



# Complexities associated with elephant impact on *Sclerocarya birrea* subsp. *caffra* in the Greater Kruger National Park

R.M. Cook<sup>a,\*</sup>, M.D. Henley<sup>a,b</sup>

<sup>a</sup> Elephants Alive, P.O. Box 960, Hoedspruit 1380, South Africa

<sup>b</sup> Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Private Bag X5, Florida 1710, South Africa

## ARTICLE INFO

### Article history:

Received 14 November 2018

Received in revised form 10 January 2019

Accepted 17 January 2019

Available online xxxx

Edited by SJ Siebert

### Keywords:

Elephant impact

*Loxodonta africana*

Marula tree mortality

Termites

Waterholes

## ABSTRACT

African elephants *Loxodonta africana* are habitat modifiers, with the ability to impose heavy impact on trees. Conservation managers are concerned about increasing elephant impact on keystone tree species such as the marula *Sclerocarya birrea* subsp. *caffra*, however, a variety of natural and management-based factors influence the likelihood of a marula receiving elephant impact. Our study focused on a marula population in the Greater Kruger National Park which has been exposed to elephants for five years. Our objectives were to (1) examine the potential factors responsible for the decline of adult marula, (2) evaluate elephant impact across marula size classes, and (3) evaluate elephant impact on male and female marula. We modelled tree mortality as a response variable to factors, which included previous elephant impact, sex of the tree, distance to water, distance to roads, and termite presence. Of the sampled trees, 38% were dead. We found that a combination of elephant impact and termite presence within trees best explained tree mortality, with the presence of water and roads having relatively uniform effects on tree mortality because of an overabundance of these features. Trees in the smaller height classes had the highest annual mortality levels, whilst female trees had heavier impact levels in comparison to males. Our results highlight the complexity of a marula tree mortality, and how both natural and management-based factors can influence tree survival. We propose that environmental management alterations can decrease elephant-tree encounter rates and increase tree survival.

© 2019 SAAB. Published by Elsevier B.V. All rights reserved.

## 1. Introduction

The ability of African elephants *Loxodonta africana* to structurally modify vegetation in extreme measures has resulted in a number of studies focusing on how elephants transform their surrounding environment (Ben-Shahar, 1998; Gandiwa et al., 2011; Asner et al., 2016) and the effects that this transformation may have on other species (Kerley and Landman, 2006; Hrabar and Du Toit, 2014; Joseph et al., 2018). Past management strategies in protected areas such as South Africa's Greater Kruger National Park (KNP) have focused on controlling elephant numbers in an attempt to control the impact that elephants have on large tree species (Whyte et al., 1999). Culling, however, did not reach its management objectives of preventing the decline of large trees and so current management strategies focus on a macroscale level of altering elephant distributions across the landscape (SANParks, 2012; Purdon and van Aarde, 2017; Robson and Aarde,

2017), as well as on a microscale level of directly protecting the large trees (Derham et al., 2016; Cook et al., 2018).

One tree species of particular concern to conservation managers is the marula tree *Sclerocarya birrea* subsp. *caffra*, an ecologically important keystone species which provides both food (Palmer and Pitman, 1972) and habitat (Shackleton et al., 2002) to a variety of species. Marula trees are actively selected for by elephants (Greyling, 2004; Shannon et al., 2008), with heavy impact being recorded on adult trees across the Greater KNP landscape (Jacobs and Biggs, 2002; Helm et al., 2009; Helm and Witkowski, 2013; Cook et al., 2017). Elephants also appear to favour female marula trees in comparison to their male counterparts due to the fruit in the female trees (Hemborg and Bond, 2007), whilst trees between the heights of 5 and 11 m are particularly vulnerable to elephant impact (Jacobs and Biggs, 2002; Shannon et al., 2008; Cook et al., 2017).

The relationship between the number of elephants and large trees in a protected area is highly complex, as the encounter rate between elephants and large trees is influenced by the density of elephants and their spatial distribution (O'Connor et al., 2007). The presence of surface water is a primary attractant for elephants (Smit et al., 2007; Robson and Aarde, 2017), with elephant impact usually greatest around surface water points (Gaylard et al., 2003; Chamailé-Jammes et al., 2007;

\* Corresponding author at: Elephants Alive, P.O. Box 960, Hoedspruit 1380, South Africa.  
E-mail address: [robincook@elephantsalive.org](mailto:robincook@elephantsalive.org) (R.M. Cook).

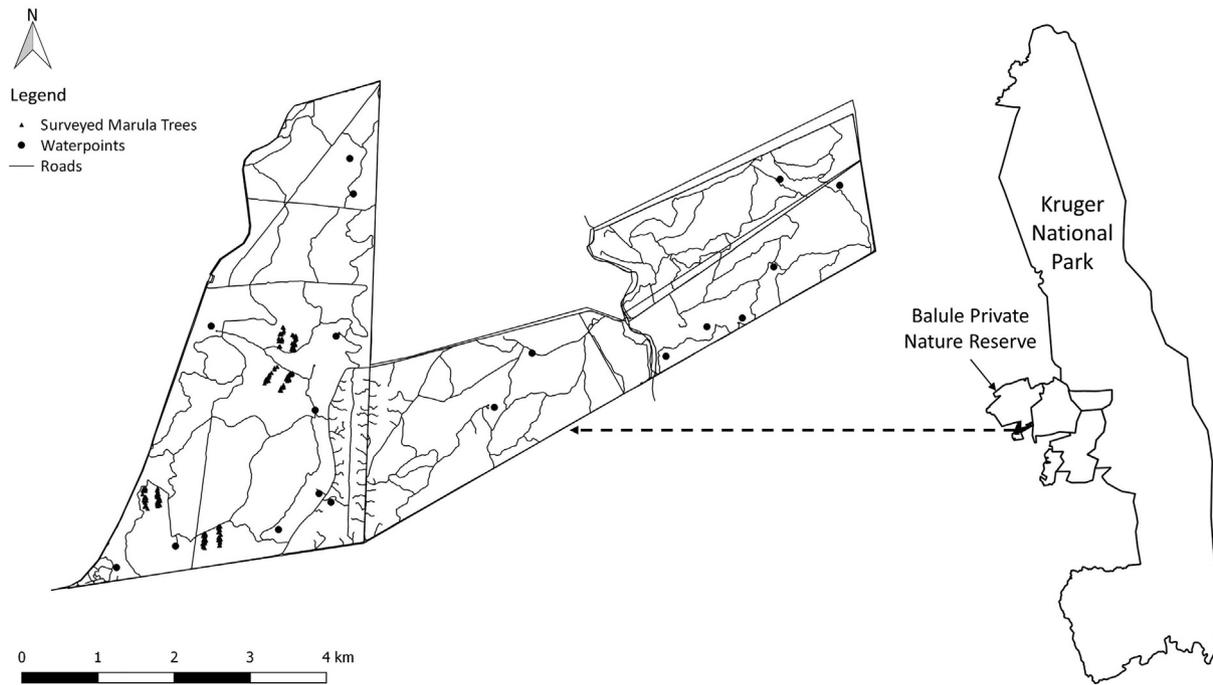


Fig. 1. Location of the surveyed marula trees across eight transects in Jeje Private Nature Reserve, Greater Kruger National Park.

Sianga et al., 2017). Furthermore, large trees closest to roads within protected areas may be more at risk to elephant impact, as bull elephants, in particular, make frequent use of roads within their home ranges (Pienaar, 1968; Coetzee et al., 1979). Added to this complexity, the condition of the tree prior to its encounter with an elephant may influence its survival rate. Termites (*Coptotermes* species) for example, attack older stressed trees with lower water content and larger gaps present (Cowie et al., 1989; Gould et al., 1993; Werner et al., 2008). A tree's susceptibility to termite entry is increased through exposure to fires (Midgley et al., 2010) or bark-stripping by elephants and other species (Helm et al., 2011). Trees may be internally hollowed out, leaving them more vulnerable to animal- (Holdo, 2003) or wind-impact (Koizumi and Hirai, 2006).

Therefore, in order to further understand how complex factors affect the survival of large trees in a small protected area, we conducted surveys on a subsample of marula trees in Jeje Private Nature Reserve (JPNR), a reserve within the Greater KNP. The marula trees in JPNR have been surveyed both before elephants were present in the reserve (Helm and Witkowski, 2012), as well as three years after elephants moved into the reserve from the Greater KNP area due to the removal of fences (Cook et al., 2017). Whilst high rates of marula tree mortality (23.8% of resampled trees) were recorded in the first three years of exposure to elephants, there was also a high presence of termites within

these trees (66.7%) (Cook et al., 2017). JPNR also has a high density of artificial surface water points (Cook et al., 2017). Understanding the factors affecting the decline of adult marula trees, in conjunction with elephant impact, will help inform conservation managers as to the best management practices to use for protecting adult marula trees. Therefore, after five years of elephant presence in JPNR, our study objectives were to: (1) examine the potential factors responsible for the decline of adult marula trees, (2) evaluate elephant impact across marula tree size classes, and (3) evaluate elephant impact on male and female marula trees.

## 2. Material and methods

### 2.1. Study area

JPNR (S24.29045; E30.97664) is a 21 km<sup>2</sup> shareholders block situated within Balule Private Nature Reserve, forming a part of the Greater KNP (Fig. 1). JPNR occurs in the savanna biome's granite lowveld vegetation unit (SVI 3), a moderately open savanna type dominated by large trees such as *Sclerocarya birrea* and *Senegalia nigrescens* (Mucina and Rutherford, 2006). JPNR receives a mean annual rainfall of 400–600 mm (Cook et al., 2017) and has an artificial surface water point density of 1 per 1.78 km<sup>2</sup> in the wet season and 1 per 3.35 km<sup>2</sup> in the dry

Table 1  
Impact scores to assess elephant impact on marula trees.

Score	Score description
0	No damage
1	<50% of the bark around the main stem's circumference has been removed and/or secondary branches have been broken off
2	>50% of the bark around the main stem's circumference has been removed, or one primary branch has been broken off
3	>50% of the bark around the main stem's circumference has been removed and one primary branch has been broken off, or more than one primary branch has been broken off
4	The tree has had its main stem snapped but is coppicing or alive
5	Tree is dead

Table 2

Results from the top eight logistic regression models investigating characteristics which explain marula tree mortality in combination with elephant impact in Jeje Private Nature Reserve. The models are arranged from best (table top) to worst (table bottom) based on the corrected Akaike's information criteria (AICc). Columns include AICc score,  $\Delta$  AICc (difference in AICc score from the best model), and the Akaike's model weight ( $\omega_i$ ).

Model	AICc	$\Delta$ AICc	$\omega_i$
Elephant impact * Height * Termites	89.61	0	0.649
BSD * Elephant impact * Termites	92.46	2.85	0.156
Elephant impact * Height * Road distance * Termites	93.75	4.14	0.082
Elephant impact * Termites	94.15	4.54	0.067
Elephant impact * Height * Sex	97.76	8.15	0.011
Elephant impact * Sex * Termites	98.48	8.87	0.007
Elephant impact * Termites * Water distance	99.01	9.40	0.006

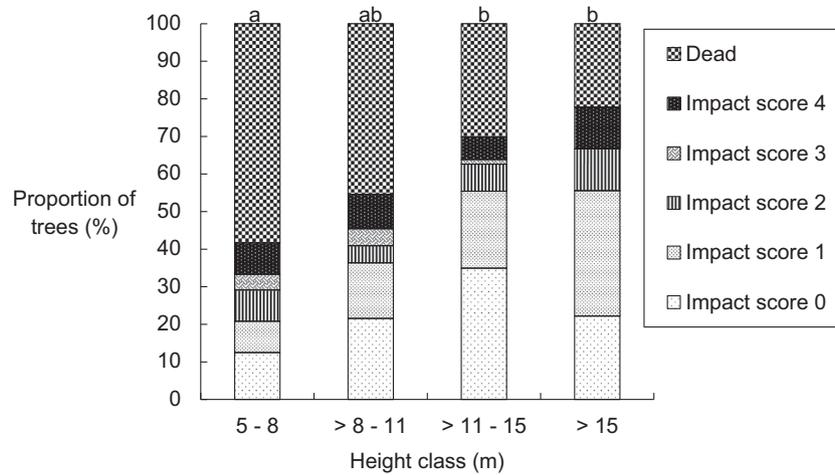


Fig. 2. Elephant impact levels on marula tree height classes in Jejeane Private Nature Reserve. Different letters indicate significant differences in elephant impact levels.

season (Cook et al., 2017). JPNR had not had any elephants in over a century, with the first elephants moving into the reserve in 2013 (Thomson, 2013). No management-controlled fires are conducted in JPNR (Cook et al., 2017).

## 2.2. Field surveys

One the 16 and 17 February 2018, 202 marula trees, first surveyed by Helm and Witkowski (2012) in 2009 and then by Cook et al. (2017) in 2016, were resurveyed. The trees were located in eight transects along the western section of JPNR, with each transect ranging from 203 to 289 m in length and 40 m in width (Fig. 1). Unfortunately, as no surveys were conducted in 2013, we cannot accurately assume that all 202 trees recorded in 2009 were alive in 2013. However, using unpublished data of Elephants Alive collected from 1219 trees across the Greater KNP, our results suggest that other agents such as wind toppling, insects, fungi, as well as unknown causes were responsible for the mortality of 0.49% of adult trees in a single year. No fire occurs in JPNR and so fire was excluded from this analysis. This equates to 1 tree per year of the 202 surveyed marula trees, or 4 trees between 2009 and 2013. As this mortality rate is minimal and not accurately accounted for, we have not included it in our analysis. We do, however, recognise the potential loss of trees prior to their exposure to elephants.

Relocated trees were classified as 'mature and standing', 'snapped or toppled but alive', and 'dead'. Elephant impact on each tree was measured according to scoring standards previously used by Helm and Witkowski (2013) and Cook et al. (2017) (Table 1). These scores were further grouped into the following categories: light impact (scores 0–1), moderate impact (scores 2–3), and heavy impact (scores 4–5). Tree height was measured using the *VolCalc* digital photography method for estimating tree dimensions (Barrett and Brown, 2012) and heights were placed into the following size categories: <5, 5–8, 8–11, 11–15, and >15 m. The basal stem diameter (BSD) of each tree was measured and placed into the following size categories: 20–30, 30–40,

40–50, 50–60, and 60–70 cm. The presence or absence of termites (*Coptotermes* species) were recorded on every tree. Trees had previously been sexed by Helm and Witkowski (2012) and Cook et al. (2017) by using the presence of kernels underneath the tree as an indication of a female tree. Each tree's distance to the nearest road and permanent surface water point was subsequently measured by a distance matrix on QGIS (QGIS Development Team, 2018).

## 2.3. Data analysis

### 2.3.1. Marula tree mortality

A moderately strong positive correlation existed between tree height and BSD (Pearson's correlation,  $r = 0.62$ ,  $n = 202$ ,  $p < .001$ ) and therefore height was used as a proxy for overall tree size when comparing elephant impact across size classes. A generalised linear model with a binary response (tree alive = 0, tree dead = 1) and a logit-link function was used to determine the covariates that best explained tree mortality between the survey periods. The following covariates were used: grouped elephant impact on the tree (Elephant impact), height of tree (Height), basal stem diameter of the tree (BSD), distance of tree to nearest road (Road distance), distance of tree to nearest permanent surface water point (Water distance), and presence or absence of termites on tree (Termites). All models were ranked using the corrected Akaike's information criteria (AICc), where the model with the lowest AICc was selected for as the best model (Burnham and Anderson, 2004). Analyses were conducted in R statistical software version 3.5.0. (R Core Team), using the *glm2* package (Marschner, 2011). Pearson's correlations were run to test for relationships between trends in elephant and marula tree densities and the number of years in which elephants have been within the study site.

**2.3.1.1. Tree mortality across height classes.** Differences in elephant impact scores across height classes were compared using a Kruskal–Wallis by ANOVA rank test. A preference ratings assessment was used to identify whether elephants were selecting for trees of a particular height class (Petrides, 1975). Preference ratings are calculated as a dividend of percentage diet choice over diet availability ( $p = d/A$ ). This method is further described by Petrides (1975). Total tree mortality (%) and annual mortality rates (% per annum) were compared across height classes and between survey years (2016 and 2018 surveys), and a log rank test was used to test for differences in the probability of tree survival across height classes using the survival package (R Development Core Team, 2016) (Therneau and Lumley, 2009).

**2.3.1.2. Tree mortality between female and male trees.** Differences in mortality levels between female and male trees were analysed using a Chi-

Table 3

Elephant preference ratings for marula tree height classes in Jejeane Private Nature Reserve. Preference ratings >1.00 indicate that the height class is sought after or preferred by elephants.

Height class	Quantities		Preference rating
	Trees available	Trees removed	
5–8 m	17	13	1.97
8–11 m	79	38	1.29
11–15 m	98	25	0.66
>15 m	8	1	0.32
Totals	202	78	–

**Table 4**  
Comparison of the total mortality percentages and annual mortality rates of marula trees since 2013 across height classes for the 2016 and 2018 surveys in Jejeane Private Nature Reserve.

	Height class			
	5–8 m (n = 17)	8–11 m (n = 78)	11–15 m (n = 98)	> 15 m (n = 8)
Total tree mortality (%)				
2016 survey (3-year elephant presence)	41.18	28.21	19.39	12.50
2018 survey (5-year elephant presence)	76.47	50.00	25.51	12.50
% change between survey years	35.29	21.79	6.12	0
Annual mortality rate (% dead trees per year)				
2016 survey (3-year elephant presence)	13.73	6.46	6.46	4.17
2018 survey (5-year elephant presence)	15.29	10.00	5.10	2.50
% change between survey years	1.56	3.54	–1.36	–1.67

square test. A Log rank test was used to test for differences in the probability of survival between male and female trees (R Core Team) (Therneau and Lumley, 2009).

### 3. Results

#### 3.1. Marula tree mortality

Of the 202 resurveyed trees in JPNR, 54% ( $n = 110$ ) were mature and standing, 6.4% ( $n = 13$ ) have been stem snapped or toppled but were still alive, whilst 38% ( $n = 78$ ) were dead. The surveyed JPNR tree density had significantly decreased from 25.6 trees/ha in 2009 to 15.7 trees/ha in 2018 (Analysis of variance,  $F_{(2,21)} = 5.21$ ,  $n = 8$ ,  $p < .05$ ). Termites were present in 43.5% ( $n = 88$ ) of all surveyed trees, whilst 24.8% ( $n = 31$ ) of trees which were still alive had termite activity. Tree distance from artificial water points ranged from 389 m - 1205 m, with 90.6% ( $n = 183$ ) of trees < 1 km from a water point.

Results from the GLM analysis are presented in Table 2. The best model for explaining tree mortality included 'Elephant impact', 'Height', and 'Termites' and had a model weight of 0.649. The next best model, with a delta of 2.85 and weight of 0.156, included 'Elephant impact', 'BSD', and 'Termites'. 'Road distance' featured in the third best model, along with 'Elephant impact', 'Height', and 'Termites' with a model weight of 0.082. 'Sex' occurs in the fifth best model, along with 'Elephant impact' and 'Termites' with model weight of 0.011. 'Water distance' only occurs in the seventh best model, along with 'Elephant impact', 'Height', and 'Termites' with a model weight of 0.006.

The JPNR marula tree density has continually decreased since being exposed to elephants (Pearson's correlation,  $r = -0.99$ ,  $n = 3$ ,  $p < .05$ ), however, elephant densities have varied between <0.2 and 2.1 elephants/km<sup>2</sup> since the fences have dropped, with no correlation between elephant numbers and the years in which they have been present within the study site (Pearson's correlation,  $r = 0.25$ ,  $n = 7$ ,  $p < .059$ ).

##### 3.1.1. Tree mortality across height classes

The highest elephant impact scores were recorded for trees in the 5–8 m height class, with impact scores decreasing with an increase in height class (Fig. 2.). Both the 5–8 m and 8–11 m height classes had preference ratings > 1.00 (Table 3), indicating that these height classes were selected for by elephants in comparison to the larger height classes. Whilst the log rank test did not find statistical differences between the survival probabilities of trees across the height classes (Log Rank Test,  $X^2_3 = 2.3$ ,  $p = .5$ ), the greatest total tree mortalities have occurred in the 5–8 m (76.47%) and 8–11 m (50.00%) height classes (Table 4). The annual mortality rates of both of these height classes have also increased between the 2016 and 2018 surveys (Table 4). Lower total mortalities have occurred in trees in the 11–15 m (25.51%) and > 15 m (12.50%) height classes, with the mortality rates of both height classes decreasing between the 2016 and 2018 surveys (Table 4).

##### 3.1.2. Tree mortality between female and male trees

Female tree mortality was significantly higher in comparison to male tree mortality  $X^2_2 = 4.15$ ,  $p < .05$ ,  $n_{\text{♀}} = 74$ ,  $n_{\text{♂}} = 127$ , with 49% of the 74 female trees dead in comparison to 33% of the 127 male trees. The female to male sex ratio has changed from 1 ♀:1.72 ♂ trees in 2009, to 1 ♀:2.24 ♂ trees in 2018, with female trees having a significantly lower probability of survival versus male trees (Log Rank Test,  $X^2_1 = 4.9$ ,  $n_{\text{♀}} = 74$ ,  $n_{\text{♂}} = 127$ ,  $p < .05$ ). Of the female trees, 50% ( $n = 37$ ) have been either uprooted or main stem snapped, versus 37% ( $n = 47$ ) of the male trees. A greater percentage of male trees (65%,  $n = 83$ ) have received some form of bark-stripping versus 55% ( $n = 41$ ) of the female trees.

### 4. Discussion

After five years of exposure to elephants, 38% of the surveyed marula trees are dead, with the highest mortality levels recorded on female trees and trees under a height of 11 m. The presence of termites in trees during the 2016 surveys (43.5% of surveyed trees) was a significant factor for predicting tree mortality for the 2018 surveys.

High levels of elephant impact on marula trees less than 11 m in height have been recorded elsewhere (Jacobs and Biggs, 2002; Shannon et al., 2008; Cook et al., 2017), as these individuals are small enough to be toppled over by elephants during foraging activities (Stokke and Du Toit, 2000). Furthermore, female trees may be targeted more by elephants in comparison to males because of the presence of fruit in female trees during the fruiting season (Hemborg and Bond, 2007). In our study, more female trees were subjected to heavier levels of elephant impact (stem snapping and uprooting) in comparison to male trees, potentially in an attempt by elephants to gain access to the fruit. However, our results also suggest that the presence of termites in marula trees may affect a tree's survival and susceptibility to elephant impact and subsequent tree mortality. Termites are prevalent in unburnt savannas (Abensperg-Traun and Milewski, 1995) and *Coptotermes* species are capable of penetrating trees through fractures in the bark (Gould et al., 1993; N'Dri et al., 2011) and establishing secondary nests inside of the trees' cavities (Harris, 1966). The susceptibility of trees to termite penetrations is increased when bark is removed by animals such as elephants or porcupines *Hystrix africaeustralis* (Helm et al., 2011), leaving the trees hollowed out from the inside (Werner et al., 2008). These hollowed out sections of the trees may be more vulnerable to various degrees of elephant impact. Reports of termites preventing the regrowth of marula trees have been recorded in the Greater KNP (Coetzee et al., 1979) and our results highlight the importance considering termite activity when focusing on the persistence of trees exposed to elephants. We suggest that further research is required in this field, where levels of termite infestation are scored in conjunction with elephant impact levels (Gould et al., 1993), thereby monitoring how superficial or internal termite damage may increase a trees susceptibility to elephant-induced mortality. Our correlations of changes in marula tree and elephant densities over time suggest that the

relationship between the two densities are nonlinear, as marula tree densities have continued to significantly decline with varied elephant densities. However, elephant impact which promotes a tree's susceptibility to termite invasions may explain the continued decline of adult marula trees, even when elephant densities are low. This pattern of accumulated mortality was recorded on *Vachellia tortilis* in the Sengwa Wildlife Ranching Area, where ring-barking in combination with borer attack were thought to be the primary drivers for tree mortality (Anderson and Walker, 1974). A tree's internal state is important to monitor, and further research into savanna trees' susceptibility to accumulated mortality will help explain the complexities surrounding elephant impact and the lag effects associated with this impact.

Our model indicated a nonsignificant but general increase in elephant impact on trees closer to roads. Whilst previous studies have recorded a greater level of elephant impact on trees closer to roads (Pienaar, 1968; Coetzee et al., 1979; but see Gadd, 2002), JPNR has an extensive road network within a small area that may decrease such a pattern. Interestingly, distance to water was only present in the seventh highest model and no significant trend was evident. Surface water is an important attractant for elephants (Smit et al., 2007; Purdon and van Aarde, 2017) and elephant impact on trees is usually greatest in the immediate areas surrounding surface water (Sianga et al., 2017; Teren et al., 2018). Ideally, this promotes heterogeneity within the landscape, as elephant impact on large trees decreases in areas further from surface water (Chamaillé-Jammes et al., 2007; Sianga et al., 2017). JPNR, however, is a water saturated landscape (Cook et al., 2017), where 90.6% of our surveyed trees were less than 1 km from a surface water point. This high density of surface water points homogenises elephant impact across the area, thereby leading to increased tree mortality within JPNR because of an increased encounter rate between the elephants and the trees (O'Connor et al., 2007). The density of surface water points, combined with the road network, may explain why the marula tree mortality levels in JPNR are so high when compared with other marula tree mortality levels across the Greater KNP (Helm et al., 2009). Furthermore, JPNR had a relatively high density of adult marula trees prior to the return of elephants into the reserve when compared with other Greater KNP sites (Helm and Witkowski, 2012), which add to the elevated tree mortality levels currently being experienced within JPNR.

Our results highlight the complexity surrounding tree mortality in protected areas containing elephants, and how both natural (i.e. termite presence) and management-based factors (i.e. road and artificial water point density) can affect the likelihood of elephant-induced tree mortality. Whilst the closure of the majority of artificial surface water points may seem ideal, this management decision would need to be applied across the entire Greater KNP to produce the desired effect (Robson and Aarde, 2017) and is not a practical solution for smaller, private reserves within the Greater KNP. Mitigation methods that increase the survival rate of individual large trees against elephant impact may be beneficial in the water-saturated private sector of the Greater KNP (Derham et al., 2016; Cook et al., 2018; Wright et al., 2018). However, it would also be beneficial to focus on large tree protection across all life history stages, where the survival of both the seeds (Helm et al., 2011) and seedlings (Moe et al., 2009) of large tree species are taken into account. Furthermore, the impact of both termites and other wood-borer species require further monitoring to understand how they affect the survival rates of African savanna trees, both with and without the presence of elephants.

#### Declarations of interest

None.

#### Acknowledgements

We wish to thank Elephants Alive for funding and logistics support throughout this study. JPNR management are thanked for allowing us

to conduct research within their property and for providing information on elephant census counts. All field assistants are thanked for their support within JPNR. T. Lotter is thanked for electronically measuring the heights of all field surveyed trees using the methods described.

#### References

- Abensperg-Traun, M., Milewski, A.V., 1995. Abundance and diversity of termites (Isoptera) in imburnt versus burnt vegetation at the Barrens in Mediterranean Western Australia. *Australian Journal of Ecology* 20, 413–417. <https://doi.org/10.1111/j.1442-9993.1995.tb00557.x>.
- Anderson, B.H., Walker, G.D., 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *South African Journal of Wildlife Research* 4, 1–14. [https://hdl.handle.net/10520/AJA03794369\\_3310](https://hdl.handle.net/10520/AJA03794369_3310).
- Asner, G.P., Vaughn, N., Smit, I.P., Levick, S., 2016. Ecosystem-scale effects of megafauna in African savannas. *Ecography* 39, 240–252. <https://doi.org/10.1111/ecog.01640>.
- Barrett, A.S., Brown, L.R., 2012. A novel method for estimating tree dimensions and calculating canopy volume using digital photography. *African Journal of Range & Forage Science* 29, 153–156. <https://doi.org/10.2989/10220119.2012.727471>.
- Ben-Shahar, R., 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology* 136, 189. <https://doi.org/10.1023/A:1009708021735>.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33, 261–304. <https://doi.org/10.1177/0049124104268644>.
- Chamaillé-Jammes, S.I.M.O.N., Valeix, M., Fritz, H., 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology* 44, 625–633. <https://doi.org/10.1111/j.1365-2664.2007.01300.x>.
- Coetzee, B.J., Engelbrecht, A.H., Joubert, S.C.J., Retief, P.F., 1979. Elephant impact on *Sclerocarya caffra* trees in *Acacia nigrescens* tropical plains thornveld of the Kruger National Park. *Koedoe* 22, 39–60. <https://doi.org/10.4102/koedoe.v22i1.650>.
- Cook, R.M., Witkowski, E.T.F., Helm, C.V., Henley, M.D., Parrini, F., 2017. Recent exposure to African elephants after a century of exclusion: Rapid accumulation of marula tree impact and mortality, and poor regeneration. *Forest Ecology and Management* 401, 107–116. <https://doi.org/10.1016/j.foreco.2017.07.006>.
- Cook, R.M., Parrini, F., King, L.E., Witkowski, E.T.F., Henley, M.D., 2018. African honeybees as a mitigation method for elephant impact on trees. *Biological Conservation* 217, 329–336. <https://doi.org/10.1016/j.biocon.2017.11.024>.
- Cowie, R.H., Logan, J.W., Wood, T.G., 1989. Termite (Isoptera) damage and control in tropical forestry with special reference to Africa and Indo-Malaysia: a review. *Bulletin of Entomological Research* 79, 173–184. <https://doi.org/10.1017/S0007485300018150>.
- Derham, K., Henley, M.D., Schulte, B.A., 2016. Wire netting reduces African elephant (*Loxodonta africana*) impact to selected trees in South Africa. *Koedoe* 58, 1–7. <https://doi.org/10.4102/koedoe.v58i1.1327>.
- Development Team, Q.G.I.S., 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project <http://qgis.osgeo.org>.
- Gadd, M.E., 2002. The impact of elephants on the marula tree *Sclerocarya birrea*. *African Journal of Ecology* 40, 328–336. <https://doi.org/10.1046/j.1365-2028.2002.00385.x>.
- Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T., Tafangenyasha, C., 2011. The impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National Park, Zimbabwe. *Journal of Arid Environments* 75, 809–814. <https://doi.org/10.1016/j.jaridenv.2011.04.017>.
- Gaylard, A., Owen-Smith, R.N., Redfern, J., 2003. Surface water availability: Implications for heterogeneity and ecosystem processes. In (Eds.), In: du Toit, J.T., Rogers, K.H., Biggs, H.C. (Eds.), *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington, DC, pp. 171–188.
- Gould, M.S., Lowe, A.J., Clarke, G.P., 1993. The frequency of termite (Isoptera) damage to tree species in Namakutwa forest, Tanzania. *Sociobiology* 23, 189–198.
- Greyling, M.D., 2004. Sex and Age Related Distinctions in the Feeding Ecology of the African Elephant, *Loxodonta africana*. PhD Thesis. Faculty of Science, University of the Witwatersrand, Johannesburg <http://hdl.handle.net/10539/7489>.
- Harris, W.V., 1966. Termites and trees. A review of recent literature. *Forestry Abstracts* 27, 173–178.
- Helm, C.V., Witkowski, E.T.F., 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. *Forest Ecology and Management* 263, 175–188. <https://doi.org/10.1016/j.foreco.2011.09.024>.
- Helm, C.V., Witkowski, E.T., 2013. Continuing decline of a keystone tree species in the Kruger National Park, South Africa. *African Journal of Ecology* 51, 270–279. <https://doi.org/10.1111/aje.12032>.
- Helm, C.V., Witkowski, E.T.F., Kruger, L., Hofmeyr, M., Owen-Smith, N., 2009. Mortality and utilisation of *Sclerocarya birrea* subsp. *caffra* between 2001 and 2008 in the Kruger National Park, South Africa. *South African Journal of Botany* 75, 475–484. <https://doi.org/10.1016/j.sajb.2009.03.004>.
- Helm, C.V., Scott, S.L., Witkowski, E.T.F., 2011. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. *South African Journal of Botany* 77, 650–664. <https://doi.org/10.1016/j.sajb.2011.02.003>.
- Hemborg, Å.M., Bond, W.J., 2007. Do browsing elephants damage female trees more? *African Journal of Ecology* 45, 41–48. <https://doi.org/10.1111/j.1365-2028.2006.00666.x>.
- Holdo, R.M., 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology* 19, 189–196. <https://doi.org/10.1017/S0266467403003213>.

- Hrbar, H., Du Toit, J.T., 2014. Interactions between megaherbivores and microherbivores: elephant browsing reduces host plant quality for caterpillars. *Ecosphere* 5, 1–6. <https://doi.org/10.1890/ES13-00173.1>.
- Jacobs, O.S., Biggs, R., 2002. The status and population structure of the marula in Kruger National Park. *South African Journal of Wildlife Research* 32, 1–12. [10.520/EJC117144](https://doi.org/10.520/EJC117144).
- Joseph, G.S., Seymour, C.L., Coetzee, B.W., Ndlovu, M., Deng, L., Fowler, K., Hagan, J., Brooks, B.J., Seminara, J.A., Foord, S.H., 2018. Elephants, termites and mound thermoregulation in a progressively warmer world. *Landscape Ecology* 1. <https://doi.org/10.1007/s10980-018-0629-9>.
- Kerley, G.L., Landman, M., 2006. The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets: elephant conservation. *South African Journal of Science* 102, 395–402. <http://hdl.handle.net/10520/EJC96608>.
- Koizumi, A., Hirai, T., 2006. Evaluation of the section modulus for tree-stem cross sections of irregular shape. *Journal of Wood Science* 52, 213–219. <https://doi.org/10.1007/s10086-005-0747-2>.
- Marschner, I.C., 2011. *glm2: Fitting generalized linear models with convergence problems*. *The R Journal* 3, 12–15.
- Midgley, J.J., Lawes, M.J., Chamaillé-Jammes, S., 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58, 1–11. <https://doi.org/10.1071/BT09034>.
- Moe, S.R., Rutina, L.P., Hytteborn, H., Du Toit, J.T., 2009. What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology* 46, 223–230. <https://doi.org/10.1111/j.1365-2664.2008.01595.x>.
- Mucina, L., Rutherford, M.C., 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.
- N'Dri, A.B., Gignoux, J., Konaté, S., Dembélé, A., Aidara, D., 2011. Origin of trunk damage in West African savanna trees: the interaction of fire and termites. *Journal of Tropical Ecology* 27, 269–278. <https://doi.org/10.1017/S026646741000074X>.
- 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. *Biological Conservation* 136, 329–345. <https://doi.org/10.1016/j.biocon.2006.12.014>.
- Palmer, E., Pitman, N., 1972. *Trees of Southern Africa*. Vol. 2. Struik, Cape Town, South Africa.
- Petrides, G.A., 1975. Principal foods versus preferred foods and their relations to stocking rate and range condition. *Biological Conservation* 7, 161–169. [https://doi.org/10.1016/0006-3207\(75\)90012-9](https://doi.org/10.1016/0006-3207(75)90012-9).
- Pienaar, U.D.V., 1968. The ecological significance of roads in a national park. *Koedoe* 11, 169–174.
- Purdon, A., van Aarde, R.J., 2017. Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments* 141, 45–51. <https://doi.org/10.1016/j.jaridenv.2017.01.014>.
- R Development Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna Available from. <http://www.Rproject.org> ISBN: 3-900051-07-0 (cited 02 July 2018).
- Robson, A.S., Aarde, R.J., 2017. Changes in elephant conservation management promote density-dependent habitat selection in the Kruger National Park. *Animal Conservation* 21, 302–312. <https://doi.org/10.1111/acv.12393>.
- SANParks, 2012. *Elephant management plan. Kruger National Park. 2013–2022*. SANParks, Skukuza, South Africa.
- Shackleton, S.E., Shackleton, C.M., Cunningham, T., Lombard, C., Sullivan, C.A., Netshiluvhi, T.R., 2002. Knowledge on *Sclerocarya birrea* subsp. *caffra* with emphasis on its importance as a non-timber forest product in south and southern Africa: a summary: part 1: taxonomy, ecology and role in rural livelihoods. *The Southern African Forestry Journal* 194, 27–41. <https://doi.org/10.1080/20702620.2002.10434589>.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R., Slotow, R., 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* 24, 281–289. <https://doi.org/10.1017/S0266467408004951>.
- Sianga, K., van Telgen, M., Vrooman, J., Fynn, R.W., van Langevelde, F., 2017. Spatial refuges buffer landscapes against homogenisation and degradation by large herbivore populations and facilitate vegetation heterogeneity. *Koedoe* 59, 1–13. <https://doi.org/10.4102/koedoe.v59i2.1434>.
- Smit, I.P.J., Grant, C.C., Whyte, I.J., 2007. Elephants and water provision: what are the management links? *Diversity and Distributions* 13, 666–669. <https://doi.org/10.1111/j.1472-4642.2007.00403.x>.
- Stokke, S., Du Toit, J.T., 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23, 70–80. <https://doi.org/10.1111/j.1600-0587.2000.tb00262.x>.
- Teren, G., Owen-Smith, N., Erasmus, B.N., 2018. Elephant-mediated compositional changes in riparian canopy trees over more than two decades in northern Botswana. *Journal of Vegetation Science* 29, 585–595. <https://doi.org/10.1111/jvs.12638>.
- Therneau, T.M., Lumley, T., 2009. *Survival Analysis, Including Penalized Likelihood*, Original R Port by Thomas Lumley [Internet]. Available from. <http://www.r-project.org/>.
- Thomson, G., 2013. *Mohlabetsi South Nature Reserve Warden's Report - 24th June 2013*.
- Werner, P.A., Prior, L.D., Forner, J., 2008. Growth and survival of termite-piped *Eucalyptus tetrodonta* and *E. miniata* in northern Australia: implications for harvest of trees for didgeridoos. *Forest Ecology and Management* 256, 328–334. <https://doi.org/10.1016/j.foreco.2008.04.027>.
- Whyte, I.J., Biggs, H.C., Gaylard, A., Braack, L.E.O., 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe* 42, 111–132. <https://doi.org/10.4102/koedoe.v42i1.228>.
- Wright, M.G., Spencer, C., Cook, R.M., Henley, M.D., North, W., Mafra-Neto, A., 2018. African bush elephants respond to a honeybee alarm pheromone blend. *Current Biology* 28, R778–R780. <https://doi.org/10.1016/j.cub.2018.06.008>.