Chapter 4

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The impact of elephants on plant community variables of the Tembe Elephant Park

Robert A.R. Guldemond & Rudi J. van Aarde

Summary

1 Elephants confined to protected areas may affect local biological diversity. We expect measurable deviations in woody plant community variables such as density, species composition, abundance-incidence and rank-abundance patterns when exposed to elephant browsing.

2 We examined these plant community variables in the presence and absence of elephants for both mixed woodlands (closed and open woodland types) and sand forests inside Tembe Elephant Park and adjacent communal land in South Africa.

3 Mixed woodlands and sand forest species composition differed significantly between the Park and the communal land. Woody plant densities, abundance-incidence and rank-abundance relationships inside the Park were not, however, significantly different from those recorded in communal land.

4 Regional and local ecological processes such as plant metapopulation dynamics, niche partitioning and other disturbance events (*e.g.* frequent fires) may mask the localised impact elephants have for rare woody plant species in the Park.

Key-words: abundance, composition, density, incidence, species rank, woodlands

Introduction

Ecological assemblages typically comprise of few dominant species and a large number of relatively rare species (Sugihara 1980; Tokeshi 1993; Gaston 1994; Lennon *et al*. 2004). A number of models predict these rank abundance patterns (e.g. Magurran & Henderson 2003; Ulrich & Ollik 2004). Further, plant and animal assemblages across a wide range of spatial and temporal scales (Guo *et al*. 2000) and disturbance regimes (Gaston & Warren 1997) are characterised by positive abundance incidence relations (Hanski 1982; Brown 1984; Gotelli & Simberloff 1987; Collins & Glenn 1990; Maurer 1990; Hanski & Gyllenberg 1993; but see Gaston & Lawton 1990; Gaston 1996). This may be explained by plant meta-population dynamics (Hanski & Gyllenberg 1993; van Rensburg *et al*. 2000), niche-breadth / resource partitioning (Brown 1984; Guo *et al*. 2000) and the related resource availability hypothesis (Gaston 1994; Hanski *et al*. 1993). Recently, neutral models suggest an alternative explanation for relative species abundance distributions (Hubbell 2001; Volkov *et al*. 2003; but see McGill 2003; Gilbert & Lechowicz 2004; Magurran 2005).

Savanna elephants (*Loxodonta africana*) influence biological diversity especially when confined and occurring at relatively high densities (Laws 1970; Cumming *et al*. 1997; Western & Maitumo 2004; but see Wiseman *et al*. 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 *et al*. 1990; Lock 1993; Barnes *et al*. 1994; Leuthold 1996; Ben-Shahar 1998; Trollope *et al*. 1998; van de Vijver *et al*. 1999; Eckhardt *et al*. 2000; Mosugelo *et al*. 2002). Such conversion may be associated with changes in the abundance-incidence and rank-abundance functions that described woody plant communities. An investigation into these relationships in areas exposed to elephant browsing then may illustrate how disturbance may affect these community variables.

The Tembe Elephant Park in the Maputaland centre of plant endemism (van Wyk 1996) represents a case of confined elephants occurring at relatively high densities. In addition to elephants, the Park protects a unique sand forest ecotype that supports several endemic plant species (van Wyk 1996). Elephants may negatively affect these unique sand forest elements (Matthews *et al*. 2001; van Rensburg *et al*. 1999) and like elsewhere this may call for management operations such as elephant culling (e.g. van Aarde *et al*. 1999; Whyte *et al*. 2003) or the application of contraceptives (Pimm & van Aarde 2001).

The present study investigates the consequences of elephant presence for the abundance-incidence and relative rank-abundance relationships of woody plants in Tembe Elephant Park. Other herbivores also occur in the Park, and therefore, for this study, the presence of elephants describes a "park effect". The surrounding study area has few herbivores, no elephants and hardly any people living there. This allows us to use the comparative method to determine if elephants, along with other browsers, modify the abundance-incidence and rank-abundance relationships for woody species. We expected a reduction in the abundance of woody species when exposed to these animals, which through selection for certain species could change the slope and intercepts of the lines describing the abundance-incidence and rank-abundance relationships.

Materials & Methods

The study area

The study was conducted in Tembe Elephant Park (27°01'S 32°24'E) (300 km^2) and adjacent communal land (200 km^2) situated within the Maputaland region of northern KwaZulu-Natal, South Africa. Elephants always occurred in Maputaland, but have been confined to the Park since 1989 following the fencing of its northern boundary, which borders southern Mozambique. During 2001 an estimated 179 elephants (95% CI of 136 to 233) resided in the Park, and the population is presently increasing at a rate of 4.64±0.06% per annum (Morley 2005).

From 1959/60 until 2001/02 (corrected for the June-July rainfall season) the area received a mean (±SD) annual rainfall of 748±388 mm. 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 closed and open woodland types (adapted from Edwards 1983; One-tailed t-test t_{257}=13.45, P<0.0001). Dense stands (mean ± SD; 2,423.3±873.1 / ha^{-1}) of trees, shrubs and undergrowth, with an enclosed and layered canopy cover characterise the closed woodland. Grass swards and sparsely spaced mature trees and shrubs (1,060.9±728.9 / ha^{-1}) dominate the open woodland.

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 inside the Park as the trial. We selected sites based on a classified satellite image for the Park and 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 livestock at the selected sites. Our follow-up visit to these sample sites in the communal land confirmed low human habitation, no subsistence farming and limited resource extraction.

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 16X16m quadrats within each site (Kent & Coker 1992). The number of quadrats per woodland type varied and range from 60 for the sand forests, 120 in the open and 139 in the closed woodlands. We identified, enumerated and documented all trees and shrubs standing higher than 0·5m within each quadrat.

Data analysis

We expressed tree and shrub densities as the total number of individuals enumerated within each quadrate, and analysis of variance (ANOVA) (Sokal & Rohlf 1995) to test for significant difference in densities between inside and outside the Park. We investigated differences in species composition for each woodland type between inside and outside the Park using a Bray-Curtis similarity coefficient in an analysis of similarity (ANOSIM) with the PRIMER-E software package (Clarke & Warwick 2001). Mean abundance values for each species were only calculated from quadrats in which the species occurred (Wright 1991; Gaston 1996). These were $\log_{10}$-transformed before analysis due to non-normality in species abundance distributions (Sokal & Rohlf 1995). Due to uneven number of quadrats (between 10 and 25) for each of the sampling sites, incidence is expressed as the proportional number of quadrats in which each species occurred. We used least square regression analysis (Blackburn & Gaston 1998) to quantify the relationship between woody species abundance and incidence, and ANOVA to test for significant differences between the slopes of the relationships inside and outside the Park. Rank-abundance curves were constructed (Krebs 1999) and a Kolmogorov-Smirnov two-sample test (Tokeshi 1993) used to statistically compare abundance values for the woody species inside and outside the Park. We used the geometric-series models to compare plant community patterns between the three woodland types (Tokeshi 1993).

Results

Tree and shrub densities inside and outside the Park were similar for the three woodland types ($F_{1,313}$=0.26, P=0.61). Based on an ANOSIM, species composition inside and outside the Park, however, differed significantly from each other for all 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). Expressing abundance as a function of incidence yielded a positive relationship for all the woodland types inside and outside the Park (Table 4.1). Only a small amount of the variation in abundances, however, could be explained by incidence, especially for the closed and open woodlands (Table 4.1).

The slopes of the relationships (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) for trees and shrubs were similar, as were the intercept values for assemblages inside and outside the Park (sand forest: $F_{1,99}$=3.54, P=0.06; closed woodland: $F_{1,213}$=0.09, P=0.76; open woodland: $F_{1,121}$=0.01, P=0.93) (Fig. 4.1).

Table 4.1 Regression statistics for abundance-incidence relationships for woody species inside and outside the Park indicating significant deviation from zero for the respective woodland types. However, no significant difference was found in 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 respectively; refer Fig. 4.1).

	Sand forest		Closed woodland		Open woodland	
	Inside	Outside	Inside	Outside	Inside	Outside
Deviation	$F_{1,58}$=58.68***	$F_{1,40}$=58.30***	$F_{1,99}$=16.20***	$F_{1,113}$=35.73***	$F_{1,58}$=4.182*	$F_{1,58}$=13.37***
Intercept	1.09±0.04	1.04±0.04	1.17±0.03	1.15±0.03	1.19±0.03	1.17±0.03
Slope	0.78±0.10	0.67±0.09	0.44±0.11	0.60±0.10	0.32±0.16	0.48±0.13
r^2	0.50	0.59	0.14	0.24	0.06	0.19

*P < 0.05; **P < 0.01; ***P < 0.001

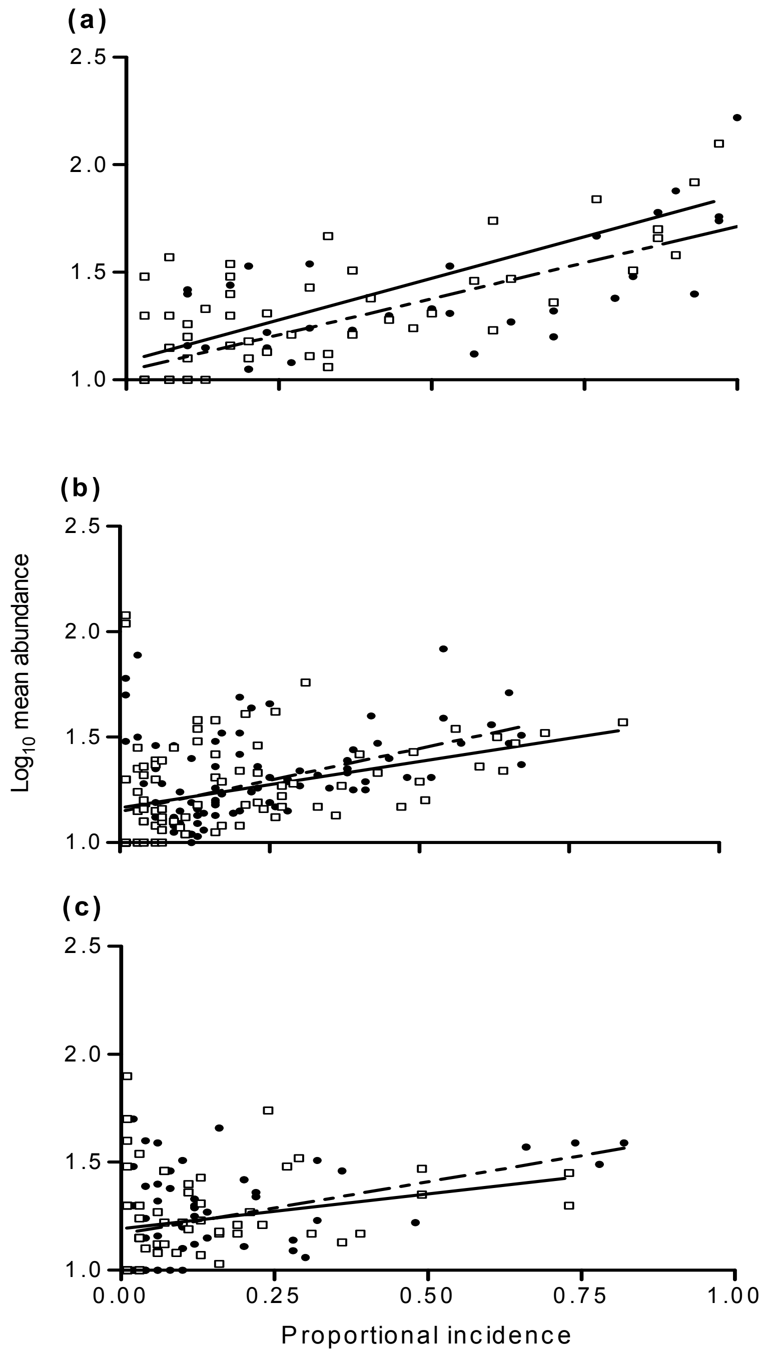

Fig. 4.1 Log_{10} mean abundance as a function of the proportional incidence for a) sand forests, b) closed woodland and c) open woodland for trees and shrubs inside (open squares & solid lines) and outside (solid circles & dashed lines) the Tembe Elephant Park.

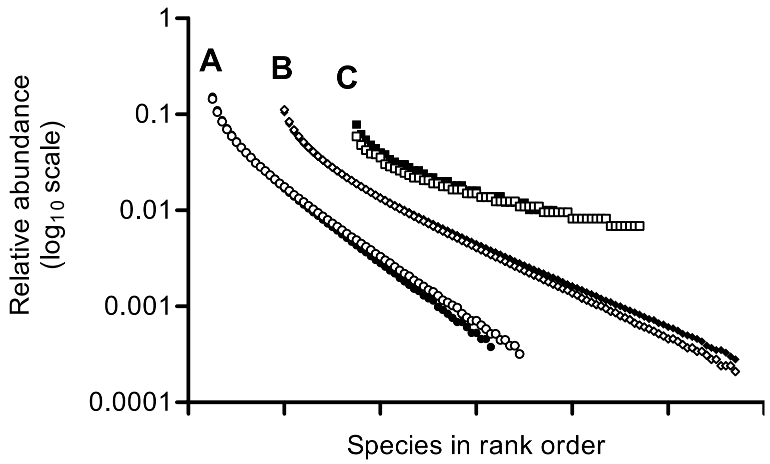

Fig. 4.2 The relative abundance ranked for trees and shrubs in the (A) open woodland, (B) closed woodland and (C) sand forests inside (open) and outside (solid) Tembe Elephant Park.

Likewise, species-specific abundance did not differ significantly inside and outside the Park (Kolmogorov-Smirnov test (α=0.01) for sand forest: D_{α}=2.298 n=60; closed woodland: D_{α}=2.304, n=114; open woodland: D_{α}=2.302, n=65; Fig. 2). The geometric-series models indicated a significant change in the species abundance pattern between the three woodland types ($F_{5,429}$=20.26, P<0.0001). These differences appear to be independent of elephant presence, with the open woodland having the steepest slope, then the closed woodland, with most evenly spread species abundance in sand forests (Fig. 4.2).

Discussion

Consequences of the feeding and foraging behaviour of confined elephant populations are important for woody species, especially when developing conservation management options (e.g. Whyte *et al*. 1999, 2003). The present study aimed at identifying the impact of a disturbance brought about by elephants and other herbivores for selective plant assemblage characteristics. The Park supports a suite of browsers other than elephants, none of who also occur outside the Park. However, elephants dominate the mammalian browser guild and most of the impact noted may therefore be ascribed to elephant browsing *per se*. Fire too can suppress woody seedlings and saplings from attaining maturity (Higgins *et al*. 2000); and we therefore refer to the apparent impact recorded through our comparative approach as the "park effect" rather than the elephant effect.

The scatter of the data points around the abundance-incidence regression line, especially within the closed and open woodlands, displays the typical curvilinear and triangularity encountered in numerous other studies (for summary see Gaston 1994). Low correlation values for plant species may be due to plant species either having a high biomass but low densities and/ or high biomass due to small individual size and high numbers (see Hanski *et al*. 1993). For all three woodland types inside and outside the Park, we recorded positive and similar relationships in the abundance-incidence relationships for trees and shrubs. Plant species abundance was, therefore, unaffected by the "park effect". Similarly, Gaston & Warren (1997) showed that under controlled laboratory experiments disturbance does not affect the slopes, intercepts, or coefficients of determination of the interspecific abundance-distribution relationships. Our findings, under more natural conditions in the Tembe Elephant Park, suggest that the abundance-incidence relationships of woodland species were resistant to elephant-induced changes. More importantly, the interspecific positive abundance-incidence relationships defined over a wide range of spatial and temporal scales (Guo *et al*. 2000), assemblages and disturbance regimes (Gaston & Warren 1997), may be assigned as one of the general rules in ecology (Hanski *et al*. 1993; but see Gaston & Lawton 1990). Elephants, along with the other herbivores, may therefore be unable to alter the abundance-incidence for woody plant species.

The plant community structure, as reflected in the rank-abundance pattern, shows typical dominance in abundance of a few common species, with most species only represented by a few individuals (Gaston 1994). The "park effect" on trees and shrubs seem to have little consequence for this pattern. The plant community structures for the three woodland types, that is the presence of mostly rare species with a few dominant species, remain intact in the presence of elephants. The slopes describing rank-abundance, however, differed significantly between the landscape types, both inside and outside the Park. The steepness of the slopes was higher for the sand forest than those for the closed and open woodlands. This suggests that the latter woodland type could represent an early successional stage of the more complex closed woodland or sand forest type; Tokeshi (1993) gives a similar scenario. On the other hand, frequent fires may prevent open woodlands from developing into closed woodlands (see Higgins *et al*. 2000).

Both regional and local ecological processes could still mask the potential impact of especially, elephants on trees and shrubs in Tembe Elephant Park. These processes may include other disturbance events (e.g. fire), meta-population dynamics (Hanski & Gyllenberg 1993, van Rensburg *et al*. 2000) and resource partitioning / niche-based models (Brown 1984; Guo *et al*. 2000), which are currently believed to structure ecological communities (Gaston *et al*. 1997). The rank-abundance patterns we found also suggest that at current densities elephants have no impact on the rare species within the Park and that the plant community structure remain intact. This is particularly important for the conservation of the rare and endemic sand forest species. We conclude that elephants in Tembe Elephant Park, under current densities, do not change the slopes and intercepts of the lines describing the abundance-incidence and rank-abundance relationships, despite the differences in species compositions between inside and outside the Park.

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