



Woody vegetation damage by the African elephant during severe drought at Pongola Game Reserve, South Africa

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Abstract

Elephants (*Loxodonta africana*) significantly alter ecosystem structure and composition through browsing (e.g. pollarding, debarking and toppling). Such browsing is predicted to intensify during severe drought which may become more common with climate change. Here, we make use of an elephant impact survey from 2012 to 2015 and during the El Niño drought of 2015–2016 at Pongola Game Reserve (107 km²), KwaZulu-Natal, to investigate how severe drought influenced damage severity of different tree heights and species by elephants in this small reserve. Contrary to expectations, damage to common species did not change with severe drought. Crown damage had the highest predicted probability across heights (29%–90%) and species (46%–75%) regardless of drought. However, we found severe drought increased the predicted probabilities of crown damage to smaller trees <4 m, mortality >6 m and severe damage at 4–6 m. Consequently, elephant damage during severe drought may alter vegetation structure by severely damaging or killing large trees (>4 m) and extensively damaging the crowns of trees <4 m. Long-term monitoring of elephant effects on woody vegetation is essential to enable science-based management in response to future drought and elephant damage (e.g. range expansion, beehive deterrents) to protect elephants and conserve woody vegetation.

Résumé

L'abrutissement (ex. : écimage, écorçage et déracinement) des éléphants (*Loxodonta africana*) a un impact considérable sur la structure et la composition de l'écosystème. Nous pouvons penser que ce phénomène d'abrutissement s'intensifiera au cours des périodes de grande sécheresse à venir, qui deviendront certainement de plus en plus fréquentes à cause du changement de climat. Notre recherche s'appuie sur une étude portant sur l'impact des éléphants réalisée entre 2012 et 2015 et pendant la période de sécheresse causée par le phénomène El Niño entre 2015 et 2016 dans la réserve animalière de Pongola (107 km²) du KwaZulu Natal, afin de déterminer la façon dont les périodes de grande sécheresse influencent la gravité des dommages causés et la sélection de divers hauteurs et espèces d'arbres par les éléphant dans cette petite réserve. Contrairement aux attentes, l'ampleur des dommages infligés

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aux espèces courantes n'a connu aucune variation au cours des périodes de grande sécheresse. Les dommages causés sur les couronnes des arbres constituaient la probabilité prévue la plus élevée pour toutes les hauteurs (29%-90%) et espèces (46%-75%), quelle que soit l'ampleur de la sécheresse. Néanmoins, nous avons conclu que les périodes de grande sécheresse avaient pour effet d'augmenter les probabilités prévues de dommages causés à la couronne des arbres de petite taille (<4 m, mortalité >6 m) et de dommages importants survenant entre 4 et 6 mètres de hauteur. Par conséquent, les dommages causés par les éléphants au cours des périodes de grande sécheresse peuvent altérer la structure de la végétation en endommageant gravement ou en provoquant la mort de grands arbres (d'une hauteur supérieure à 4 m) et en causant des dommages encore plus graves aux couronnes des arbres d'une hauteur inférieure à 4 mètres. Un suivi à long terme de l'impact des éléphants sur la végétation ligneuse est essentiel afin de mettre en place une gestion scientifique (ex. : expansion, ruches d'abeilles à effet dissuasif) du problème pour faire face aux dommages causés par la sécheresse et les éléphants à l'avenir, tout en protégeant ces mêmes animaux et cette même végétation.

KEYWORDS

browser, climate change, ecosystem engineers, large herbivore ecology, large trees, multinomial regression

1 | INTRODUCTION

African elephants (*Loxodonta africana*, Blumenbach) are the world's largest terrestrial animal (Owen-Smith, 1988). As bulk feeders, they consume large quantities of biomass such as grasses, herbs and woody vegetation, and their behaviour can strongly influence vegetation states while fulfilling their huge nutritional requirements (Codron et al., 2011; Loarie, van Aarde, & Pimm, 2009a, 2009b). Thus, they have the ability to profoundly alter ecosystem structure and composition, and in doing so act as ecosystem engineers within African savannahs (Coverdale et al., 2016; Haynes, 2012; Owen-Smith, 1988).

Elephant resource selection is typically seasonally flexible and varies between grasses, leaves and herbs (wet season), and woody vegetation such as branches, bark and roots (dry season; Loarie, van Aarde, & Pimm, 2009a; Seloana, Jordaan, Potgieter, & Kruger, 2018). The use of woody vegetation by elephants can result in significant damage through debarking, toppling (pushing over or snapping of trunk), uprooting and pollarding of trees (Parker, 2017), and their effects can drive the loss of large (>5 m, Shannon et al., 2008) and iconic tree species (e.g. Marula (*Sclerocarya birrea*), Helm & Witkowski, 2013; Baobab, Kassa et al., 2014). The loss of large and iconic tree species, when combined with damage to smaller trees, can result in the conversion of established woodland to open grassland or thicket and can prevent woody vegetation from establishing beyond the proposed 'browse trap'—a height where tree growth is suppressed through extensive browsing (Asner & Levick, 2012; Staver & Bond, 2014). Reduced structural

complexity of vegetation through elephant-induced tree mortality can promote canopy and landscape homogeneity (O'Connor & Page, 2014) and reduce the abundance and diversity of animals that rely on structural diversity to persist in savannah ecosystems (e.g. Southern-Ground Hornbill (*Bucorvus leadbeateri*), Combrink, Combrink, Botha, & Downs, 2017).

Elephants select preferred woody species based on low secondary metabolite levels and high relative nutrient quality, consequently exposing favoured species to an increased risk local extirpation when subject to extensive elephant damage (Holdo, 2003; Schmitt, Ward, & Shrader, 2016; Seloana et al., 2018). The ability of favoured woody species to resist extirpation relies on their ability to withstand and regenerate from elephant damage while recruiting juvenile trees into heights where they are less vulnerable to elephant browsing (O'Connor, Goodman, & Clegg, 2007). With persistent elephant damage, species with poor regenerative ability and low browsing tolerance are at greater risk of extirpation, which can result in the simplification of woody species diversity and structure within elephant ranges (Johnson, Cowling, & Phillipson, 1999; O'Connor & Page, 2014).

During the 1960–1970s, elephants transformed Tsavo National Park, Kenya, from a landscape dominated by *Commifera* and *Acacia* woodland (Bax & Sheldrick, 1963) to an open grassland savannah, with the primary disturbance agent switching from herbivory to fire (Dublin, Sinclair, & McGlade, 1990). Subsequently, drought and severe poaching substantially reduced elephant densities at Tsavo but fire then hindered the ability of the woody species to recover by killing many young trees before they reached maturity (Leuthold,

1996). The capacity for elephants to alter the structure and functioning of savannahs is, therefore, of concern to many conservation managers and ecologists across Africa, who fear that high elephant densities may result in a Tsavo-like situation (Owen-Smith, Kerley, Page, Slotow, & van Aarde, 2006).

The negative effects of elephant browsing may be exacerbated during low rainfall periods (drought). As a result of reduced seasonal resources, elephants are placed under enormous nutritional stress that drives increased browsing of woody vegetation in an effort to maintain their body condition (Chamaille-Jammes, Fritz, & Murindagomo, 2006). Consequently, during drought elephants can rely on browse for 70%–94% of food intake (Owen-Smith, 1988; Owen-Smith & Chafota, 2012). Elephant browsing may have a particularly negative effect on woody species during these times and could result in structural and compositional changes feared by ecologists and managers (Birkett & Stevens-Wood, 2005; O'Connor et al., 2007).

Nonetheless, elephant impact, in moderation, has been shown to positively influence biodiversity. For example, elephant impact has been shown to increase plant species richness by up to 49%

(Coverdale et al., 2016) and create habitats in trees and deadwood that increases both herpetofauna (Nasseri, Mcbrayer, & Schulte, 2011), and small invertebrate (Pringle, 2012) species richness and abundance. However, widespread spatial-temporal damage to woody vegetation can cancel out any positive benefits by extensively homogenising savannah ecosystems and extirpating highly damaged woody species and associated species (O'Connor et al., 2007; O'Connor & Page, 2014).

Concern over elephant-induced habitat change has motivated controversial management techniques particularly in Southern Africa, with culling by South Africa National Parks (SANParks) in Kruger National Park (Kruger) removing 13,000 individuals over a 35-year period (Dickson & Adams, 2009). However, this practice was condemned by the international community for the severely detrimental effects it has on elephant behaviour and social structure (Kuiper, Druce, & Druce, 2018; Shannon et al., 2013), while also being ineffective at preventing woody vegetation decline. This continued decline was, in part, due to the high spatial and temporal availability of artificial surface water that resulted in repeated, and high damage levels to woody vegetation, despite culling (Cook

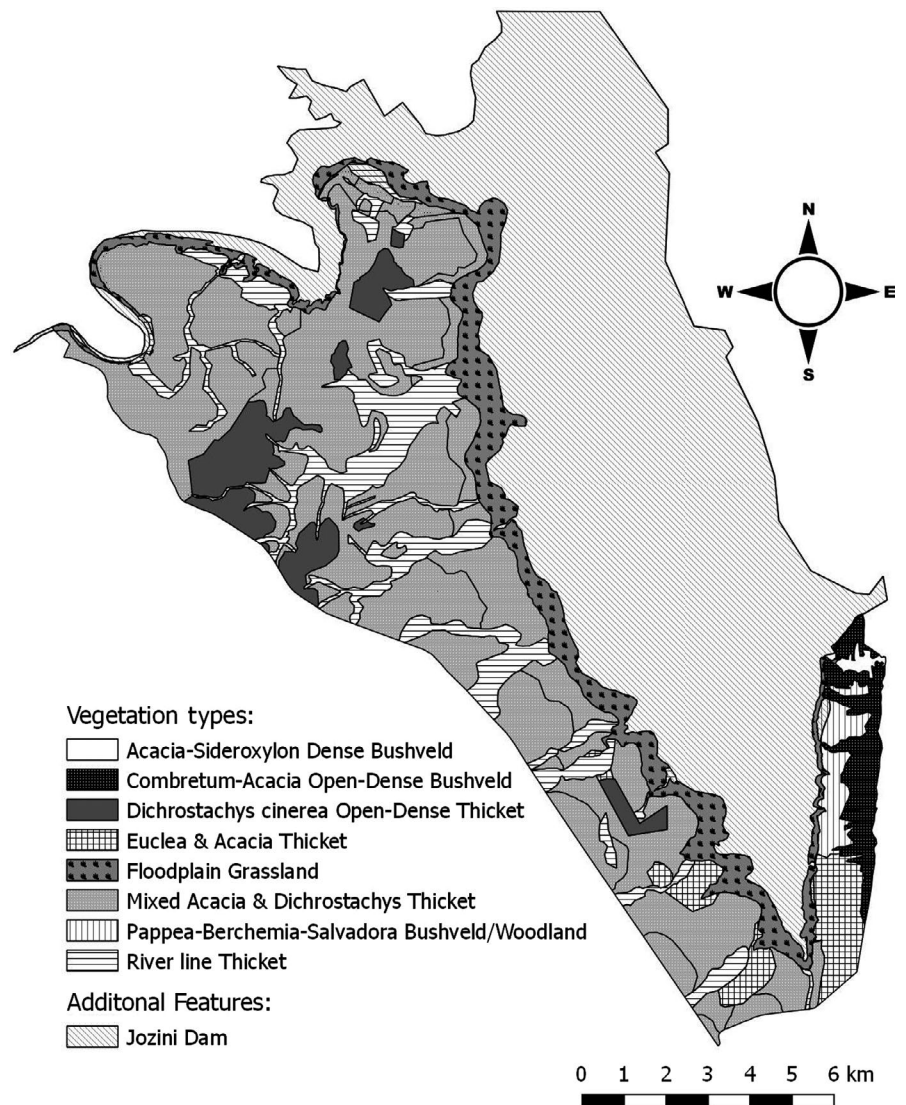


FIGURE 1 Vegetation of PGR-PNR, updated from Shannon et al., 2006

& Henley, 2019; O'Connor et al., 2007; Owen-Smith et al., 2006). Subsequently, SANParks largely ceased culling in 1995 and initiated live removals of elephants to 55 small reserves (<300 km²) in an attempt to maintain low elephant densities (7,500 elephants or <0.380 km⁻², Eckhardt, Wilgen, & Biggs, 2000). However, this also displaced the problem of extensive woody vegetation damage to their re-established ranges (Selier, Slotow, & Balfour, 2018).

It is now apparent that the threats posed to woody vegetation are particularly acute when elephants are confined to small reserves where populations have little spatial or temporal dispersal ability (Loarie et al., 2009b; Shrader, Pimm, & van Aarde, 2010). The decline of woody vegetation on small reserves has been confounded by limited evidence of density-dependent regulation (Owen-Smith et al., 2006), substantial elephant population growth (>5%, Slotow, Garaï, Reilly, Page, & Carr, 2005) and the high spatial and temporal availability of artificial surface water (Chamaillé-Jammes, Valeix, & Fritz, 2007). Consequently, space use intensity is high, particularly when elephants are exposed to environmental stressors such as drought (Midgley, Balfour, & Kerley, 2005; Slotow et al., 2005). This is made worse because elephants are unable to disperse out of fenced reserves, in which there are no refuges from elephant browsing for woody vegetation (Loarie et al., 2009a). However, few studies have explored the interaction between severe drought, the comparatively recent reintroduction of elephants to small reserves, and subsequent high elephant population density.

Here, we investigate how drought affected elephant browsing, and associated damage, at Pongola Game Reserve, South Africa. We take advantage of vegetation monitoring data collected prior to and during the El Nino drought of 2014/2016. Specifically, we examined the following: (a) Does type and severity of elephant damage change

with drought? (b) Does drought increase the probability of damage within different tree height classes? and (c) Do elephants increase selection of certain woody species more during drought than others? We expected to see (a) increase in all damage categories (crown (pollarding) damage, damaged roots/trunk or toppled and dead trees) as resource availability decreases and elephants exploit woody vegetation for an extended period during drought. (b) That instances of damaged trunk, roots and toppling would increase in larger trees (>4 m), but that crown damage would increase to smaller trees (<4 m) that are closer to elephants' optimal foraging height. Furthermore, we predicted that dead trees will increase across height categories as a result of increased elephant damage. (c) That all woody species would experience increased damage during drought, including those usually least selected for (e.g. *Dichrostachys cinerea*).

2 | METHODS

2.1 | Study site

The study was carried out at Pongola Game Reserve (27°23'47.91", 31°50'11.83"), and the Pongolapoort Nature Reserve (27°25'21.2", 32°03'89.7") located in north-east KwaZulu-Natal, South Africa. Pongola Game Reserve covers 97.81 km² of fenced, former agricultural land established in 1993 and is open to the neighbouring 10.23 km², Pongolapoort Nature Reserve (hereafter referred to collectively as PGR-PNR for ease) in the south-east. The reserve is bordered by the Jozini Dam, and the Pongola River to the north. The Lebombo mountains mark its eastern border. The soil types and topography are described by Shannon, Page, Slotow, & Duffy, 2006. The reserve is dominated by *Dichrostachys cinerea*/*Acacia* thicket, mixed *Acacia* woodland/thicket (*Senegalia nigrescens*/*Vachellia karroo*) and *Acacia* (*Senegalia nigrescens*/*Vachellia karroo*)/*Euclea* thicket. The area of floodplain grassland, and therefore graze availability, increases for a time during drought as the level of water stored in the Jozini Dam decreases in the absence of seasonal rains (15 km² in 2015, Figure 1).

The reserve is home to four of the big five (excluding lions, *Panthera leo*) numerous bird species and an array of competing mammalian browsers, notably giraffe (*Giraffa camelopardalis*, $n = 90$), kudu (*Tragelaphus strepsiceros*, $n = 600$), nyala (*Tragelaphus angasii*, $n = 800$) and black rhino (*Diceros bicornis*, $n =$ undisclosed) (H. R. Zitzer, unpublished data).

The climate is hot and arid, with a dry season (mean temperature 20.7°C, April–September) and wet season (mean temperature, 23°C, October–March). Rainfall varies annually with an average of 543 mm \pm (SD) 167 (2003–2015, Figure 2, [Zitzer & Boulton, 2018]). There was below average rainfall in 2014–2015 (total of 349.5 mm and 312 mm, respectively) caused by the changing El Nino weather cycles (Blamey, Kolu, Mahlalela, Todd, & Reason, 2018; Bond & Midgley, 2019; Figure 2). Therefore, we used 'nondrought' to denote normal meteorological conditions in 2012–2013, and 'drought years' to denote below average annual rainfall during our data collection in 2014–2015.

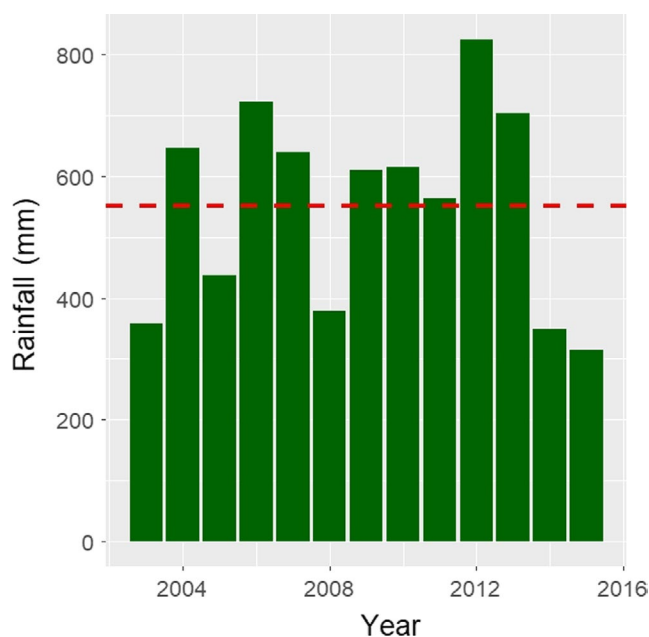


FIGURE 2 Total annual rainfall (mm, 2003–2015), mean (red line) = 552 mm (\pm (SD) 167), Zitzer & Boulton, 2018

2.2 | Elephant population

In 2012, there were a total of 77 (0.71 km⁻²) elephant individuals in the reserve (eight bulls, and 69 cows & juveniles), and in 2015, there were 83 (0.76 km⁻², 13 bulls and 70 females and juveniles). The population has only experienced an 8% growth rate over the four-year study period despite vasectomies and the birth control hormone, GnRH, being used in an attempt to limit population growth (Doughty, Slater, Zitzer, Avent, & Thompson, 2014; Zitzer & Boulton, 2018). Although density is lower than Kruger National Park (0.85 km⁻², Ferreira, Greaver, & Simms, 2017), concern among managers regarding elephant-mediated change in vegetation remains high (Knights, 2012).

The elephants at PGR-PNR were never more than 6 km from surface water at Lake Jozini, the Pongola River or 24 artificial water points across the reserve. Accordingly, distance to water was not considered a limiting factor of elephant distribution or damaging of vegetation (Harris, Russell, van Aarde, & Pimm, 2008; Shannon et al., 2006) and was not included in our analysis. As there were no spatial or temporal barriers between surveyed areas on the reserve, it was assumed elephants had equal access to all sites.

2.3 | Woody species data collection

Data collection was carried out annually from 2012 to 2015 in June–August. Habitat assessment sites were selected using ESRI ArcGIS (Redlands, USA) to generate 1,500 random GPS points across the reserves. GPS points were excluded if they overlapped with man-made features such as buildings, roads and train tracks and were at

TABLE 1 Elephant browsing damage categories

Category	Damage type
Dead	Pulled/Kicked out, dead
	Toppled, dead
	Main trunk broken, dead
Damaged trunk/ roots or toppled	Main trunk broken but resprouting
	Toppled but alive
	Main trunk debarked
	Roots exposed and eaten but alive
Crown Damage	Primary branches broken
	Secondary and/or smaller branches broken
None	No elephant damage

TABLE 2 ANOVA table showing likelihood ratio tests for each term in the best-fitting model for the effects of drought, height and species on predicted probability of elephant damage

Model Terms	df	Likelihood ratio statistic	p Value
Drought + Height + Species + Drought × Height	9	24.73	<0.001
Drought + Height+Species	15	227.31	<0.001
Drought + Height	9	684.209	<0.001
Drought	3	40.09	<0.001

least 25 m apart to avoid pseudo-replication. A random number generator was then used to produce 37 sites across the reserve, which were our annual study sites. Temporal change from 2012 to 2015 was investigated by sampling vegetation at these same 37 sites in each year.

The woody vegetation was sampled within a 25 m × 25 m quadrat at the exact GPS coordinate of sample site, running north and east from the south-west point with the plot corners kept constant throughout the study to ensure the same individuals were sampled each year. The species, damage and height category (1–2 m, 2–4 m, 4–6 m, 6 m+) were recorded for every individual over 1 m within each quadrat, using a 3-m wooden pole as a reference height (Holdo, 2003). Elephant damage, defined as the toppling of, or removal of woody biomass from a tree, was categorised based on observed damage to each tree (Table 1). Damage that could be clearly attributed to browsing by other species, fire or weather (e.g. lightning strikes) was recorded separately to prevent misclassification of damage.

Tusk slashes to trees represented only five data points over the study period, too few to be biologically meaningful, and so were excluded from the analysis.

2.4 | Statistical analysis

To determine how drought affected the probability of elephant damage on different tree species and at different heights, we used a multinomial logistic regression (Qian, Cuffney, & McMahon, 2012), implemented in the package *nnet* in R 3.5.2 (R Foundation for Statistical Computing, 2019; Venables & Ripley, 2002, section 7.3). Multinomial logistic regression differs from ANOVA and normal regression in having a categorical response variable (in our case, elephant damage category). In addition, unlike normal regression, multinomial regression does not require the assumptions of normality or homoscedasticity, making it ideal to analyse our exclusively categorical variables. Multinomial logistic regression is closely related to binary logistic regression but has a response variable in which more than two categories are possible. We used a baseline-category model, in which the logs of the ratios of probabilities of all but one of the categories to the probability of a baseline category are modelled as linear functions of the explanatory variables (Agresti, 2002, section 7.1). The choice of baseline category does not affect inferences from the model: we used 'No Elephant Damage' as the baseline category. This is similar to the most common logistic regression approach, in which the log of the ratio of success probability to failure probability is modelled. We pooled our data collections

years into two categories 'nondrought' (2012–2013) and 'drought' (2014–2015) for our analysis.

We started with a plausible initial model for the probability of each damage category, which was then simplified through a model-selection process. In the initial model, we analysed the probability of membership of our four elephant damage categories in response to several biologically meaningful predictor variables: drought, height and species, with interactions between drought and height, drought and species and drought, height and species. The species variable consisted of the top fourteen woody species, which represented 80.1% of our data set and each individual species having an agglomerated abundance over the 4-year study of >50 data points over the 4 years (Appendix 3). The remaining 19.9% (77 species), which individually constituted too few data points over the four-year study period to be analysed in a biologically meaningful way, were excluded. A model-selection process based on Akaike's Information Criterion (AIC) was performed using the *dredge()* function in the R

package *MuMIn* (Burnham & Anderson, 2002). There was no need to perform model averaging as all models, other than our best-fitting model, had delta values >2 and so were considered an ill fit for our data (Johnson & Omland, 2004; Symonds & Moussalli, 2011). Further analyses were based on this best-fitting model.

To test the significance of each of our model terms, we used maximum likelihood ratio tests (Venables & Ripley, 2002, section 7.3). We calculated the predicted probability of damage in relation to our predictor variables species, drought and height with 95% confidence intervals (Fox & Hong, 2015; Fox & Weisberg, 2019).

By including both height and species effects, we controlled for the height difference when estimating species effects (although we assumed that the height effect was the same for all species, we cannot estimate a height:species interaction from our data). However, because height distributions differed among species (e.g. *Grewia spp.* and *Dichrostachys cinera* were more likely to occur in the smaller height categories [<4 m]), further analysis was required to determine the

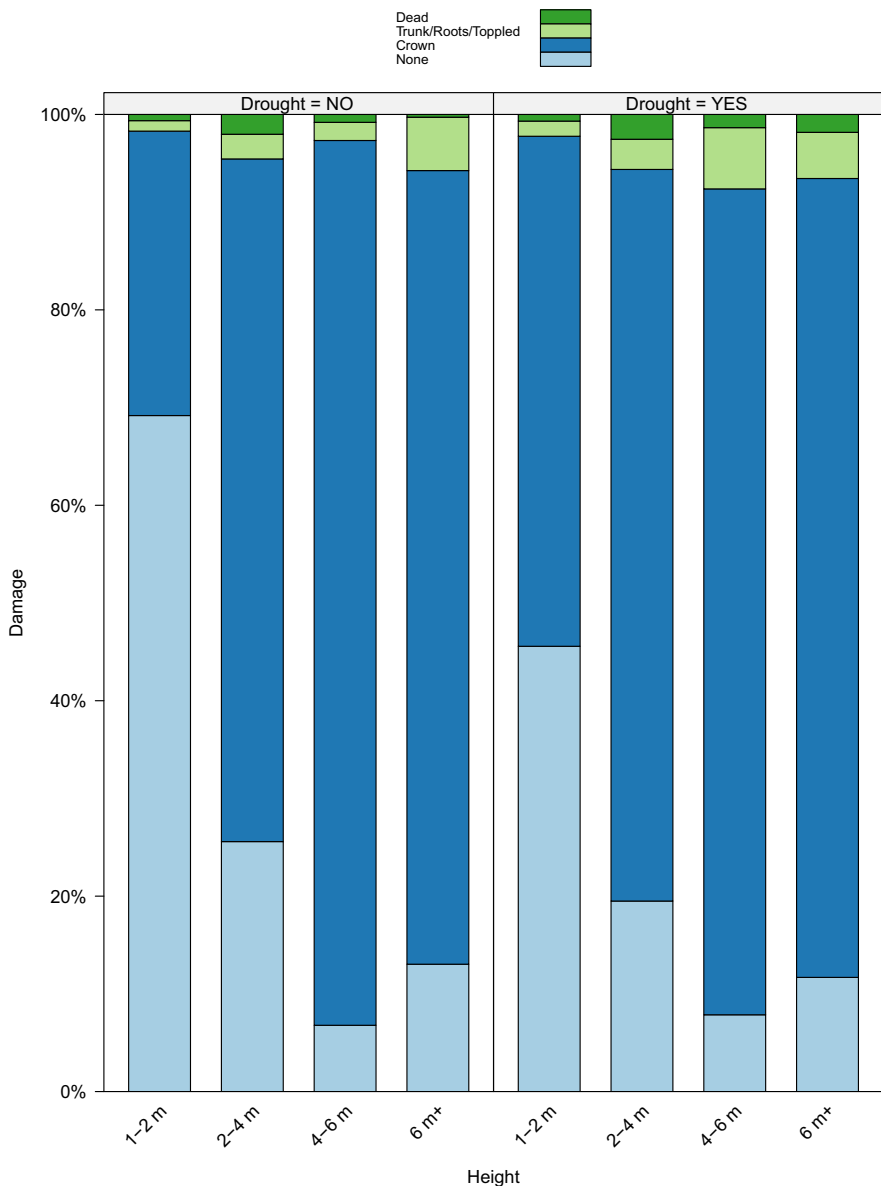


FIGURE 3 Predicted probability of elephant damage category at different heights before and during drought

TABLE 3 Predicted probability (% , ± 95% CI) of each damage category by height and drought

Height category	Category of damage	Probability predrought	Lower 95% CI	Upper 95% CI	Probability in drought	Lower 95% CI	Upper 95% CI
1–2 m (n = 2,878, 65% of all trees)	No damage	69	65	73	45	42	49
	Crown (Pollarding)	29	26	32	52	49	55
	Damaged trunk/roots or toppled	1	0.06	2	2	1	2.4
	Dead	1	<0.001	38	1	<0.001	40
2–4 m (n = 1,120, 25%)	No damage	25	21	31	19	15	25
	Crown (Pollarding)	70	61	77	75	64	83
	Damaged trunk/roots or toppled	3	1	4	3	2	5
	Dead	2	<0.001	67	3	<0.001	72
4–6 m (n = 326, 7%)	No damage	7	3	13	8	3	12
	Crown (Pollarding)	91	83	94	85	76	89
	Damaged trunk/roots or toppled	2	0.8	4	6	1	11
	Dead	1	<0.001	45	1	2	9
>6 m (n = 131, 3%)	No damage	14	6	27	11	5	18
	Crown (Pollarding)	81	68	90	82	66	92
	Damaged trunk/roots or toppled	5	2	13	5	2	12
	Dead	0.3	<0.001	30	2	<0.001	67

extent to which height and species effects could be separated (e.g. to ensure that changes in damage <2 m were not in fact selection for smaller trees or bushes such as *Grewia villosa*). Therefore, we calculated generalised variance inflation factors (GVIF) for the terms in the final model using the *vif()* function in the *car* package (Fox & Monette, 1992). We report $GVIF^{1/(2 \cdot DF)}$ for each term, where DF is the degrees of freedom associated with the term. This gives a measure of variance inflation that is comparable across terms of different dimensions.

3 | RESULTS

3.1 | Best-fitting model

Our best-fitting model according to AIC contained the predictor variables drought, height, species and an interaction between height and drought (Appendix 1). In the best-fitting model, the effect of drought on the probability of each damage category depended on height (Table 2, Drought:Height interaction). However, there was little support for our hypothesis that damage to common species would increase during drought because the Drought:Species interaction was not included in our best-fitting model.

The largest values of $GVIF^{1/(2 \cdot DF)}$ for terms in the best-fitting model were only slightly above 2 (Appendix 2). The squares of these values (slightly above 4) have the same interpretation as the usual variance inflation factors (Fox & Weisberg, 2011, p. 325). Typical rules of thumb for interpreting variance inflation factors suggest that this level of collinearity is unlikely to be problematic (O'Brien, 2007). Thus, estimation of separate height and species effects, both

before and during drought, is possible from this model with the data we have.

3.2 | Drought and height effects on browsing damage

Crown damage was the most common form of elephant damage at PGR-PNR in both the nondrought and drought periods (Figure 3). In the 1–2 m, 2–4 m and 6 m + height categories, there was an increase in the predicted probability of crown damage during drought, and a decrease in the predicted probability of 'no damage' (Figure 3, Table 3). The predicted probability of trunk/root/toppling damage during drought increased slightly at 1–2 m but most notably at 4–6 m (Table 3). Drought increased the probability of dead trees at 2–4 m and >6 m, with instances of dead trees in the remaining height categories being unaffected by drought (Figure 2, dark green bars, Table 3).

Contrary to our predictions, all damage and instances of dead trees did not increase across height categories during drought, nor did instances of trunk/root/toppling damage to large trees (>4 m; Figure 3, Table 3).

3.3 | Woody species and browsing damage

Woody species when used as a predictor variable contributed significantly to explaining the level of elephant damage (Table 2), although the selection of woody species by elephants was unaffected by the

TABLE 4 Probability of browsing categories of our top 14 most common species from 2012–2015

Species	Category of damage	Probability (%)	Lower 95% CI	Upper 95% CI
<i>Dichrostachys cinerea</i> (n = 1,428, 32% of all trees)	No damage	50	47	54
	Crown (Pollarding)	47	43	49
	Damaged trunk/roots or toppled	1	0.7	2
	Dead	2	0.1	3
<i>Grewia villosa</i> (n = 482, 11%)	No damage	33	30	39
	Crown (Pollarding)	65	60	69
	Damaged trunk/roots or toppled	0.6	0.1	2
	Dead	0.3	<0.001	2
<i>Senegalia nigrescens</i> (n = 233, 5%)	No damage	34	27	44
	Crown (Pollarding)	51	41	57
	Damaged trunk/roots or toppled	7	4	12
	Dead	8	5	14
<i>Vachellia karroo</i> (n = 231, 5%)	No damage	30	25	39
	Crown (Pollarding)	66	56	70
	Damaged trunk/roots or toppled	2	1	5
	Dead	2	0.8	5
<i>Spirostachys africana</i> (n = 184, 4%)	No damage	39	30	49
	Crown (Pollarding)	53	43	61
	Damaged trunk/roots or toppled	3	1	7
	Dead	5	3	10
<i>Gymnosporia senegalensis</i> (n = 157, 3.5%)	No damage	55	46	63
	Crown (Pollarding)	41	34	51
	Damaged trunk/roots or toppled	3	0.8	8
	Dead	1	0.02	6
<i>Gymnosporia buxifolia</i> (n = 158, 3.5%)	No damage	34	26	43
	Crown (Pollarding)	60	50	67
	Damaged trunk/roots or toppled	6	3	12
	Dead	<0.001	0.003	0.4
<i>Ehretia nervifolia</i> (n = 139, 3.1%)	No damage	33	25	42
	Crown (Pollarding)	65	57	73
	Damaged trunk/roots or toppled	2	0.4	6
	Dead	<0.001	<0.001	100
<i>Euclea divinorum</i> (n = 119, 2.8%)	No damage	21	14	32
	Crown (Pollarding)	70	60	79
	Damaged trunk/roots or toppled	6	3	13
	Dead	0.8	0.1	5
<i>Vachellia tortilis</i> (n = 105, 2.4%)	No damage	29	20	39
	Crown (Pollarding)	61	51	70
	Damaged trunk/roots or toppled	6	3	12
	Dead	4	2	10
<i>Croton menyhartii</i> (n = 100, 2.3%)	No damage	49	38	60
	Crown (Pollarding)	50	39	60
	Damaged trunk/roots or toppled	1	0.4	6
	Dead	<0.001	<0.001	100

(Continues)

TABLE 4 (Continued)

Species	Category of damage	Probability (%)	Lower 95% CI	Upper 95% CI
<i>Grewia flava</i> (n = 74, 1.7%)	No damage	34	24	47
	Crown (Pollarding)	59	47	70
	Damaged trunk/roots or toppled	6	2	14
	Dead	1	0.003	8
<i>Vachellia grandicornuta</i> (n = 74, 1.6%)	No damage	18	11	33
	Crown (Pollarding)	75	61	85
	Damaged trunk/roots or toppled	4	1	13
	Dead	1	0.01	8
<i>Vachellia nilotica</i> (n = 69, 1.5%)	No damage	15	7	27
	Crown (Pollarding)	66	54	77
	Damaged trunk/roots or toppled	9	4	19
	Dead	9	4	18

drought (Appendix 1, Table 2); in other words, elephants did not become less selective during drought.

The most common species on the reserve was *Dichrostachys cinerea* (32% of all individuals), which, along with *Gymnosporia senegalensis*, were the species least likely to show damage by elephants on the reserve (>50% predicted probability of no damage, Table 4). All of the remaining species exhibited a higher predicted probability of damage than no damage and were most commonly affected by crown damage (Figure 4, Table 4). The highest predicted probability of severe damage, trunk/root/topping damage and death was recorded in *Senegalia nigrescens* and *Vachellia nilotica* (Figure 4, Table 4). In contrast, *Grewia villosa* and *Ehretia nervifolia* had a low probability of severe damage and death but a higher probability of crown damage (Table 4, Figure 4). *Spirostachys africana* showed a relatively high predicted probability of crown damage and death despite a low probability of roots/trunk/toppling damage; in other words, if damaged by elephants, the consequences for the tree may be more severe (Figure 4, Table 4).

4 | DISCUSSION

Our study partially confirmed previous work that suggests drought increases elephant damage to woody vegetation (e.g. O'Connor et al., 2007): we revealed that severe drought increased the predicted probability of crown damage to smaller trees (<4 m) and was associated with a higher predicted probability of mortality (>6 m) and severe damage in larger trees (4–6 m). However, there was no support for our third prediction of a change in damage to common species during drought.

Though elephants showed some changes in the patterns of damage during drought, we found inconsistent support for our first prediction of an overall increase in elephant damage. Crown damage remained the most likely damage category across all heights, and there was no evidence of a major shift in the drought towards

more severe forms of damage such as debarking, toppling or elephant-induced mortality. This may be because instances of severe damage (trunk/toppling/root) require significantly more harvesting effort by elephants in comparison with crown damage during a physically demanding period (O'Connor et al., 2007; Owen-Smith, 1988). Although an increase in severe damage should be expected as elephants adapt and attempt to maintain their body condition during drought, elephants should be expected to focus the majority of their browsing efforts on the crown as they try to harvest the greatest amount of biomass at the lowest physical cost (Clegg & O'Connor, 2016; Makhabu, 2005).

Our second prediction that crown damage would increase during drought for trees <4 m was supported by our model. This is likely due to limited resource availability and ease of accessibility of this section of the canopy during physically challenging conditions. Generally, trees are resilient to moderate crown damage; however, extensive damage can significantly influence canopy structure, and the removal of >76% of a tree's canopy can result in mortality (Tchamba & Mahamat, 1992; Wiseman, Page, & Connor, 2004). Our predicted probability of crown damage (29%–90%) may be a cause for concern if crown damage influences tree mortality at PGR-PNR. Furthermore, crown damage in trees <4 m, in combination with severe damage and mortality in trees >4 m, may keep trees within the 'browse trap' (<5 m) where they may be susceptible to further herbivory and fire hindering recruitment and growth while promoting canopy homogenisation (Eckhardt et al., 2000; Staver & Bond, 2014).

The mortality of trees >6 m increased considerably from 0.2% (nondrought) to 2% (during drought) but was still below the level of mortality to large trees found in Kruger National Park during non-drought conditions (4%, Shannon et al., 2008). Although there is an extremely limited dispersal potential for elephants in which to move into in response to environmental stress at PGR-PNR (10,733 hectares), in comparison with the Kruger (1.93 million hectares), elephant-induced tree mortality was still considerably lower. This is possibly because elephant density was substantially lower at PGR-PNR

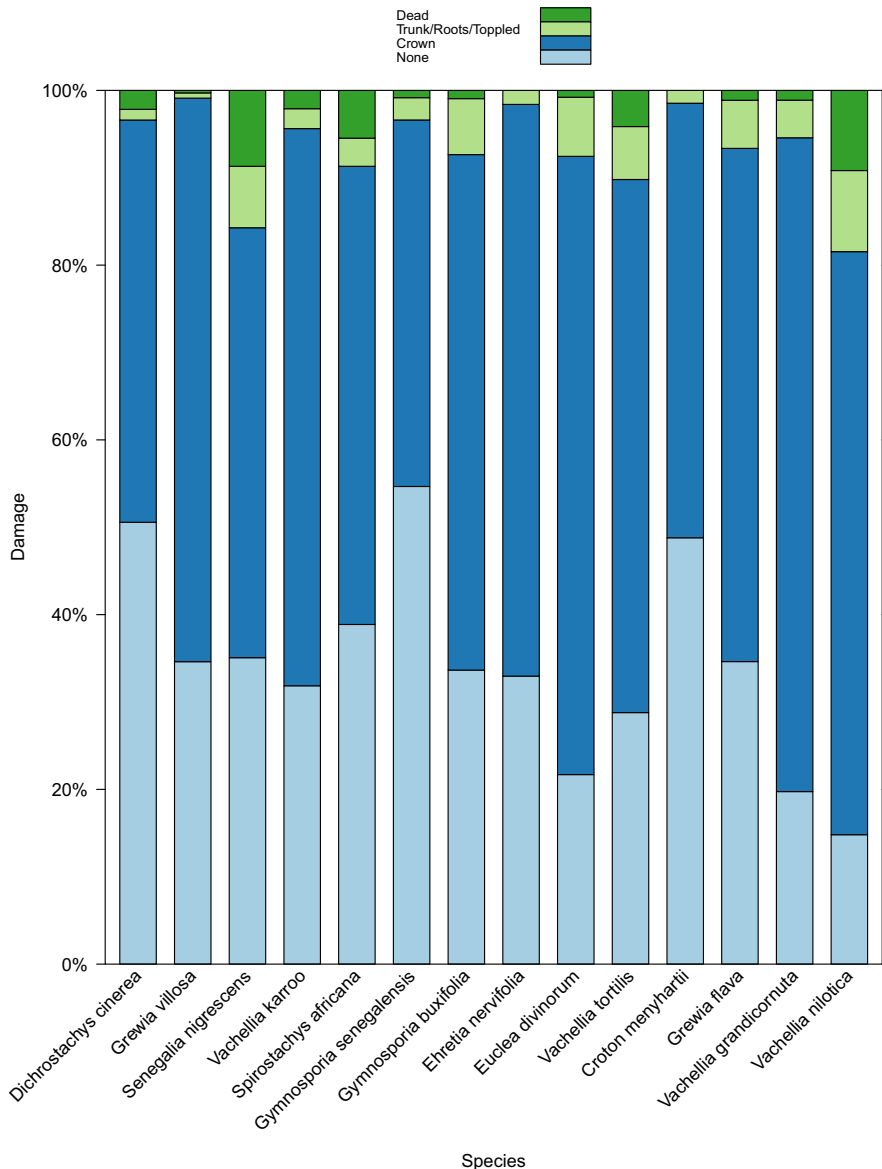


FIGURE 4 Predicted probability of elephant damage category for top 14 most common species

(0.76 km⁻²) in comparison with the local Kruger study site (1.13 km⁻², Shannon et al., 2008). Consequently, intraspecific competition between elephants may be lower at PGR-PNR than at Kruger and could explain the less severe browsing damage by elephants during drought despite their restricted dispersal potential at PGR-PNR. This could indicate that it is the level of interspecific competition, driven by elephant density (particularly bull density, Owen-Smith, 1988), that drives substantially higher impact to large trees and structural changes in the savannah canopy and not the restriction of elephants' ranges per se. However, it must be noted that our approach only considered the top 14 most abundant species, and so a full assessment of elephant impact on large trees and rare species is not represented by our approach and therefore warrants future investigation taking all species into consideration.

In our model, we interpreted high predicted probability of no damage as an indication of elephant avoidance of a particular height or species. Our model did not support our third prediction of an increase in woody species damage. Surprisingly, our model predicted

that woody vegetation had a high predicted probability of no damage (high probability of avoidance) at elephants' proposed 'optimal foraging height' of 1–2 m during normal conditions; this is atypical of other elephant populations across Africa (see Guy, 1974; Jachmann & Bell, 1985; Owen-Smith, 1988). The reserve's most common yet most avoided species, *Dichrostachys cinerea*, is usually a woody shrub <2 m (Appendix 4); thus, the lack of elephant damage at 1–2 m may be a consequence of their tendency to avoid this unpalatable species. Furthermore, the abundance of *D. cinerea* was higher at PGR-PNR (50%, 33%) than Kruger (15.5%, 20.1%, respectively [Scogings, Johansson, Hjältén, & Kruger, 2012]) although it was damaged more commonly by elephants in Kruger region (Greyling, 2004), in contrast with PGR-PNR (Table 4, Figure 4) and Atherstone National Park where *D. cinerea* was classified as a 'least preferred' species (Seloana et al., 2018). Somewhat counter-intuitively, our results suggest that the least selected species, *D. cinerea* and *Vachellia karroo*, may require management attention as both species have been implicated in bush encroachment (Stafford et al., 2017; Walters, Midgley, &

Somers, 2004). As these species exhibit a low mortality rate, even at high elephant densities during severe drought, it is unlikely that they will be controlled by elephant damage alone.

Senegalia nigrescens, for example, had one of the highest predicted probabilities of mortality (8%) and severe browsing (trunk/root/toppling, 7%). Mortality in *S. nigrescens* is strongly associated with instances of elephant debarking that can increase susceptibility to fire (Moncrieff, Kruger, & Midgley, 2008) and insect infestations (Owen-Smith, 1988). However, severe damage (e.g. debarking) and mortality to this species from elephant browsing are common and have been recorded at various locations (e.g. Northern Botswana (12% and 13%, Teren, Owen-Smith, & Erasmus, 2018), Mkhuze Game Reserve [5.3%, 3.2%, White & Goodman, 2010]). However, unlike other species (see below), no studies have reported complete extirpation, and significant regeneration from elephant damage has been recorded (e.g. Vogel et al., 2014), which suggests this species recruits and recovers from elephant damage sufficiently rapidly to avoid local extirpation. The fact that species selection was unaffected by drought highlights the complex nature of elephant browsing, suggesting that factors other than resource and species abundance, such as tannin concentrations or bark thickness, may influence elephant damage during drought.

Commonly damaged species can be severely reduced in abundance by destructive elephant browsing, and in extreme cases, this can result in the local extirpation of woody species from elephant ranges (O'Connor et al., 2007). For example, *Sclerocarya birrea*, a once dominant species at PGR-PNR (Shannon et al., 2006), is now almost entirely absent from the reserve ($n = 2$ in our study) and has been extirpated or suffered heavy elephant damage at many other reserves across South Africa (Cook, Witkowski, Helm, Henley, & Parrini, 2017; Helm & Witkowski, 2013). The threat posed by elephants will require long-term monitoring of highly selected species to allow intervention if substantial declines become apparent. However, in this regard, it is also important to consider the context and historic baseline for elephant damage to woody vegetation: the impact to particular woody species may appear large, but this may be due to unnaturally inflated woody species abundance prior to the reintroduction of elephants and other seedling browsers (Gillson & Duffin, 2007).

As a caveat to our study, it should be noted that often there is lag between elephant damage events (e.g. debarking) and mortality in some species (e.g. *Vachellia tortilis*, MacGregor & O'Connor, 2004). It is therefore possible that mortality from elephant damage inflicted before the study started may have been recorded during our pre-drought data collection. Furthermore, severe damage inflicted during the drought resulting in later mortality may not have been detected during our study and may have only become apparent in subsequent years (e.g. 2016–2017). Drought damage may also have made trees more susceptible to mortality from insects or fire in subsequent years. Subsequently, this could have reduced the ability of our frequency-based model to truly represent changes in elephant damage resulting from severe drought. Moreover, the binary classification of damage (i.e. not quantifying percentage damage per tree) did not

allow us to discern the percent of crown or severe damage to individual trees and consequently reduced our ability to make direct comparisons with some previous studies. Further investigations quantifying individual damage are needed in the future to address this limitation.

The severe resource limitation during drought may have also affected browsing patterns with potentially higher levels of browsing damage and interspecific competition between elephants and other browsers (e.g. Birkett & Stevens-Wood, 2005). We attempted to control for the effect of increased browsing by other species during drought by recording and attributing browsing damage where possible. However, it is not always possible to assign all damage with a high level of certainty. Consequently, there may be a margin of error associated with our classification of damage that could have potentially under or overrepresented elephant damage during our study.

Methods such as elephant exclusion zones, wire netting of tree trunks or beehive deterrents may reduce severe damage and mortality to large trees and protect vulnerable species while facilitating the recruitment of trees into maturity, although this could prove logistically challenging and costly over large areas (Cook, Parrini, King, Witkowski, & Henley, 2018; Derham, Henley, & Schulte, 2016). Water point closure has been an effective tool used to manage elephant impact on vegetation through density-dependent regulation and manipulation of populations and could be used at other reserves in South Africa (Robson & van Aarde, 2018). However, the extremely high availability of water at the Jozini Dam and Pongola River (see Figure 1) make this physically impossible to implement at PGR-PNR. Range expansion could be an effective way to reduce elephant density and the associated spatial and temporal stress high elephant densities cause to woody vegetation during low rainfall periods. However, the benefits of lowered density via range expansions may be limited in a future where drought is expected to increase in duration, frequency and intensity (IPCC, 2018; Trenberth et al., 2014).

Our study has highlighted the dynamic nature of elephant damage during drought at PGR-PNR where the increased probability of crown damage to smaller trees and severe damage to larger trees during drought has the potential to change structural composition locally. As droughts are predicted to become more frequent and severe (IPCC, 2018; Trenberth et al., 2014), elephant-induced structural change is likely to also intensify. Consequently, the long-term monitoring of elephant-vegetation interactions is essential to better understand emerging patterns. The proactive implementation of aforementioned conservation measures is therefore crucial to ensure the long-term co-existence of elephants and woody species on small reserves in an increasingly unpredictable world.

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DATA AVAILABILITY STATEMENT

Data were made available through collaboration with Operation Wallacea and WEI South Africa. To access to these data, please contact Heather Gilbert at heather.gilbert@opwall.ac.uk.

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REFERENCES

- Agresti, A. (2002). *Categorical Data Analysis* (2nd ed.). Hoboken, New Jersey: John Wiley & Sons.
- Asner, G. P., & Levick, S. R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters*, 15(11), 1211–1217. <https://doi.org/10.1111/j.1461-0248.2012.01842.x>
- Bax, P. N., & Sheldrick, D. L. W. (1963). Some Preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *African Journal of Ecology*, 1(1), 40–51. <https://doi.org/10.1111/j.1365-2028.1963.tb00177.x>
- Birkett, A., & Stevens-Wood, B. (2005). Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *African Journal of Ecology*, 43(2), 123–130. <https://doi.org/10.1111/j.1365-2028.2005.00555.x>
- Blamey, R. C., Kolusu, S. R., Mahlalela, P., Todd, M. C., & Reason, C. J. C. (2018). The role of regional circulation features in regulating El Niño climate impacts over southern Africa: A comparison of the 2015/2016 drought with previous events. *International Journal of Climatology*, 38(11), 4276–4295. <https://doi.org/10.1002/joc.5668>
- Bond, W. J., & Midgley, J. J. (2019). The worst drought in 50 years in a South African savannah: Limited impact on vegetation. *African Journal of Ecology*, (October 2018), 1–10. <https://doi.org/10.1111/aje.12640>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer-Verlag.
- Chamaille-Jammes, S., Fritz, H., & Murindagomo, F. (2006). Spatial patterns of the NDVI-rainfall relationship at the seasonal and interannual time scales in an African savanna. *International Journal of Remote Sensing*, 27(23), 5185–5200. <https://doi.org/10.1080/01431160600702392>
- Chamaille-Jammes, S., Valeix, M., & Fritz, H. (2007). Managing heterogeneity in elephant distribution: Interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, 44(3), 625–633. <https://doi.org/10.1111/j.1365-2664.2007.01300.x>
- Clegg, B. W., & O'Connor, T. G. (2016). Harvesting and chewing as constraints to forage consumption by the African savanna elephant (*Loxodonta africana*). *PeerJ*, 4, e2469. <https://doi.org/10.7717/peerj.2469>
- Codron, J., Codron, D., Lee-Thorp, J. A., Sponheimer, M., Kirkman, K., Duffy, K. J., & Sealy, J. (2011). Landscape-scale feeding patterns of African elephant inferred from carbon isotope analysis of feces. *Oecologia*, 165(1), 89–99. <https://doi.org/10.1007/s00442-010-1835-6>
- Combrink, L., Combrink, H. J., Botha, A. J., & Downs, C. T. (2017). Habitat structure and diversity influence the nesting success of an endangered large cavity-nesting bird, the Southern Ground-hornbill. *Koedoe*, 59(1), 1–8. <https://doi.org/10.4102/koedoe.v59i1.1438>
- Cook, R. M., & Henley, M. D. (2019). Complexities associated with elephant impact on *Sclerocarya birrea* subsp. *caffra* in the Greater Kruger National Park. *South African Journal of Botany*, 121, 543–548. <https://doi.org/10.1016/j.sajb.2019.01.016>
- 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>
- 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>
- Coverdale, T. C., Kartzinel, T. R., Grabowski, K. L., Shriver, R. K., Hassan, A. A., Goheen, J. R., ... Pringle, R. M. (2016). Elephants in the understory: Opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology*, 97(11), 3219–3230. <https://doi.org/10.1002/ecy.1557>
- 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), 1–8. <https://doi.org/10.4102/koedoe.v58i1.1327>
- Dickson, P., & Adams, W. M. (2009). Science and uncertainty in South Africa's elephant culling debate. *Environment and Planning C: Government and Policy*, 27(1), 110–123. <https://doi.org/10.1068/c0792j>
- Doughty, L. S., Slater, K., Zitzer, H., Avent, T., & Thompson, S. (2014). The impact of male contraception on dominance hierarchy and herd association patterns of African elephants (*Loxodonta africana*) in a fenced game reserve. *Global Ecology and Conservation*, 2, 88–96. <https://doi.org/10.1016/j.gecco.2014.08.004>
- Dublin, H. T., Sinclair, A. R. E., & McGlade, J. (1990). Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *Journal of Animal Ecology*, 59(3), 1147–1164. <https://doi.org/10.4271/2002-01-2197>
- Eckhardt, H. C., Van Wilgen, B. W., & Biggs, H. C. (2000). Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, 38, 108–115.
- Ferreira, S. M., Greaver, C., & Simms, C. (2017). Elephant population growth in Kruger National Park, South Africa, under a landscape management approach. *Koedoe*, 59(1), 1–6. <https://doi.org/10.4102/koedoe.v59i1.1427>
- Fox, J., & Hong, J. (2015). Effect displays in R for multinomial and proportional-odds logit models: Extensions to the effects package. *Journal of Statistical Software*, 32(1), 1–24. <https://doi.org/10.18637/jss.v032.i01>
- Fox, J., & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the American Statistical Association*, 87(417), 178–183. <https://doi.org/10.1080/01621459.1992.10475190>
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (p. 327). Los Angeles, CA: Sage Publications.
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Thousand Oaks, CA: Sage Publications.
- Gillson, L., & Duffin, K. I. (2007). Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1478), 309–319. <https://doi.org/10.1098/rstb.2006.1988>
- Greyling, M. D. (2004). *Sex and age related distinctions in the feeding ecology of the African elephant* (pp. 1–186.). Johannesburg, South Africa: Faculty of Science, University of the Witwatersrand.
- Guy, P. R. (1974). The feeding ecology of the Elephant (*Loxodonta africana*) in the Sengwa Area, Rhodesia. *Journal of South African Wildlife*

- Research, 6(1), 55–63. [https://doi.org/10.1016/0003-3472\(63\)90296-3](https://doi.org/10.1016/0003-3472(63)90296-3)
- Harris, G. M., Russell, G. J., Van Aarde, R. I., & Pimm, S. L. (2008). Rules of habitat use by elephants *Loxodonta africana* in southern Africa: Insights for regional management. *Oryx*, 42(1), 66–75. <https://doi.org/10.1017/S0030605308000483>
- Haynes, G. (2012). Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology*, 157–158, 99–107. <https://doi.org/10.1016/j.geomorph.2011.04.045>
- Helm, C. V., & Witkowski, E. T. F. (2013). Continuing decline of a keystone tree species in the Kruger National Park, South Africa. *African Journal of Ecology*, 51(2), 270–279. <https://doi.org/10.1111/aje.12032>
- Holdo, R. M. (2003). Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology*, 19(2), 189–196. <https://doi.org/10.1017/S0266467403003213>
- IPCC. (2018). *Global Warming of 1.5 °C - SR15*. In *lppc - Sr15*.
- Jachmann, H., & Bell, R. H. V. (1985). Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*, 23(4), 245–258. <https://doi.org/10.1111/j.1365-2028.1985.tb00955.x>
- Johnson, C. F., Cowling, R. M., & Phillipson, P. B. (1999). The flora of the Addo Elephant National Park, South Africa: Are threatened species vulnerable to elephant damage? *Biodiversity and Conservation*, 8(11), 1447–1456. <https://doi.org/10.1023/A:1008980120379>
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19(2), 101–108. <https://doi.org/10.1016/j.tree.2003.10.013>
- Kassa, B. D., Fandohan, B., Azihou, A. F., Assogbadjo, A. E., Oduor, A. M. O., Kidjo, F. C., ... Glèlè Kakaï, R. (2014). Survey of *Loxodonta africana* (Elephantidae)-caused bark injury on *Adansonia digitata* (Malvaceae) within Pendjari Biosphere Reserve, Benin. *African Journal of Ecology*, 52(4), 385–394. <https://doi.org/10.1111/aje.12131>
- Knights, K. (2012). *Calculating the carrying capacity of the Pongola Game Reserve for elephant, South Africa*. Internal Report for Operation Wallacea, Unpublished. <https://doi.org/10.1007/s00393-018-0552-0>
- Kuiper, T. R., Druce, D. J., & Druce, H. C. (2018). Demography and social dynamics of an African elephant population 35 years after reintroduction as juveniles. *Journal of Applied Ecology*, 55(6), 2898–2907. <https://doi.org/10.1111/1365-2664.13199>
- Leuthold, W. (1996). Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–94. *African Journal of Ecology*, 34(2), 101–112. <https://doi.org/10.1111/j.1365-2028.1996.tb00605.x>
- Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009a). Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation*, 142(12), 3099–3107. <https://doi.org/10.1016/j.biocon.2009.08.021>
- Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009b). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, 142(12), 3086–3098. <https://doi.org/10.1016/j.biocon.2009.08.008>
- MacGregor, S. D., & O'Connor, T. G. (2004). Response of *Acacia tortilis* to utilization by elephants in a semi-arid African savanna. *South African Journal of Wildlife Research*, 34(1), 55–66.
- Makhabu, S. W. (2005). *Interactions between woody plants, elephants and other browsers in the Chobe* (Vol. 1). Trondheim, Norway: Norwegian University of Science and Technology.
- Midgley, J. J., Balfour, D., & Kerley, G. I. (2005). Why do elephants damage savanna trees? *South African Journal of Science*, 101(5–6), 213–215.
- Moncrieff, G. R., Kruger, L. M., & Midgley, J. J. (2008). Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. *Journal of Tropical Ecology*, 24(6), 655–662. <https://doi.org/10.1017/S0266467408004951>
- Nasseri, N. A., Mcbrayer, L. D., & Schulte, B. A. (2011). The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. *African Journal of Ecology*, 49(2), 133–140. <https://doi.org/10.1111/j.1365-2028.2010.01238.x>
- O'Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality and Quantity*, 41(5), 673–690. <https://doi.org/10.1007/s11135-006-9018-6>
- 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(3), 329–345. <https://doi.org/10.1016/j.biocon.2006.12.014>
- O'Connor, T. G., & Page, B. R. (2014). Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants. *Biological Conservation*, 180, 122–133. <https://doi.org/10.1016/j.biocon.2014.09.036>
- Owen-Smith, N. (1988). *Mega-Herbivores - The influence of very large body size on ecology* (1st ed., Vol. 1). Cambridge, UK: Cambridge University Press.
- Owen-Smith, N., & Chafota, J. (2012). Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, 93(3), 698–705. <https://doi.org/10.1644/11-MAMM-A-350.1>
- Owen-Smith, N., Kerley, G. I. H., Page, B., Slotow, R., & van Aarde, R. J. (2006). A scientific perspective on the management of elephants in the Kruger National Park and Elsewhere. *South African Journal of Science*, October, 389–394. <https://doi.org/10.1080/0197243.1992.9960125>
- Parker, D. M. (2017). The composition and complexity of the woody and succulent components of Albany thicket with and without elephants. *South African Journal of Botany*, 112(1), 19–28. <https://doi.org/10.1016/j.sajb.2017.05.004>
- Pringle, R. M. (2012). Elephants as agents of habitat creation for small vertebrates at the patch. *Ecological Society of America*, 89(1), 26–33.
- Qian, S. S., Cuffney, T. F., & McMahon, G. (2012). Multinomial regression for analyzing macroinvertebrate assemblage composition data. *Freshwater Science*, 31(3), 681–694. <https://doi.org/10.1899/11-026.1>
- R Foundation for Statistical Computing. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Robson, A. S., & van Aarde, R. J. (2018). Changes in elephant conservation management promote density-dependent habitat selection in the Kruger National Park. *Animal Conservation*, 21(4), 302–312. <https://doi.org/10.1111/acv.12393>
- Schmitt, M. H., Ward, D., & Shrader, A. M. (2016). Incorporating secondary metabolites, tannin-binding proteins, and diet breadth into carrying-capacity models for African elephants. *Ecological Modelling*, 332, 8–18. <https://doi.org/10.1016/j.ecolmodel.2016.03.016>
- Scogings, P. F., Johansson, T., Hjältén, J., & Kruger, J. (2012). Responses of woody vegetation to exclusion of large herbivores in semi-arid savannas. *Austral Ecology*, 37(1), 56–66. <https://doi.org/10.1111/j.1442-9993.2011.02249.x>
- Selier, S. A. J., Slotow, R., & Balfour, D. (2018). Management of African elephant populations in small fenced areas: Current practices, constraints and recommendations. *Bothalia*, 48(2), 2311–2313. <https://doi.org/10.4102/abc.v48i2.2414>
- Seloana, M. Q., Jordaan, J. J., Potgieter, M. J., & Kruger, J. W. (2018). Feeding patterns of elephants at the Atherstone Collaborative Nature Reserve. *African Journal of Ecology*, 56(3), 445–454. <https://doi.org/10.1111/aje.12422>
- 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(3), 281–289. <https://doi.org/10.1017/S0266467408004951>
- Shannon, G., Page, B., Slotow, R., & Duffy, K. (2006). African elephant home range and habitat selection in Pongola Game Reserve. *South*

- Africa. *African Zoology*, 41(1), 37–44. <https://doi.org/10.1080/15627020.2006.11407333>
- Shannon, G., Slotow, R., Durant, S. M., Sayialel, K. N., Poole, J., Moss, C., & McComb, K. (2013). Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology*, 10(1), <https://doi.org/10.1186/1742-9994-10-62>
- Shrader, A. M., Pimm, S. L., & van Aarde, R. J. (2010). Elephant survival, rainfall and the confounding effects of water provision and fences. *Biodiversity and Conservation*, 19(8), 2235–2245. <https://doi.org/10.1007/s10531-010-9836-7>
- Slotow, R., Garaï, M. E., Reilly, B. K., Page, B. R., & Carr, R. D. (2005). Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, 35(1), 23–32.
- Stafford, W., Birch, C., Etter, H., Blanchard, R., Mudavanhu, S., Angelstam, P., ... Marais, C. (2017). The economics of landscape restoration: Benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. *Ecosystem Services*, 27(January), 193–202. <https://doi.org/10.1016/j.ecoser.2016.11.021>
- Staver, A. C., & Bond, W. J. (2014). Is there a "browse trap"? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology*, 102(3), 595–602. <https://doi.org/10.1111/1365-2745.12230>
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Tchamba, M., & Mahamat, H. (1992). Effects of elephant browsing on the vegetation in Kalamaloue National Park, Cameroon. *Mammalia*, 56(4), 533–540.
- Teren, G., Owen-Smith, N., & Erasmus, B. F. N. (2018). Elephant-mediated compositional changes in riparian canopy trees over more than two decades in northern Botswana. *Journal of Vegetation Science*, 29(4), 585–595. <https://doi.org/10.1111/jvs.12638>
- Trenberth, K. E., Dai, A., Van Der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22. <https://doi.org/10.1038/nclimate2067>
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. (4th ed.). New York, NY: Springer-Verlag. <https://doi.org/10.2307/2685660>
- Vogel, S. M., Henley, M. D., Rode, S. C., van de Vyver, D., Meares, K. F., Simmons, G., & de Boer, W. F. (2014). Elephant (*Loxodonta africana*) impact on trees used by nesting vultures and raptors in South Africa. *African Journal of Ecology*, 52(4), 458–465. <https://doi.org/10.1111/aje.12140>
- Walters, M., Midgley, J. J., & Somers, M. J. (2004). Effects of fire and fire intensity on the germination and establishment of *Acacia karroo*, *Acacia nilotica*, *Acacia luederitzii* and *Dichrostachys cinerea* in the field. *BMC Ecology*, 4(3), 1–13. <https://doi.org/10.1186/1472-6785-4-3>
- White, A. M., & Goodman, P. S. (2010). Differences in woody vegetation are unrelated to use by African elephants (*Loxodonta africana*) in Mkhuzo Game Reserve, South Africa. *African Journal of Ecology*, 48(1), 215–223. <https://doi.org/10.1111/j.1365-2028.2009.01105.x>
- Wiseman, R., Page, B. R., & Connor, T. G. O. (2004). Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research*, 34(1), 25–37.
- Zitzer, H. R., & Boulton, V. L. (2018). Vasectomies of male African elephants as a population management tool: A case study. *Bothalia - African Biodiversity and Conservation*, 48(2), 1–9.

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APPENDIX 1

Model selection based on AIC, delta values giving the best-fitting model (row 1). + = included in model iteration.

	(Intercept)	drought	height	species	drought: height	drought: species	drought: height: species	df	logLik	AICc	delta	weight
16	+	+	+	+	+			63	-2705.875	5,540.061	0	0.953349
8	+	+	+	+				54	-2718.239	5,546.175	6.114495	0.044824
32	+	+	+	+	+	+		93	-2680.78	5,552.613	12.55192	0.001793
24	+	+	+	+		+		84	-2694.198	5,560.512	20.45073	3.45E-05
7	+		+	+				51	-2768.502	5,640.519	100.4579	1.46E-22
64	+	+	+	+	+	+	+	255	-2568.931	5,687.45	147.3892	9.42E-33
12	+	+	+		+			24	-2820.976	5,690.292	150.2312	2.27E-33
4	+	+	+					15	-2831.894	5,693.923	153.8625	3.70E-34
3	+		+					12	-2884.895	5,793.879	253.8177	7.30E-56
22	+	+		+		+		75	-2885.213	5,923.703	383.6425	4.70E-84
6	+	+		+				45	-2916.61	5,924.4	384.3392	3.32E-84
5	+			+				42	-2947.069	5,979.166	439.1055	4.25E-96
2	+	+						6	-3173.998	6,360.02	819.9592	8.46E-179
1	+							3	-3194.043	6,394.092	854.0316	3.38E-186

APPENDIX 2

Generalised variance inflation factors (GVIF) for the terms used in our best-fitting model. GVIF is the generalised variance inflation factor, which extends the concept of variance inflation factor to terms with more than one degree of freedom (Fox & Monette, 1992). DF is the degrees of freedom for the term. $GVIF^{1/(2*DF)}$ indicates the reduction in precision due to collinearity, is comparable across terms of different dimension, and has the same interpretation as the square root of the usual variance inflation factor (Fox & Weisberg, 2011, p. 325). Calculations done using the function `vif()` in the R package `car`.

Explanatory variables	GVIF	df	$GVIF^{1/(2*DF)}$
Drought	4.26	1	2.06
Height	79.05	3	2.07
Species	110.25	13	1.9
Drought:Height	83.17	3	2.08

APPENDIX 3

Species and their total agglomerated abundance 2012–2015.

Species	N
1. <i>Dichrostachys cinerea</i>	1,428
2. <i>Grewia villosa</i>	482
3. <i>Senegalia nigrescens</i>	233
4. <i>Vachellia karroo</i>	231
5. <i>Spirostachys africana</i>	184
6. <i>Gymnosporia senegalensis</i>	157
7. <i>Gymnosporia buxifolia</i>	156
8. <i>Ehretia nervifolia</i>	139
9. <i>Euclea divinorum</i>	119
10. <i>Croton menyhartii</i>	109
11. <i>Vachellia tortilis</i>	104
12. <i>Grewia flava</i>	78
13. <i>Vachellia grandicornuta</i>	71
14. <i>Vachellia nilotica</i>	67
15. <i>Grewia flavescens</i>	45
16. <i>Ehretia Rigida</i>	41
17. <i>Combretum apiculatum</i>	39
18. <i>Ziziphus mucronata</i>	38
19. <i>Euclea daphnoides</i>	37
20. <i>Searsia gueinzii</i>	36
21. <i>Grewia monticola</i>	28
22. <i>Grewia bicolor</i>	27
23. <i>Senegalia caffra</i>	26
24. <i>Schotia capitata</i>	26
25. <i>Tecomaria capensis</i>	26
26. <i>Grewia hexamita</i>	23
27. <i>Ximenia americana</i>	23

Species	N
28. unidentified	22
29. <i>Vachellia luederitzii</i>	21
30. <i>Canthium inerme</i>	21
31. <i>Searsia dentata</i>	20
32. <i>Bolusanthus speciosus</i>	19
33. <i>Combretum hereroense</i>	19
34. <i>Capparis tomentosa</i>	18
35. <i>Terminalia phanerophlebia</i>	18
36. <i>Euclea crispa</i>	17
37. <i>Gymnosporia hemipterocarpa</i>	17
38. <i>Commiphora pyracanthoides</i>	15
39. <i>Pappia capensis</i>	14
40. <i>Azima tetraacantha</i>	13
41. <i>Ehretia species</i>	13
42. <i>Salvadora australis</i>	13
43. <i>Capparis fascicularis</i>	12
44. <i>Ehretia amoena</i>	12
45. <i>Gymnosporia maranguensis</i>	12
46. <i>Cordia monoica</i>	10
47. <i>Euclea undulata</i>	10
48. <i>Gymnosporia glaucophylla</i>	8
49. <i>Ehretia rigida</i>	7
50. <i>Grewia microthyrsa</i>	7
51. <i>Rhus gueinzii</i>	7
52. <i>Croton Gratissimus</i>	6
53. <i>Gardenia volkensii</i>	6
54. <i>Vachellia xanthophloea</i>	5
55. <i>Commiphora schimperii</i>	5
56. <i>Dovyalis caffra</i>	5
57. <i>Gymnosporia heterophylla</i>	5
58. <i>Commiphora africana</i>	4
59. <i>Diospyros natalensis</i>	4
60. <i>Euclea natalensis</i>	4
61. <i>Grewia Monticola</i>	4
62. <i>Gymnosporia spp.</i>	4
63. <i>Monodora junodii</i>	4
64. <i>Rhus gerrardii</i>	4
65. <i>Senegalia senegal</i>	3
66. <i>Cadaba natalensis</i>	3
67. <i>Capparis spp.</i>	3
68. <i>Ehretia rigida</i>	3
69. <i>Euclea spp</i>	3
70. <i>Gardenia thunbergia</i>	3
71. <i>Grewia caffra</i>	3
72. <i>Grewia hornbyi</i>	3

Species	N
73. <i>Grewia</i> spp.	3
74. <i>Vepris lanceolata</i>	3
75. <i>Vachellia</i> spp.	2
76. <i>Albizia</i> spp.	2
77. <i>Boscia albitrunca</i>	2
78. <i>Cammiphora africana</i>	2
79. <i>Capparis sepiaria</i>	2
80. <i>Catha edulis</i>	2
81. <i>Combretum collinum</i>	2
82. <i>Commiphora</i> spp.	2
83. <i>Croton gratissimus</i>	2
84. <i>Euphorbia ingens</i>	2
85. <i>Flacourtia indica</i>	2
86. <i>Gossypium</i> spp.	2
87. <i>Gymnosporia nemorosa</i>	2
88. <i>Gymnosporia woodii</i>	2
89. <i>Putterlickia verrucosa</i>	2
90. <i>Sclerocarya birrea</i>	2
91. <i>Vachellia swazica</i>	1

APPENDIX 4

The agglomerated sample size of each species in relation to height category over the 4 years of our study (2012–2015).

Species	Height			
	1–2 m	2–4 m	4–6 m	6 m+
<i>Dichrostachys cinerea</i>	1,116	311	5	1
<i>Grewia villosa</i>	465	17	0	0
<i>Senegalia nigrescens</i>	53	53	72	55
<i>Vachellia karroo</i>	118	61	30	23
<i>Spirostachys africana</i>	51	43	67	23
<i>Gymnosporia senegalensis</i>	145	11	1	0
<i>Gymnosporia buxifolia</i>	73	69	13	1
<i>Ehretia nervifolia</i>	121	17	1	0
<i>Euclea divinorum</i>	50	35	31	3
<i>Vachellia tortilis</i>	57	34	9	5
<i>Croton menyhartii</i>	50	43	6	1
<i>Grewia Flava</i>	48	25	1	0
<i>Vachellia grandicornuta</i>	17	34	14	2
<i>Vachellia nilotica</i>	24	34	10	1