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**Ants, fire and bark traits affect how African savanna trees recover following damage**

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1 ABSTRACT

2 Bark damage resulting from elephant feeding is common in African savanna trees with  
3 subsequent interactions with fire, insects and other pathogens often resulting in tree mortality.  
4 Yet, surprisingly little is known about how savanna trees respond to bark damage. We  
5 addressed this by investigating how the inner bark of marula (*Sclerocarya birrea*), a  
6 widespread tree species favoured by elephants, recovers after bark damage. We used a long-  
7 term fire experiment in the Kruger National Park to measure bark recovery with and without  
8 fire. At 24 months post-damage, mean wound closure was 98, 92, and 72% respectively in  
9 annual and biennial burns and fire exclusion treatments. Fire exclusion resulted in higher  
10 rates of ant colonisation of bark wounds, and such ant colonisation resulted in significantly  
11 lower bark recovery. We also investigated how ten common savanna tree species respond to  
12 bark damage and tested for relationships between bark damage, bark recovery and bark traits  
13 while accounting for phylogeny. We found phylogenetic signal in bark dry matter content,  
14 bark N and bark P, but not in bark thickness. Bark recovery and damage was highest in  
15 species which had thick moist inner bark and low wood densities (*Anacardiaceae*),  
16 intermediate in species which had moderate inner bark thickness and wood densities  
17 (*Fabaceae*) and lowest in species which had thin inner bark and high wood densities  
18 (*Combretaceae*). Elephants prefer species with thick, moist inner bark, traits that also appear  
19 to result in faster recovery rates.

20

21 KEY-WORDS: bark damage, bark traits, elephants, interactions, Kruger National Park, long-  
22 term fire experiment

23 ELEPHANTS HAVE A RANGE OF EFFECTS IN SAVANNA ECOSYSTEMS RANGING FROM POSITIVE,  
24 (e.g., dispersal of seeds, facilitation of feeding by other herbivores, Rutina et al. 2005, Young  
25 et al. 2005, Pringle 2008, Nasser et al. 2011) to negative, e.g., limiting tree survival and  
26 recruitment and decreasing woody densities, as well as simplification of vegetation structure,  
27 which decreases habitat for other fauna (Dublin et al. 1990, Cumming et al. 1997, McCauley  
28 et al. 2006, Landman & Kerley 2014, McCleery et al. 2018). Elephants can cause significant  
29 tree mortality through different mechanisms including ringbarking and pollarding (Coetzee et  
30 al. 1979; Gadd 2012; Helm et al. 2009, 2011; Midgley et al. 2010; Moncrieff et al. 2008;

31 O'Connor et al. 2007; Shannon et al. 2011; Vanak et al. 2012). Elephants have been  
32 observed to disproportionately damage some species (e.g. marula, *Sclerocarya birrea*)  
33 leading to increased mortality of these species and their eventual replacement by others  
34 (Coetzee et al. 1979, Helm et al. 2009, 2011, Shannon et al. 2011, Gadd 2012, Vanak et al.  
35 2012). Although ringbarking by elephants – the stripping of bark around the entire  
36 circumference of the trunk or stem – is a major cause of tree mortality, there is no clear  
37 consensus on why elephants prefer the bark of certain species (Anderson & Walker 1974,  
38 Croze 1974, Bash 2002, O'Connor et al. 2007, Boundja & Midgley 2010).

39 Previous studies have related the degree of bark damage by elephants to several  
40 factors which include calcium and water content (Anderson & Walker 1974, Croze 1974,  
41 Bash 2002), ease of debarking (O'Connor et al. 2007) and the structure of the main stem  
42 (Anderson & Walker 1974, O'Connor et al. 2007, Boundja & Midgley 2010). However these  
43 are not necessarily mutually exclusive (e.g., thick easy to peel bark is also often high in water  
44 and sugar content, O'Connor et al. 2007, Rosell et al. 2014). Ultimately, the net effect of  
45 elephants on savanna vegetation depends not only on which species they utilise, but also on  
46 how well different species respond to, and recover from, damage from both elephants and  
47 fires, which commonly occur in savannas. Bark removal, even if relatively limited, has been  
48 shown to negatively affect post-fire recovery of savanna trees (Yeaton 1988, Moncrieff et al.  
49 2008, Midgley et al. 2010). In fact, the synergistic effects of fire and elephants appear to be  
50 more important for tree mortality than either disturbance alone, with previous studies  
51 showing that bark damage when combined with fire can result in increased rates of tree  
52 mortality in African savannas (Laws 1970, Moncrieff et al. 2008, Shannon et al. 2011,  
53 Owen-Smith & Chafota 2012, Vanak et al. 2012, Pringle et al. 2015).

54 This study attempts to improve our understanding of bark recovery in savanna trees  
55 by addressing the following main objectives: 1) To determine rates of bark recovery and  
56 examine the interaction between bark recovery and fire in marula (*Sclerocarya birrea*); a  
57 widespread species that is heavily utilized by elephants in Southern African savannas. We  
58 hypothesize that the interaction between fire and bark damage should result in slower bark  
59 recovery rates. 2) To measure rates of inner bark recovery in ten widespread savanna tree  
60 species and determine how recovery is related to bark and stem traits, and the extent to which  
61 these species are damaged by elephants. We hypothesize that trees with thicker inner bark  
62 will have lower bark dry matter content (i.e. higher moisture) and recover faster from damage

63 than species with thin inner bark. We also expect elephants to preferentially select for  
64 species with thicker inner bark and higher moisture content.

65

## 66 **METHODS**

67 **STUDY SITES** — The study took place in the 20 000 km<sup>2</sup> Kruger National Park (KNP) situated  
68 in the north-eastern corner of South Africa, bordering Zimbabwe to the north and  
69 Mozambique to the east. A long-term fire experiment, established in 1954 (called the  
70 experimental burn plots or EBPs), presented the ideal opportunity to study the effects of  
71 different fire regimes on bark recovery of trees. The experiment has 12 different burning  
72 treatments that manipulate burning season (i.e. August, December, October, February, April)  
73 and frequency of burn (i.e. annual, biennial and triennial), including one fire-exclusion  
74 treatment and is replicated in four of the six major vegetation types of KNP (see Biggs et al.  
75 (2003), Higgins et al. (2007) for a more comprehensive background). In each of the four  
76 vegetation types, there are four replicate blocks, called strings, each consisting of the 12  
77 burning treatments applied over plots of ~7 ha. We explored the interaction between fire and  
78 bark recovery in marula (*Sclerocarya birrea* (A. Rich) Hochst. subsp. *caffra*), in the EBPs  
79 established in the Sourveld vegetation type around Pretoriuskop. The soils of the  
80 Pretoriuskop region are derived from the underlying Nelspruit granite suite consisting of  
81 migmatite, gneiss and granite (Barton et al. 1986) and the mean annual rainfall for the area is  
82 approximately 750 mm. Our study was restricted to three of the 12 burning treatments at the  
83 site: annual August burn (moderate fire intensity in dry season), biennial August burn (higher  
84 fire intensity in dry season because of an additional season of fuel accumulation), and fire-  
85 exclusion. We used all four replicate strings, referred to as Shabeni (25.117133° S,  
86 31.237050° E), Fayi (25.193144° S, 31.283546° E), Numbi (25.133364° S, 31.210246° E)  
87 and Kambeni (25.15540° S, 31.264882° E), for our study.

88 The second part of our study, which considered bark recovery of ten common savanna  
89 tree species, took place at five sites in the central and southern parts of Kruger National Park  
90 (Table 1). Soils at the five study sites are derived from granite, gabbro and basalt, and mean  
91 annual rainfall ranges from ~500 to 700 mm (Table1). Rain falls mainly between October  
92 and April and consists predominantly of convective thunderstorms from the north and  
93 northeast or tropical cyclones off the Indian Ocean. Mean monthly temperatures are between  
94 26.3 °C and 17.5 °C. Species nomenclature is based on Coates-Palgrave (2002).

## 96 SAMPLING METHODOLOGY

97 BARK RECOVERY RATES IN MARULA TREES AND INTERACTIONS WITH FIRE — In each of the  
98 three fire treatments (annual August burn, biennial August burn, and fire exclusion) we  
99 selected five fully grown healthy adult marula trees in each of the four replicate strings (i.e. N  
100 = 20 per treatment). We removed a circular section of bark of 50 mm diameter ( $\sim 20 \text{ cm}^2$ )  
101 from each tree in July 2016 using a hammer and sharpened soil corer. The bark of marula  
102 trees is predominantly composed of living inner bark with a thin layer of flaky dead outer  
103 bark (see Fig. 1a). For the purposes of this study, we were interested in the recovery of the  
104 living inner bark as defined by Romero (2006) and Baldauf and Dos Santos (2014), and  
105 therefore removed the thin layer of outer bark (i.e. periderm/cork) using a wood chisel and  
106 then removed the entire layer of inner bark (i.e. secondary phloem), while ensuring not to  
107 damage the underlying wood. The bark cores were removed at a height of 0.5 m above  
108 ground level to ensure that they were within the flame zone of subsequent fires. For each of  
109 the selected trees, we measured stem diameter at the height at which the cores were removed.  
110 Each tree was then tagged and a GPS location recorded. Both of the fire treatments were  
111 burnt in August 2016 and the annual August burn was burnt again in August 2017 and 2018.  
112 All trees were resurveyed in June 2017, September 2017 and again in July 2018. As recovery  
113 only took place from the outer edges of the removed bark sections (i.e. all inner bark was  
114 removed), the diameter of the recovered proportions of inner bark was measured on both the  
115 vertical and horizontal planes and then converted to percentage recovered, and a photograph  
116 taken. During our surveys, we noticed a number of ant nests in the bark wounds, and to  
117 determine if ant presence influenced bark recovery, we made a note of the presence/absence  
118 of ant nests in the wounds to include as a co-variate in our analyses.

119 BARK RECOVERY IN TEN COMMON SAVANNA TREE SPECIES AND RELATIONSHIPS WITH BARK  
120 DAMAGE, BARK TRAITS AND WOOD DENSITY — Bark cores were removed from five healthy  
121 (i.e. undamaged) adult individuals for each of ten dominant species (see Table 1) in October  
122 2015. For this part of the study we were again only interested in the recovery of living inner  
123 bark and therefore removed the outer phellogen (if present) before sampling. All trees were  
124 resurveyed in January 2016, June 2016 and September 2017. The removal of bark and  
125 measures of recovery were performed using the same methodology as described above. After  
126 removal from the tree, bark cores were kept on ice and wet weights and inner bark thickness

127 measured once back at the laboratory. Bark dry matter content (BDMC) is the oven-dry mass  
128 (mg) of a bark core divided by wet weight (g) expressed as  $\text{mg g}^{-1}$ . Inner bark thickness was  
129 measured on two sides of the core using vernier calipers. Relative bark thickness was  
130 calculated as the ratio of total (i.e. inner and outer) bark thickness (measured on the trees  
131 during sampling) to stem radius (Hoffmann et al. 2012). The inner bark cores were oven  
132 dried at 65 °C, weighed and then finely ground for the analysis of bark total nitrogen (N) and  
133 phosphorus (P). Bark N concentrations were determined using a Leco TruSpec CN Analyser  
134 (LECO Corporation, St. Joseph, MI). Bark P was analysed using inductively coupled  
135 plasma-optical emission spectrometry (ICP-OES, Varian Vista MPX, Palo Alto, CA, USA).  
136 Wood density ( $\text{mg mm}^{-3}$ ) was measured on five different individuals of the same species at  
137 each site using the volume displacement method outlined in Cornelissen et al. (2003).

138 MEASURES OF BARK DAMAGE — Data from two different sources were combined and  
139 averaged to provide a measure of elephant bark damage for the ten species. The first dataset  
140 was collected by sampling ten adult individuals for each of the species selected at each of the  
141 five sites (Table 1). For each tree the stem diameter, height, number of stems and the  
142 presence of bark damage on the main stem/stems were noted. The percentage bark damage  
143 for both the circumference and height of the trunk was then visually estimated and recorded.  
144 The second dataset was collected as part of a broader study, which aimed to assess both the  
145 susceptibility to elephant stripping and recovery response of the dominant tree species in  
146 southern KNP. This dataset was collected by walking widespread transects in the southern  
147 KNP between 2014 and 2017. For each individual tree of the ten dominant species we  
148 encountered along these transects; species identity, height (m) and diameter (cm) were  
149 recorded. We then estimated and recorded how much of the total circumference of bark on  
150 the stem had been damaged and to what height. This allowed us to calculate the total  
151 percentage of bark damage for each tree stem.

152 STATISTICAL ANALYSES — All analyses were performed using R version 3.4.2 (R  
153 Development Core Team 2016). To test for differences in rates of bark recovery among  
154 treatments (annual burn, biennial burn and no burn) and for trees with and without ant nests,  
155 we used the function ‘glm’ in the stats package in R. To model bark recovery, we ran  
156 Generalized Linear Models (GLM) using a quasibinomial distribution (bark recovery data  
157 were measured as continuous proportions) with a logit link function. A model which  
158 included both treatment and sampling month (i.e. 10, 14 and 24 months) showed no  
159 significant interaction, we therefore tested if bark recovery differed between treatments at 24

160 months only. We then ran a model which included both treatment and presence of ant nests  
161 which showed no significant interaction, we therefore tested if bark recovery differed  
162 between trees with ant nests vs. trees with no ant nests present. We used the chi-square test to  
163 check if the occurrence of ant nests was equally likely across the three treatments.

164 For our second objective, the phylogenetic tree (81 species; (Wigley et al. 2016)) was  
165 trimmed to include only the ten species sampled for bark traits using the function ‘drop.tip’ in  
166 the *ape* package for R (version 3.5, Paradis et al. 2004). To test for relationships between  
167 bark damage, bark recovery and the measured bark and stem traits, we performed  
168 phylogenetic generalised least squares (PGLS) regression on species means to account for  
169 phylogenetic dependence (Duncan et al. 2007), using the *caper* package (version 0.5.2; Orme  
170 et al. 2013) in R. For the PGLS analyses,  $\lambda$  (the extent to which covariance in traits depends  
171 on phylogenetic branch length) was estimated using the Brownian Motion model of evolution  
172 (Pagel 1999). Ordinary least squares (OLS) models, ignoring phylogenetic relatedness, and  
173 PGLS models were fitted for each comparison. We then tested for the most appropriate  
174 model using the Akaike Information Criterion (AIC). We also explored the influence of  
175 phylogenetic relatedness on recovery and bark and stem traits by plotting trait values onto the  
176 phylogenetic tree for the 10 species in this study and then tested for significant phylogenetic  
177 signal (Blomberg’s K, Blomberg et al. 2003) in the traits using the function  
178 ‘multiPhyloSignal’ as implemented in the R package *picante* (Version 1.7, Kembel et al.  
179 2010).

180

## 181 **RESULTS**

182 **BARK RECOVERY RATES IN MARULA TREES AND INTERACTIONS WITH FIRE** — Bark recovery  
183 was significantly lower in unburned plots than in either the annual and biennial burn  
184 treatments ( $F = 4.73$ ,  $df = 57$ ,  $p = 0.03$ ). Trees in all treatments had recovered at least 72% of  
185 bark within 24 months (98%, 92% and 72%, for annual burn, biennial burn and no burn,  
186 respectively). Although bark recovery continued to increase over time, rates of increase were  
187 mostly low after 10 months (Fig. 2) for all three treatments. Thus, in the studied marula  
188 trees, the majority of bark recovery appears to occur within the first year after damage. The  
189 presence of ant nests in bark wounds resulted in lower net bark recovery across all treatments  
190 ( $F = 32.1$ ,  $df = 58$ ,  $p = <0.0001$ , Fig. 3a). However, bark recovery in trees without ant nests  
191 present did not differ between annual burn, biennial burn and no burn treatments (Fig 3a).  
192 Overall, the proportion of trees with ant nests present was significantly higher in unburned

193 plots compared to annual ( $\chi^2 = 18.5$ ,  $p < 0.001$ ) and biennial burn treatments ( $\chi^2 = 8.3$ ,  $p =$   
194 0.004, Fig 3b).

195 BARK RECOVERY IN TEN COMMON SAVANNA SPECIES AND PHYLOGENETIC RELATIONSHIPS WITH  
196 BARK DAMAGE, BARK TRAITS AND WOOD DENSITY — Bark recovery in the ten common tree  
197 species found in southern KNP was highly variable (Table 2). The two species in the  
198 Anacardiaceae family had the highest bark recovery rates (47 – 100%) compared to the four  
199 species in the Fabaceae (22 – 46%, Fig. 5, Table 2). Bark recovery in the Combretaceae was  
200 the lowest (3 – 13%, Table 2). Bark damage and bark thickness were both highest in the  
201 Anacardiaceae, followed by the Fabaceae and lowest in the Combretaceae (Table 2, Fig. 4).

202 Bark dry matter content showed the strongest phylogenetic signal (Blomberg's  $K =$   
203 0.3,  $p = 0.007$ ), followed by bark [N] ( $p = 0.04$ ), while wood density also showed some  
204 evidence for phylogenetic signal ( $p < 0.10$ , Table 3). Bark damage was positively correlated  
205 with bark recovery, i.e. species that were more utilized recovered faster ( $F = 6.40$ ,  $\lambda = 0.34$ ,  $p$   
206  $= 0.04$ , Table 3). Bark damage was also positively related to bark thickness ( $F = 6.93$ ,  $\lambda = 0$ ,  $p$   
207  $= 0.03$ ) and marginally related to wood density ( $F = 3.91$ ,  $\lambda = 0$ ,  $p = 0.08$ ). Bark recovery  
208 was positively correlated with bark thickness ( $F = 34.4$ ,  $\lambda = 0$ ,  $p < 0.001$ ), negatively related  
209 to BDMC ( $F = 7.83$ ,  $\lambda = 0$ ,  $p = 0.02$ ) and marginally correlated with wood density ( $F = 3.80$ ,  
210  $\lambda = 0$ ,  $p = 0.09$ ), however none of these relationships were influenced by phylogeny (i.e.  $\lambda =$   
211 0). Bark recovery was not significantly correlated with bark [N] or bark [P] ( $p > 0.5$ , Table  
212 3).

213

## 214 DISCUSSION

215 Contrary to our prediction, we found that bark recovery rates were higher in plots that burned  
216 compared to unburnt plots. Slower bark recovery rates were associated with the presence of  
217 ant nests in the wounds, the frequency of which was higher in unburned compared to burned  
218 plots (i.e. recovery did not differ between the three treatments when ant nests were not  
219 present). We also found significant variability across tree species and families in bark  
220 recovery rates following damage. Recovery rates were most strongly related with bark  
221 thickness and moisture content and were highest in the Anacardiaceae and slowest in the  
222 Combretaceae. As expected, species with thicker bark were also preferentially utilised by  
223 elephants and recovered bark relatively rapidly following damage compared to less-preferred  
224 species.

225 Previous studies have shown that debarked savanna trees that are subsequently  
226 exposed to fire have much higher rates of mortality than those that recover without exposure  
227 to fire (Moncrieff et al. 2008, Helm et al. 2011, Owen-Smith & Chafota 2012). Surprisingly,  
228 our results show that fire itself did not impede bark recovery in marula; to the contrary, trees  
229 in burnt treatments recovered bark more rapidly (96% recovery in trees uncolonized by ants  
230 in annual burn over 24 months) than uncolonized trees in unburned treatments (86%, Fig. 2a).  
231 Such high recovery rates are likely related to the high relative bark thickness in marula; an  
232 important plant functional trait that has been shown elsewhere to be positively related with  
233 higher survival rates after disturbance in savanna species (Hoffmann et al. 2003, 2012,  
234 Midgley et al. 2010, Lawes et al. 2011, 2013). Thick bark, with high water content, is  
235 advantageous during fires as a high proportion of the heat may be absorbed by warming and  
236 vaporising water in the bark (Poorter et al. 2014) and species with thick bark can recover  
237 rapidly following fire (Pinard & Huffman 1997, Schoonenberg et al. 2003). However, we  
238 predict that the interactive effects of bark damage and fire would depend on the size of the  
239 area initially damaged; larger wounds would probably be more susceptible to damage from  
240 subsequent fires than the relatively small areas damaged in this study.

241 Our findings suggest that if the damaged area is not colonised by ants, bark recovery  
242 in marula trees can be rapid, even if the trees are subsequently exposed to fires (see Fig. 1b).  
243 However, the colonization of bark wounds by ants – which we found to be negatively related  
244 to fire frequency – significantly impaired bark recovery (e.g. Fig. 1c). Fire seldom has direct  
245 long-term negative effects on ants, although it has been shown to decrease ant colonisation in  
246 the short term (Kimuyu et al. 2014) and drive changes in ant species composition by altering  
247 vegetation structure and associated micro-climate (Andersen 1991, Sensenig et al. 2017).  
248 Parr et al. (2004) working on the same long-term fire experiment found significant  
249 differences in the composition of ant assemblages between burn and no burn treatments, as  
250 has been shown elsewhere (Andersen 1991, Andersen et al. 2006, Frizzo et al. 2012).  
251 Furthermore, Frizzo et al. (2012) suggested that fire can destroy the nests of arboreal species.  
252 Our results suggest that fire exclusion can benefit arboreal nesting ants such as  
253 *Crematogaster castanea*; the main nest-building ant species in the removed bark cores on the  
254 fire experiment plots. This genus is known to build nests in the large galls of some *Acacia*  
255 species, e.g. *A. depanolobium* and *A. seyal* (Young et al. 1996, Palmer et al. 2008), as well as  
256 in rotten wood and under bark (Slingsby 2017). *Crematogaster* spp. are often forest-

257 associated species and have also been shown to increase with fire exclusion in Australian  
258 savannas (Andersen et al. 2006).

259 Several previous studies have reported that insect (and fungal) damage, particularly  
260 by species that burrow into dry wood such as beetles and borers, can slow bark recovery,  
261 especially in tree species with slow recovery rates (Geldenhuys et al. 2006, Delvaux et al.  
262 2009, Vermeulen et al. 2012). On the other hand, the presence of termite tunnels in  
263 *Warburgia salutaris* and several other woodland species has also been shown to benefit  
264 wound recovery by keeping wounds from drying out (Geldenhuys et al. 2006). At present,  
265 we are unaware of any literature that documents how species that live or make nests on the  
266 surface (e.g., ants) influence bark recovery, and the mechanisms by which ants impede bark  
267 recovery remain unclear.

268 Bark recovery was highly variable among the ten common savanna tree species at the  
269 study sites and was not phylogenetically determined (see Table 3). The lack of phylogenetic  
270 signal in bark recovery was surprising as recovery was highest amongst species belonging to  
271 the Anacardiaceae (thick moist bark), lowest in the Combretaceae (thin bark with low  
272 moisture), and intermediate in the Fabaceae (intermediate bark thickness and moisture  
273 content). Bark recovery was most strongly related to bark thickness with no phylogenetic  
274 dependence ( $\lambda = 0$ ); species with thicker inner bark had higher rates of recovery following  
275 damage. Faster rates of recovery in thick barked species compared to species with thin bark  
276 has been reported from other systems such as the Bolivian Amazon (Romero & Bolker 2008,  
277 Baldauf & dos Santos 2014).

278 As predicted, the species with thicker moist bark were preferentially utilized by  
279 elephants. Our results show that bark damage was not related to bark N or P which is in  
280 contrast to patterns previously reported (Anderson & Walker 1974, Croze 1974, Thomson  
281 1975, Field & Ross 1976, O'Connor et al. 2007). Although we don't rule out that elephants  
282 may prefer thick barked species because of compounds not measured in our study (e.g.,  
283 sugars and other compounds), they appear to preferentially select for trees with high bark  
284 moisture content. Species with thick, moist bark also recovered more rapidly from bark  
285 damage, which would prevent further damage from fire and boring insects. Similarly,  
286 Romero & Bolker (2008) found that species with thick bark (and exudates and trunk thorns)  
287 had the fastest recovery rates in Amazonian forest trees. Delvaux et al. (2013) also showed  
288 that the thickness of the conducting phloem was an important factor explaining bark recovery

289 rates. On the other hand, species with thin inner bark, high bark dry matter content, high  
290 wood densities (which may combine with low growth rates such as in Combretaceae) had  
291 slow or limited bark recovery (see Fig. 1d) and these species were not preferred by elephants  
292 and tended to suffer little bark damage. However, if these species are damaged it is likely  
293 that compartmentalisation of wound damage occurs quickly and stem decay is limited  
294 (Romero & Bolker 2008, Ngubeni et al. 2017).

295 To conclude, the removal of fire resulted in changes in ant communities (either  
296 directly or indirectly), such that arboreal ant species nested more frequently in damaged bark,  
297 resulting in lower bark recovery. These findings remind us of the importance of the often-  
298 overlooked indirect effects of fires in savanna ecosystems. We highlight the need for further  
299 studies that examine the interactions between invertebrates, fire, elephants and tree mortality.  
300 Our second major finding was that certain bark and stem traits were influenced by the  
301 phylogenetic relatedness of the ten species in this study, which in turn determined the degree  
302 of utilisation or damage by elephants. Tree species with moist (and thicker) inner bark were  
303 favoured by elephants but at the same time, better able to recover after damage. Our results  
304 also suggest that bark recovery is largely limited to the first year since damage for many of  
305 the studied species. Phylogenetic constraints on bark traits may thus act as a filter on tree  
306 species assembly in fire-prone and herbivore-rich habitats.

307

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313

#### 314 **DATA AVAILABILITY**

315 The data used in this study will be archived at the Dryad Digital Repository

316

#### 317 **LITERATURE CITED**

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## TABLES

Table 1. Dominant tree species, underlying geology, mean annual rainfall (MAP), latitude and longitude for the five sites in the southern Kruger National Park, South Africa.

Site name	Species	Geology	MAP (mm)	CO-ORD E	CO-ORD S
Nhlangwini	<i>Sclerocarya birrea</i>	Granite	678	31.293	-25.199
	<i>Terminalia sericea</i>				
Ship Mountain	<i>Acacia nigrescens</i>	Gabbro	676	31.373	-25.213
	<i>Combretum apiculatum</i>				
Makhohlolo	<i>Acacia gerrardii</i>	Basalt	550	31.914	-25.262
	<i>Albizia harveyi</i>				
Satara Basalt	<i>Acacia tortilis</i>	Basalt	525	31.815	-24.277
	<i>Combretum imberbe</i>				
Satara Granite	<i>Combretum zeyheri</i>	Granite	576	31.643	-24.526
	<i>Lanea schweinfurthii</i>				

Table 2. Mean  $\pm$  se for bark damage (% circumference damaged), bark recovery (% core recovered), bark thickness (BT, mm), relative bark thickness (RBT, %), wood density (WD, mg mm<sup>-3</sup>), bark dry matter content (BDMC, mg g<sup>-1</sup>), bark nitrogen (N, %) and bark phosphorus (P, %) for the species in each of the three families. No se is shown for N and P as they were measured using pooled bark samples from five individuals.

Species	Family	Damage	Recovery	BT	RBT	WD	BDMC	N	P
<i>Lanea schweinfurthii</i>	Anacardiaceae	17.5 $\pm$ 3.8	47.0 $\pm$ 9.70	9.80 $\pm$ 1.50	8.70 $\pm$ 1.50	0.54 $\pm$ 0.02	514 $\pm$ 18.1	0.06	0.024
<i>Sclerocarya birrea</i>	Anacardiaceae	37.5 $\pm$ 5.6	100 $\pm$ 0.00	21.8 $\pm$ 0.70	4.70 $\pm$ 0.70	0.63 $\pm$ 0.04	537 $\pm$ 12.5	0.08	0.017
<i>Combretum apiculatum</i>	Combretaceae	14.2 $\pm$ 3.1	12.7 $\pm$ 6.90	4.00 $\pm$ 0.50	2.10 $\pm$ 0.50	0.79 $\pm$ 0.02	895 $\pm$ 15.3	0.27	0.014
<i>Combretum imberbe</i>	Combretaceae	0.0 $\pm$ 0.0	11.5 $\pm$ 8.80	3.90 $\pm$ 0.30	2.90 $\pm$ 0.50	0.90 $\pm$ 0.01	665 $\pm$ 20.9	0.13	0.019
<i>Combretum zeyheri</i>	Combretaceae	7.50 $\pm$ 3.8	3.30 $\pm$ 5.70	5.20 $\pm$ 0.30	5.60 $\pm$ 0.30	0.66 $\pm$ 0.03	775 $\pm$ 18.0	0.27	0.028
<i>Terminalia sericea</i>	Combretaceae	16.3 $\pm$ 4.2	12.5 $\pm$ 8.30	8.90 $\pm$ 0.70	3.00 $\pm$ 0.70	0.70 $\pm$ 0.05	758 $\pm$ 29.3	0.11	0.001
<i>Acacia gerrardii</i>	Fabacea	15.0 $\pm$ 7.6	45.6 $\pm$ 20.3	7.40 $\pm$ 0.50	11.5 $\pm$ 0.50	0.75 $\pm$ 0.03	719 $\pm$ 46.1	1.04	0.011
<i>Acacia nigrescens</i>	Fabacea	25.9 $\pm$ 4.6	29.4 $\pm$ 6.50	10.9 $\pm$ 0.40	3.70 $\pm$ 0.40	0.79 $\pm$ 0.02	659 $\pm$ 18.8	1.14	0.024
<i>Acacia tortilis</i>	Fabacea	20.0 $\pm$ 6.2	27.7 $\pm$ 13.6	6.20 $\pm$ 0.90	6.50 $\pm$ 0.90	0.81 $\pm$ 0.02	679 $\pm$ 17.4	0.70	0.037
<i>Albizia harveyi</i>	Fabacea	3.80 $\pm$ 2.0	21.6 $\pm$ 6.50	5.50 $\pm$ 0.40	6.60 $\pm$ 0.40	0.72 $\pm$ 0.02	700 $\pm$ 15.9	0.50	0.009

Table 3 Tests for phylogenetic signal in the measured bark traits (Blomberg's K) and results from the phylogenetic generalised least squares (PGLS) models showing  $R^2$ ,  $\lambda$ , F and p values for correlations between bark damage, bark recovery, inner bark thickness, bark dry matter content (BDMC), wood density, bark nitrogen and bark phosphorus concentrations.

Trait	Blombergs K	bark damage				bark recovery			
		$R^2$	$\lambda$	F	p	$R^2$	$\lambda$	F	p
bark recovery	0.14 (p = 0.14)	0.37	0.34	6.34	0.04				
bark thickness	0.11 (p = 0.28)	0.40	0	6.93	0.03	0.79	0	34.4	<0.001
BDMC	0.30 (p = 0.007)	0.15	0.95	2.53	0.15	-0.43	0	7.83	0.02
wood density	0.14 (p = 0.09)	0.24	0	3.91	0.08	0.24	0	3.8	0.09
bark [N]	0.22 (p = 0.04)	-0.06	0	0.47	0.51	-0.1	0.68	0.04	0.85
bark [P]	0.03 (p = 0.93)	-0.11	0.25	0.10	0.76	-0.1	0.73	0.45	0.52

434 **FIGURE LEGENDS**

435 Figure 1. a) A fresh wound caused by removing a bark core from a marula (*Sclerocarya*  
436 *birrea*) tree. b) A fully recovered bark wound 24 months after removing a bark core from a  
437 marula tree in the annual burn treatment of the long-term fire experiment. c) An ant  
438 (*Crematogaster castanea*) nest in the wound area from which a bark core was removed from  
439 a marula tree growing in the no burn treatment of the long-term fire experiment. The ant nest  
440 resulted in zero bark recovery in this marula tree. d) A photo of the wound where a bark core  
441 was removed from a *Combretum apiculatum* tree after 21 months, note the lack of recovery  
442 and thin bark found in this species.

443 Figure 2. Mean  $\pm$  se bark recovery, measured as the percentage of the original removed core  
444 that recovered after ten, fourteen and twenty-four months in the annual, biennial and no burn  
445 fire treatments in the Pretoriuskop strings of the Kruger National Park long-term fire  
446 experiment. N = 20 for each treatment.

447 Figure 3. a) Mean  $\pm$  se bark recovery after twenty-four months in trees with and without ant  
448 nests present in damaged areas from which bark cores were removed in annual, biennial, no  
449 burn and across all treatments. b) Percentages of trees with ant nests present in the no burn,  
450 annual and biennial fire treatments. Total n for each treatment = 20, for number of trees with  
451 ants present n = 3 for annual burn, n = 5 for biennial burn and n = 10 for no burn.

452 Figure 4. Phylogenetic relationships among the ten species included in this study and  
453 associated relative trait values, squares of similar size and colour indicate similar trait values.

454

**FIGURES**

Figure 1

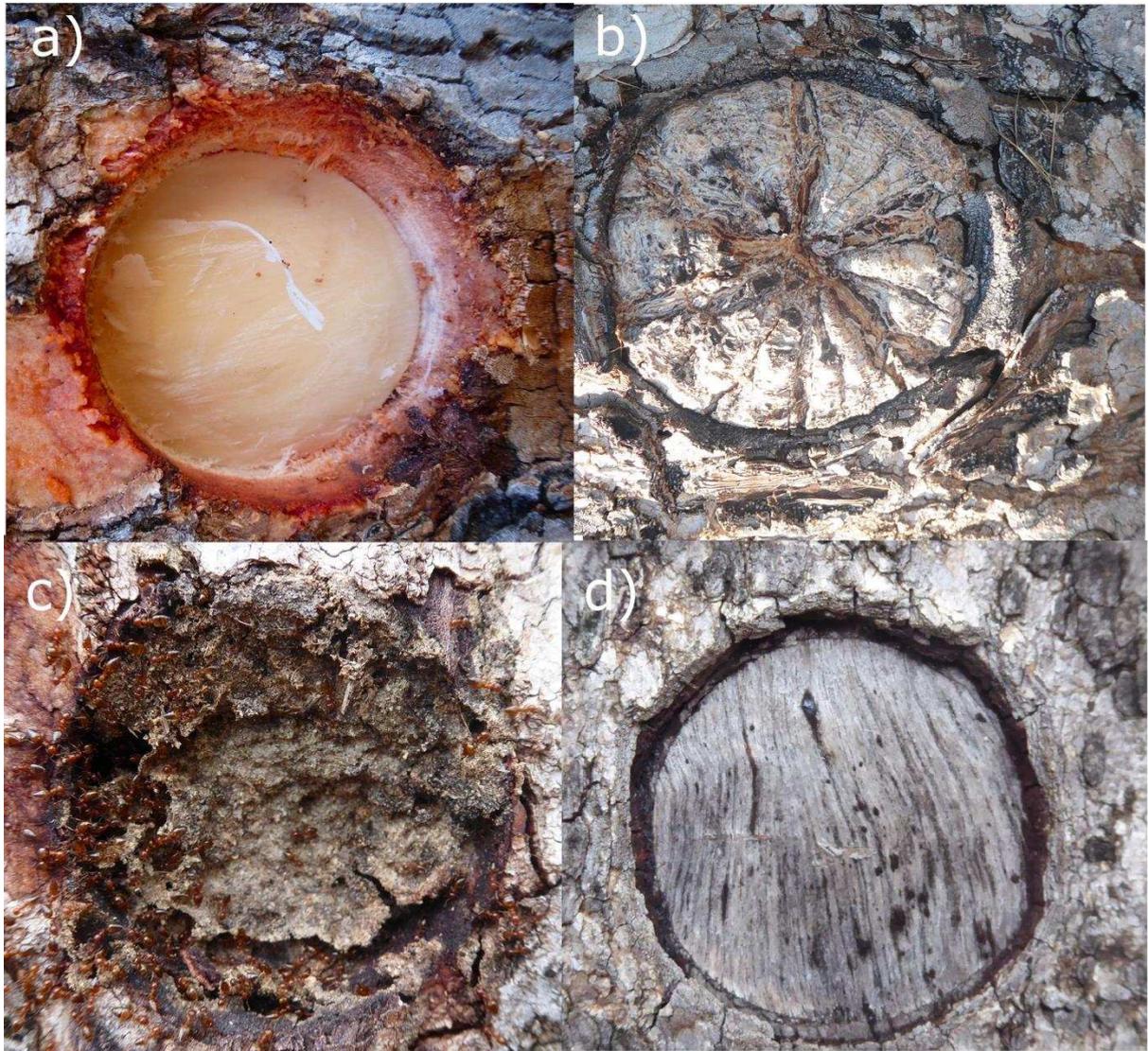


Figure 2

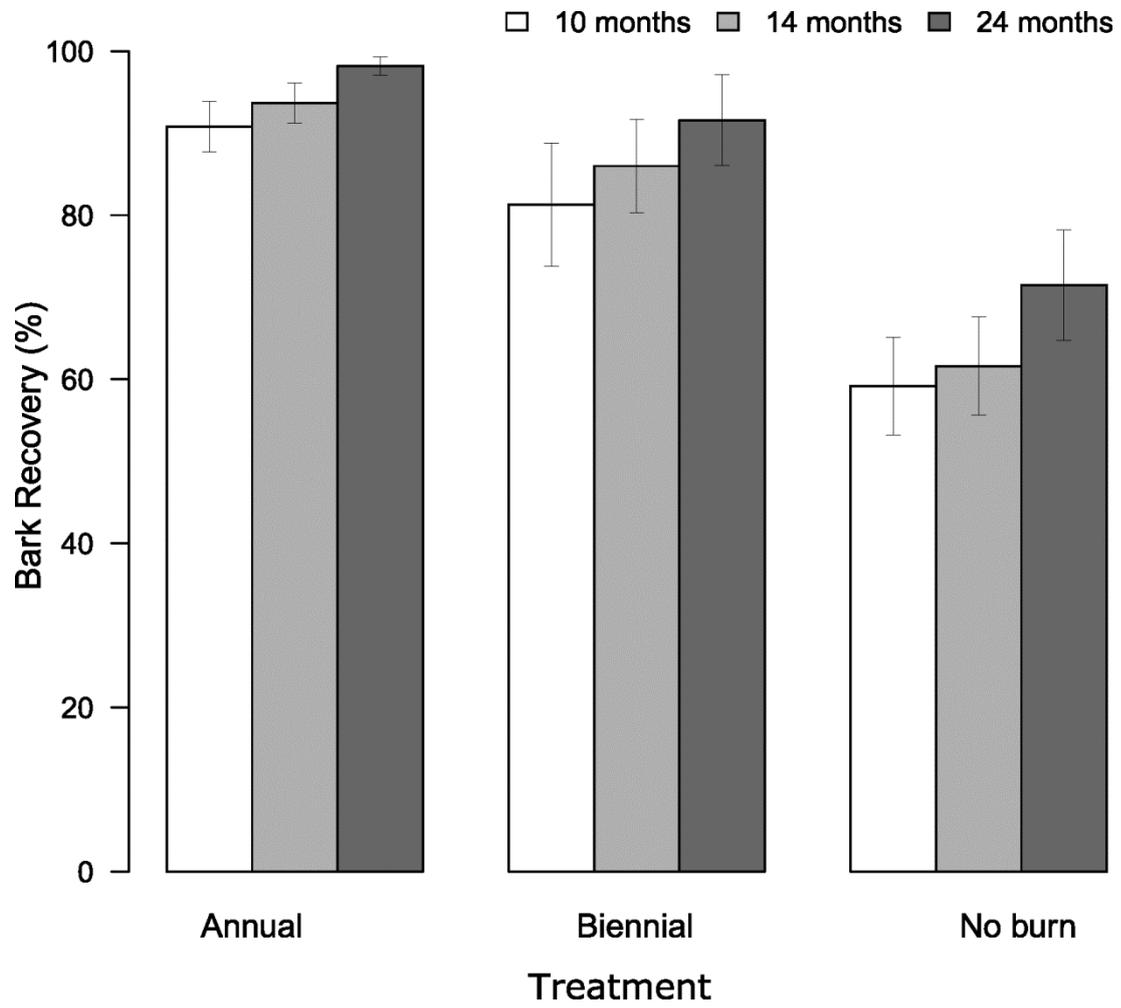


Figure 3

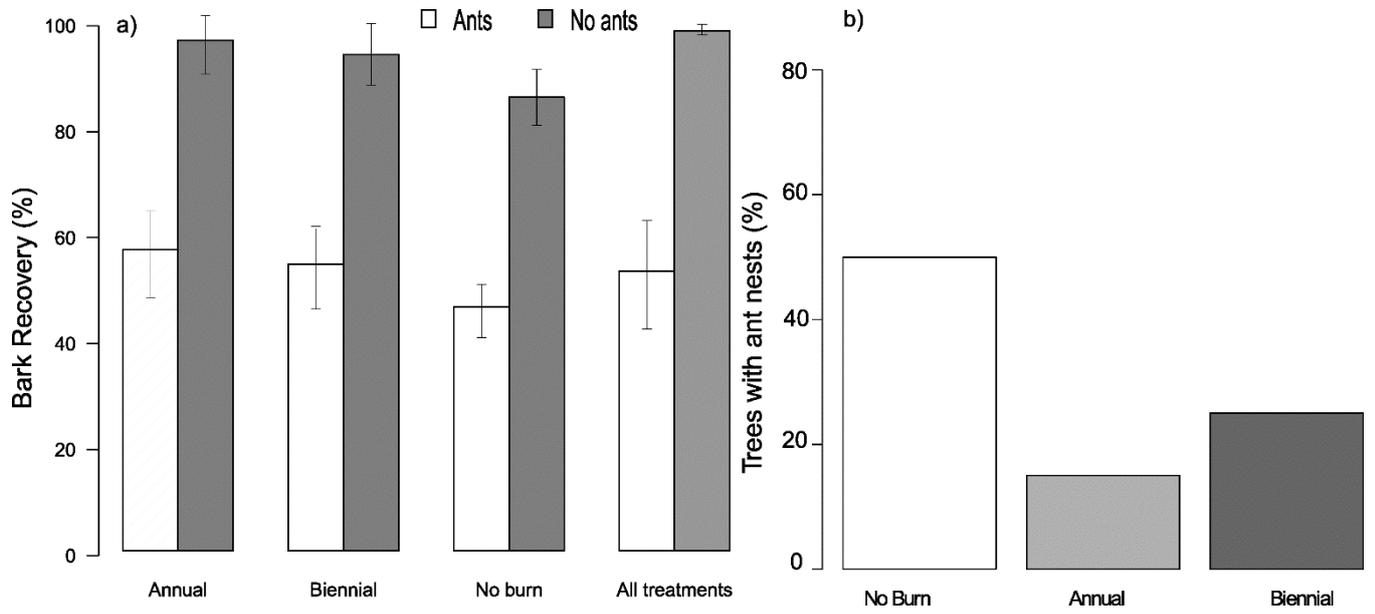


Figure 4

