

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/267208285>

# Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants

Article in *Biological Conservation* · December 2014

DOI: 10.1016/j.biocon.2014.09.036

CITATIONS

13

READS

358

2 authors:



Timothy Gordon O'Connor

77 PUBLICATIONS 2,669 CITATIONS

SEE PROFILE



Bruce Richard Page

University of KwaZulu-Natal

63 PUBLICATIONS 1,729 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Ecosystems simulation [View project](#)



Karkloof Catchment Landuse Change 1944 - 1999 [View project](#)



# Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants



T.G. O'Connor<sup>a,b,\*</sup>, B.R. Page<sup>c</sup>

<sup>a</sup>SAEON, P.O. Box 2600, Pretoria 0001, South Africa

<sup>b</sup>School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

<sup>c</sup>School of Life Sciences, University of KwaZulu-Natal, Westville, Durban, South Africa

## ARTICLE INFO

### Article history:

Received 10 July 2014

Received in revised form 22 September 2014

Accepted 23 September 2014

### Keywords:

*Colophospermum mopane*

Moisture stress

Tree density

Woody structure

## ABSTRACT

Elephant populations at high density commonly transform their habitat, but a low density population would not be expected to have a marked impact. Re-introduction of elephants into the Venetia-Limpopo Nature Reserve (320 km<sup>2</sup>) in the early 1990s established a low density population for the period of survey (0.16–0.33 individuals km<sup>-2</sup>). Accordingly, their impact on the composition and structure of the woody vegetation of three riparian and nine dryland vegetation types was measured between 1997 and 2010 using 148 permanent transects. Riparian habitat showed a greater change in composition and diversity, and also a greater decline of species richness, density of tall trees or total basal area, than dryland habitat. Change of dryland *Commiphora* Woodland was comparable to changes of riparian types. These conspicuous changes were a consequence primarily of severe use by elephants. Some species within these vegetation types declined markedly in abundance. Vegetation types dominated by *Colophospermum mopane* showed an increase in total basal area and relatively minor change in composition or structure, resulting mainly from the impact of moisture stress. Vegetation types that were severely impacted by elephants constituted <10% of reserve area; lightly impacted dryland *C. mopane* types constituted >70% of area. Some uncommon, selected dryland species were heavily impacted by elephants. A number of species may therefore be trending toward local extirpation. It was concluded that the coexistence of elephants and some plant species in this medium-sized, contained reserve was not possible.

© 2014 Elsevier Ltd. All rights reserved.

## 1. Introduction

Persistence of elephants (*Loxodonta africana*) within sub-Saharan Africa is rapidly becoming centered on protected areas (Blanc et al., 2007), but this species is capable of radically transforming its habitat (Laws et al., 1975; O'Connor et al., 2007). A geographic dichotomy has developed across Africa in terms of elephant impacts. Initial concern about elephant impacts arose in the large, open-ended national parks of East Africa during the 1960s (Eltringham, 1982; Spinage, 1994, 2012), but the decimation of these populations by poaching during the 1980s allayed these concerns (Douglas-Hamilton, 1987). In contrast, the density of most southern African elephant populations, spared severe poaching impact, was controlled by management from the 1950s, after

\* Corresponding author at: P.O. Box 379, Hilton 3245, South Africa. Tel.: +27 33 3433491.

E-mail addresses: [tim@saeon.ac.za](mailto:tim@saeon.ac.za) (T.G. O'Connor), [brupage@gmail.com](mailto:brupage@gmail.com) (B.R. Page).

which populations have grown following reduced population control, resulting in increasing concern about vegetation impacts (e.g., Whyte et al., 2003). In addition, the growth of the tourism industry in southern Africa resulted in the re-introduction of elephants into over 58 medium-sized (<1000 km<sup>2</sup>) to small (<200 km<sup>2</sup>) protected areas (Garai et al., 2004). A novel challenge of managing elephants within a relatively small, closed area has therefore been created.

Current concern about elephant impacts relates not only to the effect they might have on their own population performance (e.g., Laws et al., 1975) but also their potential impact on supported animal diversity through alteration of the composition, diversity and structure of vegetation (Cumming et al., 1997; Guldmond and Van Aarde, 2008). They may also directly impact plant diversity (O'Connor et al., 2007). Elephants usually share protected areas with other large browsers or mixed feeders such as giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*) and eland (*Taurotragus oryx*). Elephants may alter the availability of food resources to these species (O'Kane et al.,

2011a, 2011b) whose impact on vegetation may be as significant as that of elephants (O'Kane et al., 2012, 2013; Pellew, 1983). If management is to respond to purported elephant impacts, then it behoves scientists to ensure that impacts of other species are not falsely attributed to elephants. Furthermore, woody vegetation in African savannas is impacted by many other agents. Fire can transform savanna vegetation on its own (Trapnell, 1959) and in conjunction with elephant impacts (Buechner and Dawkins, 1961; Laws et al., 1975). Impact of stress-related agents such as drought (O'Connor, 1999) and frost (Childes and Walker, 1987; Holdo, 2006) are usually episodic in nature but can impart an indelible imprint to ecosystem organization. The significance of elephant impacts therefore needs to be judged in relation to all other potential impacts.

Elephants, like any herbivore, do not forage randomly but usually exhibit a hierarchy of selection from landscape, through vegetation type, to species and plant part (Clegg, 2010). Use of individuals of some woody species may result in their death whereas individuals of other species may maintain sound growth, depending on the manner and extent to which an individual is used (O'Connor et al., 2007). As a consequence of selection across space and differences across species in terms of impact, elephant impacts are not spatially uniform (Mosugelo et al., 2002; Vanak et al., 2012). Distribution of watering points imparts an additional spatial pattern (Chamaillé-Jammes et al., 2009; Mukwashi et al., 2012; Owen-Smith, 1996; Redfern et al., 2005; Tafangenyasha, 1997). Owing to the pronounced seasonal character of southern African savannas, elephant impacts on riparian vegetation may become pronounced during the dry season (Loarie et al., 2009). The majority of studies on elephant impacts have focused on systems in which elephants have always occurred. In the case of systems from which elephants have been absent for a number of decades, it can be expected that vegetation has altered in response to relaxation of their use. As a corollary, it should be expected that vegetation should respond to their re-introduction. Long-term study is needed to assess such responses in order that conclusions are based on vegetation that has had an opportunity to respond to a new impact through regeneration and growth.

Case studies can contribute to a deeper understanding of elephant impacts provided the similarities and differences to other cases are identified. The Venetia-Limpopo Nature Reserve (VLNR), South Africa, offered an opportunity to examine the impact of a recently re-introduced elephant population on a semi-arid savanna from which it had been effectively absent for over a century. A population of low density was established in this medium-sized (318 km<sup>2</sup>) reserve. Animals used in the re-introduction were familiar with the vegetation as they had been sourced from areas with comparable vegetation. Fire could be excluded as a compounding factor because no fires had occurred for half a century, and all areas of the reserve were accessible to elephants owing to the density and distribution of water points. The reserve thus offered a special case of examining the impact of a low density elephant population within a medium-sized, closed system that had not been impacted by elephants for about a century.

The aim of this study was to determine whether the composition, diversity and structure of the woody vegetation of the VLNR had changed following the re-introduction of elephants. The following two hypotheses were addressed.

1. Conspicuous changes in the composition and structure of vegetation types selected by elephants would occur, of which riparian vegetation types were a prime candidate.
2. Other agents which can affect the composition or structure of woody vegetation were not expected to account for meaningful change because they have been operating within the region prior to the re-introduction of elephants.

## 2. Study area

The VLNR is a 31,855 ha wildlife reserve situated in the Limpopo Province of South Africa. This semi-arid region experiences a mean annual rainfall of about 366 mm (36% coefficient of variation) (31-year record) that falls during summer (November to March) (O'Connor, 1992, 1999). Annual rainfall over the period of study was highly variable (Supplementary Material 1). The first ten years of monitoring and the years preceding were generally below average with the exception of the highest rainfall season on record (1999/2000); but there was a three-year sequence of above-average rainfall from 2008 to 2010. Temperature at Musina (80 km E but comparable) ranges from 7.2 °C (June, July) to 20.3 °C (December) for average minimum monthly, and from 24.7 °C (June) to 32 °C (October, November, December) for average maximum monthly. Severe black frost is an uncommon (and unquantified) occurrence but occurred during the winter of 2010.

Topography of most of the reserve is relatively flat, on which vegetation is broadly described as Musina Mopane Bushveld, with small hills occupying about 20% of the reserve and supporting Limpopo Ridge Bushveld (Mucina and Rutherford, 2006). At a finer spatial scale, 20 main vegetation types have been described (O'Connor, 1992, unpublished). Dryland vegetation of the VLNR, which is dominated by the ubiquitous *Colophospermum mopane*, shows a close correspondence between topo-edaphic-geologic units and vegetation types (O'Connor, 1992). Geology includes base-rich, base-poor and calcium-rich rock types supporting soils with corresponding properties. A distinctive feature is a flat region underlain by deep (>3 m) palaeo-fluvial deposits of clay-loam texture occupying a third of the reserve and supporting *C. mopane* Woodland. Old crop lands are dominated by *Acacia* (now *Vachellia*) *tortilis*. (*Acacia* is retained in this paper because not all species reported on have yet been ascribed to a new genus.) Three non-perennial rivers that flow only after large storms traverse the reserve. Their associated alluvial soils that cover about 5% of the reserve support riparian vegetation types including *Acacia* Woodland on former hydromorphic grassland (MacGregor and O'Connor, 2004; O'Connor, 2001).

The VLNR was established in 1991 through the amalgamation of livestock farms. All livestock were removed at time of purchase. The population sizes for mammalian browser or mixed feeder species in 1993 was 12 for giraffe, 968 for kudu, 256 for eland, 770 for impala, and small numbers of bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), and steenbok (*Raphicerus campestris*). Populations of kudu, eland and impala declined between 1993 and 2010; that of giraffe increased. Five black rhinoceros (*Diceros bicornis*) were re-introduced in 2004. Fire has not been an ecological factor in the VLNR since before 1950, bar a small area (<100 ha) that burnt in the north-west corner in 2002. Fourty three elephants were reintroduced into the VLNR as four separate groups between 1991 and 1994. The founder population originated from Kruger and Gona-Re-Zhou National Parks. By 2007 the founder population had increased to 68 elephants, after which 29 elephants broke into the reserve from a nearby population in Botswana in 2009. Population size was 105 elephants in 2011, occurring as seven or eight herds that merge and split frequently (Page, unpublished information).

## 3. Methods

### 3.1. Data collection

The study area was stratified first according to habitat (dryland versus riparian), and secondly according to vegetation type. A sample was drawn for the main vegetation types in which sampling

intensity varied in relation to the size of the vegetation type, its perceived importance for elephant foraging, or perceived conservation importance. Thirteen dryland and three riparian vegetation types were sampled in total. Sampling was by the use of 50 m belt transects that were permanently located in February 1997 ( $n = 148$ ) and re-sampled in 2010. Areas in close proximity of water were avoided on account of potential piosphere effects (Chamaillé-Jammes et al., 2009; Mukwashi et al., 2012). Transects were of variable width in relation to woody density. A transect was sampled in a nested fashion in which a core width was measured for the most common species, and width was then increased to accommodate any additional uncommon species of trees and shrubs. Each woody individual was measured for: (i) position along the transect to enable relocation; (ii) stem circumference of each stem above any basal swelling but below the first branching point; (iii) height of the highest living material on each plant to the nearest decametre; (iv) percentage loss of phytomass to elephant utilization, other browsers, stress (mainly moisture), frost, fire, or unknown, ranked using an eight-point scale (Walker, 1976). The age of lost phytomass was scored as less than (recent use) or greater than 2 years (old use) based on weathering of broken wood using a field experimental calibration (Page, unpublished data). Nomenclature follows the African Plants Database (2012).

Basal area was chosen as a measure of species abundance on account of its relation to phytomass (Rutherford, 1979). For each transect, total basal area, absolute basal area per species, and the proportion contributed by each species to total basal area was computed for each sampling occasion. Calculations were standardized to a measure per unit ground area in order to account for differences in the width of transects or nests within each transect.

### 3.2. Analysis

The analysis was conducted at three spatial levels. These were (i) overall trends within the reserve ( $n = 148$ ), (ii) dryland ( $n = 110$ ) and riparian ( $n = 38$ ) habitats, and (iii) 12 vegetation types for which there was a sufficient sample ( $n > 3$ ) for analysis.

The set of response variables defined below was selected to reflect composition, diversity and structure of the woody vegetation. A further set of variables defined loss of plant biomass to various agents. Each variable was examined at each level of the spatial hierarchy for whether a significant change had occurred over the period of study, using a paired test. A paired  $t$ -test was used if differences, without or with appropriate transformation, were described by a normal distribution, examined with the Shapiro–Wilk statistic. Otherwise a Wilcoxon's signed-ranks test was used.

Each variable was also examined for whether it differed between habitats or among vegetation types in terms of amount of change and, if relevant, amount at the commencement (1997) and termination (2010) of the study. Differences between the two habitats were examined with a  $t$ -test. Differences among vegetation types were examined using a Kruskal–Wallis non-parametric one-way analysis of variance. This was chosen because the pronounced right skew of all variables could not be corrected by transformation.

Compositional change per plot between 1997 and 2010 was measured using Euclidean distance ( $ED$ ):  $ED_{i,h} = \sqrt{\sum (a_{1997,j} - a_{2010,j})^2}$  where  $a_{1997,j}$  is the abundance (proportion of plot total basal area) of species  $j$  in the 1997 sample.  $ED$  was chosen because of the geometric elegance of the measure and because large differences are weighted more heavily than several small differences, resulting in greater sensitivity to species that change the most, and because the problems relating to its use in dissimilarity matrices were not relevant (McCune and Grace, 2002, p. 55).

Change in the abundance of individual species was analyzed using only transects on which a species occurred in at least one

of the sampling occasions. Only results for absolute abundance are presented because those for proportional abundance were similar. For most species this was conducted only at a reserve level owing to small sample sizes, but a few of the common species were also analyzed according to habitat.

Changes over 13 years in species richness, species diversity, and evenness were examined. Change in species richness was measured as the difference in species density per transect. 'Species flux' was defined as the total number of species that appeared in either only 1997 but not 2010, or in 2010 but not 1997. Diversity was estimated using the Shannon–Wiener diversity index  $H' = -\sum p_i \ln p_i$  where  $p_i$  is the proportion of total basal area contributed by species  $i$ . Evenness was estimated (Alatalo, 1981) as  $E = (N2 - 1) / (\exp H' - 1)$  where  $N2 = 1 / \sum p_i^2 \cdot H'$  and was calculated per unit ground area in order to accommodate the effect of different transect sizes.

Vegetation structure was reflected by total woody basal area (per unit ground area) and the density of different height classes. The height classes (m) were:  $\leq 0.3$ ;  $>0.3-1$ ;  $>1-2$ ;  $>2-3$ ;  $>3-5$ ;  $>5-7$ ; and  $>7$  m.

The impact per transect of each agent of biomass loss was calculated as summarized for each core transect by calculating a weighted average using individual basal area as the weight. The agents considered were elephants, other browsers, and stress-related dieback.

Statistical analysis was conducted using SAS 9.3 (SAS, 2010). Alpha was set at 0.5 for  $n > 30$  but at 0.1 for  $n = 5-30$  (Stewart-Oaten, 1995).

## 4. Results

### 4.1. Composition

Composition of the woody component changed between 1997 and 2010 for the reserve and in each habitat, although change was twofold greater within riparian than dryland habitat ( $Z = 3.29$ ;  $P < 0.001$ ). Composition also changed for all vegetation types except *C. mopane-Grewia flava* Woodland (Table 1), although the extent of change differed among types (KW  $\chi^2 = 48.8$ ; d.f. = 11;  $P < 0.0001$ ). Compositional change was conspicuous for *Acacia*, *Commiphora*, and Riverine Woodland types, and less so for vegetation types dominated by *C. mopane*. In correspondence, there were changes in the basal area of 22 of 47 woody species of trees and shrubs assessed, of which eight species showed an increase and 14 a decrease (Table 2). Conspicuous decreases were evident for *Acacia nilotica*, *Acacia tortilis* in riparian habitat, *Albizia anthelmintica*, *Cadaba termitaria*, most *Commiphora* species, *Ximenia americana* and *Ziziphus mucronata*. In contrast, basal area of *C. mopane* and *Terminalia prunioides*, the two most common tree species of dryland, increased, with a corresponding increase in their contribution to total basal area ( $P < 0.0001$ ). The contribution of *C. mopane* increased by 12.5% to 55.7%, by 4.6% to 49.9%, and by 7.1% to 51.7% for riparian habitat, dryland habitat, and the reserve overall, respectively, whilst *T. prunioides* increased by 0.54% to 2.84%. Ten species showed a pronounced but non-significant decline (Table 2) as a result of a dramatic decline on some transects but no change on others, illustrating marked spatial variability in patterns of change.

### 4.2. Diversity

Change in diversity variables was not as marked as change in composition. Species richness (Table 3) declined across the reserve, as well as within dryland and riparian habitats between 1997 and 2010. For vegetation types, a decline was recorded for *C. mopane* Woodland, *Commiphora* Woodland, *C. mopane* Riverine Woodland,

**Table 1**Compositional change expressed as Euclidean distance (ED) between 1997 and 2010 for the reserve, two main habitat types, and 12 vegetation types (each  $n > 3$ ).

Unit	<i>n</i>	ED <sub>x</sub>	ED S.E.	<i>P</i> <sup>a</sup>
Reserve	148	0.144	0.0126	<0.0001
Habitat				
Dryland	110	0.118	0.0127	<0.0001
Riparian	38	0.219	0.0297	<0.0001
Vegetation types				
<i>Acacia</i> woodland	7	0.349	0.0820	0.0053
<i>Commiphora</i> Woodland	6	0.240	0.0923	0.0485
Sandstone Hills	9	0.188	0.0415	0.0019
Mixed Woodland	5	0.133	0.0226	0.0041
<i>C. mopane</i> – <i>Terminalia prunioides</i> open Shrub Woodland	13	0.065	0.0176	0.0031
<i>C. mopane</i> Shrub Woodland	6	0.083	0.0453	0.0313
<i>Colophospermum mopane</i> Woodland	40	0.083	0.0146	<0.0001
Riverine Woodland	16	0.246	0.0356	<0.0001
<i>C. mopane</i> Riverine Woodland	14	0.094	0.0265	0.0001
<i>Combretum apiculatum</i> – <i>C. mopane</i> open Woodland	16	0.123	0.0123	<0.0001
<i>C. mopane</i> – <i>Grewia flava</i> Woodland	5	0.283	0.1600	0.1511
<i>Sesamothamnus lugardii</i> open Woodland	4	0.007	0.0016	0.0246

<sup>a</sup> Paired *t*-test or Wilcoxon's signed rank test, as appropriate.

and Riverine Woodland. Species flux ranged from 0.8 to 3.8 species per transect and was correlated with the total number of species recorded on a transect in 1997 for both riparian ( $r = 0.44$ ; d.f. = 36;  $P = 0.0053$ ) and dryland ( $r = 0.36$ ; d.f. = 108;  $P < 0.0001$ ) habitats. In correspondence, diversity ( $H'$ ) (Table 3) declined over the reserve, within riparian habitat and marginally within dryland habitat. Diversity declined only on Riverine Woodland and *C. mopane* Riverine Woodland types. Changes in evenness were recorded only for two vegetation types, namely Sandstone Hills and *C. mopane* Riverine Woodland. Thus changes in diversity were primarily a consequence of changes in species richness.

#### 4.3. Structure

Woody basal area (Table 3) increased over the reserve and on dryland habitat, but decreased on riparian habitat. For vegetation types, an increase was recorded for the dryland types of *C. mopane* Woodland and *C. mopane*–*Terminalia prunioides* Shrub Woodland, and a decrease for dryland *Commiphora* Woodland, riparian *Acacia* woodland, and a tendency for decrease of Riverine Woodland. Changes in the density of different height classes were relatively consistent across the reserve, two habitats and twelve vegetation types with a few marked exceptions (Fig. 1). The density of the tallest trees has in general decreased and the density of trees of medium height (2–5 m) remained stable. The changes in density of the three smallest height classes (0–2 m) indicate that regeneration had in general been successful, with the density of the smallest individuals (0–1 m) being maintained and that of 1–2 m tall individuals increasing. *Acacia* woodland was an exception to this pattern, with the density of all except the smallest height class decreasing, indicating regeneration was occurring. The decline in density of larger trees was also conspicuous for *Commiphora* Woodland. By contrast, the density of most height classes of *C. mopane*–*Terminalia prunioides* Shrub Woodland, *C. mopane*–*Grewia flava* Woodland and *Sesamothamnus lugardii* Open Woodland was stable.

#### 4.4. Causes for loss of phytomass

Stress-related dieback increased 2.2-fold across the reserve, with a 1.7- and 6.5-fold increase on dryland and on riparian habitat respectively (Fig. 2). For eight of 12 vegetation types, stress-related dieback increased between 2.1- and 7.4-fold. The greatest increases were recorded for *C. mopane* Riverine Woodland and Riverine Woodland. Stress-related dieback differed among vegetation

types in 1997 ( $X^2 = 41.5$ ; d.f. = 11;  $P < 0.0001$ ), when it was highest in *C. mopane* Woodland and *C. mopane* Shrub Woodland; for which there was a small increase in the former by 2010 but the latter remained unchanged (Fig. 2). The amount of stress-related dieback differed among vegetation types in 2010 as well ( $X^2 = 27.8$ ; d.f. = 11;  $P = 0.0034$ ), at which time it was greatest for a number of *C. mopane* dominated vegetation types, including *C. mopane* Shrub Woodland, *C. mopane* Woodland, and *C. mopane* Riverine Woodland.

Old elephant utilization (> 2 years before the survey), but not recent elephant utilization (< 2 years), increased conspicuously between 1997 and 2010 (Fig. 2). The proportion of biomass lost to old elephant use (excluding debarking) increased by 9.4-, 7.8- and 12.9-fold for the reserve, dryland and riparian habitats respectively. The two habitats did not differ in 1997 ( $t = 0.63$ ; d.f. = 102.3;  $P = 0.5294$ ) but riparian showed 2.1-fold greater use in 2010 than dryland ( $t = 3.58$ ; d.f. = 52.8;  $P = 0.0007$ ). Differences among vegetation types were relatively minor in 1997 ( $X^2 = 18.3$ ; d.f. = 11;  $P = 0.0739$ ), with especially low use of some dryland *C. mopane* vegetation types, but were pronounced by 2010 ( $X^2 = 48.1$ ; d.f. = 11;  $P < 0.0001$ ), with conspicuous old use of some riparian types and very little old use of *C. mopane* Shrub Woodland. Correspondingly, an increase in old elephant use was evident for all vegetation types other than *C. mopane* Shrub Woodland between 1997 and 2010, the extent of which differed among vegetation types ( $X^2 = 52.1$ ; d.f. = 11;  $P < 0.0001$ ). Old use of some dryland *C. mopane* vegetation types had increased markedly, whereas use of some riparian types was unchanged on account of consistently high levels of old use.

By contrast, the proportion of biomass lost to recent (<2 year old) elephant use was 3.2-fold greater for riparian than dryland habitat in 1997 ( $t = 2.53$ ;  $P = .0125$ ) but did not differ in 2010 ( $t = 0.09$ ;  $P = 0.9286$ ), and thus the extent of change between 1997 and 2010 differed between the two habitats ( $t = 5.81$ ;  $P < 0.0001$ ). Correspondingly, recent elephant use had decreased between 1997 and 2010 for riparian but not dryland habitat. Differences among vegetation types in terms of recent elephant use were stark in 1997 ( $X^2 = 61.7$ ; d.f. = 11;  $P < 0.0001$ ), with conspicuous use of riparian vegetation types as well as of *Sesamothamnus lugardii* Open Woodland and little use of dryland vegetation types dominated by *C. mopane*. By contrast, there were no differences among vegetation types for recent elephant use in 2010 ( $X^2 = 6.7$ ; d.f. = 11;  $P = 0.8196$ ). Correspondingly, there were stark differences among vegetation types in the extent of change between 1997 and 2010 ( $X^2 = 46.7$ ; d.f. = 11;  $P < 0.0001$ ).

**Table 2**Change in basal area (cm<sup>2</sup>m<sup>-2</sup>) of the main woody species between 1997 and 2010 (*P* in bold print: *P* < 0.05; *P* in italics: 0.05 < *P* < 0.1).

Species	<i>n</i>	Basal area (cm <sup>2</sup> m <sup>-2</sup> ) 1997	Basal area (cm <sup>2</sup> m <sup>-2</sup> ) 2010	Mean change (cm <sup>2</sup> m <sup>-2</sup> )	<i>P</i> <sup>a</sup>
<i>Acacia grandicornuta</i>	10	0.830	0.245	-0.585	0.2754
<i>Acacia newbrowmii</i>	9	0.205	0.213	0.008	0.8378
<i>Acacia nigrescens</i>	17	2.009	1.573	-0.437	0.7436
<i>Acacia nilotica</i>	11	2.291	0.160	-2.131	<b>0.0020</b>
<i>Acacia senegal</i>	12	0.202	.320	0.117	0.1514
<i>Acacia tortilis</i>	51	2.903	0.964	-1.939	<b>&lt;.0001</b>
<i>A. tortilis</i> dryland	25	0.706	0.283	-0.423	0.1078
<i>A. tortilis</i> riparian	26	5.015	1.618	-3.397	<b>0.0025</b>
<i>Albizia anthelmintica</i>	7	0.631	0.001	-0.630	<b>0.0156</b>
<i>Balanites pedicellaris</i>	10	0.239	0.114	-0.125	0.1934
<i>Boscia albitrunca</i>	60	0.287	0.278	-0.009	<b>0.0036</b>
<i>Boscia foetida</i>	64	0.827	0.898	0.071	<b>0.0095</b>
<i>Cadaba termitaria</i>	14	0.063	0.010	-.0528	<b>0.0040</b>
<i>Colophospermum mopane</i>	140	8.086	9.148	1.062	<b>&lt;.0001</b>
<i>C. mopane</i> dryland	108	6.996	7.898	0.903	<b>&lt;.0001</b>
<i>C. mopane</i> riparian	32	11.765	13.367	1.602	<b>0.0004</b>
<i>Combretum apiculatum</i>	33	0.739	0.771	0.031	0.9930
<i>Combretum imberbe</i>	20	8.092	8.358	0.266	0.9217
<i>Combretum microphyllum</i>	21	0.040	0.054	0.013	<b>0.0209</b>
<i>Combretum mosambicense</i>	5	0.026	0.091	0.066	0.1608
<i>Commiphora africana</i>	17	0.026	0.032	0.006	0.4954
<i>Commiphora glandulosa</i> <sup>*</sup>	36	0.940	0.340	-0.600	<b>0.0158</b>
<i>Commiphora mollis</i> <sup>*</sup>	33	0.643	0.456	-0.187	<b>0.0034</b>
<i>Commiphora pyracanthoides</i> <sup>*</sup>	25	0.309	0.108	-0.200	<b>&lt;.0001</b>
<i>Commiphora schimperi</i>	5	0.056	0.036	-0.021	0.4985
<i>Commiphora tenuipetiolata</i>	5	1.493	0.635	-0.859	0.0599
<i>Commiphora viminea</i> <sup>*</sup>	12	2.663	2.189	-0.474	<b>0.0320</b>
<i>Cordia ovalis</i>	10	0.110	0.116	0.006	0.7346
<i>Croton megalobotrys</i>	11	2.191	0.996	-1.195	0.5571
<i>Dichrostachys cinerea</i>	81	0.095	0.070	-0.025	<b>0.0173</b>
<i>Ehretia rigida</i>	15	0.031	0.034	0.003	0.6753
<i>Flueggia virosa</i>	21	0.035	0.064	0.029	<b>0.0002</b>
<i>Grewia bicolor</i>	56	0.088	0.190	0.102	<b>0.0088</b>
<i>G. bicolor</i> dryland	43	0.106	0.245	0.138	<b>0.0019</b>
<i>G. bicolor</i> riparian	13	0.028	0.010	-0.019	0.0936
<i>Grewia flava</i>	56	0.135	0.177	0.042	0.1409
<i>G. flava</i> dryland	38	0.148	0.244	0.096	<b>0.0051</b>
<i>G. flava</i> riparian <sup>*</sup>	18	0.109	0.037	-0.072	0.1473
<i>Grewia flavescens</i>	23	0.135	0.086	-0.049	0.9531
<i>Grewia tenax</i>	17	0.041	0.063	0.021	0.7730
<i>Grewia villosa</i>	18	0.015	0.028	0.013	0.2199
<i>Kirkia acuminata</i>	8	2.161	1.545	-0.616	0.1878
<i>Lannea schweinfurthii</i> <sup>*</sup>	15	1.301	0.912	-0.389	0.1074
<i>Lycium schizocalyx</i>	10	0.016	0.006	-0.007	<b>0.0874</b>
<i>Maerua parvifolia</i>	64	0.041	0.048	0.006	0.0760
<i>Philenoptera violacea</i>	23	1.839	1.915	0.076	0.6856
<i>Rhigozum zambesiicum</i>	28	0.102	0.185	0.083	0.0833
<i>Salvadora angustifolia</i>	32	1.264	1.491	0.284	<b>0.0478</b>
<i>Schotia brachypetala</i>	7	2.226	1.708	-0.517	0.4085
<i>Sclerocarrya birrea</i>	11	1.095	0.539	-0.555	0.1230
<i>Sesamothamnus lugardii</i>	9	48.881	48.498	-0.383	0.3750
<i>Sterculia rogersii</i>	15	5.128	3.736	-1.396	0.5416
<i>Terminalia prunioides</i>	72	0.812	0.977	0.165	<b>&lt;.0001</b>
<i>Ximania americana</i>	47	0.250	0.133	-0.117	<b>0.0001</b>
<i>Ziziphus mucronata</i>	28	0.296	0.171	-0.125	<b>0.0001</b>

<sup>\*</sup> Test undertaken using log-transformed data.<sup>a</sup> Paired *t*-test or Wilcoxon's signed rank test, as appropriate.

Overall elephant use (irrespective of age) was thus also greater for riparian than dryland habitat for both 1997 ( $t = 2.41$ ;  $P = 0.0173$ ) and 2010 ( $t = 3.93$ ;  $P = 0.0001$ ) by 2.5- and 2-fold respectively, but the extent of change over time did not differ ( $t = 0.0$ ;  $P = 0.9998$ ). However, dryland and riparian habitat, as well as the reserve, showed an increase in overall elephant use between 1997 and 2010 (Fig. 2). Overall elephant use of eight of 12 vegetation types increased between 1997 and 2010. Vegetation types differed in the extent of overall elephant use in both 1997 ( $X^2 = 41.7$ ; d.f. = 11;  $P < 0.0001$ ) and 2010 ( $X^2 = 46.3$ ; d.f. = 11;  $P < 0.0001$ ). In 1997, overall use of *Acacia* Woodland was particularly high whereas that of *C. mopane* Shrub Woodland, *C. mopane* Woodland,

and *Combretum apiculatum*-*C. mopane* Open Woodland was low. By 2010, overall use of Riverine Woodland and *C. mopane* Riverine Woodland was high but that of *C. mopane* Shrub Woodland remained low.

The spatial pattern of debarking impact changed over time (Fig. 3). Debarking impact was 2.4-times greater in 1997 than 2010 across the reserve but the pattern of change differed between habitats. Debarking impact was 8-fold greater on riparian than dryland habitat in 1997 ( $t = 2.57$ ; d.f. = 37.6;  $P = 0.0144$ ), but by 2010 there was no difference between habitats ( $t = 0.09$ ; d.f. = 146;  $P = 0.9286$ ). Correspondingly, the change in debarking impact between the two surveys differed between habitats

**Table 3**

Change in woody basal area, species richness (S), 'species flux' (F), Shannon–Wiener diversity ( $H'$ ), and evenness ( $E$ ) between 1997 and 2010 for the VLNR, its two main habitats, and 12 main vegetation types ( $P$  in bold print:  $P < 0.05$ ;  $P$  in italics:  $0.05 < P < 0.1$ ).

Unit	$n$	Basal area 1997 (cm <sup>2</sup> m <sup>-2</sup> )	Change in basal area to 2010 (cm <sup>2</sup> m <sup>-2</sup> )	$P$	S 1997	Change in S to 2010	$P$ for S	Species flux	$H'$ 1997	Change in $H'$ to 2010	$P$ for $H'$	$E$ 1997	Change in $E$ to 2010	$P$ for $E$
Reserve Habitat	148	17.1603	-0.4219	0.4700	8.43	-0.76	<b>&lt;0.0001</b>	2.230	0.8861	-0.2021	<b>0.0002</b>	0.6000	-0.0074	0.5675
Dryland	110	15.1851	0.3650	<b>0.0010</b>	8.12	-0.56	<b>0.0008</b>	1.755	0.863	-0.1330	<b>0.0353</b>	0.5903	-0.0135	0.6492
Riparian	38	22.8777	-2.7000	<b>0.0109</b>	9.32	-1.32	<b>0.0005</b>	3.605	0.953	-0.4024	<b>0.0016</b>	0.6271	0.0101	0.6718
<i>Vegetation types</i>														
Acacia woodland	7	8.8359	-5.9822	<b>0.0002</b>	6.00	-1.57	0.2500	3.143	0.870	-0.3497	0.1473	0.662	0.0990	0.2163
Commiphora Woodland	6	13.2308	-2.2820	<b>0.0561</b>	10.83	-2.17	<b>0.0625</b>	3.667	1.319	-0.9202	0.1563	0.733	-0.1051	0.2347
Sandstone Hills	9	12.5134	-0.4745	0.6497	12.11	-0.22	0.5000	1.556	1.508	-0.3368	0.3136	0.712	-0.0555	<b>0.0665</b>
Mixed Woodland	5	14.1700	0.3179	0.7956	13.60	-1.80	0.1250	2.600	1.551	-0.3000	0.4331	0.604	0.0255	0.1608
<i>C. mopane</i> - <i>T. prunioides</i> Shrub Woodland	13	8.8091	1.1070	<b>0.0215</b>	7.85	0.38	0.3984	1.308	0.922	0.0156	0.8259	0.576	-0.0052	0.7354
<i>C. mopane</i> Shrub Woodland	6	8.7843	0.4340	0.5058	6.33	-0.83	0.1250	0.833	0.588	-0.0120	0.4375	0.593	-0.0424	0.2969
<i>Colophospermum mopane</i> Woodland	40	13.1650	1.4377	<b>&lt;0.0001</b>	6.25	-0.60	<b>0.0033</b>	1.450	0.561	-0.0651	0.1837	0.536	-0.0022	0.7216
Riverine Woodland	16	25.5471	-3.7638	<b>0.0740</b>	10.88	-1.38	<b>0.0703</b>	3.813	1.211	-0.5660	<b>0.0192</b>	0.699	0.0069	0.8731
<i>C. mopane</i> Riverine Woodland	14	28.0360	0.1341	0.9129	9.21	-1.14	<b>0.0449</b>	3.786	0.681	-0.3046	<b>0.0580</b>	0.527	-0.0233	<i>0.0906</i>
<i>Combretum apiculatum</i> - <i>C. mopane</i> Open Woodland	16	9.3066	0.7511	0.2225	9.13	-0.56	0.1484	1.813	1.167	-0.0467	0.7568	0.619	0.0102	0.5588
<i>C. mopane</i> - <i>Grewia flava</i> Woodland	5	16.0320	-3.8984	0.4271	6.60	-1.60	0.1250	2.000	0.540	-0.2866	0.3530	0.537	-0.0548	0.4653
<i>Sesamothamnus lugardii</i> Open Woodland	4	111.8424	-1.4560	0.8025	9.50	0.25	1.0000	2.750	0.160	-0.0031	0.8112	0.328	0.0052	0.6388

( $t = 4.18$ ; d.f. = 40.5;  $P = 0.0010$ ). In 1997, debarking impact was recorded in effect for only six of 12 vegetation types ( $X^2 = 50.0$ ; d.f. = 11;  $P < 0.0001$ ), and was especially prominent for *Acacia* Woodland and Riverine Woodland. There were no differences among vegetation types in 2010 ( $X^2 = 6.7$ ; d.f. = 11;  $P = 0.8196$ ) although *C. mopane* Shrub Woodland was, in effect, not impacted by debarking. Correspondingly vegetation types differed in the extent of change in debarking between 1997 and 2010 ( $X^2 = 34.8$ ; d.f. = 11;  $P = 0.0003$ ), which was most pronounced for some riparian vegetation types and for *Commiphora* Woodland.

Browsing by other herbivores was a minor impact on habitats or vegetation types; results are therefore not presented.

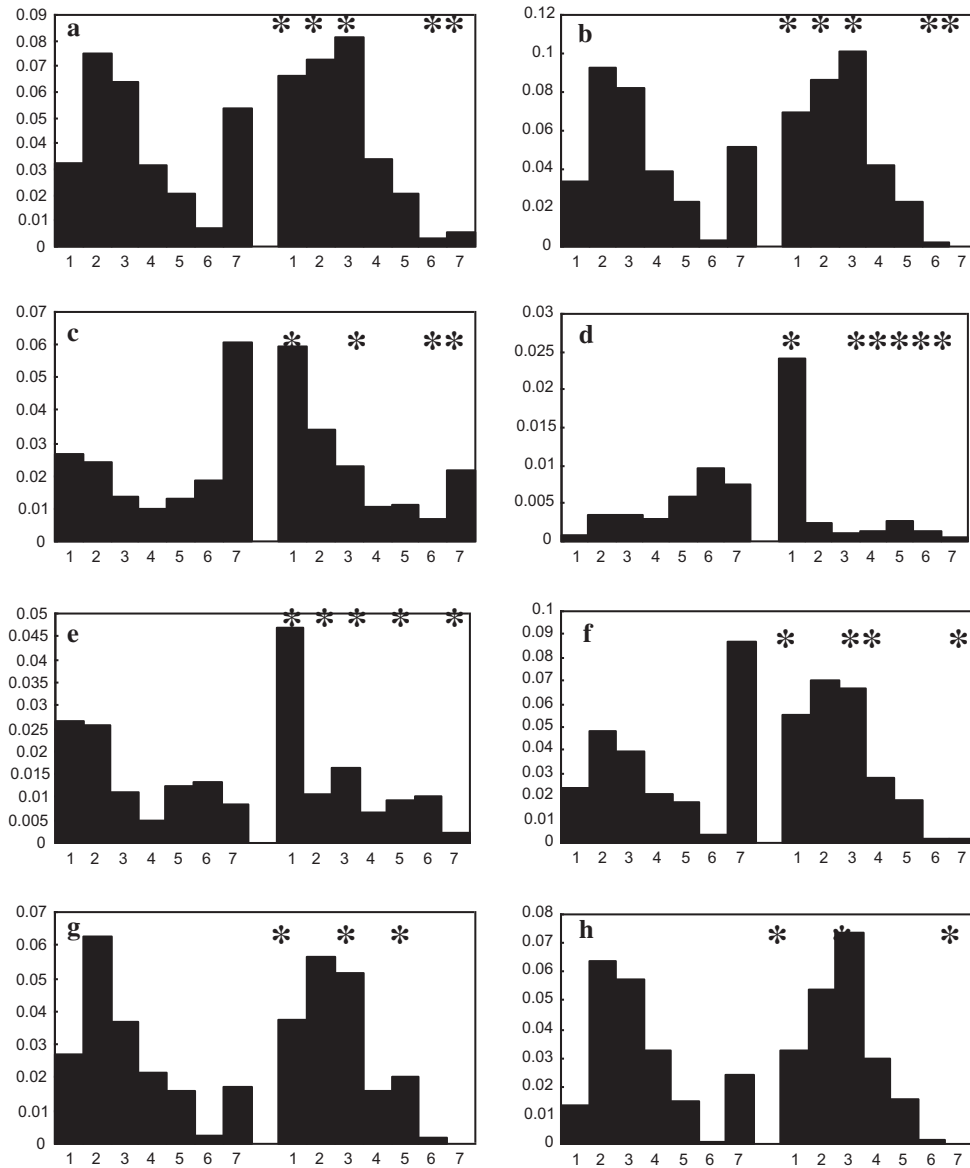
## 5. Discussion

### 5.1. Pattern of changes

During the 19 years since elephants were re-introduced, changes have occurred in the composition, diversity, and structure of the woody vegetation of the VLNR. These were not equally distributed between habitats or among vegetation types. Riparian habitat showed a greater change in composition (Table 1) and diversity (Table 3), and a greater decline of species richness (Table 3), density of tall trees (Fig. 1) or total basal area (Table 3), than dryland habitat showed. Most riparian vegetation types mirrored this pattern of change, but *Commiphora* Woodland, a dryland vegetation type, showed comparable changes. By contrast, total basal area of dryland vegetation types dominated by *C. mopane*

increased. The relative influence of elephants and stress-related agents varied across vegetation types (Fig. 2).

The general pattern of changes corresponds with what has been recorded elsewhere in Africa in areas in which elephants occur. Severe elephant impact has been reported for *Acacia* woodlands of various types (Barnes, 1983, 1985; Botha et al., 2002; Field and Ross, 1976; Harrington and Ross, 1974; Okula and Sise, 1986; Tchamba and Mahamat, 1992; Vesey-Fitzgerald, 1974), specifically for *Acacia tortilis*-dominated woodlands (Anderson and Walker, 1974; Mwalyosi, 1987, 1990; Pellew, 1983; Ruess and Halter, 1990), *Commiphora* Woodlands (Barnes, 1983, 1985; Leuthold, 1977), and riverine woodland (Anderson and Walker, 1974; Skarpe et al., 2004). The effects of moisture and temperature stress on plant survival or loss of phytomass have not, to our knowledge, been previously examined in the context of savanna systems. Determining the relative contributions of elephants and stress, and their interaction, to overall phytomass loss or mortality for correlated data is difficult. However, several conclusions are possible. Dryland vegetation types strongly dominated by *C. mopane*, which covered more than 70% of the VLNR, showed less change despite stress-related dieback and elephant use (Fig. 2). *C. mopane* has a growth habit of strong coppicing in response to loss of biomass to elephants or to drought die-back (Smallie and O'Connor, 2000; Styles and Skinner, 2000). Taller trees can, however, be lost to elephant use (Anderson and Walker, 1974; Lewis, 1991), which was evident in the extent of compositional change and decline in the density of tall trees of *C. mopane* Riverine Woodland compared with dryland *C. mopane* vegetation types (Fig. 1). Mortality of this species between 1997 and 2002, then 2002 and



**Fig. 1.** Change in the density (individuals m<sup>-2</sup>) per height class for (a) the reserve; (b) dryland and (c) riverine habitats; and for vegetation types: (d) *Acacia* Woodland; (e) *Commiphora* Woodland; (f) Sandstone Hills; (g) Mixed Woodland; (h) *Colophospermum mopane*-*Terminalia prunioides* Shrub Woodland; (i) *C. mopane* Shrub Woodland; (j) *C. mopane* Woodland; (k) Riverine Woodland; (l) *C. mopane* Riverine Woodland; (m) *Combretum apiculatum*-*C. mopane* Open Woodland (Sandveld); (n) *C. mopane*-*Grewia flava* Woodland; and (o) *Sesamothamnus lugardii* Woodland. Key to the height classes (m): 1, 0 to <0.3; 2, >0.3 to <1; 3, >1 to <2; 4, >2 to <3; 5, >3 to <5; 6, >5 to <7; and 7, >7. An asterisk above a column in 2010 indicates a change in density of that height class from 1997 ( $P < 0.05$ ).

2010, was 2.6% then 7% for riparian habitat compared with 0.9% to 5.8% in dryland habitat. The primary agent of deaths was elephants for 68% for riparian habitat but stress-related agents for 74% of dryland habitat (O'Connor, unpublished). The main agent of stress was drought, which has previously affected populations of *C. mopane* in the VLNR (O'Connor, 1999), with extreme impacts of patch die-back occurring on degraded areas (MacGregor and O'Connor, 2002).

## 5.2. Significance of changes

The elephant population of the VLNR is at low density by comparison with other African savanna systems not seriously impacted by poaching. By 1994, elephants were at a density of approximately 0.16 km<sup>-2</sup>, which had doubled to 0.33 km<sup>-2</sup> by 2011. Density of elephants in some large parks ranges between 0.11 (Etosha, Namibia) and 3.45 (Hwange, Zimbabwe) elephants km<sup>-2</sup> (Blanc

et al., 2007) for mean annual rainfall of 359 mm for Etosha and 600 mm for Hwange (De Beer et al., 2006; Dudley et al., 2001). Values of elephant density for comparable semi-arid systems are thus similar or 10-fold higher than those for the VLNR. Furthermore, the founding population of the VLNR did not contain any mature bulls, which generally have a greater impact on woody vegetation than cows (Barnes, 1982; Barnes et al., 1994; Clegg, 2010; Guy, 1976; Hiscocks, 1999). Notwithstanding a population of low density with an under-representation of adult bulls, some vegetation types were heavily impacted by elephants (Figs. 1 and 2; Tables 1 and 3). *Acacia* Woodland (MacGregor and O'Connor, 2004) and *Commiphora* Woodland (personal observation) had already been impacted by the late 1990s. By 2010, *Acacia* Woodland had nearly been transformed to its original state of hydromorphic grassland (Fig. 1; O'Connor, 2001) and was no longer used much by elephants (Figs. 2 and 3). *Commiphora* Woodland similarly lost most trees (Fig. 1) and correspondingly showed little use by elephants in 2010



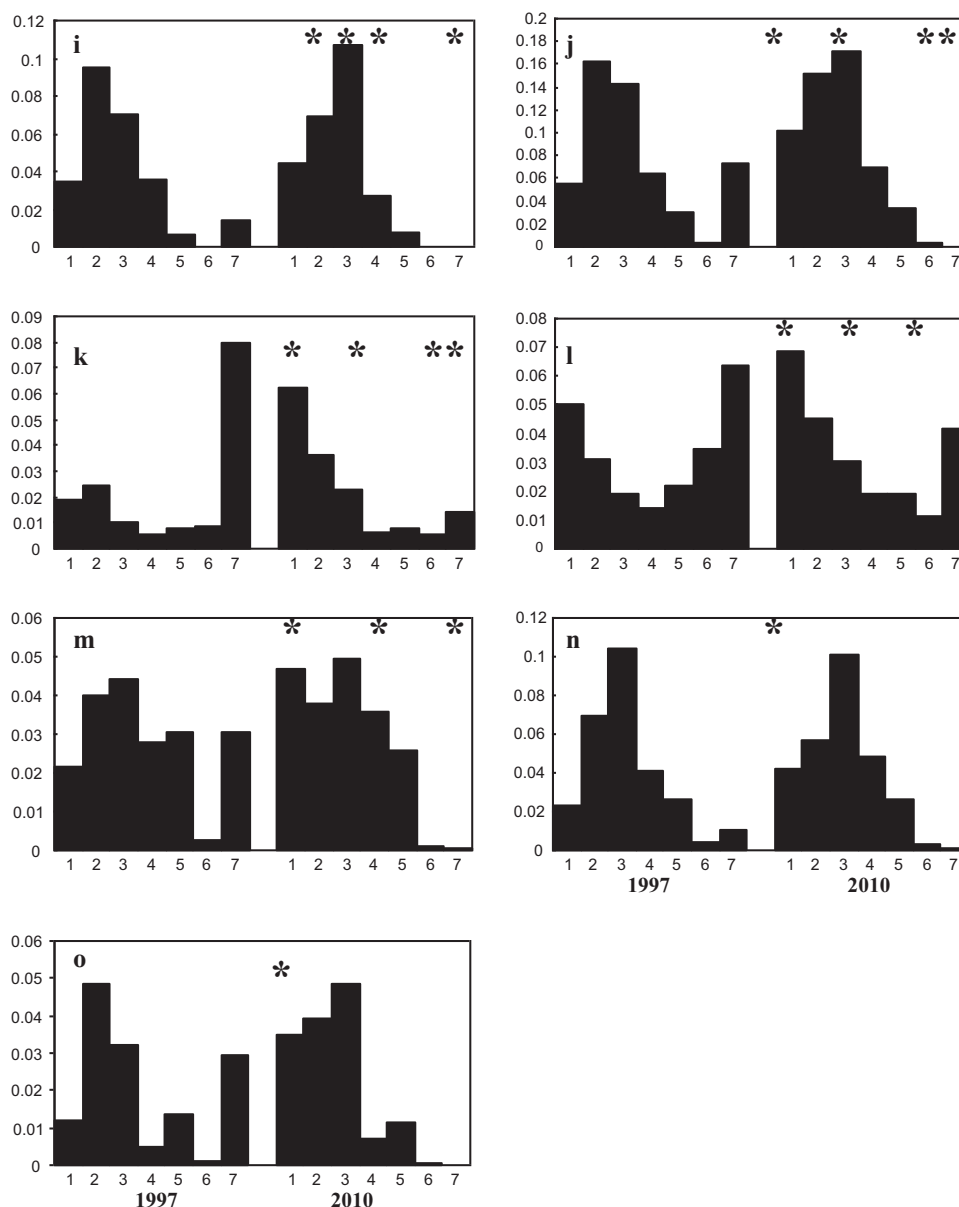


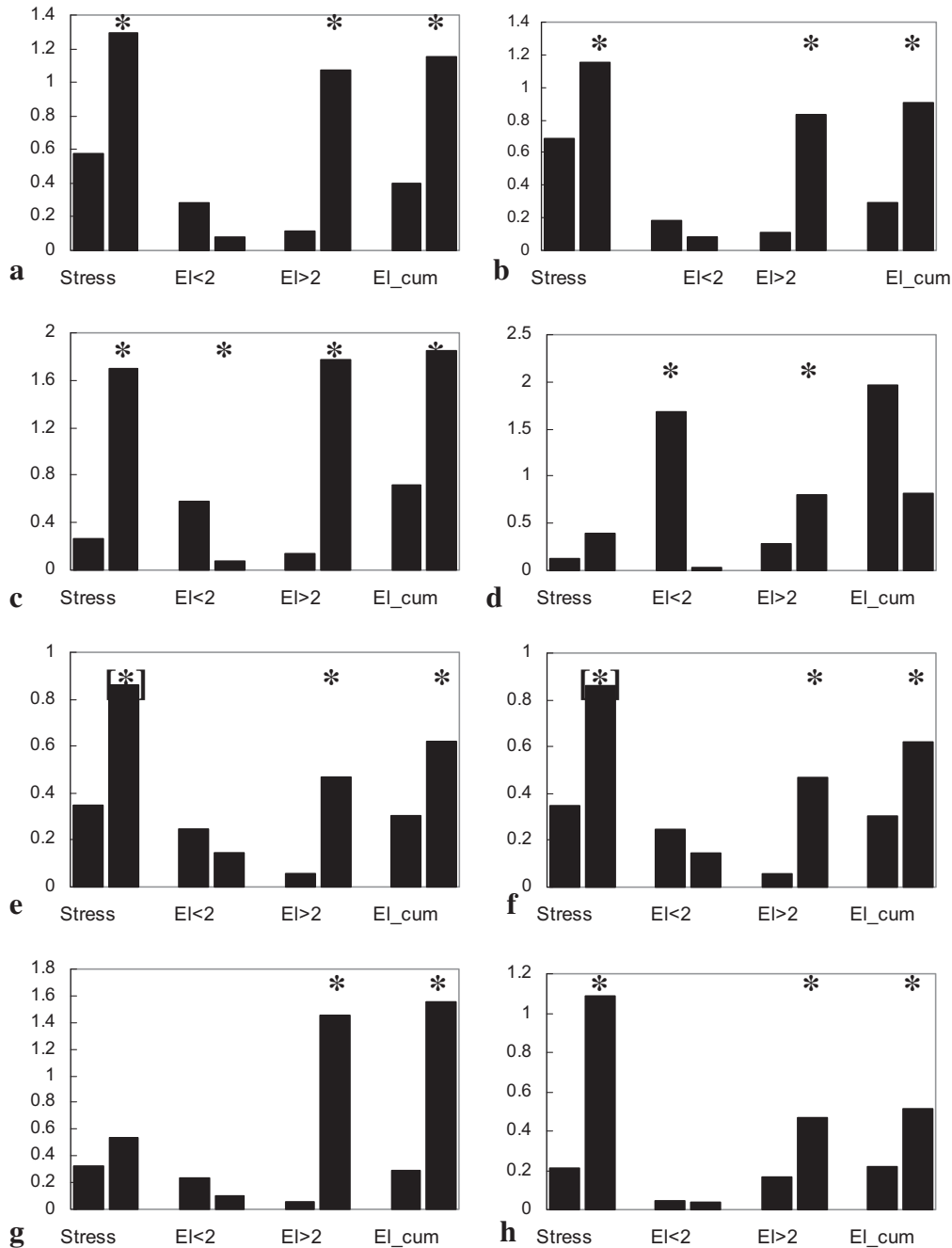
Fig. 1 (continued)

(Figs. 2 and 3). Sparse use of these vegetation types as of 2010 is attributable to their lack of desirable forage because of elephant-induced mortality, as elephants select for vegetation types within a landscape dominated by *C. mopane* that offer the best overall return (Clegg, 2010).

The vegetation types for which stark changes were evident constitute, however, less than 10% of the surface area of the VLNR (O'Connor, unpublished data). The greater part of the reserve is covered by dryland vegetation types dominated by *C. mopane*. These have been relatively stable vegetation types (Fig. 1; Tables 1 and 3), despite stress-related impacts (Fig. 2) that are most commonly experienced in response to drought episodes (O'Connor, 1999). The ability of *C. mopane* to alter its individual form through adjustment of stem number (O'Connor, unpublished data), thus producing a high proportion of multi-stemmed individuals, in conjunction with its tolerance of low matrix potentials thus providing high tolerance of moisture stress (Smit, 1994), are factors which contribute to its persistence and thus to the relative stability of vegetation types dominated by *C. mopane*.

### 5.3. Area- versus population-based monitoring

A conventional approach to monitoring vegetation change in African savannas is through the use of transects (e.g., Walker, 1976), as adopted in this study. This study suggests that such an approach is not ideal for assessing impacts on the less abundant woody species. Rare and uncommon species comprise a substantial proportion of overall species richness, and many of which are strongly selected for, have low recruitment rates, and appear not to possess survival responses to biomass removal (O'Connor, unpublished data), and thus are vulnerable to impact by elephants. Although many species declined in abundance (Table 2), no clear projection of the future abundance of individual woody species can be made using the transect data because sample sizes are too low to provide size structures of rare and uncommon species. Projections are also required in order to anticipate expected consequent changes in animal diversity (e.g., Cumming et al., 1997). By contrast, study of the population dynamics of individual woody species (O'Connor, unpublished



**Fig. 2.** Change in the proportion of phytomass lost per individual plant, weighted by the basal area of the plant, between 1997 (left-hand column of pair) and 2010 (right-hand column of pair) for (a) the reserve; (b) dryland and (c) riverine habitats; and for vegetation types: (d) *Acacia* Woodland; (e) *Commiphora* Woodland; (f) Sandstone Hills; (g) Mixed Woodland; (h) *Colophospermum mopane-Terminalia prunioides* Shrub Woodland; (i) *C. mopane* Shrub Woodland; (j) *C. mopane* Woodland; (k) Riverine Woodland; (l) *C. mopane* Riverine Woodland; (m) *Combretum apiculatum-C. mopane* Open Woodland (Sandveld); (n) *C. mopane-Grewia flava* Woodland; and (o) *Sesamothamnus lugardii* Open Woodland. For each agent, 1997 is the left-hand and 2010 is the right-hand column. Key to the agents of biomass removal: Stress, phytomass lost to plant stress; EI < 2, phytomass lost to elephant less than two years old (excluding debarking); EI > 2, phytomass lost to elephant greater than two years old (excluding debarking); and EI\_cum, total phytomass lost to elephant (i.e., sum of less than, and greater than two years old, excluding debarking). Significance of change for an agent between 1997 and 2010: \*,  $P < 0.05$ ; [ ],  $0.05 < P < 0.1$ .

data) strongly suggests that approximately half the woody species are trending toward local extirpation mainly as a consequence of elephant use. For a number of uncommon species, including *Adansonia digitata*, *Adenia spinosa*, *Albizia anthelmintica*, *Kirkia acuminata*, *Maerua angolensis* and *Sclerocarrya birrea*, a sufficient sample size could only be obtained by recording individuals outside of transects (few were recorded on transects). Monitoring of scattered individual plants is extremely demanding

of time; for example, two days are required to visit the less than 30 remaining individuals of *Adenia spinosa* spread across hills, during which time at least 400 individuals could be measured on transects. Notwithstanding this additional time demand, it is suggested that population-centered monitoring of a targeted set of species, including those both vulnerable and less vulnerable to elephants, offers better information for decision-making related to biodiversity conservation.

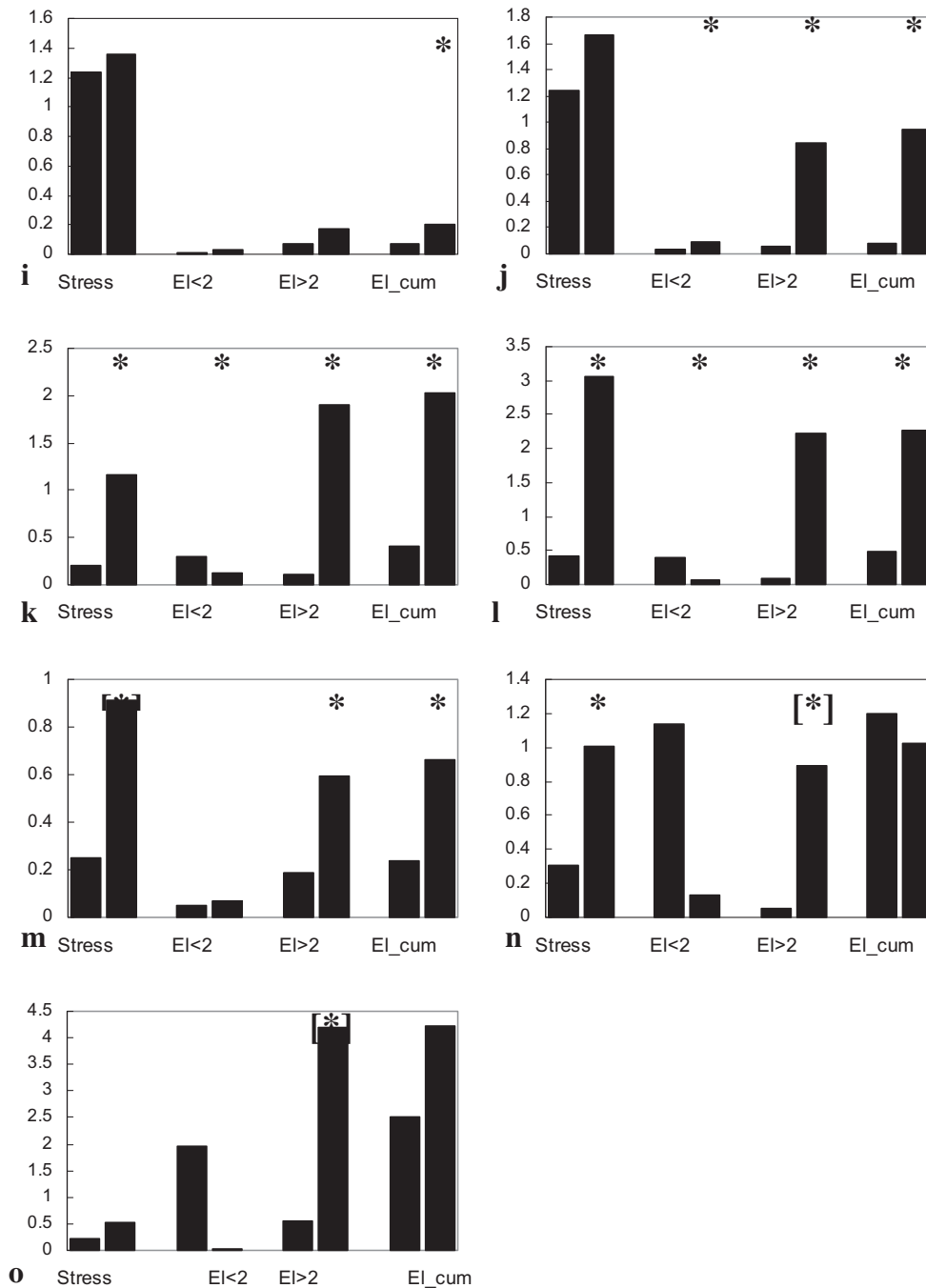
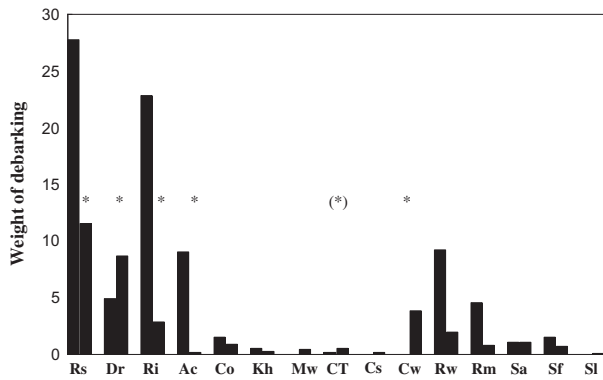


Fig. 2 (continued)

#### 5.4. Management outlook

Effective management should rely on lessons learned from experience and on anticipation of expected change. This study illustrated that an elephant population at relatively low density within a closed, medium-sized reserve in a semi-arid savanna region will cause ecological simplification through its effects on vegetation composition, diversity and structure. Simplification of the reserve is expected to continue if the current *status quo* is maintained. The elephant population of the VLNR has doubled in size in less than 20 years by immigration into the reserve as well as population growth, and is expected to continue to grow (Page, unpublished data) unless population intervention is exercised. This

expectation is based on the availability of food because *C. mopane*, the dominant woody species of dryland vegetation types (O'Connor, 1992) and a prominent species of some riparian vegetation types, is a staple food item that can tolerate relatively heavy elephant use (Smallie and O'Connor, 2000; Styles and Skinner, 2000). In addition, perennial grasses, which are important food for elephants (O'Connor et al., 2007), are relatively abundant in riparian systems and along drainage lines (O'Connor, 2014). There is no indication that the elephant carrying capacity for the VLNR is being approached. Thus, with increasing elephant numbers underpinned by ubiquitous staple food items, sustained and increasing impact can be expected on selected, uncommon woody species and the trend of declining local species richness and diversity



**Fig. 3.** The extent of debarking (proportion of circumference debarked weighted by circumference) in 1997 and 2010 for the reserve (Rs), Dryland (Dr) and riparian (Ri) habitats, and vegetation types: Ac, *Acacia* Woodland; Co, *Commiphora* Woodland; Kh, Sandstone (Karoo) Hills; Mw, Mixed Woodland; CT, *Colophospermum mopane-Terminalia prunioides* Shrub Woodland; Cs, *C. mopane* Shrub Woodland; Cw, *C. mopane* Woodland; Rw, Riverine Woodland; Rm, *C. mopane* Riparian Woodland; Sa, *Combretum apiculatum*–*C. mopane* Open Woodland (Sandveld); Sf, *C. mopane-Grewia flava* Woodland; and SI, *Sesamothamnus lugardii* Woodland. The 1997 and 2010 values are the left- and right-hand columns of each pair, respectively. A significant change in the extent of debarking for a unit between 1997 and 2010: \* –  $P < 0.05$ ; (\*) –  $0.05 < P < 0.1$ .

(Table 3) and possibly local extirpation of a number of species is an expected future outcome that is at odds with the biodiversity conservation objectives of the reserve.

A management response is required if conservation objectives are to be met but the options are limited. There is no scope for manipulation of access to foraging areas through manipulation of water supplies (Owen-Smith, 1996) because the size of the reserve in conjunction with the distribution of perennial water ensures elephants have access to all corners of the reserve. Increasing the size of the reserve through the acquisition of additional adjacent properties, ignoring obvious social and financial constraints, would create an enlarged but closed system functioning in a similar manner. Some of the impacts recorded in this reserve became apparent shortly after the re-introduction of elephants (MacGregor and O'Connor, 2004) at very low elephant densities, especially of mature bulls; the inference is that areas not currently impacted and added to the current range would be similarly affected. Such a response would be a tactic of deferment rather than a solution unless future additions offer an improved spatial constellation of resources and improve connectivity with other systems containing elephants (Van Aarde and Jackson, 2007). Management of numbers begs the question of the number of elephant that can be supported and at the same time ensuring that all woody species persist. What that number might be has not been defined for any system nor is there a generally accepted approach for defining a stocking rate for elephants at which biodiversity in general would not decline in any given system, nor at which any rare species selected by elephants might be maintained. It is relevant to note that declines in some rare, selected species began soon after introduction of elephants at very low densities. For most of the declining species, regeneration is absent, very low or low. Under such circumstances the question arises as to whether, even at very low elephant densities, coexistence between the selected rare plant species and elephants is possible. As mentioned, there are no areas within the VLNR that elephants cannot access easily within a day, and whilst occupancy and impact are heterogeneous over the landscape, selected rare species are used wherever they occur.

With the benefit of hindsight, elephants should perhaps not have been re-introduced into the VLNR if maintaining biodiversity conservation is a primary objective, unless population size had

been controlled from the outset at a low (unknown) density considered safe for maintaining plant diversity. This is presented as a key lesson for management on similar reserves as yet without elephants. An alternative approach for medium-sized reserves similar to the VLNR is to accept that the re-introduction of elephants will result in system simplification, but to achieve conservation of woody species on other land uses based on natural vegetation (e.g., livestock ranching), a debate beyond the scope of this paper. What does not appear to be an option is to alter the inherent foraging patterns of elephants (Loarie et al., 2009) – negative consequences for plant diversity appear to be an inevitable outcome of re-introducing elephants into a medium-sized, closed reserve in semi-arid savanna. There is, however, a caveat in that many larger reserves have distributions of food and water that similarly preclude the existence of refugia for rare species. Consequently, size of a reserve is not necessarily a criterion ensuring persistence of susceptible species, but rather size and the configuration of resource distribution in both space and time might create refugia for plants to which elephants do not have access. This being the case, the corollary regarding biodiversity conservation that emerges from a conclusion that the coexistence between elephants and some tree species is not possible, is that botanical reserves adjoining or included in protected areas with elephants may be necessary as a conservation strategy.

#### Acknowledgements

We thank De Beers (Pty.) Ltd., especially M. Berry and G. Main, for having initiated this exercise. We further thank reserve managers, especially W. Mostert-Davies and J. Zylstra, for support on the ground. The first author thanks SAOON for an opportunity to complete the work in 2010, and S. O'Connor for assistance with field work for this season.

#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.09.036>.

#### References

- African Plants Database, 2012. African Plant Database (version 3.4.0). Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute. <http://www.ville-ge.ch/musinfo/bd/cjb/africa/> (retrieved 22.05.12).
- Alatalo, R.V., 1981. Problems in the measurement of evenness in ecology. *Oikos* 37, 199–204.
- Anderson, G.D., Walker, B.H., 1974. Vegetation composition and elephant damage in the Sengwa Wildlife research area, Rhodesia. *J. S. Afr. Wildlife Manage. Assoc.* 4, 1–14.
- Barnes, R.F.W., 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 20, 123–136.
- Barnes, R.F.W., 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *J. Appl. Ecol.* 20, 521–540.
- Barnes, R.F.H., 1985. Woodland changes in Ruaha National park (Tanzania) between 1976 and 1982. *Afr. J. Ecol.* 23, 214–221.
- 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.
- Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I., Hart, J.A., 2007. African Elephant Status Report: An Update from the African Elephant Database. IUCN, Gland.
- Botha, J., Witkowski, E.T.F., Shackleton, C.M., 2002. A comparison of anthropogenic and elephant disturbance on *Acacia xanthophloea* (fever tree) populations in the lowveld, South Africa. *Koedoe* 45, 9–18.
- Buechner, H.K., Dawkins, H.C., 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* 42, 752–767.
- Chamailé-Jammes, S., Fritz, H., Madzikanda, H., 2009. Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. *Ecography* 32, 871–880.

- Childes, S.L., Walker, B.H., 1987. Ecology and dynamics of the woody vegetation on the Kalahari sands in Hwange National Park, Zimbabwe. *Vegetatio* 72, 111–128.
- Clegg, B.W., 2010. Habitat and diet selection by African elephant at the landscape level: a functional integration of multi-scale foraging processes. PhD thesis. University of the Witwatersrand, Johannesburg.
- 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, C.V.R., 1997. Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* 93, 231–236.
- De Beer, Y., Kilian, W., Versfeld, V., Van Aarde, R.J., 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *J. Arid Environ.* 64, 412–421.
- Douglas-Hamilton, I., 1987. African elephants: population trends and their causes. *Oryx* 21, 11–24.
- Dudley, J.P., Craig, G.C., Gibson, D.St.C., Haynes, G., Klimowicz, J., 2001. Drought mortality of bush elephants in Hwange National park, Zimbabwe. *Afr. J. Ecol.* 39, 187–194.
- Eltringham, S.K., 1982. Elephants. Poole, Dorset.
- Field, C.R., Ross, I.C., 1976. The savanna ecology of Kidepo Valley National Park II. Feeding ecology of elephant and giraffe. *East Afr. Wildlife J.* 14, 1–15.
- Garai, M.E., Slotow, R., Carr, R.D., Riley, B., 2004. Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm* 37, 28–36.
- Guldmond, R., Van Aarde, R., 2008. The impact of elephants on plants and their community variables in South Africa's Moputaland. *Afr. J. Ecol.* 45, 327–335.
- Guy, P.R., 1976. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area, Rhodesia. *S. Afr. J. Wildlife Res.* 6, 55–63.
- Harrington, G.N., Ross, I.C., 1974. The savanna ecology of Kidepo Valley National Park I. The effects of burning and browsing on the vegetation. *East Afr. Wildlife J.* 12, 93–105.
- Hiscocks, K., 1999. The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe* 42, 47–55.
- Holdo, R.M., 2006. Elephant herbivory, frost damage and topkill in Kalahari sand woodland savanna trees. *J. Veg. Sci.* 17, 509–518.
- Laws, R.M., Parker, I.S.C., Johnstone, R.C.B., 1975. Elephants and their Habitats. Clarendon Press, Oxford.
- Leuthold, W., 1977. Changes in tree populations of Tsavo East National Park, Kenya. *East Afr. Wildlife J.* 15, 61–69.
- Lewis, D.M., 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *Afr. J. Ecol.* 29, 207–221.
- Loarie, S.R., Van Aarde, R.J., Pimm, S.L., 2009. Elephant seasonal vegetation preferences across dry and wet savannas. *Biol. Conserv.* 142, 3099–3107.
- MacGregor, S.D., O'Connor, T.G., 2002. Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid African savanna. *Austral Ecol.* 27, 385–395.
- 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. Wildlife Res.* 34, 55–66.
- McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- Mosugelo, D.K., Moe, S.R., Ringrose, S., Nellemann, C., 2002. Vegetation change during a 36-year period in northern Chobe National Park, Botswana. *Afr. J. Ecol.* 40, 232–240.
- Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.
- Mwalyosi, R.B.B., 1987. Decline of *Acacia tortilis* in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.* 25, 51–53.
- Mwalyosi, R.B.B., 1990. The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.* 28, 189–199.
- Mukwashi, K., Gandiwa, E., Kativu, S., 2012. Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. *Int. J. Environ. Sci.* 2, 1355–1368.
- O'Connor, T.G., 1992. Woody vegetation-environment relations in a semi-arid savanna in the northern Transvaal. *S. Afr. J. Bot.* 58, 268–274.
- O'Connor, T.G., 1999. Impact of sustained drought on a semi-arid *Colophospermum mopane* savanna. *Afr. J. Range Forage Sci.* 15, 83–91.
- O'Connor, T.G., 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in a semi-arid African savanna. *J. Appl. Ecol.* 38, 1314–1325.
- O'Connor, T.G., 2014. Long-term response of the herbaceous component to reduced grazing pressure in a semi-arid savanna, Venetia-Limpopo Nature Reserve, South Africa. *African Journal of Range and Forage Science* (submitted for publication).
- O'Connor, T.G., Goodman, P.S., Clegg, B., 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biol. Conserv.* 136, 329–345.
- O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W., 2011a. Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephants? *Acta Oecol.* 37, 393–398.
- O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W., 2011b. Overlap and seasonal shifts of use in woody plant species amongst a guild of savanna browsers. *J. Trop. Ecol.* 27, 249–258.
- O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W., 2012. Heavy impact on seedlings by impala suggests a central role in woodland dynamics. *J. Trop. Ecol.* 28, 291–297.
- O'Kane, C.A.J., Duffy, K.J., Page, B.R., Macdonald, D.W., 2013. Model highlights likely long-term influences of mesobrowsers versus those of elephant on woodland dynamics. *Afr. J. Ecol.* 52, 192–208.
- Okula, J.P., Sise, W.R., 1986. Effects of elephant browsing on *Acacia seyal* in Waza National Park, Cameroon. *Afr. J. Ecol.* 24, 1–6.
- Owen-Smith, N., 1996. Ecological guidelines for waterpoints in extensive protected areas. *S. Afr. J. Wildlife Res.* 26, 107–112.
- Pellew, R.A.P., 1983. The impacts of elephant, giraffe, and fire upon the *Acacia tortilis* woodlands of Serengeti. *Afr. J. Ecol.* 21, 41–74.
- Redfern, J.V., Grant, C.C., Gaylard, A., Getz, W.M., 2005. Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *J. Arid Environ.* 63, 406–424.
- Ruess, R.W., Halter, F.L., 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *Afr. J. Ecol.* 28, 259–275.
- Rutherford, M.C., 1979. Plant-based techniques for determining available browse and browse utilization: a review. *Bot. Rev.* 45, 203–228.
- SAS Institute Inc., 2010. SAS 9.3 for Windows. Cary, NC, USA.
- Skarpe, C. et al., 2004. The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33, 276–282.
- Smallie, J.J., O'Connor, T.G., 2000. Elephant utilisation of *Colophospermum mopane*: possible benefits of hedging. *Afr. J. Ecol.* 38, 352–359.
- Smit, G.N., 1994. The influence of intensity of tree thinning on mopane veld (volumes 1 and 2). PhD thesis, University of Pretoria, Pretoria.
- Spinage, C.A., 1994. Elephants. In: Poyser, T., Poyser (Eds.), AD Ltd., London.
- Spinage, C.A., 2012. African Ecology – Benchmarks and Historical Perspectives. Springer, Berlin.
- Stewart-Oaten, A., 1995. Rules and judgments in statistics: three examples. *Ecology* 76, 2001–2009.
- Styles, C.V., Skinner, J.D., 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve. *Afr. J. Ecol.* 38, 95–101.
- Tafangenyasha, C., 1997. Tree loss in Gonarezhou National Park (Zimbabwe) between 1970 and 1993. *J. Environ. Manage.* 49, 355–366.
- Tchamba, M.N., Mahamat, H., 1992. Effects of elephant browsing on the vegetation in Kalamaloue National Park, Cameroon. *Mammalia* 56, 533–540.
- Trappell, C.G., 1959. Ecological results of woodland burning experiments in Northern Rhodesia. *J. Ecol.* 47, 129–168.
- Van Aarde, R.J., Jackson, T.P., 2007. Megaparks for meta-populations: addressing the causes of locally high elephant numbers in southern Africa. *Biol. Conserv.* 134, 289–297.
- Vanak, A.T., Shannon, G., Thaker, M., Page, B., Grant, R., Slotow, R., 2012. Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. *Ecography* 35, 315–321.
- Vesey-Fitzgerald, D.F., 1974. The changing state of *Acacia xanthophloea* groves in Arusha National Park, Tanzania. *Biol. Conserv.* 6, 40–47.
- Walker, B.H., 1976. An approach to the monitoring of changes in the composition and utilisation of woodland and savanna vegetation. *S. Afr. J. Wildlife Res.* 6, 1–32.
- Whyte, I.J., Van Aarde, R., Pimm, S., 2003. Kruger National Park's elephant population: its size and consequences for ecosystem heterogeneity. In: Du Toit, J., Biggs, H., Rogers, K. (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington DC, pp. 332–348.