



Recent exposure to African elephants after a century of exclusion: Rapid accumulation of marula tree impact and mortality, and poor regeneration



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ABSTRACT

Concerns exist over the continual decline of marula trees (*Sclerocarya birrea* subsp. *caffra*), a large ecologically and economically important tree species in southern Africa, primarily as a consequence of impact by African elephants (*Loxodonta africana*) and poor regeneration. We assessed changes to marula tree population structure in a protected area that was only recently opened to elephants. Jejane Private Nature Reserve (JPNR) has been subjected to elephants from the Greater Kruger National Park (Greater KNP) since 2013, as it was fenced off beforehand. A previous survey of the marula population in JPNR was done in 2009 and again in 2016. Therefore this study aimed to (i) assess elephant-induced impact and mortality levels on the previously surveyed JPNR marula tree population, (ii) compare these levels with previously recorded impact and mortality levels on marula trees across the Greater KNP, and (iii) assess marula seed predation and seedling recruitment in JPNR. The resurveyed marula population had declined by 23.8% post-elephant movement into JPNR, with the highest annual mortality rates (AMR) and elephant impact scores for trees in the 5–8 m height class. The JPNR marula tree AMR of 8.1% was higher than that of Greater KNP (4.6%). Only two marula seedlings were found across all transects, whilst 84.2% of all endocarps' locules had seeds missing, with bite marks present on 42.3% of all endocarps. This suggests potential high levels of seed predation and a lack of seedling recruitment. The concern over the impact by elephants on adult marula trees is therefore escalated as a consequence of the lack of regeneration, primarily because of seed and seedling predation. Management policies should be focused on protection methods for individual trees, seedlings and seeds, together with a large scale artificial surface water management plan to manipulate herbivore densities and pressures on marula tree populations.

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1. Introduction

African elephants (*Loxodonta africana*) are considered to be one of the major drivers of ecosystem functioning, owing to their ability to alter landscapes and promote habitat heterogeneity (Dublin et al., 1990; White and Goodman, 2010; Coverdale et al., 2016). However, concerns have been raised over the potential negative impacts that can result from high densities of elephants in protected areas (Ben-Shahar, 1998; Gandiwa et al., 2011). This is of particular importance in South Africa's Greater Kruger National Park (Greater KNP), where long-term studies have reported significant declines in the density of large trees (Shannon et al., 2008;

Helm and Witkowski, 2013; Asner et al., 2015). Large trees are important for ecosystem services, providing foraging opportunities and habitats for numerous species (Shackleton et al., 2002; Vogel et al., 2014; Mograbi et al., in press), as well as being critical for the cycling of nutrients (Scholes and Archer, 1997). A tree species of particular concern to conservationists is the marula tree (*Sclerocarya birrea* subsp. *caffra*; Anacardiaceae), with elephant impact on marula trees having been extensively studied because of its cultural, ecological and economical importance (Coetzee et al., 1979; Jacobs and Biggs, 2002a; Shackleton et al., 2002; Helm and Witkowski, 2013). Studies suggest that marula trees are actively selected for by elephants and are consequently foraged more intensely in comparison to other large tree species (Shannon et al., 2008; Henley, 2013). Elephants therefore, have been largely recognised as a major factor responsible for the decline of adult

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marula trees within protected areas (Helm et al., 2009; Helm and Witkowski, 2013).

The decline in marula tree numbers is not, however, solely due to elephant impact. A lack of regeneration is a concern in various populations (Helm et al., 2011a; Helm and Witkowski, 2012). Regeneration of trees can be affected by a variety of factors including seed predation (Eriksson and Ehrlén, 1992) and herbivory (Lewis, 1987; Moe et al., 2009). Seed predation is a common seed fate that occurs once either primary or secondary seed dispersal has occurred (Helm et al., 2011a; Midgley et al., 2012), with birds and small mammals being recorded preying on marula seeds by manually opening the endocarps to feed on the stored seeds (Manson et al., 2001; Symes and Perrin, 2003). Furthermore, marula seeds which develop into seedlings are highly palatable (Walker et al., 1986), and studies have suggested a negative correlation between seedling survival and herbivore densities, especially those of impala (*Aepyceros melampus*) (Lewis, 1987; Kauffman and Maron, 2006). These recruitment studies indicate that it is necessary to investigate factors that may be influencing marula tree population structure at both the adult and recruitment demographic stages.

In January 2009, Helm and Witkowski (2012) assessed the size class distributions of marula tree populations, both within and bordering the Greater KNP. One of the bordering study sites, Jeje Private Nature Reserve (JPNR), displayed an adult-dominated marula tree population with a lack of seedling recruitment. At the time of the 2009 assessments, JPNR had not had any elephants present within the protected area in over 100 years, and no fires had occurred since the year 2000 (JPNR Management, pers. comm., November 23, 2016). In March 2013, JPNR proceeded to remove the fence-line between itself and the Greater KNP, allowing for elephants to move into JPNR (Thomson, 2013). Subsequent reports have suggested a decline in the number of large trees across JPNR, as well as a growing concern amongst management regarding the impact of elephants on marula trees (Weber, 2014). Therefore, by surveying the JPNR marula trees previously surveyed by Helm and Witkowski (2012), this paper aims to (i) assess elephant-induced impact and mortality levels on the previously surveyed JPNR marula tree population, (ii) compare these levels with previously recorded impact and mortality levels on marula trees across the Greater KNP, as published in Helm et al. (2009), and (iii) assess marula seed predation and seedling recruitment in JPNR. It is predicted that the impact and mortality levels of marula trees in JPNR will exceed those of previously recorded sites in the Greater KNP because of the abundance of marula trees in JPNR as a consequence of having no elephants for so many years. It is further predicted that high levels of seed predation may account for the lack of recruitment in JPNR.

2. Materials and methods

2.1. Study area

JPNR, a 21 km² protected area (S24.29045; E30.97664), is situated in the western region of the Greater KNP (Fig. 1). JPNR receives a mean annual rainfall (MAR) of 400–600 mm (JPNR Management, pers. comm., March 16, 2016) and is located in the Granite Lowveld vegetation unit (SVI 3) in the Savanna biome (Mucina and Rutherford, 2006). This vegetation unit is a moderately open savanna that is dominated by tall tree species such as *Sclerocarya birrea*, *Combretum apiculatum* and *Senegalia nigrescens* (Mucina and Rutherford, 2006). The marula trees which were previously surveyed in the Greater KNP by Helm et al. (2009) (Objective ii) were located in the following ecozones: Marula-knobthorn savanna, Delagoa-thorn thickets, Sabie thorn thickets, Mixed bush-

willow woodlands, and Gabbro thornveld (Helm et al., 2009). This portion of the Greater KNP receives a MAR of 500–700 mm (Venter and Gertenbach, 1986) and is similarly predominantly located in the Granite Lowveld vegetation unit (SVI 3; Mucina and Rutherford, 2006).

2.2. Study species

The marula tree (Anacardiaceae) is a fast growing dioecious and deciduous tree, reaching heights of 7–17 m (Shackleton et al., 2002). Marula is often a community dominant and is a keystone species with both ecological and economical uses (Shackleton et al., 2002). Marula trees occur on a wide variety of soil-types, but are most commonly found on well-drained soil crests in areas with a MAR of 200–1500 mm (Lewis, 1987). Female trees produce sweet fleshy fruits, which may each contain 0–4 seeds (Leakey et al., 2005). Marula trees have been listed as a protected species in South Africa since 1962 (Shackleton and Shackleton, 2005).

2.3. Elephant impact and mortality levels

During 29 April–01 May 2016, 202 previously surveyed marula trees by Helm and Witkowski (2012) were resurveyed for elephant impact. These trees had not been previously assessed for elephant impact. The surveys had been done along eight transects which were all 40 m in width and ranged from 203 to 289 m in length. All trees had been previously georeferenced using a Global Positioning System (GPS). Upon arrival at the GPS location of each tree, methodology followed Helm et al. (2009) and Helm and Witkowski (2012, 2013). The located tree was classed into the following three tree fates: 'Surviving', 'Missing' and 'Dead'. Trees classified as 'Dead' were further categorised into the cause of the death, being 'Stem snapping', 'Uprooting' or 'Bark stripping'. Trees that were classified as 'Surviving' were further categorised into the following tree fate categories: 'Mature' (tree alive and >2 m in height), 'Stem snapped' (main stem broken but tree coppicing), or 'Toppled' (tree has been pushed over but coppicing). Each surviving tree had its height measured to a level of accuracy of 1 cm using the *VolCalc* digital photography method for estimating tree dimensions (Barrett and Brown, 2012). To compare height class distributions to those previously measured by Helm and Witkowski (2012), surviving trees were placed into the same 12 height classes (Table 1). The basal stem diameter (BSD) of each tree was measured 30 cm from the ground. To compare BSD class distributions to those previously measured by Helm and Witkowski (2012), surviving trees were placed into the same ten BSD size classes (Table 1). Elephant impact scores (Table 2), as previously used by Jacobs and Biggs (2002a), Helm et al. (2009) and Helm and Witkowski (2013), were assessed on all 'Surviving' trees that were categorised as 'Standing' and 'Stem snapped'. As these impact scores would be compared to impact scores on marula trees in the Greater KNP, the trees were separated into an additional arrangement of height classes (Table 1) to correspond with the previously assessed trees by Helm et al. (2009) in 2001 and 2008. Impact score comparisons were only carried out on trees >5 m, as only one tree from the 2009 survey by Helm and Witkowski (2012) was <5 m. Additional notes were recorded on the presence or absence of bracket fungus (class Basidiomycetes), termites (*Coptotermes* species) and woodborer activity. The age of any elephant impact was estimated into the following age classes using parameters established by Henley (2013): 1 (within the past month); 2 (1–6 months); 3 (6–12 months); and 4 (more than a year old). Previous research has indicated that elephants may have a preference for female trees because of the fruit they bear (Hemborg and Bond, 2007), and therefore the sex of each tree was determined by searching for fruit endocarps beneath the tree's canopy (Helm et al., 2009, 2011a).

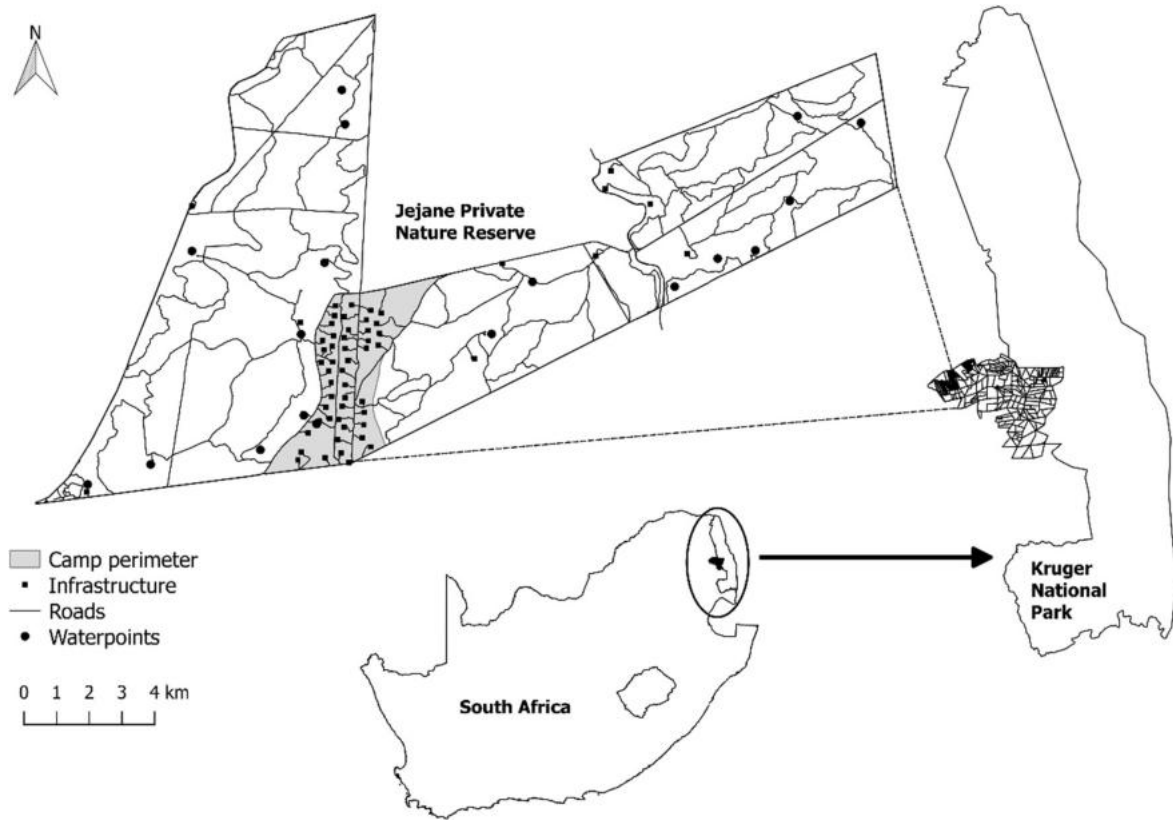


Fig. 1. Location of Jeje Private Nature Reserve (JPNR) along the western border of the Greater Kruger National Park (Greater KNP). JPNR is a section of Balule Nature Reserve, a member of the Associated Private Nature Reserves which opened up their border to the Kruger National Park, forming the Greater KNP.

Table 1

Height and BSD size classes into which the 2016 JPNR marula trees were categorised for comparisons with the Helm and Witkowski (2012) population structure and Helm et al. (2009) elephant impact surveys.

Study comparison	Class											
	1	2	3	4	5	6	7	8	9	10	11	12
Change in height distribution (m): Helm and Witkowski (2012)	<0.25	0.25–1	1–2	2–3	3–4	4–5	5–6	6–8	8–10	10–12	12–15	>15
Change in BSD distribution (cm): Helm and Witkowski (2012)	0.5–2	2–5	5–9	9–14	14–20	20–30	30–40	40–50	50–60	60–70		
Elephant impact comparison across heights (m): Helm et al. (2009)	2–5	5–8	8–11	11–15	>15							

Table 2

Impact scores to assess elephant impact on marula trees, as described by Jacobs and Biggs (2002a), Helm et al. (2009) and Helm and Witkowski (2013).

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

Proportions were used to represent the number of trees in each tree fate category, as well as the number of trees in the height, BSD, and impact score classes. A Kolmogorov-Smirnov two-sample test was used to test for differences in the height and BSD size class distributions between the 2009 and 2016 assessments. A Kruskal-Wallis by ANOVA Rank test was used to test for impact score differences between height classes in JPNR. Furthermore, tree height selection preference by elephants was assessed using preference ratings (Petrides, 1975) to identify if elephants were target-

ing a specific height class. A paired *t*-test was used to test for differences between the tree densities of 2009 and 2016, whilst a Chi-squared test was used to test for differences in the JPNR marula tree sex ratio between 2009 and 2016. Tree annual mortality rates (AMR) were calculated and divided into two separate time periods for JPNR, 2009–2016 and 2013–2016. The 2009–2016 AMR assumed that tree mortality occurred both prior- and post-elephant movement into JPNR, whilst the 2013–2016 AMR assumed that tree mortality occurred only post-elephant movement into JPNR from 2013.

JPNR elephant impact scores and tree AMRs were compared to those previously surveyed in 2001 and 2008 in the Greater KNP by Helm et al. (2009). A Mann-Whitney *U* test was used to test for impact score differences between JPNR trees in 2016 and KNP trees in 2001 and 2008, respectively. All statistical analyses were performed using R statistical software (R v. 3.2.2, R Core Team, 2016).

2.4. Seed predation and seedling recruitment

Seed bank sampling in JPNR was carried out on 02–03 May 2016 on 30 female trees following methodology described in Helm et al.

(2011a). For each tree, the following microsites were assessed: inner canopy (tree trunk to half radius of tree canopy); outer canopy (half radius of tree canopy to canopy edge); subcanopy (tree trunk to canopy edge); and outside canopy (≤ 10 m outside of canopy edge). Eight quadrats (0.5×0.5 m) in total were sampled for each of the 30 female trees. Four quadrats were sampled in the inner canopy of each tree on the northern, southern, western and eastern bearings of the trunk. Two quadrats were sampled within the outer canopy of each tree on the northern and southern bearings of the tree trunk, and two quadrats were randomly sampled outside the canopy of each tree, >5 m apart from one another. For each quadrat, marula endocarps within the litter layer and the soil layer (5 cm in depth) were collected. Endocarps were separated from the soil and debris using a 120×70 cm sieve (12 mm diameter holes). Each endocarp was labelled according to its microsite, quadrat bearing and soil layer position. Notes were taken on whether each endocarp had flesh, dried skin or pulp surrounding it, indicating that the endocarp was 'new' and from the most recent fruiting season. For each endocarp, the total number of locules were recorded, representing the total number of potential seeds per endocarp prior to primary dispersal. Of these locules, the total number of open and closed locules were recorded. The number of open locules (operculum removed) was indicative of the number of seeds which had been removed from the endocarp, representing either seed predation or germination. The number of closed locules (intact operculum) was indicative of the number of potential seeds still present within the endocarp. The presence of bite marks on the operculum were also recorded. Endocarp densities between microsites were compared using a Kruskal-Wallis by ANOVA Rank test, and a Wilcoxon signed-rank test was used to test for differences in endocarp densities between the litter and soil layers across the microsites.

The number of marula seedlings and saplings were recorded within each of the eight transects, with a search effort of 1 h per transect and an additional 10 min around each female marula tree. Seedlings were placed into one of the following two seedling height classes: 1 (<0.25 m) and 2 (≥ 0.25 –1 m). Individuals in height class 1 represented new seedlings from the current season, whilst individuals in height class 2 represented older seedlings or saplings from previous growing seasons.

3. Results

3.1. Elephant impact and mortality levels

Of the 202 resurveyed trees in JPNR, there was a significant shift in the number of trees from higher to lower height classes between 2009 and 2016 ($D = 0.56$; $p < 0.00001$) (Fig. 2a). Most trees, however, were in the higher BSD size classes and did not significantly change between the 2009 and 2016 assessments ($D = 0.11$; $p = 0.29$) (Fig. 2b). Overall, JPNR still displayed an adult dominated population with the majority of trees in the larger height and BSD size classes.

Of the resurveyed trees in JPNR, 23.8% ($n = 48$) were dead, whilst 64.3% ($n = 130$) were alive and mature (Fig. 3). One tree (previously 9.8 m in height) could not be found and was thus classified as missing. It was also noted that 100% ($n = 201$) of the resurveyed and located trees in JPNR had wood borer activity, 66.7% ($n = 134$) had termite activity, and 3% ($n = 6$) had fungi present. When estimating the age of the elephant impact on the trees, 82% was >1 year old (age class 4), placing this impact within the first two years that JPNR has had elephants, whilst 6.5% of the total impact had occurred within one month prior to surveying (age class 1).

Impact scores on the resurveyed trees in JPNR differed significantly across the height classes ($H_{(3)} = 9.579$; $p < 0.05$; $n = 153$)

with the greatest impact scores recorded in the 5–8 m and 8–11 m height classes (Fig. 4). There was no significant difference between the impact scores on male and female trees ($U = 4641$; $p = 0.33$; $n_3 = 89$; $n_2 = 112$), nor was there a significant change in the JPNR male-to-female tree sex ratio between 2009 (89_3 and 113_2) and 2016 (64_3 and 89_2) ($\chi^2_1 = 0.184$; $p = 0.89$; $n_{2009} = 202$; $n_{2016} = 153$). Overall, elephant impact scores on trees in JPNR were significantly higher than impact scores recorded on Greater KNP trees in 2001, and equal to or lower than impact scores recorded on Greater KNP trees in 2008 (Fig. 4).

There was a significant decrease in the JPNR marula tree density from 25.6 ± 2.3 trees/ha in 2009 to 19.6 ± 2.2 in 2016 ($t_{(7)} = 7.61$; $p < 0.001$; $n = 8$). The highest total tree mortality (2009–2016) in JPNR occurred in the 5–8 m height class (35.3%), followed by the 8–11 m height class (28.2%) (Fig. 5a). Elephants displayed a high preference rating for trees in the 5–8 m height class, followed by the 8–11 m height class (Table 3). These trends in total mortality levels were similar to those recorded in the Greater KNP by Helm et al. (2009), where the highest mortalities were also recorded in the 5–8 m height class (58.3%), followed by the 8–11 m height class (28.2%) (Fig. 5a). For the 2009–2016 period, the AMR of trees in JPNR (3.5% per annum) was lower than in the Greater KNP (4.6% per annum) when measured over a similar period (eight years), albeit at staggered times. However, for 2013–2016, the JPNR AMR of 8.1% per annum was higher than that of the Greater KNP surveyed in earlier years. The highest AMRs occurred in the smaller height classes for both JPNR and the Greater KNP (Fig. 5b). For the 2009–2016 period, JPNR AMRs were equal to or smaller than AMRs in the Greater KNP across most height classes (Fig. 5b). For the 2013–2016 period however, AMRs of trees in JPNR were always greater than those of the Greater KNP.

3.2. Seed predation and seedling recruitment

A total of 1033 endocarps were collected and analysed from 30 female trees. The number of locules present per endocarp ranged from 1 to 4 (mean \pm S.E. = 2.2 ± 0.02). Endocarp density differed significantly across the microsites ($H_{(3)} = 65.253$; $p < 0.0001$; $n = 1033$), with most of the endocarps within the inner canopy (Fig. 6). Endocarps were predominantly found in the litter layer (69.4%; $n = 717$) compared to the soil layer (30.6%; $n = 316$) (Fig. 6). Bite marks were present on 42.3% ($n = 307$) of endocarps. Overall, 97.1% ($n = 1003$) of the endocarps had at least one missing seed, whilst only 2.1% ($n = 22$) were untouched and had all of the locules enclosed with no bite marks present. A total of 2289 locules were counted from the 1033 endocarps, of which 84.2% ($n = 1928$) had been opened and had empty locules. Four endocarps still had a fleshy covering, indicating that they were from the most recent fruiting season. Of the fleshy endocarps, six of the seven opercula had been removed and the locules were empty, indicating a seed predation level of 85.7% on these new seeds.

A total of only two seedlings were recorded (both in seedling height class 1) across all transects. Both seedlings were located under the subcanopy of female trees within 4 m of the main stems.

4. Discussion

4.1. Elephant impact and mortality levels

There was a significant shift in the number of JPNR marula trees from higher to lower height classes, with the highest elephant impact scores occurring in height classes 2 (5–8 m) and 3 (8–11 m). The resurveyed population had declined by 23.8% over a three year period since the movement of elephants into JPNR, with the highest AMRs in height classes 2 (11.8%) and 3 (9.4%).

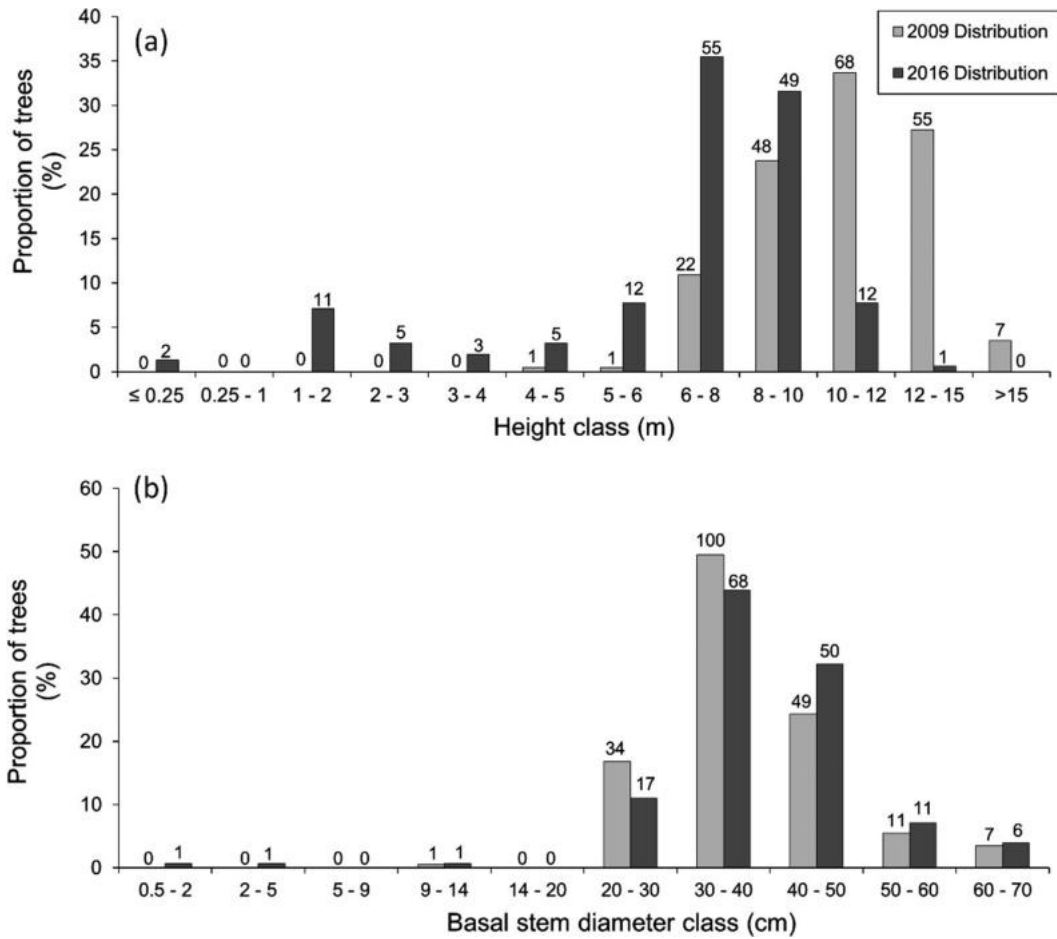


Fig. 2. Changes in (a) height and (b) basal stem diameter class distributions of marula trees in Jejene Private Nature Reserve between the 2009 (Helm and Witkowski, 2012) and 2016 assessments. Numbers above each bar represent the number of live trees in each height and basal stem diameter class.

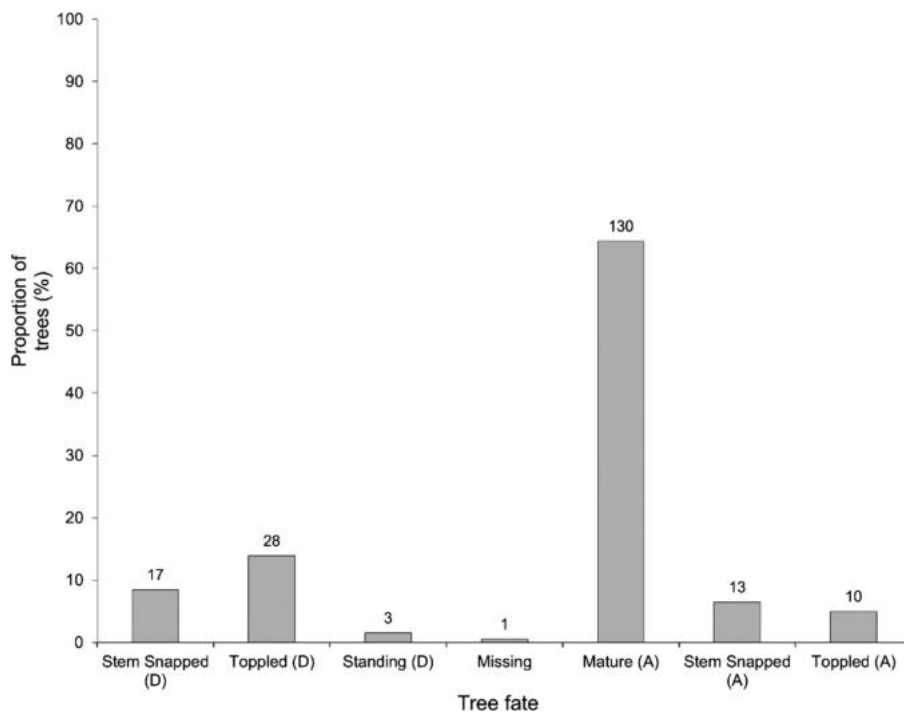


Fig. 3. Tree fate of resurveyed marula trees in Jejene Private Nature Reserve (n = 202). Numbers above each bar represents the number of trees in each tree fate. 'A' represents live trees; 'D' represents dead trees.

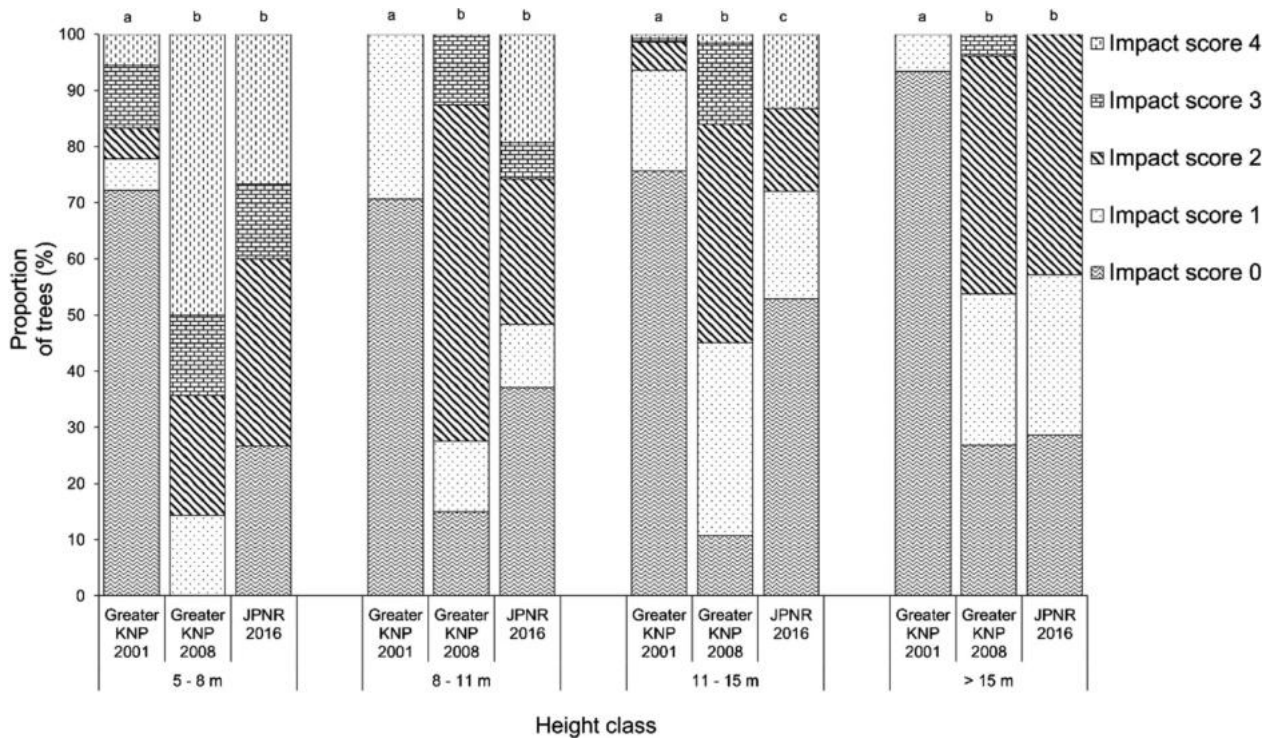


Fig. 4. Comparison of elephant impact score across marula tree height classes between Jejeane Private Nature Reserve (2016) and the Greater Kruger National Park (2001 and 2008; Helm et al., 2009). Highest elephant impact levels were recorded in the 5–8 m and 8–11 m height classes. Different letters indicate significant differences between the survey periods' impact scores within each height class.

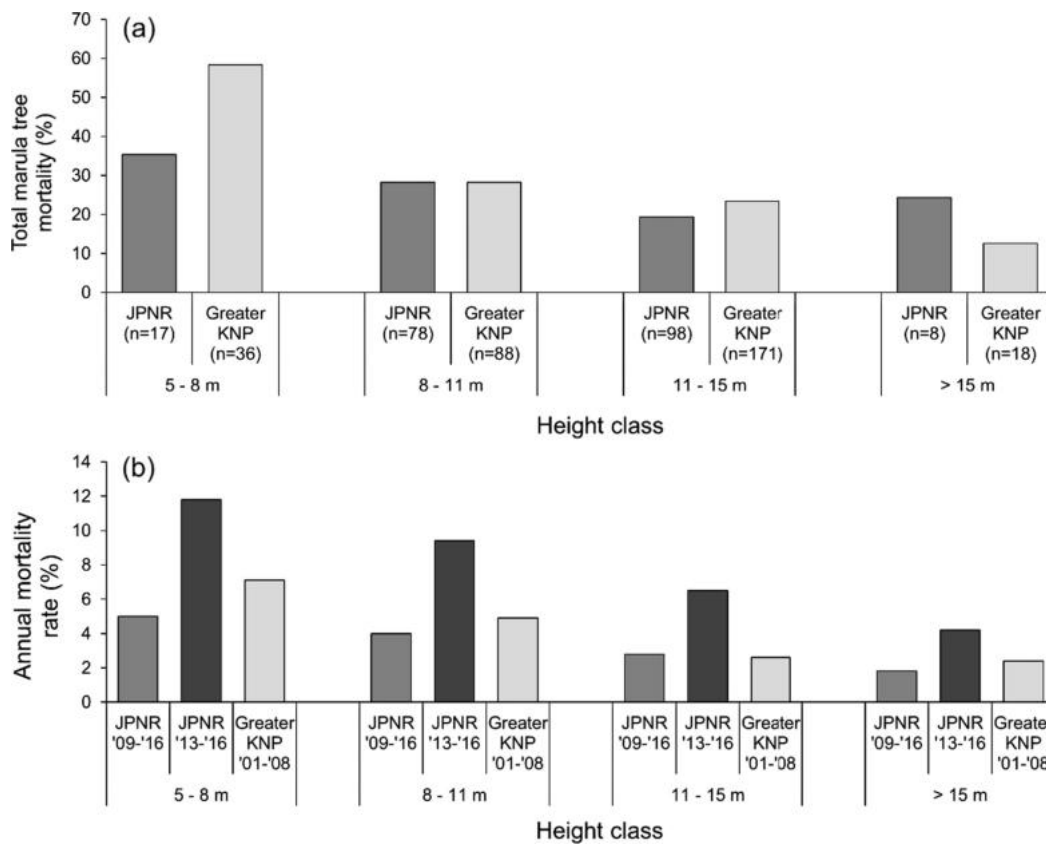


Fig. 5. Marula tree (a) total mortality percentage and (b) annual mortality rates across height classes in Jejeane Private Nature Reserve ($n = 201$) and the Greater Kruger National Park ($n = 313$; Helm et al., 2009). Annual mortality rates for JPNR were divided into two time periods: '2009–2016', assuming tree mortality had occurred prior to the movement of elephants into JPNR from 2013; and '2013–2016', assuming tree mortality only occurred post-elephant movement into JPNR from 2013.

Table 3

Elephant preference ratings for marula tree height classes in Jejane 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	7	1.69
8–11 m	78	22	1.16
11–15 m	98	19	0.80
>15 m	8	1	0.51
Totals	201	49	–

The significant shift in the number of JPNR trees from higher to lower height classes was largely due to main stem snapping and primary branch breakage. Main stem snapping and branch breakage alters a tree's structure and can lead to a stunted growth form (Coetzee et al., 1979). Although there was no significant change in the number of trees across the BSD size classes, diameter at breast height (DBH) measurements may have revealed a more accurate pattern of elephant impact because of the smaller cross-sectional areas of coppiced shoots in comparison to intact basal stems. In the Greater KNP, Jacobs and Biggs (2002a) also measured heavy elephant impact on trees between 5 and 11 m in height, whilst Shannon et al. (2008) found the greatest proportion of toppled trees in the 5–8 m height class. The preferred feeding height of elephants is 2–3 m (Jachmann and Croes, 1991), but elephants may push over taller trees to gain access to the out-of-reach portions of these trees (Stokke and Toit, 2000). Increased elephant impact on trees between these size classes in JPNR may further amplify the adult-dominated population within the protected area.

JPNR trees were not exposed to fire occurrence during the study period as a result of the low fuel loads within the protected area (JPNR Management, pers. comm., September 06, 2016), however, a high number of individuals had either termite- or wood borer-activity (personal observation). Termites in trees are particularly prevalent in unburnt savannas (Abensperg-Traun and Milewski,

1995) and can result in the deterioration of individuals from the inside (Cowie et al., 1989). This deterioration causes these infested trees to become hollow, and therefore more vulnerable to being toppled over by wind and elephants (Jacobs and Biggs, 2002a). Elephant bulls are also more likely to explore newly opened regions in comparison to breeding herds (Druce et al., 2008), and an early study in JPNR indicated a high presence of young 'pilot' bulls post-fence removal (Weber, 2014). Bulls are hypothesised to heavily impact trees as an act of 'confidence building' and muscular training, in addition to browsing (Midgley et al., 2005). It is likely that the high levels of elephant impact on JPNR's trees was a direct result of an initial influx of elephants, particularly bulls, into the protected area. During the first year that the fence was removed (2013), the elephant density in JPNR and the immediate surrounding protected areas was 2.16 elephants/km² (JPNR Management, pers. comm., September 06, 2016). This density was more than double that of the adjacent transect zones in the Greater KNP, which ranged from 0.31 to 0.94 elephants/km² during the period for which Helm et al. (2009) recorded elephant impact (Whyte, 2007). Elephant densities in the Associated Private Nature Reserves (APNR), of which JPNR is a part of, have increased from 0.65 elephants/km² in 2001 to 1.49 elephants/km² in 2015, partly as a result of immigration from the open border with the KNP (Whyte, 2007; Peel, 2015). However, the elephant density in JPNR post-fence removal is still greater than that of the surrounding areas and may explain why almost a quarter of the resurveyed trees had died after only three years. Furthermore, JPNR had not had any elephants present in the region in over 100 years and had the highest density of adult marula trees (BSD > 14 cm) in the Greater KNP prior to the removal of the fence-line (Helm and Witkowski, 2012). JPNR's adult marula tree density in 2009 (25.6 ± 2.3 trees/ha) is far greater than those of Helm et al. (2009) transect sites in the Greater KNP, which ranged from 2 to 7 adult trees/ha (Helm and Witkowski, 2012). Therefore, the high density of trees in JPNR, coupled with the high elephant density, would likely increase the probability of encounters between elephants and trees, thereby increasing tree mortality (O'Connor

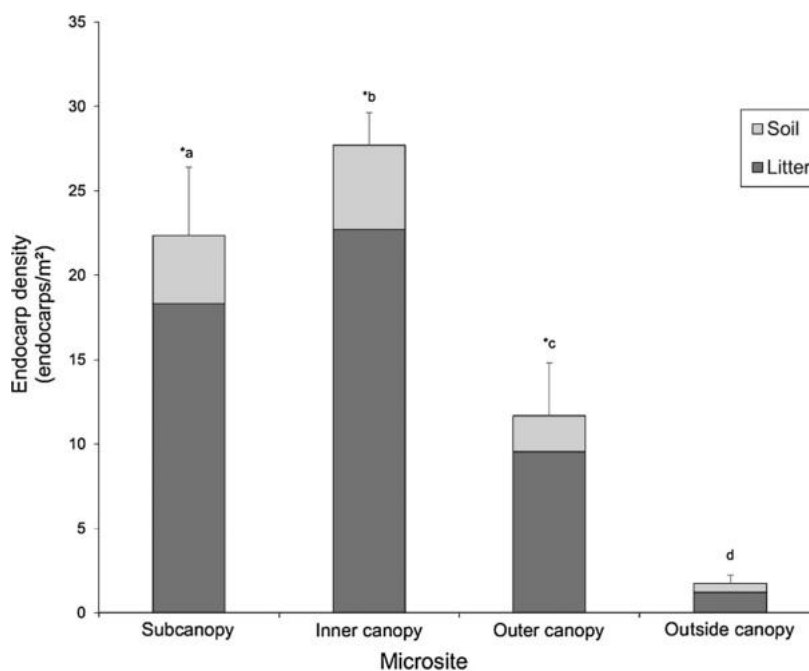


Fig. 6. A comparison of the endocarp density (endocarps/m²; mean ± SE) between the litter and soil (0–5 cm depth) layers across the four microsites of 30 female marula trees in Jejane Private Nature Reserve. The highest endocarp densities were found in the litter layer of the inner canopies. * Indicates significant differences between litter and soil layer endocarp densities, while different letters indicate significant differences between microsite endocarp densities.

et al., 2007). This would explain why mortality rates in JPNR were greater than those previously recorded in the Greater KNP by Helm et al. (2009). No fires occurred within JPNR during the 2009–2012 period (JPNR Management, pers. comm., January 10, 2017), which could have killed smaller trees and seedlings (Jacobs and Biggs, 2001; Helm et al., 2011b). Therefore we suggest that the 2013–2016 mortality rates are a more accurate representation compared to those of 2009–2016. There is, however, a temporal difference in the data collection periods of tree impact in the JPNR and Greater KNP survey sites. Observed differences in tree impact may be due to differences in surface water availability, vegetation types, elephant densities, or marula tree density. JPNR is situated 12 km south of the perennial Olifants River and contains numerous artificial surface waterholes, whilst the survey sites within the Greater KNP were either <5 km from the perennial Sabie River, or within the vicinity of artificial surface waterholes (Helm and Witkowski, 2012). Furthermore, both the JPNR and Greater KNP survey sites occurred mostly on granite catenas within a MAR range of 400–700 mm (Mucina and Rutherford, 2006). Therefore, whilst the temporal differences between the two survey periods is a limitation of this study, our results suggest that increased marula tree mortality will occur when both elephant and tree densities are high.

4.2. Seed predation and seedling recruitment

97.1% of sampled endocarps had at least one seed missing, whilst 84.2% of the endocarps' locules had been opened. Only two seedlings (<25 cm in height) were found across transects, indicating a lack of recruitment in the JPNR population.

Large irregular seeds, or seeds with large endocarps such as marula seeds, do not easily enter the soil layer (Thompson et al., 1993). This exposes the seeds to seed predators (Reader, 1991) and Helm et al. (2011a) recorded varying seed predation levels of 19–74% for marula seeds across the Greater KNP. A lack of fire in savannas can result in an increase in vegetation cover (Stephens et al., 2009), thereby leading to an increase in rodent numbers and seed predation levels (Reader, 1991; Helm et al., 2011a). Midgley et al. (2012) recorded that tree squirrels (*Paraxerus cepapi*) were common predators of marula seeds in the Greater KNP, often gnawing through the opercula to obtain the enclosed seeds. Tree squirrels collecting endocarps were able to consume all of the enclosed seeds in a single endocarp within 10 min (Midgley et al., 2012). High levels of seed predation could ultimately cause seed limitation within a population, restricting the regeneration of its individuals (Kurkjian et al., in press). Therefore, the high number of missing seeds in this present study, especially from new endocarps, suggests that marula recruitment in JPNR may also be seed limited. Elephants are important seed dispersal agents of marula trees, being able to transport seeds up to 65 km away from their parent trees (Bunney et al., 2017), as well as by facilitating seed germination through acid treatment in the digestion system (Lewis, 1987). However, Midgley et al. (2012) hypothesise that tree squirrels may target the seeds of endocarps found inside elephant faeces, as these opercula will have been loosened by the acid treatment. Further investigation into this hypothesis is required.

JPNR displayed an adult-dominated marula tree population (Group 1 classification; Helm and Witkowski, 2012), evident by the lack of individuals with a BSD < 14 cm. Marula tree populations with a group 1 classification are representative of a population where recruitment has not occurred in many years, representing a pattern of distinct episodic recruitment (Helm and Witkowski, 2012). Similar episodic recruitment patterns have been identified for baobab trees (*Adansonia digitata*) in southern Africa (Venter and Witkowski, 2010). Populations that experience such bottlenecks at the seed and seedling levels are potentially proceeding towards local extirpation (O'Connor et al., 2007). In 2009, Helm

and Witkowski (2012) did not find any seedlings in JPNR, indicating a lack of recruitment in this population prior to the movement of elephants into JPNR. A number of factors affect seedling recruitment, including seed limitation (Eriksson and Ehrlén, 1992), herbivory (Moe et al., 2009), fires (Jacobs and Biggs, 2001), and rainfall (Venter and Witkowski, 2013). Impala are one of the main seedling predators in African savannas and correlations have been observed between increased impala densities and a decrease in seedlings (Lewis, 1987; Moe et al., 2009). The mean impala density in JPNR and the immediate surrounding protected areas was 17.74 ± 5.29 individuals/km² between the years 2010 and 2015 (JPNR Management, pers. comm., September 06, 2016). This is higher than the neighbouring Greater KNP impala density, ranging from 8.12 to 11.7 individuals/km² across the protected area (Ferreira et al., 2013). Thus, the high impala densities may be preventing seedlings from developing into saplings and adults.

4.3. Management implications

Elephant culling in the Greater KNP has been discontinued due to a combination of animal welfare concerns and evidence that elephant culling did not meet conservation goals (Owen-Smith et al., 2006). There has also been a scientific paradigm shift towards managing the impacts and distributions of species, rather than species' numbers alone (Owen-Smith et al., 2006; Ferreira et al., 2011). Impala and elephant distributions specifically, are positively correlated with the presence of surface water (Smit et al., 2007a,b). JPNR and the immediate surrounding protected areas currently have an artificial waterhole density of 1 per 1.78 km² in the wet, and 1 per 3.35 km² in the dry season (JPNR Management, pers. comm., December 06, 2016). These artificial waterhole densities are far greater in comparison to the Greater KNP (1 per 88.57 km² in the dry season, depending on the waterhole closure plan; Gaylard et al., 2003). Although closing down artificial waterholes within JPNR may decrease the density of impala within the immediate area (Smit et al., 2007a), and therefore their impact on marula seedlings (Moe et al., 2009), the closure of artificial waterholes on a large scale across the Greater KNP system would be required to reduce elephant densities by creating a surface water gradient across the system (Smit et al., 2007b; Purdon and van Aarde, 2017). Therefore, mitigation methods which directly influence elephant impact on large trees may be a more effective management option for JPNR. These include wire-netting a tree's main stem to prevent ring barking (Derham et al., 2016), and most recently, the use of African honeybees to deter elephants from impacting trees (Cook et al., in preparation). These methods can be applied to selected tree species in need of protection, thereby allowing managers to mitigate elephant impact within the protected areas under their control.

Furthermore, our results suggest that seed predation may be causing a bottleneck effect on the JPNR population. Whilst the use of fire as a management option to control rodent numbers may be effective when fuel loads are sufficient, the negative impact of fire on marula seedlings and saplings will have to be taken into account (Jacobs and Biggs, 2001; Helm et al., 2011b). The use of exclusion plots may provide artificial refugia for marula seeds and seedlings where there is protection against rodents and smaller herbivores (Jacobs and Biggs, 2002b). However, consideration for exclusion plot locations is required for protected areas containing megaherbivores which are capable of breaking through the enclosure fencing.

5. Conclusion

The JPNR marula tree population surveyed in 2009 by Helm and Witkowski (2012) had declined by 23.8% in 2016 and displayed an

adult-dominated population with a lack of recruitment and high seed predation levels. Our results suggest that the relatively high tree mortality levels which have occurred in JPNR, in comparison to the Greater KNP, are due to a combination of a high elephant density and marula tree availability within JPNR post-fence removal. As JPNR had an adult-dominated marula tree population prior to the movement of elephants into the protected area from 2013, it is also necessary to focus on factors at the various demographic stages that are preventing seeds from establishing into seedlings, as well as seedlings recruiting into saplings and adult trees. The high seed predation levels may be indicative of rodent predation (Midgley et al., 2012), as rodent numbers increase in unburnt savannas (Stephens et al., 2009). Furthermore, the extensive density of artificial surface waterholes within and around JPNR may be contributing to the relatively high densities of both elephants and impala within the protected area, thereby having an effect on the marula tree population at various demographic stages. Management strategies should focus on methods to protect individual trees, seedlings and seeds, together with a large scale landscape management plan through the manipulation of artificial surface waterholes.

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