

The effects of elephants and fire on vegetation at Marakele National Park, South Africa

*Piet J van Staden*¹, *Hugo Bezuidenhout*^{2,4*}, *Sam Ferreira*³ and *George J Bredenkamp*¹

¹Department of Plant Sciences, University of Pretoria, South Africa

²Scientific Services, SANParks, Kimberley, South Africa

³Scientific Services, SANParks, Skukuza, South Africa

⁴Applied Behavioural Ecology and Ecosystem Research Unit, UNISA, Private Bag X6, Florida, 1717, South Africa

*corresponding author: hugo.bezuidenhout@sanparks.org

Abstract

Elephants and fire can modify African savanna ecosystems. The authors evaluated the influence that elephants and fires had on five mountainous plant communities in Marakele National Park. These plant communities were surveyed from 1996 to 2010 with the first sampling in 1996 in the absence of elephants. Initially thirty-nine elephants, introduced in 1996, increased to 150 by 2010 while fires occurred roughly every second year. Over this period vegetation changed and in four of the five cases these associated with structural damage indices, assumed to reflect the effects of elephants. Fire played a role in one of the five mountainous plant communities. The expansion of areas available for elephants partially resulted in halting vegetation changes. The authors conclude that existing resource gradients still impose intensity of use by elephants that can degrade plant communities. In some instances elephant disturbance may facilitate fire disturbance in future. The management should focus on restoring spatial and temporal limitation of resource gradients such as water, and on how elephants use landscapes, while protecting unique plant communities in the interim.

Additional key words: plant species composition, vegetation structure, Euclidean distance

Résumé

Les éléphants et l'incendie peuvent modifier les écosystèmes de la savane africaine. Les auteurs ont évalué l'influence des éléphants et des incendies sur cinq communautés de plantes montagneuses dans le parc national Marakele. On a étudié ces communautés végétales de 1996 à 2010 avec le premier échantillonnage fait en 1996 en l'absence des éléphants. A l'origine, trente-neuf éléphants, introduits en 1996, se sont multipliés jusqu'à 150 en 2010 alors que les incendies se produisaient approximativement tous les deux ans. Au cours de cette période, la végétation a changé et, dans quatre cas sur cinq, ceux associés aux indices de dommages structurels semblaient refléter les effets des éléphants. L'incendie a joué un rôle dans l'une des cinq communautés de plantes montagneuses. L'expansion des zones disponibles pour les éléphants a entraîné en partie l'arrêt des changements de végétation. Les auteurs concluent que les gradients de ressources existants imposent toujours une intensité d'utilisation par les éléphants qui peuvent dégrader les communautés végétales. Dans certains cas, la perturbation par les éléphants peut faciliter celle de l'incendie à l'avenir. La gestion devrait se concentrer sur la restauration de la limitation spatiale et temporelle des gradients de ressources, comme l'eau, et sur la façon dont les éléphants utilisent les paysages tout en protégeant les communautés végétales uniques dans l'entre-temps.

Mots clés supplémentaires: composition des espèces végétales, structure végétale, distance euclidienne

Introduction

Small conservation areas may accentuate the effect of influences such as fire and invasive plant species, specifically when sources of these are largely from outside protected areas. In African savannas, fire and mammal activity are key disturbances that influence ecosystem composition, structure integrity, resistance and resilience within a climatic and geological template (Sankaran et al. 2008; Shannon et al. 2011).

Several protected areas in South Africa are smaller than the home range size of mega-herbivores (e.g. elephant *Loxodonta africana* home range typically vary between 32 km² to 12,800 km²—van Aarde et al. 2008). National Parks in South Africa range from 35 km² to 19,000 km², but most are below 1,000 km². The constraints that small areas impose on spatial and temporal variation in landscape use or regulation of population sizes may result in effects on other biological values (de Boer et al. 2015).

When a protected area is small in size the impacts of fires may be accentuated with large proportions being burnt at one time. In savannas, natural fire intensity varies according to wet and dry seasons. Increased incidences of high intensity fires across most landscapes may also affect biodiversity objectives of conservation authorities (Govender et al. 2006).

The combination of increased herbivory and fire intensity across all landscapes disrupt variability of disturbance agents across space and time (Roxburgh et al. 2004) that reduce biological diversity and hence ecological resilience (Peterson et al. 1998). Marakele National Park (NP), including the area managed by Marakele Park Pty Ltd (combined Marakele ecosystem), presents such a case in South Africa. The mammal community at Marakele originated from introductions of species to achieve the biodiversity objectives of the Park. Re-introduction of elephants into Marakele sought to address ecological challenges such as bush densification (Hall-Martin 2003).

It was anticipated that elephants and fire induced non-linear vegetation changes because species respond differently to disturbances (Baxter 2003). For instance, regional species pools may constrain recovery and resilience in the face of disturbance when not all original species exist in the region. Species also have specific niche requirements (Cornell and Lawton 1992), while changing diversity

of disturbed plots may induce variable colonization rates by other species. This predicts exponential directional change in plant community characteristics (Wassenaar et al. 2005).

In this paper the trends in herbivores and fire incidences at Marakele were recorded. The next step was to evaluate whether plant communities changed between 1996 and 2010. If so, how were these changes associated with indicators of elephant use and fire incidences?

Study area

Authorities proclaimed Kransberg National Park, established during June 1988, as Marakele National Park during 1994 (van Staden 2002). During 2001, Marakele Pty Limited joined the Park through entering a contractual agreement that allows their property to be managed as part of the Marakele National Park ecosystem and under the national park management. The current size of the Park is 678 km² and it is situated in the south-western corner of the Waterberg Mountain Range, South Africa (Figure 1; see colour plates: page iv). The Waterberg Mountains and the Bushveld plains comprise the Park's landscapes (van Staden 2002). Rainfall during September to March varies from 400 mm in the plains to 1,197 mm in the mountains. The Park has mild winter temperatures as low as -3.7 °C while in summer they may reach 40 °C (Agricultural Research Council 2012). Mucina and Rutherford (2006) classified the vegetation as Western Sandy Bushveld—(SVcb 16), Waterberg Mountain Bushveld—(SVcb 17), Waterberg Magaliesberg Summit Sourveld—(Gm 29) and the Northern Afrotropical Forest (FOz 2) vegetation units.

A total number of 39 elephants were first introduced into the Park in 1996 and the population has increased ever since, with smaller groups introduced between 1996 and 1998. Furthermore, a long list of mammal species such as rhino, disease free buffalo and roan, were introduced and moved from and to Marakele NP. Authorities started vegetation sampling shortly before introducing elephants to a 300 km² section of Marakele. The removal of fences between Marakele National Park and Marakele Pty Limited during 2001 allowed elephants to move out of the mountainous areas into these lower-lying areas also (Hall-Martin 2003). By 2010 the population had increased to more than 150¹ elephants. While this is

¹SANParks Data Depository, Judith Botha, judith.botha@sanparks.org

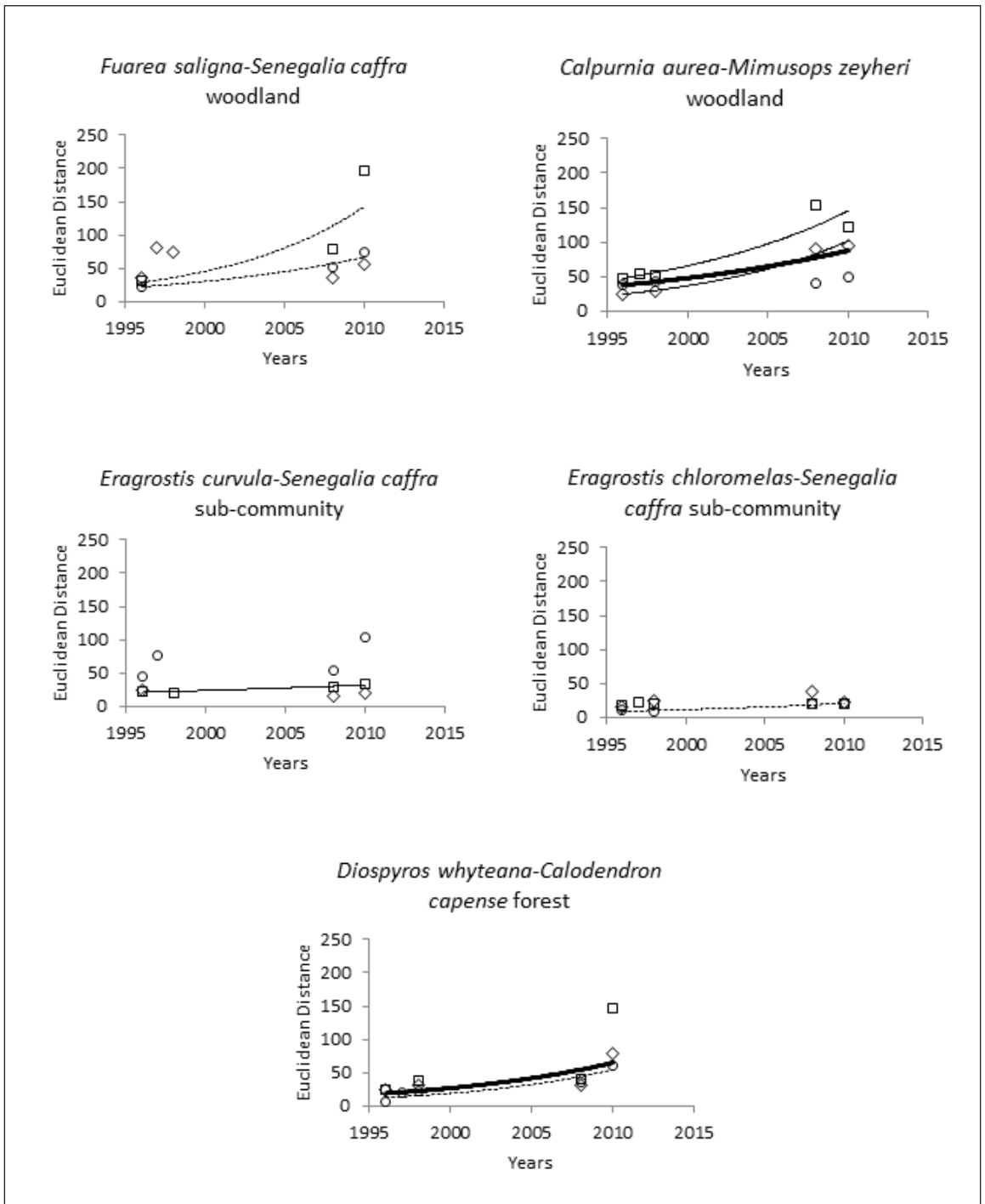


Figure 2. Euclidean distances for survey plots from super plant communities noted for each plant community at Marakele. Thick solid lines represent significant directional change across the plant community. Thin solid lines represent plots with significant directional change and thin broken lines plot with near-significant directional change. Plot 1–Square symbol, Plot 2–Diamond symbol, Plot 3–Circular symbol per plant community.

seen as a success, small populations of elephants often show aberrant growth because of stochastic effects such as skewed sex-ratios in favor of females (Mackey et al. 2006).

Incidents of fire largely occurred in the mountains ignited by seasonal lightning strikes associated with thunderstorms from the end of September to February. Sections of the park burned almost every second year (van Staden 2002). National Department of Agriculture legislation sought to prevent fire on the Bushveld plains of Marakele (van Staden 2002) that, combined with overgrazing, resulted in densification of the woody plant species (Brown 1997).

Methods

Data collection

We collated herbivore census data from 1996 to 2010 (SANParks records²). Surveys were not conducted in all years. Herbivore aerial census—which include elephant counts—were conducted using helicopters to systematically search the total

area of Marakele. The counts derived are thus minimum numbers known to be alive at the time. Fire records from 1996 to 2010 (van Staden 2002) allowed us to summarize historic trends in the area of Marakele that burned each year.

Vegetation sampling focused on fifteen plots within five of the plant communities previously identified as suitable elephant habitat (van Staden 2002; Table 1, Figure 1). Five plant communities were monitored (1) *Faurea saligna-Senegalia caffra* woodland (*Faurea saligna* woodland) (Plot numbers: 1, 2 and 3); (2) *Calpurnia aurea-Mimusops zeyheri* woodland (*Calpurnia aurea* woodland) (Plot numbers: 4, 5 and 6); (3) *Eragrostis curvula-Senegalia caffra* sub-community (*Eragrostis curvula* woodland) (Plot numbers: 7, 8, 9); (4) *Eragrostis chloromelas-Senegalia caffra* sub-community (*Eragrostis chloromelas* woodland) (Plot numbers: 10, 11 and 12); and the (5) *Diospyros whyteana-Calodendron capense* forest (*Diospyros whyteana* forest) (Plot numbers: 13, 14 and 15).

Sampling started in March 1996 before elephant introduction, and were repeated in 1997, 1998, 2008 and 2010. At each plot, we took fixed-point photographs, GPS readings, identified and counted all woody species.

Table 1. Vegetation surveys conducted in five plant communities. Numbers refer to sample plots (1996) and Y indicates sampling not done.

Plant communities	Plot	Size (m)	1996	1997	1998	2008	2010
<i>Faurea saligna-Senegalia caffra</i> woodland	1	30X30	Y	-	-	Y	Y
	2		Y	Y	Y	Y	Y
	3		Y	-	-	Y	Y
<i>Calpurnia aurea-Mimusops zeyheri</i> woodland	4	5X5	Y	Y	Y	Y	Y
	5		Y	-	Y	Y	Y
	6		Y	-	Y	Y	Y
<i>Eragrostis curvula-Senegalia caffra</i> sub-community	7	30X30	Y	-	Y	Y	Y
	8		Y	-	-	Y	Y
	9		Y	Y	-	Y	Y
<i>Eragrostis chloromelas-Senegalia caffra</i> sub-community	10	30X30	Y	Y	Y	Y	Y
	11		Y	-	Y	Y	Y
	12		Y	-	Y	Y	Y
<i>Diospyros whyteana-Calodendron capense</i> forest	13	5X5	Y	-	Y	Y	Y
	14		Y	-	Y	Y	Y
	15		Y	Y	Y	Y	Y

²SANParks Data Depository, Judith Botha, judith.botha@sanparks.org

The Variable Quadrat Plot vegetation sampling method (Coetzee and Gertenbach 1977) were used to determine woody species density. Trees were categorised into the following growth form: (1) Tree—individual with a single stem; (2) Light shrub—individual with 2-4 stems; and (3) Dense shrub—individual with five or more stems. We also classified plant species according to height as follows: < 0.5m; 0.5-<1m; 1-<1.5m; 1.5-<2m; 2-<3m; 3-<4m; > 4m. Quadrant size for each plot varied from 30x30m to 5x5m (Table 1).

Within each plot, all individuals of woody plant species were counted, the different growth forms assigned and canopy cover recorded by measuring the diameter of each individual tree. Also noted was structural damage to (individual) trees of different plant species, and classified as elephant (debarking, felled trees and browsing/broken branches) and black rhino (feeding and/or other browsing) damage. Fire damage was recorded as partially burned, secondary burns and dead trees.

Data analyses

The vegetation plot data was reduced to a species by plot matrix with percentage cover (i.e. total canopy cover for each species as a percentage of the total area of a plot) as an index of abundance for each plant species and calculated total average cover for the three plots in each plant community. We first investigated whether directional changes had taken place in plant species composition since 1996. For this an index of an “original” plant community was constructed for each of the five plant communities with the mean abundance of each plant species calculated from the abundances of the three plots representing a specific plant community found during 1996. The Euclidean distance was calculated for each of the different sampling periods (Faith et al. 1987) between the observed plant species composition at any sampling time and the “original” community for that specific plant community.

The Euclidean distance was plotted against time and we fitted an exponential model to the data. The analyses considered plots separately as an index of plot specific change relative to the “original” plant community of 1996. We then combined plots as an index of plant community change relative to the “original” plant community in 1996. When the F -statistic of the model had a p -value of ≤ 0.05

it was regarded as significant change. In cases where few repeat surveys were conducted, we concluded near-significant change when the confidence intervals of the slope of the regression excluded zero.

Next, we sought to define an accumulation of damage associated with fire and structural features (used as an index of elephant damage). The definition of fire and structural damage were snapshots at each plot with variable time lapses between monitoring occasions. Fire and elephant effects may be cumulative over time—therefore a time series of cumulative damage (i.e. the sum of all the scores upto and including the time in question) for fire and elephants were constructed separately for each plot in the five different plant communities. The missing data was interpolated by estimating exponential change between the two sequential previous data points smoothed by what the next available data point was. When a new interpolated data point was available, we repeated the process.

For the final analyses, it was anticipated that plot-specific variance in plant species composition may be important and we sought to evaluate the association of such variation with the cumulative indices of fire and structural damage. Euclidean distances were plotted first against cumulative indices of fire and structural damage for each plot and plant community separately. Linear regressions allowed us to evaluate whether plant communities became less similar to what they had been during 1996 as cumulative fire or structural damage indices increased. Again, we concluded that there is a significant relationship when the F -statistic of the model had a p -value of ≤ 0.05 . Furthermore, it was concluded that there was near-significant change when the confidence intervals of the slope of the regression excluded zero.

Damage indices may interact and we thus included all plots in the model selection approaches (Johnson and Omland 2004) within a specific plant community to identify the most plausible model of Euclidean distance associated with structural, fire, or structural and fire cumulative damage indices. When the most plausible models were also statistically significant as judged by the F -statistic of the multiple linear regression with a p -value of ≤ 0.05 , we concluded that factors included in that specific model may have significant influences on plot specific species composition in a specific plant community. In some instances the F -statistic generated p -values only slightly higher than 0.05. Because of small sample sizes, more lenient criteria were included to identify near-plausible models when the F -statistic of the

multiple linear regression had a p -value of ≤ 0.10 .

Results

Changes in disturbance agents

Elephants increased to 150 individuals by 2010. Note that some of the park burned each year, but this varied over time. Therefore our focal sources of disturbances varied over time between elephants and fire. The same area(s) (plots) were examined.

Vegetation changes

The *Faurea saligna* woodland had near-significant directional change in Euclidean Distance (*i.e.* species composition) at plot one and three (Table 2 and Figure 2). From Table 3 it is evident that the number of individual trees and shrubs varied across time and between plots.

The *Calpurnia aurea* woodland had near consistent directional changes for all plots (Table 2 and Figure 2). Even so, the number of individual trees and shrubs varied across time and between plots (Table 3). In contrast, the changes in the *Eragrostis curvula* woodland were only significant on one plot (Table 2 and Figure 2). The number of trees and shrubs varied between plots and between sampling years (Table 3).

The *Eragrostis chloromelas* woodland had relatively little change with only one plot changing weakly over time (Table 2 and Figure 2). Even so, the number of trees and shrubs during 2010 was consistently less by more than 50%, than was noted during 1996 (Table 3).

Vegetation changes in the *Diospyros whyteana* forest was directional overall, although only one plot showed near significant change (Table 2 and Figure 2).

Changes in damage indicators associated with disturbance indices

The indices of the structural damage at all three plots in the *Faurea saligna* woodland increased specifically during 2008 and 2010 (Figure 3). Although fire damage indices varied between plots, the yearly added or cumulative effects also increased during the 2008 and 2010 sampling periods (Figure 4).

For the *Calpurnia aurea* woodland we noted significant changes in cumulative structural damage

from 1996 to 1998. For the last two sampling periods during 2008 and 2010, however, only one plot recorded substantial increases in the cumulative structural damage index (Figure 3).

The indices of cumulative structural damage in the *Eragrostis curvula* woodland increased during the 2008 and 2010 sampling periods (Figure 3), while indices of cumulative fire damage only substantially increased during the last sampling period on two of the three plots (Figure 4).

Two of the three plots in the *Eragrostis chloromelas* woodland had significant changes in cumulative structural damage by 1998 after which they remained relatively stable. The third plot showed major changes in cumulative structural damage during the 2008 and 2010 sample periods (Figure 3). Only one plot displayed changes in indices of cumulative fire damage by 1998. Cumulative fire damage indices increased in all plots during the 2010 sampling period (Figure 4).

Variable changes in cumulative structural damage for the *Diospyros whyteana* forest was noted (Figure 3), while the forest had no fire incidents (Figure 4).

Associations of vegetation with damage indicators

Only one of the plots in the *Faurea saligna* woodland changed slightly since 1996 as the cumulative structural damage index increased ($F_{1,1}=57.44$, $p=0.08$, Table 1), while none of the *Faurea saligna* plots showed any correlation with the cumulative fire damage index (Figure 6).

Only one plot in the *Calpurnia aurea* woodland had changed significantly since 1996 as the cumulative damage index increased ($F_{1,2}=50.96$, $p<0.02$, Figure 5). Another plot became significantly less similar to its 1996 state as the cumulative fire damage index increased ($F_{1,3}=101.54$, $p<0.01$, Figure 6). Although the most statistically plausible model for vegetation changes associated with the cumulative structural damage index of elephant effects, it explained only 37% of the variance in the data (Table 4).

The vegetation on one plot in the *Eragrostis curvula* woodland had changed significantly since 1996 as the cumulative damage index increased ($F_{1,2}=39.12$, $p<0.03$; Figure 5). Only one plot showed weak change to its vegetation composition since 1996 as the cumulative fire damage indices increased ($F_{1,2}=8.75$, $p=0.09$, Figure 6). Model selection identified the most plausible (model) for vegetation changes associated with the cumulative structural damage index of elephant effects that explained 54% of the variance in the data (Table 4).

We recorded only one plot that had a weak association

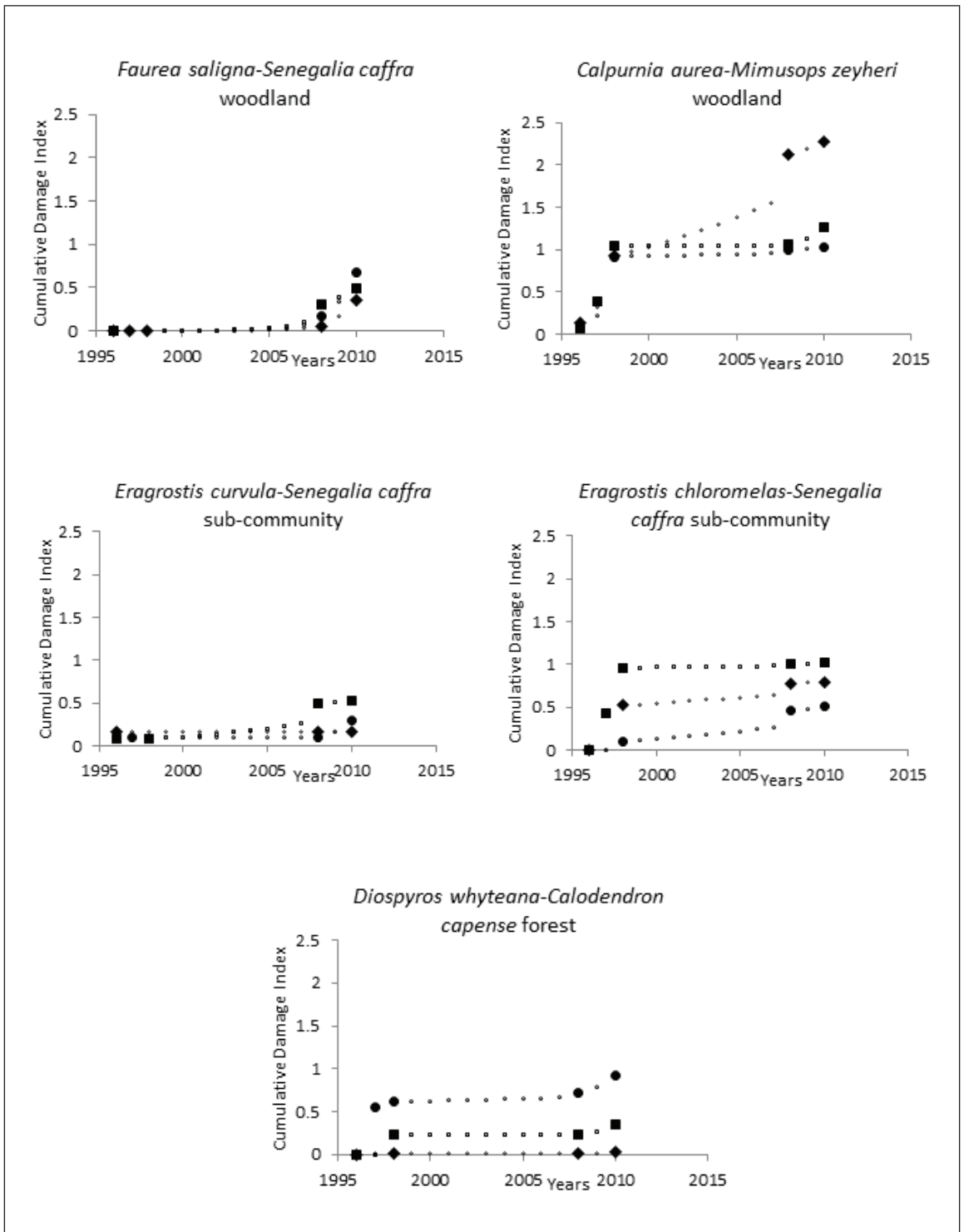


Figure 3. Indices of structural vegetation damage assigned to elephants at three plots each within a plant community. Small symbols are interpolated values. The large dark symbols are observed values. Plot 1–Square symbol, Plot 2–Diamond symbol, Plot 3–Circular symbol.

Table 2. Changes in plant communities expressed as change in Euclidean distance to the “original” plant community defined in 1996.

<i>Faurea saligna-Senegalia caffra</i> woodland					
Plot	Δ	95% CI	F-value	p-value	Significant
1	0.12	0.02–0.21	$F_{1,1} = 6.21$	0.24	Near
2	-0.02	-0.09–0.05	$F_{1,3} = 0.25$	0.65	Not
3	0.08	0.05–0.11	$F_{1,1} = 32.55$	0.11	Near
All	0.05	-0.01–0.10	$F_{1,9} = 3.10$	0.11	Near
<i>Calpurnia aurea-Mimusops zeyheri</i> woodland					
Plot	Δ	95% CI	F-value	p-value	Significant
4	0.08	0.66–0.10	$F_{1,3} = 42.47$	<0.01	Yes
5	0.10	0.09–0.12	$F_{1,2} = 189.63$	<0.01	Yes
6	0.01	-0.01–0.03	$F_{1,2} = 1.69$	0.32	Not
All	0.06	0.02–0.10	$F_{1,11} = 10.48$	<0.01	Yes
<i>Eragrostis curvula-Senegalia caffra</i> sub-community					
Plot	Δ	95% CI	F-value	p-value	Significant
7	0.03	0.02–0.04	$F_{1,2} = 20.13$	0.05	Yes
8	-0.02	-0.05–0.01	$F_{1,1} = 2.04$	0.39	Not
9	0.03	-0.03–0.09	$F_{1,2} = 0.65$	0.50	Not
All	0.01	-0.05–0.07	$F_{1,9} = 0.04$	0.85	Not
<i>Eragrostis chloromelas-Senegalia caffra</i> sub-community					
Plot	Δ	95% CI	F-value	p-value	Significant
10	0.002	-0.01–0.01	$F_{1,3} = 0.12$	0.75	Not
11	0.03	-0.03–0.09	$F_{1,2} = 1.20$	0.39	Not
12	0.06	0.02–0.10	$F_{1,2} = 10.33$	0.08	Near
All	0.03	-0.01–0.06	$F_{1,11} = 2.67$	0.13	Not
<i>Diospyros whyteana-Calodendron capense</i> forest					
Plot	Δ	95% CI	F-value	p-value	Significant
13	0.09	-0.01–0.18	$F_{1,2} = 3.59$	0.20	Not
14	0.06	-0.01–0.12	$F_{1,2} = 2.82$	0.24	Not
15	0.11	0.04–0.18	$F_{1,3} = 8.72$	0.06	Near
All	0.09	0.04–0.13	$F_{1,11} = 14.61$	<0.01	Yes

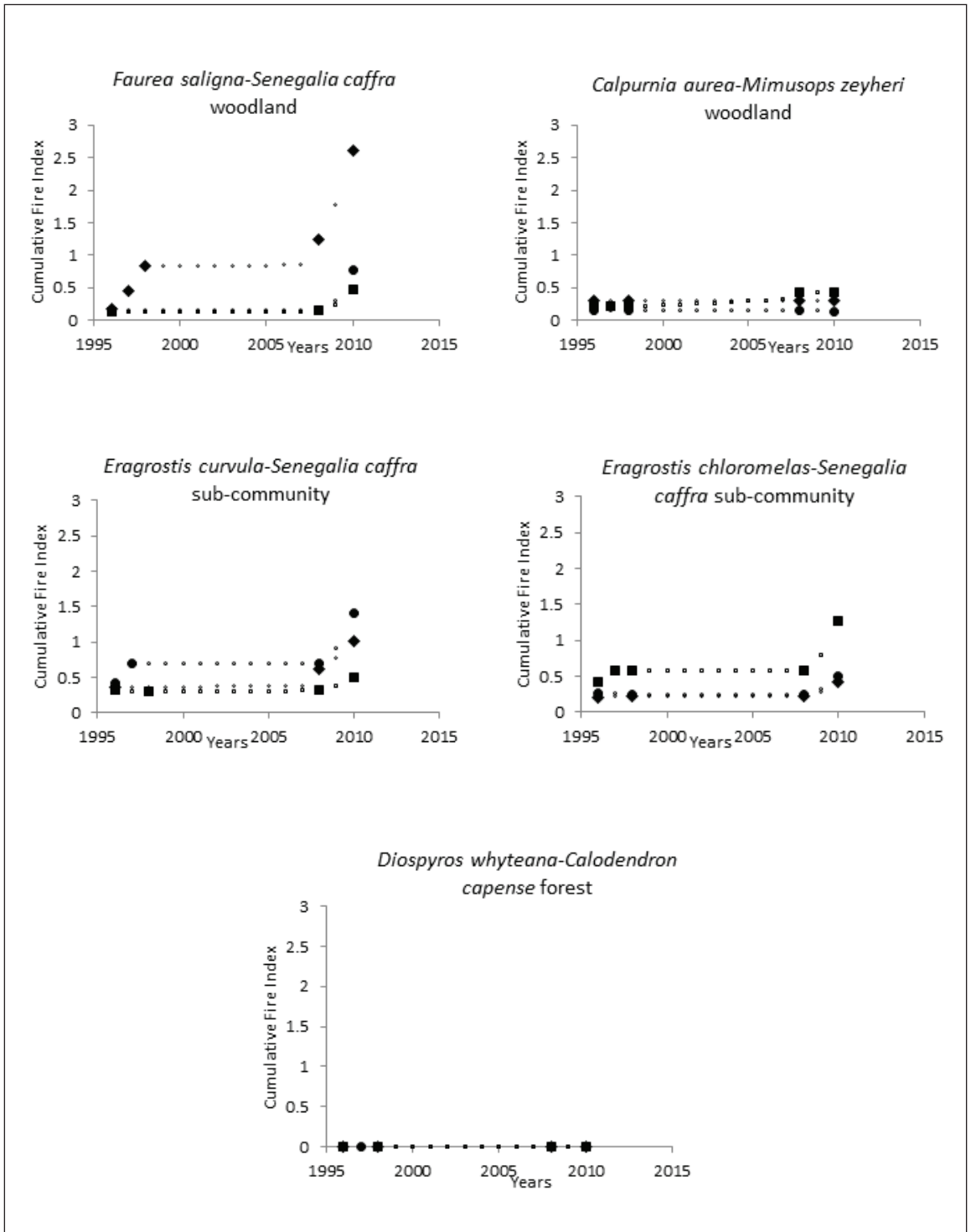


Figure 4. Indices of damage assigned to fires at three plots each within a plant community. Small symbols are interpolated values. The large dark symbols are observed values. Plot 1–Square symbol, Plot 2–Diamond symbol, Plot 3–Circular symbol.

Table 3. Number of individual woody species in the “taller than four meter” height class per plot recorded.

Plant communities	Plot	1996	1997	1998	2008	2010
<i>Faurea saligna-Senegalia caffra</i> woodland	1	25	-	-	19	19
	2	6	12	9	3	5
	3	5	-	-	9	12
	Total	36	-*	-*	31	36
<i>Calpurnia aurea-Mimusops zeyheri</i> woodland	4	42	30	26	31	16
	5	37	-	31	28	33
	6	14	-	10	6	5
	Total	93	-*	67	65	54
<i>Eragrostis curvula-Senegalia caffra</i> sub-community	7	13	-	12	10	11
	8	15	-	-	6	9
	9	32	27	-	17	23
	Total	60	-*	-*	33	43
<i>Eragrostis chloromelas-Senegalia caffra</i> sub-community	10	14	10	8	8	7
	11	16	-	6	0	0
	12	12	-	7	4	5
	Total	42	-*	21	12	12
<i>Diospyros whyteana-Calodendron capense</i> forest	13	25	-	21	8	7
	14	8	-	9	5	8
	15	7	7	4	4	7
	Total	40	-*	34	17	22

*Surveys were done only in some plots, therefore the total number of trees would be incorrect and therefore data was omitted from the table.

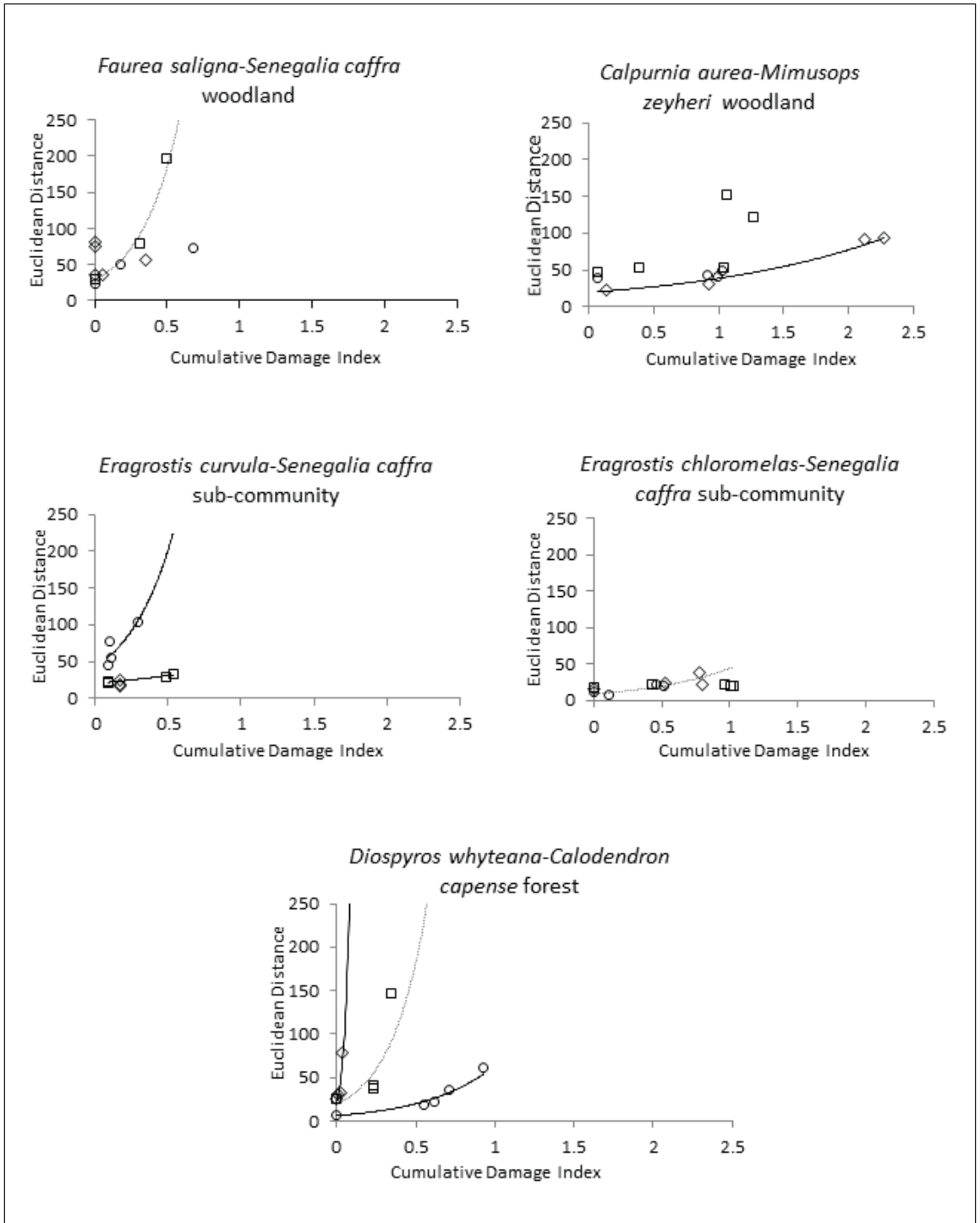


Figure 5. Associations between Euclidean distances as an index of vegetation change and cumulative damage indices as an indication of elephant usage across five plant communities in MNP. Thin solid lines represent plots with significant directional change and thin broken lines plot with near-significant directional change. Plot 1–Square symbol, Plot 2–Diamond symbol, Plot 3–Circular symbol.

Table 4. Models of association between cumulative structural and fire indices with sample plot site specific variance in plant species composition noted in five plant communities.

Plant communities	Model	R^2	AIC_c	Δ_i	W_i	P^*
<i>Faurea saligna-Senegalia caffra</i> woodland	Fire	0.28	-10.21	-	0.53	0.10
	Elephants	0.22	-9.41	0.80	0.36	0.14
	Fire + Elephants	0.33	-7.18	3.03	0.12	0.19
<i>Calpurnia aurea-Mimusops zeyheri</i> woodland	Elephants	0.37	-19.15	-	0.74	0.05
	Elephants + Fire	0.41	-16.65	2.50	0.21	0.13
	Fire	0.03	-13.52	5.62	0.04	0.63
<i>Eragrostis curvula-Senegalia caffra</i> sub-community	Elephants	0.54	-32.37	-	0.84	0.01
	Elephants + Fire	0.56	-28.86	3.51	0.15	0.06
	Fire	0.04	-24.17	8.19	0.01	0.56
<i>Eragrostis chloromelas-Senegalia caffra</i> sub-community	Elephants	0.43	-32.48	-	0.63	0.03
	Fire	0.32	-30.13	2.35	0.20	0.07
	Elephants + Fire	0.47	-29.87	2.61	0.17	0.10
<i>Diospyros whyteana-Calodendron capense</i> forest	Elephants	0.35	-14.70	-	0.81	0.06
	Elephants + Fire	0.35	-11.23	3.47	0.14	0.06
	Fire	0	-9.17	5.53	0.05	1.00

* R^2 is the coefficient of determination for each model, AIC_c is the Akaike Information Criteria corrected for small sample sizes, Δ_i is the difference between the observed AIC_c for each model and the smallest AIC_c of the candidate models, w_i is the weight of support in the information for each model, and p is the p -value of the F -statistic for the linear regression of each model.

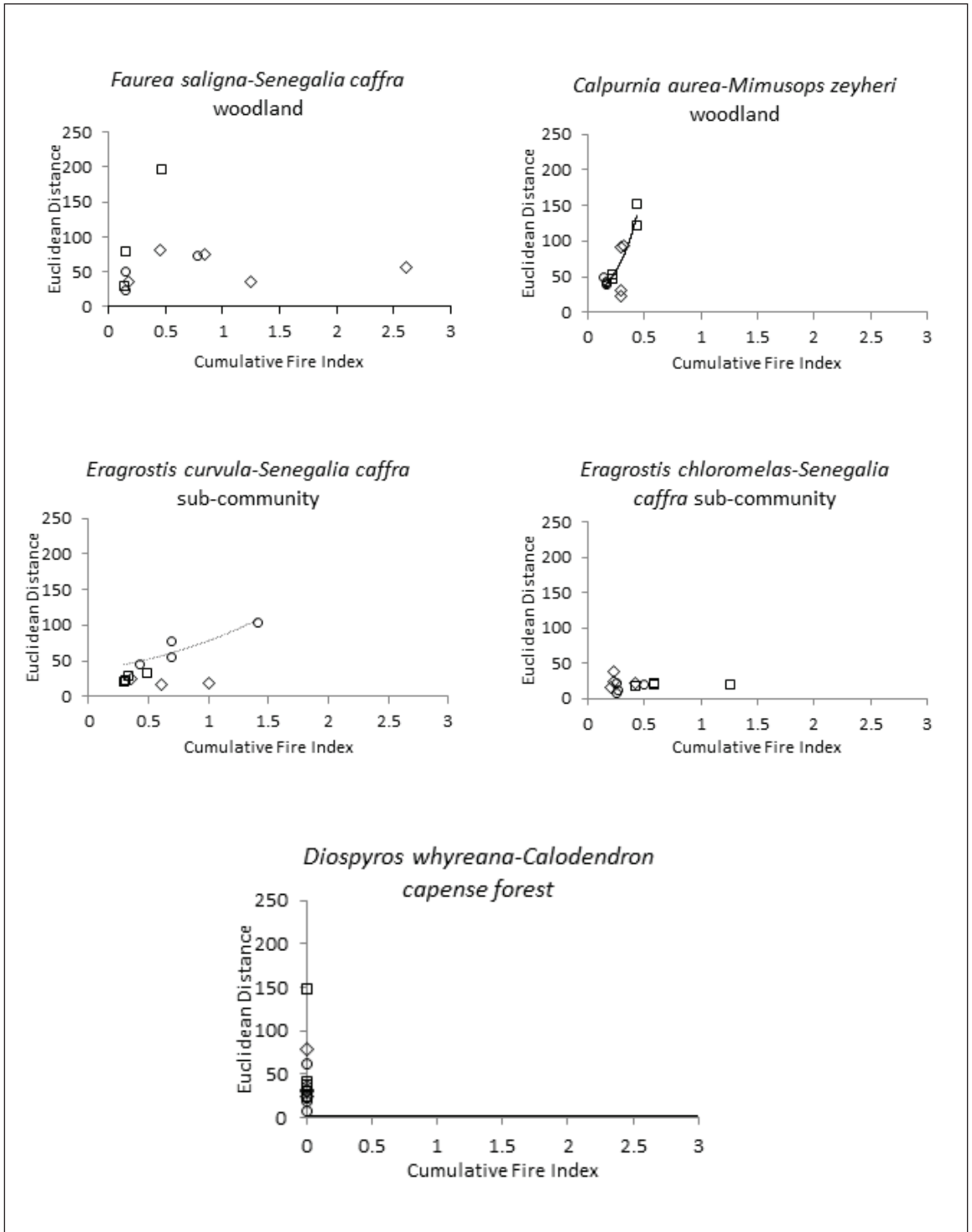


Figure 6. Associations between Euclidean distances as an index of vegetation change and cumulative fire indices as an indication of fire occurrence across five plant communities in MNP. Thin solid lines represent plots with significant directional change and thin broken lines plot with near-significant directional change. Plot 1–Square symbol, Plot 2–Diamond symbol, Plot 3–Circular symbol.

between vegetation changes and cumulative structural damage for the *Eragrostis chloromelas* woodland ($F_{1,2}=8.52$, $p=0.10$; Figure 5), while no associations were noted with cumulative fire indices (Figure 6). Even so, it was the most plausible model for vegetation changes included elephants and explains 43% of the variance in the data (Table 4).

The cumulative structural damage index had increased significantly for two plots ($F_{1,2}=102.69$; $p<0.01$; and $F_{1,2}=263.39$; $p<0.01$; Figure 5) in the *Diospyros whyteana* forest since 1996. No fires occurred in this forest (Figure 6), and no plausible model for vegetation change was identified, but a near-plausible model showed associations with cumulative structural damage indices (Table 4).

Discussion

Five plant communities in the study area exhibited changes in plant species composition and vegetation structure by 2010 compared to 1996 before elephants were introduced. Only two of the five communities displayed broad-scale directional change and became less similar to the plant species composition in 1996 (*Calpurnia aurea* woodland, *Diospyros whyteana* forest). For four of the five vegetation types, we noted variable decreases in the number of trees and shrubs greater than 4m in height as noted elsewhere (Kerley et al. 2008), due perhaps to the preference of these plant species by elephants.

Both cumulative fire and structural damage indices had changed variably since 1996. The most plausible models included vegetation changes associated with cumulative structural damage in three of the five plant communities (*Calpurnia aurea* woodland, *Eragrostis curvula* woodland, *Eragrostis chloromelas* woodland). Near-plausible models had vegetation changes associated with cumulative vegetation structural damages in four (*Diospyros whyteana* forest) of the five plant communities, with the fifth associated with cumulative fire damage indices (*Faurea saligna* woodland). If we assume that vegetation structural damage indices associate with elephant use (Shannon et al. 2011), then our results suggest that plant communities vary mostly in association with how intensely elephants use the landscape and associated vegetation and plant species.

Marakele, however, is prone to fires caused by lightning (van Staden 2002). Elephants, along with fires, may thus act as combined disturbance agents. We noted that the most plausible models were those including cumulative structural damage indices explained between 37% and 54% variation for three plant communities. In all three cases, the next best model included both cumulative vegetation, structural and fire damage indices. This suggests that interactions between elephants and fire may cause significant disturbance, especially in combination to plant communities. This result agrees with those of other studies across Africa which have noted the combined role of elephants and fire in shaping plant communities, an effect that is often accentuated in mesic savannas (Trollope et al. 1998).

At the time of elephant introduction during 1996, elephants could only use 300 km² of the mountainous landscapes of Marakele (van Staden 2002). Studies elsewhere (Landman et al. 2014; De Boer et al. 2015) noted that elephants have preferred vegetation-cum-habitats that limit their feeding localities. Elephants target specific plant communities, or even smaller micro-scale habitats within. This resulted in the variance we noted between plots representing the same plant community.

We noted rapid changes in cumulative vegetation structural damage indices from 1996 to 1998 for *Calpurnia aurea* woodland, *Eragrostis chloromelas* woodland and *Diospyros whyteana* forest. Elephants took two years to move into the newly available areas (Bezuidenhout 2004) after authorities expanded the Park during 2001. Since then, elephant use of the mountains was variable with herds only spending short periods at the study plots (SANParks, unpublished data³). Most plots for which we noted rapid change in cumulative vegetation structural damage indices by 1998 had little observed change during the 2008 and 2010 sampling periods.

The expansion of protected areas (if possible) can mitigate the accentuated intensity of use of localities by elephants, and potentially restore the variability in disturbance regimes associated with elephant activity (van Aarde et al. 2006). The consequences on biodiversity depend on whether a full spectrum of variability in resource availability for elephants is realized. At Marakele, the expansion of areas available to elephants introduced additional

³Judith Botha, judith.botha@sanparks.org

resource gradients and elephant habitat. We noted changes in cumulative vegetation structural damage indices in *Faurea saligna* woodland and the *Eragrostis curvula* woodland only during 2008 and 2010. This suggests that Marakele may still impose spatial constraints on resource gradients and use by elephants. It also suggests that density-dependent influences on landscape use and population demography (Gough and Kerley 2006) may not realize easily in Marakele.

The incidence and intensity of fires typically associated with rainfall history (Govender et al. 2006). We noted major increases in cumulative fire damage indices only during 2008 and the 2010 sampling periods. Our results support the notion that complex disturbance processes together with, and influenced by, climate and physical environmental factors (Gillson and Lindsay 2003) shape the character of ecosystems. Four plant communities had changes that associated with indices assumed to reflect elephant use, while one plant community had changes that associated with fire indices.

Conclusion

Elephants and fire are important modulators of vegetation features within the climatic regime and geomorphological features of Marakele. We recorded changes in four of the five mountainous plant communities that associated with structural damage indicative of elephant effects. Fire was largely a secondary factor. Although the expansion of the Park resulted in halting vegetation change, the remaining resource gradients at Marakele may still impose constraints on how elephants use landscapes and impact vegetation dynamics. This is particularly so when elephant disturbances facilitate fire disturbances that together can degrade unique plant communities *Diospyros whyteana* forest change contrasts park objectives, but can recover if conservationists protect such unique plant communities from undesirable disturbances while restoring the resource gradients that maintain disturbance regimes in Marakele.

Acknowledgements

Mr Abel Matsapula is thanked for assistance with the map.

References

- Agricultural Research Council (ARC). 2012. *Agricultural Research Council (ARC) weather station in Marakele National Park*. Kimberley: SANParks.
- Baxter PWJ. 2003. Modeling the impact of the African Elephant (*Loxodonta africana*) on woody vegetation in Semi-Arid Savannas. PhD. dissertation. University of California, Berkeley.
- Bezuidenhout H. 2004. Report on the impact of elephants on the vegetation of the Zwarthoek section (1996–1998 and 2002), Marakele National Park. Internal scientific report, Arid Ecosystems Research Unit, Kimberley, Conservation Services.
- Brown LR. 1997. A plant ecological study and wildlife management plan of the Borakalalo Nature Reserve, North West Province. PhD Thesis. University of Pretoria, Pretoria
- Coetzee BJ, Gertenbach WPD. 1977. Technique for describing woody vegetation composition and structure in inventory type classification, ordination and animal habitat surveys. *Koedoe* 20:67–75.
- Cornell HV, Lawton, JH. 1992. Species interactions, local and regional processes and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1–12.
- De Boer WF, Van Oort JWA, Grover M, Peel MJS. 2015. Elephants-mediated habitat modifications and changes in herbivore species assemblages in Sabi Sand, South Africa. *European Journal of Wildlife Research* Published online: DOI 10.1007/s10344-015-0919-3.
- Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetation* 69(1-3):57–68.
- Gillson L, Lindsay K. 2003. Ivory and ecology—changing perspectives on elephant management and the international trade in ivory. *Environmental Science and Policy* 6:411–419.
- Gough KF, Kerley GI. 2006. Demography and population dynamics in the elephants on savanna vegetation. *The Journal of Wildlife Management* 72(4):892–899.
- Govender N, Trollope, WS, Van Wilgen BW. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43(4):748–758.

Hall-Martin AJ. 2003. Management and Developed Plan for Marakele National Park. Part 1: Description of Marakele National Park. Internal Report, Conservation Services, SANParks.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. *Trends in ecology and evolution* 19(2):101–108.

Kerley GIH, Landman M. 2006. The impact of elephant on biodiversity in the Eastern Cape Subtropical thickets. *South African Journal of Science* 102:1–8.

Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D, De Boer WF, Gaylard A, Lindsey K, Slotow R. 2008. Effects of elephants on ecosystem and biodiversity. In: Scholes RJ, Mennell, GG (eds). *Elephant management: a scientific assessment for South Africa*. Wits University Press, Johannesburg, pp 146–205.

Landman M, Schoeman DS, Hall-Martin A, Kerley GIH. 2014. Long-term monitoring reveals differing impacts of elephants on elements of canopy shrub community. *Ecology Applications* 24(8):2002–2012.

Mucina L, Rutherford MC. (eds) 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.

Mackey RL, Page BR, Duffy KJ, Slotow R. 2006. Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research-24-month delayed open access* 36(1):33–43.

Peterson G, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1(1):6–18.

Roxburgh SH, Shea K, Wilson JB. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85(2):359–371.

Sankaran M, Ratnam J, Hanan N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17 (2):236–245.

Shannon G, Thaker M, Tamim VA, Page BR, Grant R, Slotow R. 2011. Relative impacts of elephant and fire on large trees in a savanna ecosystem. *Ecosystems* online publication: DOI: 10.1007/s10021-011-9485-z.

Trollope WSW, Trollope LA, Biggs HC, Pienaar DJ, Potgieter ALF. 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(2):103–112.

Van Aarde RJ, Ferreira, SM, Jackson TP, Page B, De Beer Y, Junker J, Gough K, Guldemond R, Olivier PJ, Ott T, Trimble MJ. 2008. Population biology and ecology. In: *Elephant Management: A Scientific Assessment for South Africa*. eds. Scholes RJ, Mennell KG pp. 84–145. Johannesburg, South Africa: Wits University Press.

Van Aarde RJ, Jackson TP, Ferreira SM. 2006. Conservation science and elephant management in South Africa. *South African Journal of Science* 102(9/10): 385.

Van Staden PJ. 2002. *An ecological study of the plant communities of Marakele National Park*. MSc Thesis. University of Pretoria, Pretoria.

Wassenaar. TD, Van Aarde, RJ, Pimm, SL., Ferreira, SM. 2005. Community convergence in disturbed subtropical dune forests. *Ecology* 86 (3):655–66