001; Volkov *et al.*, 2003; also see McGill, 2003; Gilbert & Lechowicz, 2004; Magurran, 2005).

The generality of rank-abundance and abundance-incidence patterns imply that such relationships are resilient to disturbances. For woody plants, this may be interpreted as resilience to browsing at the community level. We wanted to assess such apparent resilience to a browsing guild dominated by elephants (*Loxodonta africana* Blumenbach), that is typical for most woodland community across southern Africa (Fritz *et al.*, 2002).

Elephant dominance has conservation implications because of their impact on other species, especially when confined and/or occurring at relatively high densities (Laws, 1970; Cumming *et al.*, 1997; Western & Maitumo, 2004; also see Wiseman, Page & O'Connor, 2004). Under such conditions, their foraging and feeding habits may reduce tree densities and transform forests and intact woodlands into mixed woodlands and even grasslands (e.g. Dublin, Sinclair & McGlade, 1990; Lock, 1993; Barnes, Barnes & Kapela, 1994; Leuthold, 1996; Ben-Shahar, 1998; Trollope *et al.*, 1998; Van De Vijver, Foley & Olf, 1999; Eckhardt, Van Wilgen & Biggs, 2000; Mosugelo *et al.*, 2002). Because of selective feeding, such conversion may be associated with changes in the abundance-incidence and rank-abundance functions that describe woody plant communities. An enquiry into these relationships in areas exposed to elephant browsing may then illustrate how disturbance can affect one of the few 'universal ecological principles' (sensu Hanski *et al.*, 1993).

The Tembe Elephant Park in the Maputaland Centre of Plant Endemism (Van Wyk, 1996) represents a case where elephants are confined to a relatively small area. The park also protects a unique sand forest ecotype that supports several endemic plant species (Van Wyk, 1996). Elephants use these forests (Klingelhoefer, 1987; De Boer *et al.*, 2000) and may negatively affect the unique elements of these forests (Van Rensburg *et al.*, 1999; Matthews *et al.*, 2001). Like elsewhere this may call for the control of impact.

We studied the consequences that the presence of a browser guild, dominated by elephants, could have for densities, species number, turnover and composition, and the abundance-incidence and relative rank-abundance relationships of woody plants in Maputaland. We expected a reduction in the abundance of woody species when exposed to these browsers, which through selection for certain species could change the slope and intercepts of the regression lines describing the abundance-incidence and rank-abundance relationships.

## Materials and methods

### Study area

Our study in Maputaland (northern KwaZulu-Natal, South Africa) focussed on the Tembe Elephant Park (27°01'S; 32°24'E) (300 km<sup>2</sup>) and the communal land adjacent to the western and southern boundaries of the park (200 km<sup>2</sup>). Elephants have always occurred in Maputaland. In the South African sector, elephants have been limited to the park since its establishment in 1983 (Klingelhoefer, 1987). The fencing of the park occurred in two phases – during 1983, the eastern, western and southern boundaries on the South African side were fenced and in 1989, the northern boundary between the park and southern Mozambique was established. During 2001, some 179 elephants (95% CI of 136–233) lived there, yielding a density of 0.59 elephant per km<sup>2</sup> that increases at about 4.6% per year (Morley, 2005). Elephants dominate the browser guild and account for almost 70% of the total biomass of browsers in the park (W.S. Matthews, unpublished data). Other species in this guild include black rhino (*Diceros bicornis* Linnaeus), giraffe (*Giraffa camelopardalis* Linnaeus), kudu (*Tragelaphus strepsiceros* Pallas), nyala (*Tragelaphus angasii* Gray), impala (*Aepyceros melampus* Lichtenstein), grey duiker (*Sylvicapra grimmia* Linnaeus), red duiker (*Cephalophus natalensis* A. Smith) and suni (*Neotragus inoschatus* von Dueben). Of these, only the last two occur occasionally on the communal land adjacent to the park.

From 1959/60 to 2001/02 (calculated as a July–June rainfall season) the area received  $748 \pm 388$  mm (mean  $\pm$  SD) rain yearly. Sand forests and mixed woodlands dominate the landscape (Matthews *et al.*, 2001). Van Wyk (1996) describes sand forests as a very dense and dry semi-deciduous to deciduous forest type. Based on tree and shrub densities, we divided the mixed woodlands into

**Table 1** Species list of trees that elephants use frequently in Maputaland (from Klingelhoefer, 1987 and De Boer *et al.*, 2000) for the respective woodland types. Values indicate positional shifts in species rank based on their relative abundance inside Tembe Elephant Park. A negative sign indicates the relative abundance of that species to be lower inside than outside the Park and higher values indicate a larger positional shift.

Species	Sand forest	Closed woodland	Open woodland
<i>Acacia burkei</i> Benth.	59	15	3
<i>Acacia karroo</i> Hayne	–	–38	21
<i>Azelia quanzensis</i> Welw.	9	63	–
<i>Albizia adianthifolia</i> (Schumacher) W. F. Wight	–16	–69	–16
<i>Albizia versicolor</i> Weiw. ex Oliver	–	–39	–10
<i>Combretum molle</i> R. Br. Ex Don	–	7	8
<i>Dialium schlechteri</i> Harms	–14	9	14
<i>Garcinia livingstonei</i> T. Anders.	–	–2	9
<i>Manilkara discolor</i> (Sonder) J. H. Hemsley	–23	–26	–11
<i>Sapium integerrimum</i> (Hochst.) J. Leonard	19	5	16
<i>Sclerocarya birrea</i> (A. Rich.) Hochst.	–	3	11
<i>Spirostachys africana</i> Sonder	7	13	5
<i>Strychnos madagascariensis</i> Poirlet	–	–14	–3
<i>Terminalia sericea</i> Burch. Ex DC.	–	–15	3
<i>Trichilia emetica</i> Vahl	–	–79	–25

closed and open woodland types (adapted from Edwards, 1983). Dense stands (mean  $\pm$  SD:  $2423 \pm 873 \text{ ha}^{-1}$ ) of trees, shrubs and undergrowth, with an enclosed and layered canopy cover, characterize the closed woodland. Grass swards and sparsely spaced mature trees and shrubs ( $1061 \pm 729 \text{ ha}^{-1}$ ) dominate the open woodland.

Elephants in Maputaland feed on a variety of trees and shrubs. The studies of Klingelhoefer (1987) and De Boer *et al.* (2000), revealed that elephants feed here preferentially on two fine-leaved and thirteen broad-leaved woodland species listed in Table 1.

#### Experimental design

We considered the absence of elephants in communal land outside the park and on its fringes as a regional control, and elephant presence in the park as the trial. We selected sample sites in the communal land with areas of low human habitation and impact (e.g. no subsistence farming) and limited resource extraction, such as roots for medicinal uses and firewood for cooking. The design follows a stratified random sampling procedure (Krebs, 1999), with strata based on the woodland types (sand forests, closed and open woodlands). We selected three sampling sites inside and three outside the park for each woodland type and randomly placed  $16 \times 16 \text{ m}$  quadrats at each site (Kent & Coker, 1992). The number of quadrats per woodland type was dictated by species accumulation curves. Accordingly, we surveyed 60 in the sand forests, 120 in the open woodlands and 139 in the

closed woodlands. We identified, counted and listed all trees and shrubs higher than 0.5 m within each of the quadrats.

#### Data analysis

We analysed data on the trees preferred by elephants according to the studies of Klingelhoefer (1987) and De Boer *et al.* (2000) separately to illustrate the apparent impact on their abundances and relative rank-abundances. We expressed tree and shrub densities as the numbers counted within each quadrat, and relied on the Mann–Whitney *U*-test (Sokal & Rohlf, 1995) to illustrate statistical differences between trial (inside the park) and control values (outside the park). Whittaker's beta diversity ( $\beta$ ) index (Wilson & Shmida, 1984) was used to compare the species turnover inside and outside the park for each of the woodland types.

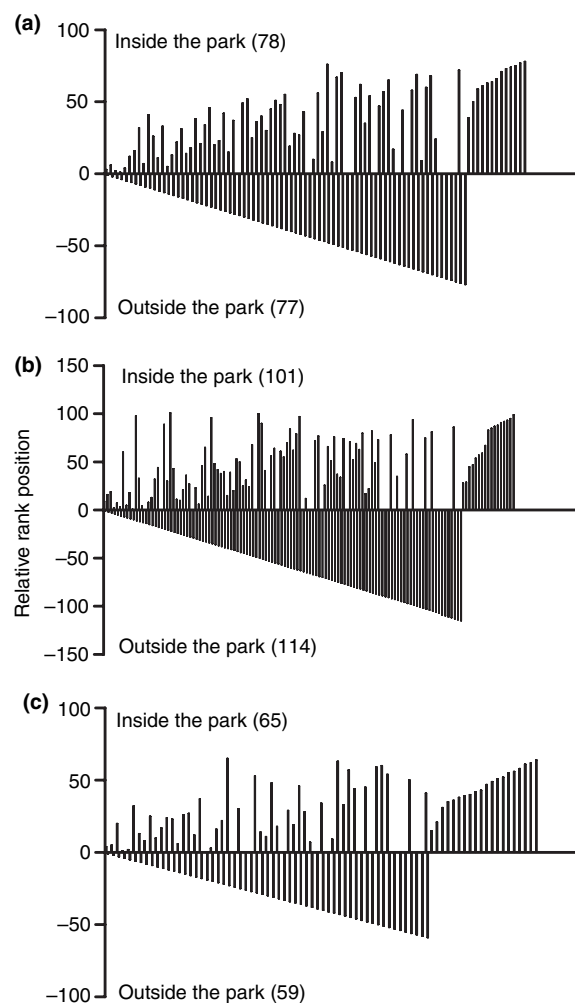
We examined the trial and control differences in species composition for each woodland type using a Bray–Curtis similarity coefficient in an analysis of similarity (ANOSIM) with the PRIMER-E software package (Clarke & Warwick, 2001). We calculated mean abundance values for each species from only those quadrats in which the species occurred (Wright, 1991; Gaston, 1996) and because of non-normality in species abundance distributions, log-transformed these values before analysis (Sokal & Rohlf, 1995). As the number of quadrats differed for each of the sampling sites, we expressed incidence as the proportional number of quadrats in which each species occurred. We

used least square regression analysis to quantify the relationship between abundance and incidence (see Blackburn & Gaston, 1998), and ANOVA to test for significant differences between the slopes of the relationships for the trial and control sites. Rank-abundance curves were constructed and we used a Kolmogorov–Smirnov two-sample test (Tokeshi, 1993) to compare abundance values for trials and controls. We used the geometric-series models to compare rank-abundance patterns of the three woodland types (Tokeshi, 1993).

## Results

We recorded 165 tree and shrub species during this study. Both sand forest and open woodland species occurred in the closed woodlands, where we identified 131 species. Sand forests harboured more species (90) than open woodlands (79). The number of species and their identities differed – some of the species that we found on trial sites were absent in control sites. The opposite was also true. For instance, open woodlands and sand forests in the park had six and one species, respectively, more than outside the park. This differed from the closed woodlands where we found thirteen more species outside than inside the park. A further thirteen of the species in sand forests in the park were not recorded outside the park. On the other hand, twelve species recorded in sand forests outside the park did not occur in the park. Seventeen of the species found in the closed woodlands outside the park did not occur in the park, while another seventeen occurred only inside the park. For open woodlands, twenty of the species recorded in the park did not occur outside the park, and fourteen species were found outside and not inside the park.

Species-specific abundances on trials and controls differed. Consequently, the ranked positions of each species in the three woodland types also differed (Figs 1a–c). In Fig. 1 the heights of bars denote the ranking of a given species, with low bars indicating high ranks. All the three woodlands had species that were either abundant or rare in the park compared with outside the park, and vice versa. For instance, several species with low abundances (rare) on the outside were either absent from the park or may have occurred at higher or equally low numbers. Based on an ANOSIM, species composition inside and outside the park differed significantly for all the woodland types (sand forest: global  $R = 0.24$ ,  $P < 0.001$ ; closed woodland: global  $R = 0.25$ ,  $P < 0.001$ ; open woodland: global  $R = 0.11$ ,  $P < 0.001$ ).



**Fig 1** Relative rank position based on the abundance of each tree species inside Tembe Elephant Park (above the horizontal line) and outside (below the line) for (a) sand forests, (b) closed woodland and (c) open woodland. We ranked species with highest abundance outside the park first; the smaller bars indicate species with higher abundance. No opposing bars across the horizontal line indicate species absence for that woodland community. Values in brackets indicate number of species

The relative abundances and related rank positions for the tree species that elephants frequently use were either lower or higher on the trial than control sites (Table 1). Woodland type also influenced the shift in the rank position of these species, which increased for some and decreased for others. For instance, *Dialium schlechteri* in sand forests, *Acacia karroo*, *Garcinia livingstonei* and *Terminalia sericea* in the closed woodlands, and *Sclerocarya birrea* in the open woodlands had lower abundances in the park

**Table 2** Mean ( $\pm$ SE) densities,  $\beta$  diversity and regression statistics: significant deviation from zero was indicated for the abundance-incidence relationships for woody species inside and outside Tembe Elephant Park. However, no significant difference was found between the slopes of the relationships inside and outside the park (for the sand forest:  $F_{1,98} = 0.56$ ,  $P = 0.46$ ; closed woodland:  $F_{1,212} = 1.21$ ,  $P = 0.27$  and open woodland:  $F_{1,120} = 0.63$ ,  $P = 0.43$ ; refer Fig. 2).

	Sand forest		Closed woodland		Open woodland	
	Inside	Outside	Inside	Outside	Inside	Outside
Densities (ind. ha <sup>-1</sup> )	6260 $\pm$ 433	5391 $\pm$ 252	2004 $\pm$ 89	2848 $\pm$ 95	983 $\pm$ 85	1170 $\pm$ 106
$\beta$ diversity	3.05	2.48	7.06	5.42	9.28	7.88
Deviation	$F_{1,58} = 58.68^{***}$	$F_{1,40} = 58.30^{***}$	$F_{1,99} = 16.20^{***}$	$F_{1,113} = 35.73^{***}$	$F_{1,63} = 4.182^*$	$F_{1,57} = 13.37^{***}$
Intercept	1.09 $\pm$ 0.04	1.04 $\pm$ 0.04	1.17 $\pm$ 0.03	1.15 $\pm$ 0.03	1.19 $\pm$ 0.03	1.17 $\pm$ 0.03
Slope	0.78 $\pm$ 0.10	0.67 $\pm$ 0.09	0.44 $\pm$ 0.11	0.60 $\pm$ 0.10	0.32 $\pm$ 0.16	0.48 $\pm$ 0.13
r <sup>2</sup>	0.50	0.59	0.14	0.24	0.06	0.19

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

than on communal land outside the park. These species were more abundant, however, in the other woodland types in the park than on communal land. The contributions of the food plants of elephants (*Albizia adianthifolia*, *A. versicolor*, *Manilkara discolor*, *Strychnos madagascariensis* and *Trichilia emetica*) to total tree densities were lower on trial than control sites (reflected in the negative positional shift in rank in the park).

Tree densities in the trial and control sites for sand forests and open woodlands were similar (sand forests:  $U = 343$ ,  $n = 60$ ,  $P > 0.05$  and open woodlands:  $U = 1454$ ,  $n = 120$ ,  $P > 0.05$ ), but trials in closed woodlands supported fewer trees than controls ( $U = 999$ ,  $n = 139$ ,  $P < 0.001$ ) (Table 2). Species turnover rates ( $\beta$  diversity) for the three landscape types were consistently higher in the park than outside (Table 2).

Abundance increased with incidence for all the woodland types inside and outside the park (Table 2). Only a small amount of variation in abundances, however, could be explained by incidence, especially for the closed and open woodlands (Table 2). The slopes of the abundance-incidence functions inside and outside the park were similar (sand forest:  $F_{1,98} = 0.56$ ,  $P = 0.46$ ; closed woodland:  $F_{1,212} = 1.21$ ,  $P = 0.27$ ; open woodland:  $F_{1,120} = 0.63$ ,  $P = 0.43$ ) as were their intercept values (sand forest:  $F_{1,99} = 3.54$ ,  $P = 0.06$ ; closed woodland:  $F_{1,212} = 0.09$ ,  $P = 0.76$ ; open woodland:  $F_{1,121} = 0.01$ ,  $P = 0.93$ ; Fig. 2a–c).

The abundance of species as a function of their ranks in the park did not differ significantly from outside the park (Kolmogorov–Smirnov test ( $\alpha = 0.01$ ) for sand forest:  $D_x = 2.298$ ,  $n = 60$ ; closed woodland:  $D_x = 2.304$ ,  $n = 114$ ; open woodland:  $D_x = 2.302$ ,  $n = 65$ ) (Fig. 3).

The geometric series models suggested that the species abundance patterns for the three woodland types differed ( $F_{5,429} = 20.26$ ,  $P < 0.0001$ ) but were similar for trial (in the park) and control sites (outside the park). The open woodland had the steepest slope, followed by the closed woodland, with the relative abundances of species in the sand forests more evenly spread than in the mixed woodlands (Fig. 3).

## Discussion

The consequences that the feeding and foraging of confined elephants may have for woody species is important for conservation, especially when developing management options (e.g. Whyte *et al.*, 1999; Whyte, Van Aarde & Pimm, 2003). Rather than focusing only on species-specific influences (e.g. Augustine & McNaughton, 2004; Wiseman *et al.*, 2004) we aimed at identifying the impact of a browsing guild, dominated by elephants, for density- and incidence-related characteristics of woody plant assemblages. Similar to Wiseman *et al.* (2004), we opted for this approach because of the effects that elephants may have had could not be separated from those of the co-occurring browsers (such as black rhino, giraffe, kudu, nyala, impala, red duiker, grey duiker and suni). None of these species, but the occasional red duiker and suni, occurred outside the park where our control sites were located. Elephants dominated the guild in the park and most of the impact noted may therefore be ascribed to their browsing. Amongst these browsers, elephants are also the only species known to destroy trees by toppling, debarking and the breaking of branches, though giraffes do break

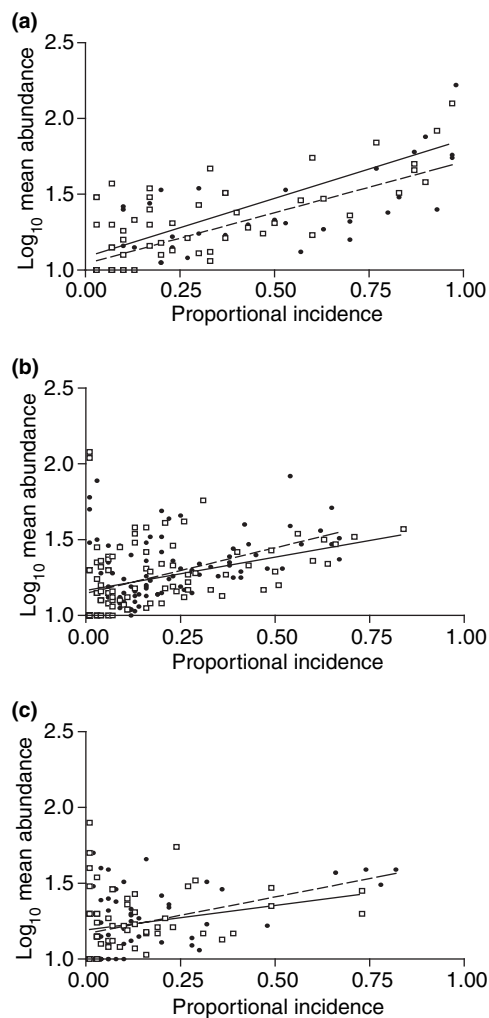


Fig 2 Log<sub>10</sub> mean abundance as a function of the proportional incidence for (a) sand forests, (b) closed woodland and (c) open woodland for trees and shrubs inside (open squares and solid lines) and outside (solid circles and dashed lines) the Tembe Elephant Park

branches occasionally (Van Aarde & Skinner, 1975; Bond & Loffell, 2001). We compared the characteristics of assemblages in a protected area where elephants live, with those in similar assemblages outside the area where no elephants occurred for at least 20 years before our study.

The scatter of the data points around the abundance-incidence regression line, especially for the closed and open woodlands, showed the typical curvilinearity and triangularity others have encountered (for summary, see Gaston, 1994). The low correlation values we recorded for the densities as functions of incidences may be due to some plants either having a high biomass but low densities and/or

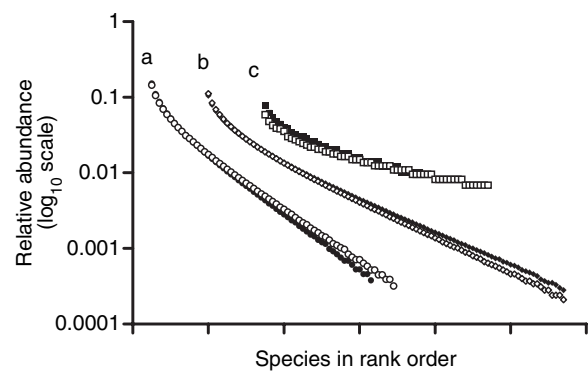


Fig 3 The relative abundance ranked for trees and shrubs in the (a) open woodland, (b) closed woodland and (c) sand forests inside (open) and outside (solid) Tembe Elephant Park

high biomass due to small individual size and high numbers (see Hanski *et al.*, 1993). At this level, we could not find an effect that we could ascribe to the browser guild because the positive abundance-incidence relationships for woody plants in the park did not differ from those outside. This finding supports Gaston & Warren's (1997) study, who show that controlled disturbances do not affect the slopes, intercepts, or coefficients of determination of the interspecific abundance-distribution relationships that they studied in the laboratory. Our findings suggest that (1) disturbances by browsers do not disrupt abundance-incidence relationships in woodlands or (2) abundance-incidence relationships in woodlands are resilient to such disturbances. Abundance-incidence relationships exist over a wide range of spatial and temporal scales (Guo *et al.*, 2000), assemblages and disturbance regimes (Gaston & Warren, 1997), and could well be one of the general rules in ecology (Hanski *et al.*, 1993; also see Gaston & Lawton, 1990). Our study suggests that elephants did not alter these functions for woody plants in Maputaland. It may also be argued that the lack of community-level responses in our study merely results from current densities of elephants being too low to have any impact on community-level variables.

In our study, few species dominated in numbers. This pattern is typical to that noted by others (see Gaston, 1994) and was not altered by browsers. The slopes of the rank-abundance curves that we constructed, however, differed between woodlands. The slopes were shallower for sand forest than for the closed and open woodlands, while those for the closed woodlands were shallower than for the open woodlands. Such a trend may be induced by succession (see Tokeshi, 1993) and in our study area frequent

fires may prevent the open woodlands from developing into closed woodlands, as has been noted elsewhere (see Higgins, Bond & Trollope, 2000). This needs further study.

Although the bivariate community characteristics did not respond to the presence of the elephants, the species-specific abundances did so. Two possible related explanations may account for this. First, compensatory responses may allow some species to increase when others are decreasing, or even replace those not encountered during the study. For instance, rare species outside the park are relatively common in the park; the opposite is also apparent. Nevertheless, species turnover ( $\beta$  diversity) in the respective woodlands in the park is higher than on communal lands out of the park. Elephants are known to destroy individual trees (e.g. MacGregor & O'Connor, 2004; Wiseman *et al.*, 2004) and reduce the densities of favoured species (e.g. Hiscocks, 1999; Gadd, 2002). This conceivably may provide other species with opportunities to thrive, as is implied by the relatively high rates of species turnover noted inside the park. We are not aware, however, of other studies that support this notion.

A second explanation for our trends is that relative abundances may mask the differences between trials and controls. It is the species abundance, and not its identity, that determines its rank. A rank abundance curve only reflects on the structure of the woodland community based on the abundances of species relative to each other within the same community.

The seven main species that elephants feed on in sand forests (*Acacia burkei*, *Azelia quanzensis*, *Albizia adianthifolia*, *Dialium schlechteri*, *Manilkara discolor*, *Sapium integerrimum* and *Spirostachys africanum*; Klingelhofer, 1987; De Boer *et al.*, 2000) occur at low numbers in the park's sand forests, but are not endemic to these forests and are relatively common in the mixed woodlands. These species may also be taken in closed and open woodlands where they occur and this may explain the relatively low abundances of some of them. This is particularly important for the conservation of the rare and endemic sand forest species. Contrary to Van Rensburg *et al.* (1999) and Matthews *et al.* (2001) this finding suggests that elephants presently are not threatening such species.

To conclude, elephants in parts of Maputaland had little consequences for community-level variables but their presence was associated with a decline in the abundances of favoured food species. This supports the findings of other studies that show that elephants do modify the composition of woodlands (Dublin *et al.*, 1990; Baxter & Getz, 2005). We

are not aware of any other studies that focused on community level responses to elephants in the manner that we did. The apparent insensitivity of these variables to elephant browsing renders them of limited value as measures of the interactions between browsers and their browse to vegetation.

## Acknowledgements

We would like to thank the National Research Foundation, the U.S. Fish and Wildlife Services and the Peace Parks Foundation for financial support. The Ezemvelo KZN Wildlife personnel of the Tembe Elephant Park provided some logistical support. Derrick Tembe and D.G. Erasmus assisted with fieldwork.

## References

- AUGUSTINE, D.J. & McNAUGHTON, S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* **41**, 45–58.
- BARNES, R.F.W., BARNES, K.L. & KAPELA, E.B. (1994) The long-term impact of elephant browsing on baobab trees at Msembe, Ruaha National Park, Tanzania. *Afr. J. Ecol.* **32**, 177–184.
- BAXTER, P.W.J. & GETZ, W.M. (2005) A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecol. Appl.* **15**, 1331–1341.
- BEN-SHAHAR, R. (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecol.* **136**, 189–194.
- BLACKBURN, T.M. & GASTON, K.J. (1998) Some methodological issues in macroecology. *Am. Nat.* **151**, 68–83.
- BOND, W.J. & LOFFELL, D. (2001) Introduction of giraffe changes acacia distribution in a South African savanna. *Afr. J. Ecol.* **39**, 286–294.
- BROWN, J.H. (1984) On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 225–279.
- CLARKE, K.R. & WARWICK, R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. Primer-E, Plymouth.
- COLLINS, S.L. & GLENN, S.M. (1990) A hierarchical analysis of species' abundance patterns in grassland vegetation. *Am. Nat.* **135**, 633–648.
- CUMMING, D.H.M., FENTON, M.B., RAUTENBACH, I.L., TAYLOR, R.D., CUMMING, G.S., CUMMING, M.S., DUNLOP, J.M., FORD, A.G., HOVORKA, M.D., JOHNSTON, D.S., KALCOUNIS, M., MAHLANGU, Z. & PORTFORS, V.R. (1997) Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* **93**, 231–236.
- DE BOER, W.F., NTUMI C.P., CORREIA, A.U. & MAFUCA, M. (2000) Diet and distribution of elephant in danger: the Maputo Elephant Reserve, Mozambique. *Afr. J. Ecol.* **38**, 188–201.

- DUBLIN, H.T., SINCLAIR, A.R.E. & MCGLADE, J. (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.* **59**, 1147–1164.
- ECKHARDT, H.C., VAN WILGEN, B.W. & BIGGS, H.C. (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1988. *Afr. J. Ecol.* **38**, 108–115.
- EDWARDS, D. (1983) A broad-scale structural classification of vegetation for practical purposes. *Bothalia* **14**, 705–712.
- FRTZ, H., DUNCAN, P., GORDON, I.J. & ILLIUS, A.W. (2002) Mega-herbivores influence trophic guilds structure in African ungulate communities. *Oecologia* **131**, 620–625.
- GADD, M.E. (2002) The impact of elephants on the marula tree *Sclerocarya birrea*. *Afr. J. Ecol.* **40**, 328–336.
- GASTON, K.J. (1994) *Rarity*. Chapman and Hall, London.
- GASTON, K.J. (1996) The multiple forms of the interspecific abundance-distribution relationship. *Oikos* **76**, 211–220.
- GASTON, K.J. & LAWTON, J.H. (1990) Effects of scale and habitat on the relationship between regional and local abundance. *Oikos* **58**, 329–335.
- GASTON, K.J. & WARREN, P.H. (1997) Interspecific abundance-occupancy relationships and the effects of disturbance: a test using microcosms. *Oecologia* **112**, 112–117.
- GILBERT, B. & LECHOWICZ, M.J. (2004) Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Nat. Acad. Sci. USA* **101**, 7651–7656.
- GOTTELLI, N.J. & SIMBERLOFF, D. (1987) The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *Am. Nat.* **130**, 18–35.
- HANSKI, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210–221.
- HANSKI, I. & GYLLENBERG, M. (1993) Two general metapopulation models and the core-satellite species hypothesis. *Am. Nat.* **142**, 17–41.
- HANSKI, I., KOUKI, J. & HALKKA, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Eds R. RICKLEFS & D. SCHLUTER). University of Chicago Press, Chicago, IL.
- HIGGINS, S.I., BOND, W.J. & TROLLOPE, W.S.W. (2000) Fire, re-sprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol.* **88**, 213–229.
- HISCOCKS, K. (1999) The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe* **42**, 47–56.
- HUBBELL, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- KENT, M. & COKER, P. (1992) *Vegetation Description and Analysis. A Practical Approach*. John Wiley & Sons, Chichester.
- KLINGELHOEFER, E.W. (1987) Aspects of the ecology of the elephant *Loxodonta africana* (Blumenbach, 1797) and a management plan for the Tembe Elephant Park in Tongaland, Kwazulu. MSc thesis, University of Pretoria, Pretoria.
- KREBS, C.J. (1999) *Ecological Methodology*, 2nd edn. Addison-Wesley Educational Publishers, Inc., Menlo Park, CA.
- LAWS, R.M. (1970) Elephants as agents of habitat and landscape change in East Africa. *Oikos* **21**, 1–15.
- LENNON, J.J., KOLEFF, P., GREENWOOD, J.J.D. & GASTON, K.J. (2004) Contribution of rarity and commonness to patterns of species richness. *Ecol. Lett.* **7**, 81–87.
- LEUTHOLD, W. (1996) Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–94. *Afr. J. Ecol.* **34**, 101–112.
- LOCK, J.M. (1993) Vegetation change in the Queen Elizabeth National Park, Uganda: 1970–1988. *Afr. J. Ecol.* **31**, 106–117.
- MACGREGOR, S.D. & O'CONNOR, T.G. (2004) Response of *Acacia tortilis* to utilization by elephants in a semi-arid African savanna. *S. Afr. J. Wildl. Res.* **34**, 55–66.
- MAGURRAN, A.E. (2005) Species abundance distributions: patterns or process? *Funct. Ecol.* **19**, 177–181.
- MAGURRAN, A.E. & HENDERSON, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature* **422**, 714–716.
- MATTHEWS, W.S., VAN WYK, A.E., VAN ROOYEN, N. & BOTHA, G.A. (2001) Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *S. Afr. J. Bot.* **67**, 573–594.
- MAURER, B.A. (1990) The relationship between distribution and abundance in a patchy environment. *Oikos* **58**, 181–189.
- MCGILL, B.J. (2003) A test of the unified neutral theory of biodiversity. *Nature* **422**, 881–885.
- MORLEY, R.C. (2005) The demography of a fragmented population of the savanna elephant (*Loxodonta africana* Blumenbach) in Maputaland. PhD thesis, University of Pretoria, Pretoria.
- MOSUGELO, D.K., MOE, S.T., RINGROSE, S. & NELLEMAN, C. (2002) Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *Afr. J. Ecol.* **40**, 232–240.
- QUO, Q., BROWN, J.H. & VALONE, T.J. (2000) Abundance and distribution of desert annuals: are spatial and temporal patterns related? *J. Ecol.* **88**, 551–560.
- SOKAL, R.R. & ROHLF, F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman & Company, New York.
- SUGIHARA, G. (1980) Minimal community structure: and explanation of species abundance patterns. *Am. Nat.* **116**, 770–787.
- TOKESHI, M. (1993) Species abundance patterns and community structure. *Adv. Ecol. Res.* **24**, 111–186.
- TROLLOPE, W.S.W., TROLLOPE, L.A., BIGGS, H.C., PIENAAR, D. & POTGIETER, A.L.F. (1998) Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe* **41**, 103–112.
- ULRICH, W. & OLLIK, M. (2004) Frequent and occasional species and the shape of relative-abundance distributions. *Divers. Distrib.* **10**, 263–269.
- VAN AARDE, R.J. & SKINNER, J.D. (1975) *The Food and Feeding Behaviour of the Giraffa camelopardalis* in the Jack Scott Nature Reserve. Publication series of the University of Pretoria no. 79. University of Pretoria, Pretoria, South Africa.
- VAN DE VIJVER, C.A.D.M., FOLEY, C.A. & OLFF, H. (1999) Changes in the woody component of an East African savanna during 25 years. *J. Trop. Ecol.* **15**, 545–564.



- VAN RENSBURG, B.J., MCGEOCH, M.A., CHOWN, S.L. & VAN JAARSVELD, A.S. (1999) Conservation of heterogeneity among dung beetles in the Maputaland Centre of Enderism, South Africa. *Biol. Conserv.* **88**, 145–153.
- VAN RENSBURG, B.J., MCGEOCH, M.A., MATTHEWS, W., CHOWN, S.L. & VAN JAARSVELD, A.S. (2000) Testing generalities in the shape of patch occupancy frequency distributions. *Ecology* **81**, 3163–3177.
- VAN WYK, A.E. (1996) Biodiversity of the Maputaland Centre. In: *The Biodiversity in African Plants* (Ed L. J. G. van der MAESEN, X. M. van der BURGT and J. M. van MEDENBACH DE ROOY). Kluwer Academic Publishers, Dordrecht.
- VOLKOV, I., BANAVAR, J.R., HUBBELL, S.P. & MARITAN, A. (2003) Neutral theory and relative species abundance in ecology. *Nature* **424**, 1035
- WESTERN, D & MAITUMO, D. (2004) Woodland loss and restoration in a savanna park: a 20-year experiment. *Afr. J. Ecol.* **42**, 111–121.
- WHYTE, I.J., BIGGS, H.C., GAYLARD, A. & BRAACK, L.E.O. (1999) A new policy for the management of the Kruger National Park's elephant population. *Koedoe* **42**, 111–132.
- WHYTE, I.J., VAN AARDE, R.J. & PIMM, S.L. (2003) Kruger elephant population: its size and consequences for ecosystem heterogeneity. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds J. T. DU TOIT, K. H. ROGERS and H. C. BIGGS). Island Press, Washington, DC.
- WILSON M.V. & SHMIDA, A. (1984) Measuring beta diversity with presence-absence data. *J. Ecol.* **72**, 1055–1064.
- WISEMAN, R., PAGE, B.R. & O'CONNOR, T.G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *S. Afr. J. Wildl. Res.* **34**, 25–37.
- WRIGHT, D.H. (1991) Correlations between incidence and abundance are expected by chance. *J. Biogeogr.* **18**, 463–466.

(Manuscript accepted 1 November 2006)

doi: 10.1111/j.1365-2028.2007.00714.x