The effect of an increasing elephant population on the allometry of trees

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Increasing elephant densities in fenced reserves reshape landscapes and modify vegetation. By comparing with an elephant-free zone, we uncover how these giants leave their mark in the trees structure.

Abstract

African savannas, which support a diverse range of plant species, from evergreen trees to deciduous shrubs, are regulated by complex interactions between climatic, fire, soil and herbivory processes. African elephants (*Loxodonta africana*) exert substantial top-down control over vegetation dynamics by utilising large amounts of plant biomass, as well as through various forms of non-consumptive effects. However, how much elephants affect the pattern of proportional growth between different tree components such as roots, stems or branches (known as allometry), remains understudied. Using vegetation data collected in 2000-2001 and 2019 for more than 3500 individual trees inside and outside Madikwe Game Reserve, South Africa, we determined the long-term effects of an increasing elephant population on allometric relationships in 13 tree species. The presence of elephants reduced logged canopy volume, and increasing elephant population in Madikwe reduced logged tree height and logged initial growth rate of the allometric relationship between tree height and tree diameter, without modifying asymptotic change in growth rate. Although not significantly, elephants seemed to increase asymptotic change in growth rate of canopy volume according to tree diameter, suggesting that compensatory mechanisms for the loss of height might happen in the longer-term. Although the species-specific elephant use index increased over the 20 years of the study, no consistent effect on allometric coefficients was detectable. Our study emphasises the necessity of long-term, species-specific studies to improve our understanding of how elephants affect allometric relationships in trees, which will ultimately guide management of savanna systems with increasing elephant numbers.

Keywords: large herbivore ecology, *Loxodonta africana*, canopy volume, tree height, tree diameter, long-term monitoring, savanna ecosystem.

Introduction

African savannas, which cover approximately half of sub-Saharan Africa (Du Toit and Cumming, 1999), are characterised by a "continuous grass understory interspersed by a discontinuous woody overstory" (Scholes and Archer, 1997). The productivity of these savannas is shaped by a complex interplay of micro- and macro-herbivory, soil dynamics, as well as fire, rainfall and frost regimes (Van Langevelde *et al*., 2003; Sankaran *et al*., 2005; Hoffmann *et al*., 2019), which contribute to the diversity of plant species and the structure of the vegetation (Sankaran *et al*., 2005). Although fire is commonly considered the dominant factor shaping savanna vegetation by reducing canopy and maintaining a continuous grass understory competing with trees (Sankaran *et al*., 2008), the herbivore community also strongly influences both vegetation structure and plant community composition through the consumption of biomass (Danell *et al*., 2006; O'Connor *et al*., 2007; Lagendijk *et al*., 2015). This effect parallels the impacts of fire at a local scale and contributes to the stabilisation of the "tree-grass" coexistence in this ecosystem (Bond *et al*., 2005). Herbivory can lead to a decrease of up to 30.6 % in tree abundance and 57 % in grass abundance (Staver *et al*., 2021). In African savannas, the woody vegetation and biomass are influenced by mega-herbivores, particularly African elephants (Cumming *et al*., 1997; Kerley and Landman, 2006; Guldemond and Van Aarde, 2008; Valeix *et al*., 2011; Morrison *et al*., 2016). As ecosystem engineers (Jones *et al*., 1994), elephants directly affect tree height (O'Connor *et al*., 2024), canopy volumes (Guldemond and Van Aarde, 2010; O'Connor *et al*., 2024; Sorokina *et al*., 2024) and understorey composition (Ferry *et al*., 2021). Elephants affect species diversity by reducing the density of more palatable tree species, such as *Senegalia mellifera* and *Sclerocarya birrea caffra* (Skarpe *et al*., 2004; Guldemond and Van Aarde, 2008; Sankaran *et al*., 2013; Wigley *et al*., 2014; Bakker *et al*., 2016; Cook *et al*., 2017; Guldemond *et al*., 2017; Sorokina *et al*., 2024). Indeed, by utilising certain species, elephants can cause rapid

declines and even local extirpation in species that are unable to cope with their feeding behaviour (*e.g.*, *Adansonia digitata*, *Aloe marlothii*, *Commiphora ugogensis*, *Sclerocarya birrea*, and *Vachellia* species; Barnes, 1983; Kerley and Landman, 2006; O'Connor *et al.*, 2007; Guldemond and Van Aarde, 2008; Helm *et al.*, 2011).

Elephants can also significantly influence the allometry (*i.e.*, the proportional relationships between different components of an individual through growth; Huxley and Teissier, 1936) of the woody plant species (Makhabu *et al.*, 2006; Shannon *et al.*, 2008; Moncrieff, *et al.*, 2011; Lagendijk *et al.*, 2015). Some species utilised by elephants change growth form, allowing them to persist (*e.g.*, *Colophospermum mopane*; Lewis, 1991; Kerley and Landman, 2006). They may experience reductions in height and total basal area (*e.g.*, *Senegalia nigrescens*; Moncrieff *et al.*, 2011), or to the contrary thicker diameters and wider canopies (*e.g.*, *Vachellia drepanolobium* and *Vachellia karroo*; Archibald and Bond 2003; Moncrieff *et al.*, 2011).

However, while earlier studies suggested that elephant activity could transform woodlands and forests into grasslands or open savannas across Africa, a concern known as "the elephant problem" (Laws, 1970; Caughley, 1976; Owen-Smith, 1988; Trollope *et al.*, 1998), more recent research indicates that elephant effect on savanna vegetation is highly variable (Guldemond and Van Aarde, 2008). A meta-analysis highlighted that these effects depend significantly on environmental conditions, such as rainfall and geographical constraints, leading to outcomes that range from negative to neutral, and even positive effects (Guldemond and Van Aarde, 2008). While numerous studies have suggested that elephants may have a negative impact on their habitats especially under sustained high population densities, the expected changes might be less striking in open systems (Skarpe *et al.*, 2004; Ferry *et al.*, 2021), or when measured over longer periods (Guldemond and Van Aarde, 2008).

In this study, we determined the effect of elephants on allometric relationships in 13 tree species. We used data from woody vegetation monitoring conducted in 2000-2001 and repeated in 2019 in Madikwe Game Reserve (hereafter MGR), which is exposed to an increasing elephant population, and in the adjacent Barokologadi Communal Property (hereafter BCP) in 2019, which does not contain elephants. We examined how elephants affected the allometric relationship between tree diameter and tree height, and the allometric relationship between tree diameter and canopy volume. We expected that repeated utilisation by elephants would lead to mature individual trees with large diameter stems being shorter and showing a reduced canopy volume, translating into the reduction of the allometric coefficients in the elephant zone (MGR) compared to the elephant-free zone (BCP, Stoinski *et al.*, 2000; Holdo, 2007). Conversely, through growth stimulation, we could alternatively expect that elephants may have a positive effect on allometric relationships, as mature trees subject to long-term elephant exposure could exhibit greater height and larger canopy volumes if they grow taller to escape browsing (Canham et al., 1994). Eventually, we expected the possibility for compensatory growth which would translate into the reduction of the tree height parameters and the increase of the canopy volume parameters in their respective allometric relationships with tree diameter (Makhabu *et al.*, 2006).

Material and methods

Study site and species

MGR (24°49′S - 26°13′E, South Africa), is a fenced reserve currently covering approximately 750 km² (Supporting information 1). MGR is situated within the central bushveld bioregion, as part of the broader savanna biome, and experiences a dry season from mid-April to mid-November (Rutherford *et al.*, 2011). The average annual rainfall is approximately 475-520 mm (Trinkel *et al.*, 2010).

In 2001, the elephant population was estimated at 389 individuals (*i.e.*, 0.60 elephants/km^2; North West Parks and Tourism Board, 2024). By 2019, the elephant population almost increased threefold, with an estimated 1318 individuals (*i.e.*, 1.76 elephants/km^2; North West Parks and Tourism Board, 2024). Elephants constituted approximately 70 % of the herbivore biomass in MGR at the time of the study (North West Parks and Tourism Board, 2024). Other browsing herbivores in MGR include giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), springbuck (*Antidorcas marsupialis*) and impala (*Aepyceros melampus*). The density of the latter increased substantially between 2011 and 2019 from 3.84 individuals/km^2 to 6.30 individuals/km^2 (Supporting information 2).

BCP, covering 160 km^2 (Supporting information 1), is separated from MGR by an elephant-proof fence, rendering it an elephant-free zone. BCP has been used for cattle, goat, and sheep farming for meat production since 2009, with occasional firewood collection (Barokologadi Communal Property Association, unpublished report). Bushbuck (*Tragelaphus scriptus*), greater kudu and impala roam freely in BCP in unknown numbers. Although unfortunately there is no written report available, BCP experienced more frequent fires than MGR over the study period, where fire frequency is controlled and maintained at a very low level (park management services, personal communication).

Sampling design

Tree morphological measurements were collected at 35 sites in MGR during three two-weeks periods in January 2000, July 2000 and January 2001, following a stratified random sampling protocol (*i.e.*, stratified across vegetation types and randomised within vegetation types, Page and Slotow, 2001). The minimal distance between sites was approximately 100 m. In each site, a 50-metre transect of variable width (from 2 m to 50 m depending on the woody vegetation density of the site) was used to record all living woody plants. A nested sampling

approach was used to identify species not found within the core transect by extending sampling to surrounding areas with a maximum transect size of 100 x 50 m. The 35 original sites from 2000-2001 were re-sampled between February and June 2019 (except for 2 sites sampled in October), as well as 27 new sites in BCP, following the same methodology. In BCP, 23 sites were sampled during a two-week period in October, and four sites were sampled between April and June. The minimum distance between sites in BCP was approximately 240 m.

We defined three spatio-temporal treatments: i) "Old", using MGR data from 2000-2001 and exposed to a relatively low elephant density (n = 2331 trees, 0.60 elephants/km^2), ii) "New", using MGR data from 2019 and exposed to a higher elephant density (n = 1583 trees, 1.76 elephants/km^2) and iii) "Out", using BCP data from 2019 and excluded from elephants (n = 1026 trees, 0 elephants/km^2). Although not completely untouched (*e.g.*, occasional livestock browsing and firewood collection), the "Out" treatment provides a good comparison point for the allometric relationships of trees in the absence of any elephant pressure.

For each living tree, we recorded the number of live stems and measured stem diameters. For the analyses, we only used the stems within the six largest stem diameters for a given individual (*i.e.*, all the stems of a similar diameter up to six classes, hereafter called "stem classes", range = 0.1 to 75 cm). We measured the total tree height (**Height**, in metres) as the vertical distance from the ground to the tree's highest point, and the height of the bottom of the canopy (*HBC*, in metres) as the vertical distance from the ground to the height where the main canopy starts. For trees larger than 2 m in height, measurements were estimated. We calculated the total tree diameter (**Diameter**, in centimetres) as the diameter of a disk of an area equal to the sum of all the stem diameters, each stem being modelled as a perfect cylinder, as explained in equation (1):

$$\boldsymbol{Diameter} = \sqrt{\sum_{i=1}^{n} \boldsymbol{nb\ stem_i} \times \boldsymbol{d_i}} \qquad \textit{equation (1)},$$

where d_i is the diameter of the stem class i and $nb\ stem_i$ is the number of stems belonging to the stem class i. We calculated the canopy volume (**Canopy Volume**, in cubic metres) using the formula of the volume of an ellipsoid (equation (2)):

$$\boldsymbol{Canopy\ Volume} = \frac{4}{3} \times \boldsymbol{\Pi} \times \left(\frac{\boldsymbol{Diameter\ max}}{2}\right)^2 \times \left(\frac{\boldsymbol{Canopy\ height}}{2}\right) \qquad \textit{equation (2)},$$

where *Diameter max* (in metres) corresponds to the widest horizontal diameter of the ellipsoid formed by the canopy, and *Canopy height* corresponds to the difference between **Height** and *HBC* and represents the vertical diameter of the ellipsoid formed by the canopy. For each individual tree, we estimated elephant utilisation as the percentage of biomass (*i.e.*, branches, leaves, stems, bark and/or roots) removed using eight categories: 0 (0 %), 1 (1 to 10 %), 2 (11 to 25 %), 3 (26 to 50 %), 4 (51 to 75 %), 5 (76 to 90 %), 6 (91 to 99 %), and 7 (100 %). We then calculated the species-specific mean elephant utilisation per treatment (hereafter called **Elephant Use**).

Statistical analyses

We identified the species that were present in all three treatments with sufficient sample size recorded (*i.e.*, ≥ 15 trees in each treatment) and included only these in our analyses to ensure between-treatments comparability and statistical robustness (n = 13 species; n_{Old} = 1693 trees, n_{New} = 1392 trees, n_{Out} = 713 trees; Supporting information 3). In other words, this study focussed on the allometric responses of common tree species in this landscape. We first investigated the changes of tree **Height** and **Canopy Volume** between treatments. We conducted a one-way ANOVA on the log-transformed (natural log to meet assumptions of normality and heteroscedasticity) tree **Height** and **Canopy Volume** of all species pooled together. We subsequently conducted a post-hoc pairwise comparison test using Tukey's test to identify significant differences between treatments. We conducted the same analysis for each species individually (see details in Supporting information 4).

211 We then determined the species-specific coefficients of the allometric relationships between
212 tree **Height** and tree **Diameter**, and between **Canopy Volume** and tree **Diameter**. One
213 commonly expected relationship in tree allometry (Kearsley *et al.*, 2013) can be written as
214 (equation (3)):

215 $$\boldsymbol{Y} = \boldsymbol{A} \times \boldsymbol{X^B} + \boldsymbol{C} \qquad \textit{equation (3)},$$

216 where *X* and *Y* are two tree measurements (*X* is tree diameter and *Y* is either tree height or
217 canopy volume), *A* corresponds to the Initial Growth Rate, *B* corresponds to the **Asymptotic**
218 **Change in Growth Rate**, and *C* is a constant close to 0 (C is 0 in nature but to fit the model
219 we allow for some parameter adjustment in the fit; if C is significantly different from 0 it
220 suggests poor fit of the model). Mathematically, the **Initial Growth Rate** illustrates the
221 intrinsic growth linking the two parameters *X* and *Y*, namely the growth potential that can be
222 reached. The **Asymptotic Change in Growth Rate** corresponds to the speed of the increase
223 in growth, namely how fast the curve increases: if $B < 1$ the growth rate in height, or canopy
224 volume, decreases as the tree diameter increases; if $B > 1$ the growth rate increases with
225 increasing tree diameter. However, in our study, visual inspection revealed non-normality and
226 heteroscedasticity associated with an important variance in the tree **Height** and **Canopy**
227 **Volume** and creating a poor fit of the data with equation (3). Therefore, we used the log-
228 transformed formula, and we fitted a linear regression instead (equation (4)):

229 $$\boldsymbol{log(Y)} = \boldsymbol{I} + \boldsymbol{B} \times \boldsymbol{log(X)} \quad \textit{equation (4)},$$

230 where *X* and *Y* are the same two tree measurements, *B* remains the **Asymptotic Change in**
231 **Growth Rate** (equation (3)) and *I* corresponds to the Logged Initial Growth Rate coupled
232 with the constant term (*A* and *C*, respectively in equation (3)), hereafter named **Logged**
233 **Initial Growth Rate** for simplicity. We fitted such a relationship for each species in each
234 treatment separately, and extracted the coefficients *B* and *I* of the allometric relationship
235 linking the dependent (*Y*, *i.e.*, tree **Height** and **Canopy Volume**, respectively) and the

explanatory (*X*, *i.e.*, tree **Diameter**) variables. Eventually, we tested the correlation between tree **Height** and **Canopy Volume** using the Spearman's test of correlation, as these two variables are known to be correlated (*e.g.*, Arzai and Aliyu, 2010).

We then determined how the treatment and the **Elephant Use** affected the coefficients *B* and *I* of the allometric relationships (between **Height** and **Diameter**, and between **Canopy Volume** and **Diameter**, respectively). We first conducted a one-way ANOVA to explore the effect of treatment on these coefficients, followed by a post-hoc pairwise comparison test using Tukey's test to identify significant differences between pairs of treatments. We then used linear regressions with an interaction between treatment and **Elephant Use** to determine the effect of **Elephant Use** on the coefficients *B* and *I* in the "Old" versus "New" treatment. All statistical analyses were conducted using R (version 4.4.0, R Core Development Team 2024).

Results

We identified 13 species present in all three treatments, which were represented by more than 15 individuals in each treatment: *Combretum hereroense*, *Dichrostachys cinerea*, *Euclea undulata*, *Flueggea virosa*, *Grewia flava*, *Grewia monticola*, *Gymnosporia buxifolia*, *Senegalia erubescens*, *Senegalia mellifera*, *Vachellia karroo*, *Vachellia tortilis*, *Ximenia americana* and *Ziziphus mucronata* (Supporting information 3). The most abundant species within all three treatments was *Dichrostachys cinerea* (n_{old} = 327, n_{new} = 482, n_{out} = 194), and the least abundant species was *Senegalia mellifera* in the "Old" and "New" treatment (n_{old} = 23, n_{new} = 15, n_{out} = 67), as well as *Vachellia karroo* in the "Out" treatment (n_{old} = 108, n_{new} = 54, n_{out} = 16). Ten species experienced a marked decrease in occurrence (between -10 and -50 %) between the "Old" and "New" treatments, while *Combretum hereroense*, *Grewia monticola* and *Dichrostachys cinerea* increased, the latter by almost 50 %. The number of

261 individuals of *Euclea undulata*, *Gymnosporia buxifolia*, *Vachellia karroo*, *Senegalia*
262 *erubescens*, *Ximenia caffra* and *Ziziphus mucronata* decreased by almost 50 % between the
263 "Old" and "New" treatments (Supporting information 3).
264 Overall, the logged tree **Height** was significantly lower in the "New" than in the "Old" ($P <$
265 0.01) and the "Out" ($P < 0.01$) treatments, and significantly higher in the "Out" than in the
266 "Old" treatment ($P < 0.01$, Fig. 1a). The logged **Canopy Volume** was similar in the "New"
267 and "Old" treatments ($P = 0.39$), but it was significantly larger in the "Out" than in both other
268 elephant treatments (both $P < 0.01$, Fig. 1b). Although these results were mostly consistent
269 among five species (*Dichrostachys cinerea*, *Grewia monticola*, *Vachellia karroo*, *Ximenia*
270 *americana* and *Ziziphus mucronata*), there were species-specific patterns (Supporting
271 information 4). Notably, *Flueggea virosa* increased in logged tree **Height** and logged
272 **Canopy Volume** between the "Old" and "New" treatments, and the differences in logged tree
273 **Height** and logged **Canopy Volume** were less pronounced between the two elephant
274 treatments ("Old" and "New") and the elephant free treatment ("Out") for *Gymnosporia*
275 *buxifolia*. No significant differences were detected for *Senegalia mellifera*.
276 We found a significant positive relationship between logged tree **Diameter** and logged tree
277 **Height** for all 13 species in each treatment, except for *Senegalia mellifera* in the "New"
278 treatment (Supporting information 5). Similarly, we found a significant positive relationship
279 between logged tree **Diameter** and logged **Canopy Volume** for all 13 species in each
280 treatment (Supporting information 6). Additionally, we found a significant and very high
281 correlation between logged tree **Height** and logged **Canopy Volume** in all species in all three
282 treatments (all $\rho > 0.6$, all $P \leq 0.01$, Table 1).
283 The **Logged Initial Growth Rate** (I) was significantly lower in the "New" than in the "Old"
284 ($P = 0.01$) and the "Out" ($P = 0.04$) treatments for the tree **Height** - tree **Diameter**
285 relationship (Fig. 2b). Although not significant, we found a similar trend for the **Logged**

Initial Growth Rate (*I*) of the **Canopy Volume** - tree **Diameter** relationship ($P = 0.06$, Fig. 2d). The **Asymptotic Change in Growth Rate** (*B*) was not significantly different in any treatment for the tree **Height** - tree **Diameter** relationship ($P = 0.10$, Fig. 2a). However, it was significantly larger in the "Out" than in the "Old" treatment for the **Canopy Volume** - tree **Diameter** relationship ($P = 0.01$, Fig. 2c).

On average, **Elephant Use** varied between 0.0 (for *Ximenia americana* in the "Old" treatment) and 2.1 (for *Senegalia erubescens* in the "New" treatment). The least used species were *Ximenia americana* and *Euclea undulata* (**Elephant Use** ranging between 0.0 and 0.2 in the "Old" and "New" treatments). Overall, there was an increase in **Elephant Use** between the "Old" and "New" treatments, except for *Euclea undulata* for which the index remained stable, and *Gymnosporia buxifolia* which was the only species to experience a decrease (from 0.8 to 0.6 in the "Old" and "New" treatments respectively, Fig. 3). *Senegalia erubescens*, *Grewia monticola* and *Grewia flava* experienced the largest increase in **Elephant Use** ($\geq$ 1.3 increase between the "Old" and "New" treatments). **Elephant Use** did not affect variation of the **Logged Initial Growth Rate** (*I*), or variation of the **Asymptotic Change in Growth Rate** (*B*) for either allometric relationship (Table 2, Fig. 3).

Discussion

In this study, we highlighted the effect of an increasing elephant population on the structure of the woody vegetation at the community scale. Elephants reduced the **Height** and **Canopy Volume** of trees, and reduced the **Logged Initial Growth Rate** of the allometric relationship between tree **Height** and tree **Diameter**, without modifying the **Asymptotic Change in Growth Rate**. Our results suggest that a compensatory mechanism for the loss of tree **Height** could start to take place after 20 years of continuously increasing exposure to elephants, with a detectable but not significant increase in the **Asymptotic Change in Growth Rate** of the

311 **Canopy Volume**. Although the species-specific **Elephant Use** index increased over the
312 period of the study, no general trend of its effect on allometric coefficients was detectable,
313 suggesting species-specific patterns.
314 Trees were shorter and had a smaller **Canopy Volume** (Fig. 1) in MGR ("Old" and "New"
315 treatments) than in BCP ("Out" treatment). Even at low density, elephants might reduce the
316 abundance of very large trees, consistent with similar studies conducted in African savannas
317 (*e.g.*, Shannon *et al*., 2008; Mapaure and Moe, 2009; Gandiwa *et al*., 2011; Cook *et al*.,
318 2017). The smaller **Logged Initial Growth Rate** (*I*) of tree **Height** in the "New" compared
319 to the "Out" treatments, coupled with the absence of modification of the **Asymptotic Change**
320 **in Growth Rate** (*B*), denotes a reduction of the overall growth potential of trees in the former
321 treatment, but not of the speed at which the final growth potential is reached. This suggests
322 that elephants might participate in the maintenance of small trees in the landscape (Kalwij *et*
323 *al*., 2010). However, the allometric coefficients (tree **Height** - tree **Diameter** relationship) in
324 the "Out" and "Old" treatments were not significantly different, suggesting that elephants
325 affect the allometric relationship between tree **Height** and tree **Diameter**, but only
326 subsequent to a long-term population increase.
327 Although there was a high correlation between tree **Height** and **Canopy Volume** (Table 1;
328 Blanchard *et al.*, 2016; Davies *et al.*, 2018), there was a trend towards an increase of the
329 **Asymptotic Change in Growth Rate** (*B*) only in the allometric relationship between
330 **Canopy Volume** and tree **Diameter** in MGR ($mean_{Old} = 2.02 \pm 0.27$, $mean_{New} = 2.20 \pm 0.53$,
331 Fig. 2c) with an increasing elephant population. Such a phenomenon could denote the
332 development of a long-term compensation mechanism, trees being shortened by elephants,
333 they would increase in canopy volume. When exposed to herbivory, trees can develop
334 compensatory mechanisms to balance the loss of biomass (McNaughton, 1983; Paige 1992;
335 Zhang *et al*., 2018), although species-specific patterns are common (Focardi and Tinelli,

336 2005). Alternatively, elephant presence is usually associated with a decreased density in trees
337 (O'Connor *et al.*, 2007; Thompson *et al.*, 2022), which might reduce light competition,
338 leading to increased tree growth (Sevillano *et al.*, 2016). This increase of the **Asymptotic**
339 **Change in Growth Rate** of **Canopy Volume** was however not significant ($P = 0.54$), and
340 further exploration is needed to confirm if this trend becomes significant in the longer-term.
341 In MGR and BCP, besides elephants, other browsing herbivores also occur, which can affect
342 tree structure. In MGR, impala, a mixed feeder (Owen-Smith, 2008), is known for its
343 negative impact on the recruitment of trees in both the seedling and sapling classes, but also
344 reducing recruitment into taller height classes as they restrain tree growth within the
345 browsing trap (O'Kane *et al.*, 2012; Lagendijk *et al.*, 2015). Similarly, the BCP area was
346 affected by fuelwood collection and livestock (e.g. goats), which can both affect the structure
347 of the woody vegetation (Stuart-Hill, 1992; Scogings and Macanda, 2005; Tripathi et al.,
348 2019). During the study period, MGR has experienced an increase in its impala population
349 (from 2879 individuals in 2011 to 6110 individuals in 2021, Supporting information 2),
350 which has likely contributed to the modification of the allometric relationships between the
351 "Old" and "New" treatments (Staver and Bond 2014). Unfortunately, there was no data
352 available regarding fire regimes in the MGR and BCP, although several studies showed that
353 fire interacts with herbivory and contributes to modifications in the woody vegetation
354 dynamics (Holdo *et al.*, 2009; Shannon *et al.*, 2011; Vanak *et al.*, 2012).
355 Although there was a general increase of **Elephant Use** in MGR, we did not find evidence
356 for a modification of the **Logged Initial Growth Rate** (I) and the **Asymptotic Change in**
357 **Growth Rate** (B) in response to this increase (Fig. 3, Table 2). The wide dispersion of these
358 species-specific coefficients prevents detecting any significant trend, and rather denotes
359 species-specific patterns as found by Levick and Rogers (2008). Some species characterised
360 by higher abundance or palatability can be preferentially selected by herbivores (e.g. kudu

361 and elephant select preferentially *Dichrostachys cinerea*, Owen-Smith and Cooper 1987; de
362 Garine-Wichatitsky *et al*., 2004; Makhabu, 2005). Depending on the tree and herbivore
363 species, different parts of the tree can be preferentially selected and exposed to various types
364 of modifications. Elephants can topple, strip and break stems (e.g. in *Vachellia tortilis*,
365 Boundja and Midgley, 2010) and/or consume the bark (e.g. in *Senegalia nigrescens*; Watson
366 *et al.*, 2020), while giraffes browse exclusively on leaves (e.g. in *Acacia spp.*; Mahenya *et al*.,
367 2016). Such preferences generate the potential for species-specific allometric responses in
368 trees (MacGregor and O'Connor, 2004).
369 Our study provides an overview of the influence of elephants on tree allometry (reduced
370 **Height** and **Canopy Volume**, reduced **Logged Initial Growth Rate** of the allometric
371 relationship between tree **Height** and tree **Diameter**). However, allometric relationships in
372 trees are the result of a complex interplay between tree species traits (e.g. regeneration by
373 regrowth in *Acacia nigrescens*, Fornara and du Toit, 2007), herbivore decisions (e.g. different
374 herbivores browse different plant parts; Cameron and du Toit, 2007) and abiotic factors (e.g.
375 fire regimes; Schafer and Mack, 2014). Further exploration is thus needed to better
376 understand how elephants interact with these coexisting factors and modify the allometric
377 relationships at the species-specific level in African savannas.

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Declarations

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Georgette Lagendijk: Methodology - Data Curation - Validation - Writing: Review & Editing; **Rob Slotow**: Methodology - Data Curation - Validation - Writing: Review & Editing - Funding acquisition; **Jan Venter**: Conceptualization - Validation - Writing: Review & Editing - Supervision - Project administration - Funding acquisition; **Hervé Fritz**: Conceptualization - Validation - Methodology - Writing: Review & Editing - Supervision - Project administration - Funding acquisition.

References

Archibald, S. and Bond, W.J., 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos*, 102(1), pp.3-14.

Arzai, A., and Aliyu B., 2010. The relationship between canopy width, height and trunk size in some tree species growing in the Savanna zone of Nigeria. *Bayero Journal of Pure and Applied Sciences*, 3(1).

Bakker, E.S., Gill, J.L., Johnson, C.N., Vera, F.W., Sandom, C.J., Asner, G.P. and Svenning, J.C., 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences*, 113(4), pp.847-855.

Barnes, R.F.W., 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology*, pp.521-539.

Barokologadi Communal Property Association. The Path Followed by Barokologadi CPA (BCPA) Since the Claim of Melorane, Barokologadi's Ancestral Land. *Unpublished report*.

Blanchard, E., Birnbaum, P., Ibanez, T., Boutreux, T., Antin, C., Ploton, P., Vincent, G., Pouteau, R., Vandrot, H., Hequet, V. and Barbier, N., 2016. Contrasted allometries between stem diameter, crown area, and tree height in five tropical biogeographic areas. *Trees*, 30, pp.1953-1968.

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165, pp. 525–538.

Boundja, R.P. and Midgley, J.J., 2010. Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park, Kwazulu-Natal, South Africa. *African Journal of Ecology*, 48(1), pp.206-214.

Cameron, E. Z. and du Toit, J. T., 2007. Winning by a neck: tall giraffes avoid competing with shorter browsers. *The American Naturalist*, 169(1), pp.130-135.

Canham, C. D., McAninch, J. B. and Wood, D. M., 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Canadian Journal of Forest Research*, 24(4), pp.817-825.

Caughley, G., 1976. The elephant problem–an alternative hypothesis. African Journal of *Ecology*, 14(4), pp.265-283.

Cook, R.M., Witkowski, E.T.F., Helm, C.V., Henley, M.D. and 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, pp.107-116.

Cumming, D.H., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Hovorka, M.D., Johnston, D.S. and Kalcounis, M., 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science*, 93(5), pp.231-236.

Danell, K., Bergström, R., Duncan, P. and Pastor, J. eds., 2006. Large herbivore ecology, ecosystem dynamics and conservation (Vol. 11). Cambridge University Press.

Davies, A.B., Gaylard, A. and Asner, G.P., 2018. Megafaunal effects on vegetation structure throughout a densely wooded African landscape. *Ecological applications*, 28(2), pp.398-408.

de Garine-Wichatitsky, M., Fritz, H., Gordon, I.J. and Illius, A.W., 2004. Bush selection along foraging pathways by sympatric impala and greater kudu. *Oecologia*, 141, pp.66-75.

Du Toit, J.T., Cumming, D.H.M., 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism, *Biodiversity and Conservation* 8, pp.1643-1661.

459 Ferry, N., Dray, S., Fritz, H., Ipavec, A., Wigley, B.J., Charles-Dominique, T., Bourgarel, M.,
460 Sebele, L. and Valeix, M., 2021. Long-term high densities of African elephants clear the
461 understorey and promote a new stable savanna woodland community. *Journal of*
462 *Vegetation Science*, 32(6), p.e13101.
463 Focardi, S. and Tinelli, A., 2005. Herbivory in a Mediterranean forest: browsing impact and
464 plant compensation. *Acta Oecologica*, 28(3), pp. 239-247.
465 Fornara, D. A. and Toit, J. D., 2007. Browsing lawns? Responses of *Acacia nigrescens* to
466 ungulate browsing in an African savanna. *Ecology*, 88(1),pp. 200-209.
467 Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T. and Tafangenyasha, C., 2011. The
468 impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National
469 Park, Zimbabwe. *Journal of Arid Environments*, 75(9), pp 809-814.
470 Guldemond, R. and Van Aarde, R., 2008. A meta-analysis of the impact of African elephants
471 on savanna vegetation. *The Journal of Wildlife Management*, 72(4), pp.892-899.
472 Guldemond, R. and Van Aarde, R., 2010. The influence of tree canopies and elephants on
473 sub-canopy vegetation in a savannah. *African Journal of Ecology*, 48(1), pp.180-189.
474 Guldemond, R.A., Purdon, A. and Van Aarde, R.J., 2017. A systematic review of elephant
475 impact across Africa. *PloS one*, 12(6), p.e0178935.
476 Helm, C.V., Scott, S.L. and Witkowski, E.T.F., 2011. Reproductive potential and seed fate of
477 *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa.
478 *South African Journal of Botany*, 77(3), pp.650-664.
479 Hoffmann, W.A., Flake, S.W., Abreu, R.C.R., Pilon, N.A.L., Rossatto, D.R., Durigan, G.,
480 2019. Rare frost events reinforce tropical savanna–forest boundaries. *Journal of Ecology*
481 107, pp. 468–477.

482 Holdo, R. M., Holt, R. D. and Fryxell, J. M., 2009. Grazers, browsers, and fire influence the
483 extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications*, 19(1),
484 pp.95-109.
485 Holdo, R.M., 2007. Elephants, fire, and frost can determine community structure and
486 composition in Kalahari woodlands. *Ecological applications*, 17(2), pp.558-568.
487 Huxley, J. S. and G. Teissier., 1936. Terminology of relative growth. *Nature*, 137, pp. 780–
488 781.
489 Jones, C. G., Lawton, J. H. and Shachak, M., 1994. Organisms as ecosystem engineers.
490 *Oikos*, 69(3): pp.373-386.
491 Kalwij, J. M., De Boer, W. F., Mucina, L., Prins, H. H. T., Skarpe, C. and Winterbach, C.,
492 2010. Tree cover and biomass increase in a southern African savanna despite growing
493 elephant population. *Ecological Applications*, 20(1), pp.222-233.
494 Kearsley, E., De Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G.,
495 Huygens, D., Kebede, Y., Defourny, P., Bogaert, J. and Beeckman, H., 2013.
496 Conventional tree height–diameter relationships significantly overestimate aboveground
497 carbon stocks in the Central Congo Basin. *Nature communications*, 4(1), p.2269.
498 Kerley, G.I. and Landman, M., 2006. The impacts of elephants on biodiversity in the Eastern
499 Cape Subtropical Thickets: elephant conservation. *South African Journal of Science*,
500 102(9), pp.395-402.
501 Lagendijk, D.G., Thaker, M., De Boer, W.F., Page, B.R., Prins, H.H. and Slotow, R., 2015.
502 Change in mesoherbivore browsing is mediated by elephant and hillslope position. *PloS*
503 *one*, 10(6), p.e0128340.
504 Laws, R.M., 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos*,
505 pp.1-15.

Levick, S. and Rogers, K., 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*, 141(2), pp.489-498.

Lewis, D., 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology*, 29(3), pp.207-221.

MacGregor, S.D. and 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), pp.55-66.

Mahenya, O., Ndjamba, J.K., Mathisen, K.M. and Skarpe, C., 2016. Giraffe browsing in response to plant traits. *Acta Oecologica*, 75, pp.54-62.

Makhabu, S. W., 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *Journal of Tropical Ecology*, 21(6), pp.641-649.

Makhabu, S.W., Skarpe, C. and Hytteborn, H., 2006. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta oecologica*, 30(2), pp.136-146.

Mapaure, I. and Moe, S.R., 2009. Changes in the structure and composition of miombo woodlands mediated by elephants (*Loxodonta africana*) and fire over a 26-year period in north-western Zimbabwe. *African journal of ecology*, 47(2), pp.175-183.

McNaughton, S. J., 1983. Compensatory plant growth as a response to herbivory. *Oikos*, pp.329-336.

Moncrieff, G.R., Chamaillé-Jammes, S., Higgins, S.I., O'Hara, R.B., Bond, W.J., 2011. Tree allometries reflect a lifetime of herbivory in an African savanna. *Ecology*, 92, pp. 2310–2315.

Morrison, T.A., Holdo, R.M., Anderson, T.M., 2016. Elephant damage, not fire or rainfall, explains mortality of overstorey trees in Serengeti. *Journal of Ecology* 104,pp. 409–418.

North West Parks and Tourism Board, 2024, Madikwe Game Reserve Annual Game Census Report. *Unpublished report*.

O'Connor, T.G., Goodman, P.S. and Clegg, B., 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*, 136(3), pp.329-345.

O'Connor, T., Ferguson, A., Clegg, B.W., Pallett, N., Midgley, J.J. and Shimbani, J., 2024. Emergent trees in *Colophospermum mopane* woodland: influence of elephant density on persistence versus attrition. *PeerJ*, *12*, p.e16961.

O'Kane, C.A., Duffy, K.J., Page, B.R. and Macdonald, D.W., 2012. Heavy impact on seedlings by the impala suggests a central role in woodland dynamics. *Journal of Tropical Ecology*, 28(3), pp.291-297.

Owen-Smith, N. and Cooper, S. M., 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, 68(2), pp.319-331.

Owen-Smith, N., 2008. The Comparative Population Dynamics of Browsing and Grazing Ungulates. In: Gordon, I.J., Prins, H.H.T. (eds) *The Ecology of Browsing and Grazing. Ecological Studies*, 195. Springer, Berlin, Heidelberg. pp.149-177.

Owen-Smith, R.N., 1988. Megaherbivores: the influence of very large body size on ecology. *Cambridge university press*.

Page, B., Slotow, R., 2001. The Influence of Browsers, Particularly Elephants, on Vegetation (Diversity) at Madikwe Game Reserve. *Preliminary Project Report*, April 2001. Amarula Elephant Research Programme, School of Life and Environmental Science, University of Natal, Durban.

Paige, K. N., 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology*, 73(6), pp.2076-2085.

R Core Development Team., 2024. R: A language and environment for statistical computing, version 4.4.0. R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rutherford, M.C., Mucina, L., Lötter, M.C., Bredenkamp, G.J., Smit, J.H.L., Scott-Shaw, C.R., Hoare, D.B., *et al.*, 2011. *Savanna Biome.* In: L. Mucina & M.C. Rutherford, eds. *The Vegetation of South Africa, Lesotho and Swaziland.* Strelitzia 19. Pretoria: South African National Biodiversity Institute (SANBI), pp.439–538.

Sankaran, M., Augustine, D.J. and Ratnam, J., 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology*, 101(6), pp.1389-1399.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F. and Ardo, J., 2005. Determinants of woody cover in African savannas. *Nature*, 438(7069), pp.846-849.

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

Schafer, J. L. and Mack, M. C., 2014. Growth, biomass, and allometry of resprouting shrubs after fire in scrubby flatwoods. *The American Midland Naturalist*, 172(2), pp.266-284.

Scholes, R.J. and Archer, S.R., 1997. Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 28(1), pp.517-544.

Scogings, P., and Macanda, M. 2005. *Acacia karroo* responses to early dormant season defoliation and debarking by goats in a semi-arid subtropical savanna. *Plant Ecology*, 179, pp.193-206.

Sevillano, I., Short, I., Grant, J. and O'Reilly, C., 2016. Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *Forest Ecology and Management*, 374, pp. 11-19.

Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R. and Slotow, R., 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of tropical ecology*, 24(3), pp.281-289.

Shannon, G., Thaker, M., Vanak, A.T., Page, B.R., Grant, R. and Slotow, R., 2011. Relative impacts of elephant and fire on large trees in a savanna ecosystem. *Ecosystems*, 14, pp.1372-1381.

Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., du Toit, J.T., Duncan, J.H., Hytteborn, H., Makhabu, S., Mari, M. and Marokane, W., 2004. The return of the giants: ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment*, 33(6), pp.276-282.

Sorokina, H.E., Nunes, M.H., Heiskanen, J., Munyao, M., Mwang'ombe, J., Pellikka, P., Raumonen, P. and Maeda, E.E., 2024. East African megafauna influence on vegetation structure permeates from landscape to tree level scales. *Ecological Informatics*, 79, p.102435.

Staver, A.C., Abraham, J.O., Hempson, G.P., Karp, A.T. and Faith, J.T., 2021. The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology*, 109(8), pp.2804-2822.

Staver, A. C. and 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), pp.595-602.

Stoinski, T.S., Daniel, E. and Maple, T.L., 2000. A preliminary study of the behavioral effects of feeding enrichment on African elephants. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, 19(6), pp.485-493.

Stuart-Hill, G. C., 1992. Effects of elephants and goats on the Kaffrarian succulent thicket of the eastern Cape, South Africa. *Journal of Applied Ecology*, pp. 699-710.

603 Thompson, K.E., Ford, A., Esteban, G., Poupard, A., Zoon, K. and Pettorelli, N., 2022.
604 Impacts of African savannah elephants (*Loxodonta africana*) on tall trees and their
605 recovery within a small, fenced reserve in South Africa. *African Journal of Ecology*,
606 60(3), pp.357-366.
607 Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C. and Slotow, R.,
608 2010. Inbreeding and density-dependent population growth in a small, isolated lion
609 population. *Animal Conservation*, 13(4), pp.374-382.
610 Tripathi, H. G., Mzumara, T. I., Martin, R. O., Parr, C. L., Phiri, C. and Ryan, C. M., 2019.
611 Dissimilar effects of human and elephant disturbance on woodland structure and
612 functional bird diversity in the mopane woodlands of Zambia. *Landscape Ecology*, 34,
613 357-371.
614 Trollope, W.S.W., Trollope, L.A., Biggs, H.C., Pienaar, D. and Potgieter, A.L.F., 1998.
615 Long-term changes in the woody vegetation of the Kruger National Park, with special
616 reference to the effects of elephants and fire. *Koedoe*, 41(2), pp.103-112.
617 Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. and Duncan, P., 2011.
618 Elephant-induced structural changes in the vegetation and habitat selection by large
619 herbivores in an African savanna. *Biological Conservation*, 144(2), pp.902-912.
620 Vanak, A. T., Shannon, G., Thaker, M., Page, B., Grant, R. and Slotow, R., 2012.
621 Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in
622 an African savanna. *Ecography*, 35(4),pp.315-321.
623 Van Langevelde, F., Van De Vijver, C.A., Kumar, L., Van De Koppel, J., De Ridder, N., Van
624 Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J. and Prins, H.H.,
625 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2),
626 pp.337-350.

Watson, L.H., Cameron, M.J. and Iifo, F., 2020. Elephant herbivory of knob-thorn *(Senegalia nigrescens*) and ivory palm (*Hyphaene petersiana*) in Bwabwata National Park, Caprivi, Namibia: The role of ivory palm as a biotic refuge. *African Journal of Ecology*, 58(1), pp.14-22.

Wigley, B.J., Coetsee, C., Fritz, H. and Bond, W.J., 2014. Herbivores shape woody plant communities in the Kruger National Park: lessons from three long-term exclosures. *Koedoe: African protected area conservation and science*, 56(1), pp.1-12.

Zhang, B., Liu, X., DeAngelis, D. L., Zhai, L., Rayamajhi, M. B. and Ju, S., 2018. Modeling the compensatory response of an invasive tree to specialist insect herbivory. *Biological Control*, 117, 128-136.

Tables

Table 1: Species-specific Spearman rank correlation (ρ) between tree height and canopy volume and their significance (P) in Madikwe Game Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa. "Old": data collected in MGR in 2000 and 2001 at relatively low elephant density; "New", data collected in MGR in 2019 at relatively high elephant density; "Out", data collected in BCP in 2019 in the absence of elephants.

Species	ρ_{old}	P_{old}	ρ_{new}	P_{new}	ρ_{out}	P_{out}
Combretum hereroense	0.95	< 0.01	0.9	< 0.01	0.94	< 0.01
Dichrostachys cinerea	0.91	< 0.01	0.95	< 0.01	0.86	< 0.01
Euclea undulata	0.82	< 0.01	0.89	< 0.01	0.97	< 0.01
Flueggea virosa	0.85	< 0.01	0.65	< 0.01	0.78	< 0.01
Grewia flava	0.82	< 0.01	0.87	< 0.01	0.72	< 0.01
Grewia monticola	0.89	< 0.01	0.9	< 0.01	0.84	< 0.01
Gymnosporia buxifolia	0.91	< 0.01	0.8	< 0.01	0.62	< 0.01
Senegalia erubescens	0.93	< 0.01	0.94	< 0.01	0.94	< 0.01
Senegalia mellifera	0.97	< 0.01	0.68	0.01	0.92	< 0.01
Vachellia karroo	0.76	< 0.01	0.86	< 0.01	0.92	< 0.01
Vachellia tortilis	0.94	< 0.01	0.9	< 0.01	0.93	< 0.01
Ximenia americana	0.77	< 0.01	0.93	< 0.01	0.81	< 0.01
Ziziphus mucronata	0.93	< 0.01	0.95	< 0.01	0.92	< 0.01

645 Table 2: Effect of the Elephant Use on the species-specific Asymptotic Change in Growth
646 Rate (*B*) and Logged Initial Growth Rate (*I*) for the tree Height - tree Diameter and the
647 Canopy Volume - tree Diameter relationships according to the treatment, in Madikwe Game
648 Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa. "Old": data
649 collected in MGR in 2000 and 2001 at relatively low elephant density; "New", data collected
650 in MGR in 2019 at relatively high elephant density.

Treatment	**Allometric relationship**	**Allometric coefficient**	**Estimate ± SE**	**P**
Old	Height - Diameter	B	0.18 ± 0.21	0.38
New	Height - Diameter	B	0.00 ± 0.10	0.99
Old	Height - Diameter	I	-0.14 ± 0.35	0.68
New	Height - Diameter	I	-0.08 ± 0.17	0.64
Old	Canopy Volume - Diameter	B	-0.14 ± 0.49	0.77
New	Canopy Volume - Diameter	B	-0.04 ± 0.24	0.85
Old	Canopy Volume - Diameter	I	-0.22 ± 0.83	0.79
New	Canopy Volume - Diameter	I	-0.01 ± 0.40	0.99

651

Figure legends

Figure 1: Variation of a) the logged tree Height and b) the logged Canopy Volume, between the three treatments in Madikwe Game Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa. “Old”, data collected in MGR in 2000 and 2001 at relatively low elephant use; “New”, data collected in MGR in 2019 at relatively high elephant use; “Out”, data collected in BCP in 2019 in the absence of elephants. All 13 tree species were pooled.

Figure 2: Asymptotic Change in Growth Rate (*B*) and Logged Initial Growth Rate (*I*) according to the treatment in Madikwe Game Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa for the tree Height - tree Diameter and the Canopy Volume - tree Diameter relationships: a) Asymptotic Change in Growth Rate (*B*) for the tree Height - tree Diameter relationship; b) Logged Initial Growth Rate (*I*) for the tree Height - tree Diameter relationship; c) Asymptotic Change in Growth Rate (*B*) for the Canopy Volume - tree Diameter relationship; d) Logged Initial Growth Rate (*I*) for the Canopy Volume - tree Diameter relationship. “Old”: data collected in MGR in 2000 and 2001 at relatively low elephant use; “New”, data collected in MGR in 2019 at relatively high elephant use; “Out”, data collected in BCP in 2019 in the absence of elephants. Letters denote significant differences between treatments, the absence of letters denoting the absence of significant difference.

Figure 3: Species-specific Asymptotic Change in Growth Rate (*B*) and Logged Initial Growth Rate (*I*) according to the Elephant Use in each treatment in Madikwe Game Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa, for the tree Height - tree

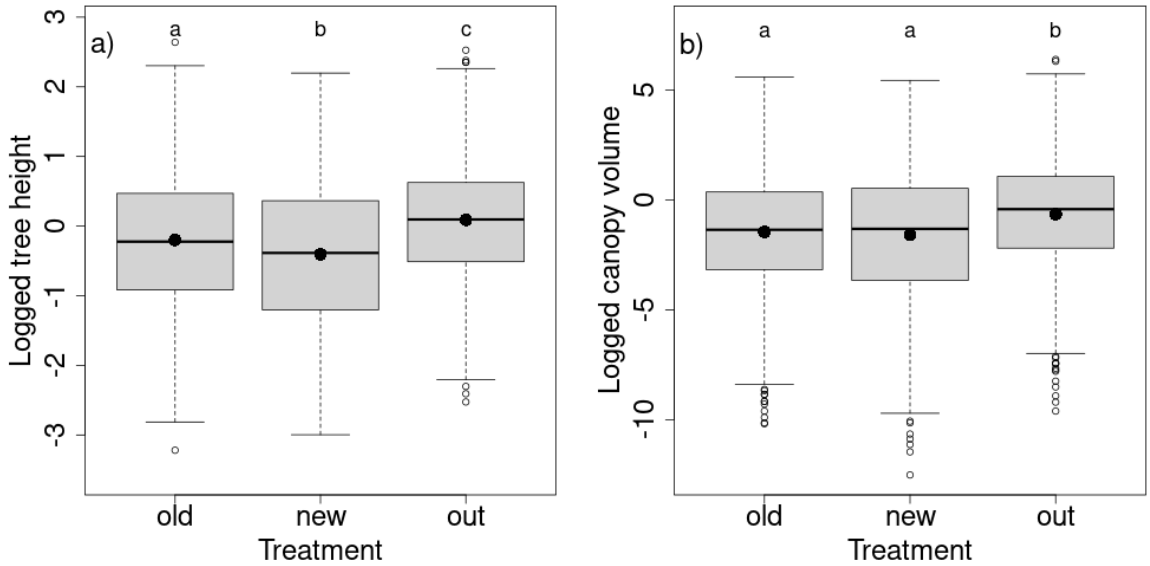
Diameter and the Canopy Volume - tree Diameter relationships: a) Asymptotic Change in Growth Rate (*B*) for the tree Height - tree Diameter relationship; b) Logged Initial Growth Rate (*I*) for the tree Height - tree Diameter relationship; c) Asymptotic Change in Growth Rate (*B*) for the Canopy Volume - tree Diameter relationship; d) Logged Initial Growth Rate (*I*) for the Canopy Volume - tree Diameter relationship. “Old”: data collected in MGR in 2000 and 2001 at relatively low elephant use, in green; “New”, data collected in MGR in 2019 at relatively high elephant use, in red. Dots correspond to the observed values, solid lines correspond to the predicted values from the model, shaded areas correspond to the 95 % confidence intervals of the model predictions.

686 **Figures**

687

688 Figure 1

689



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691 Figure 2

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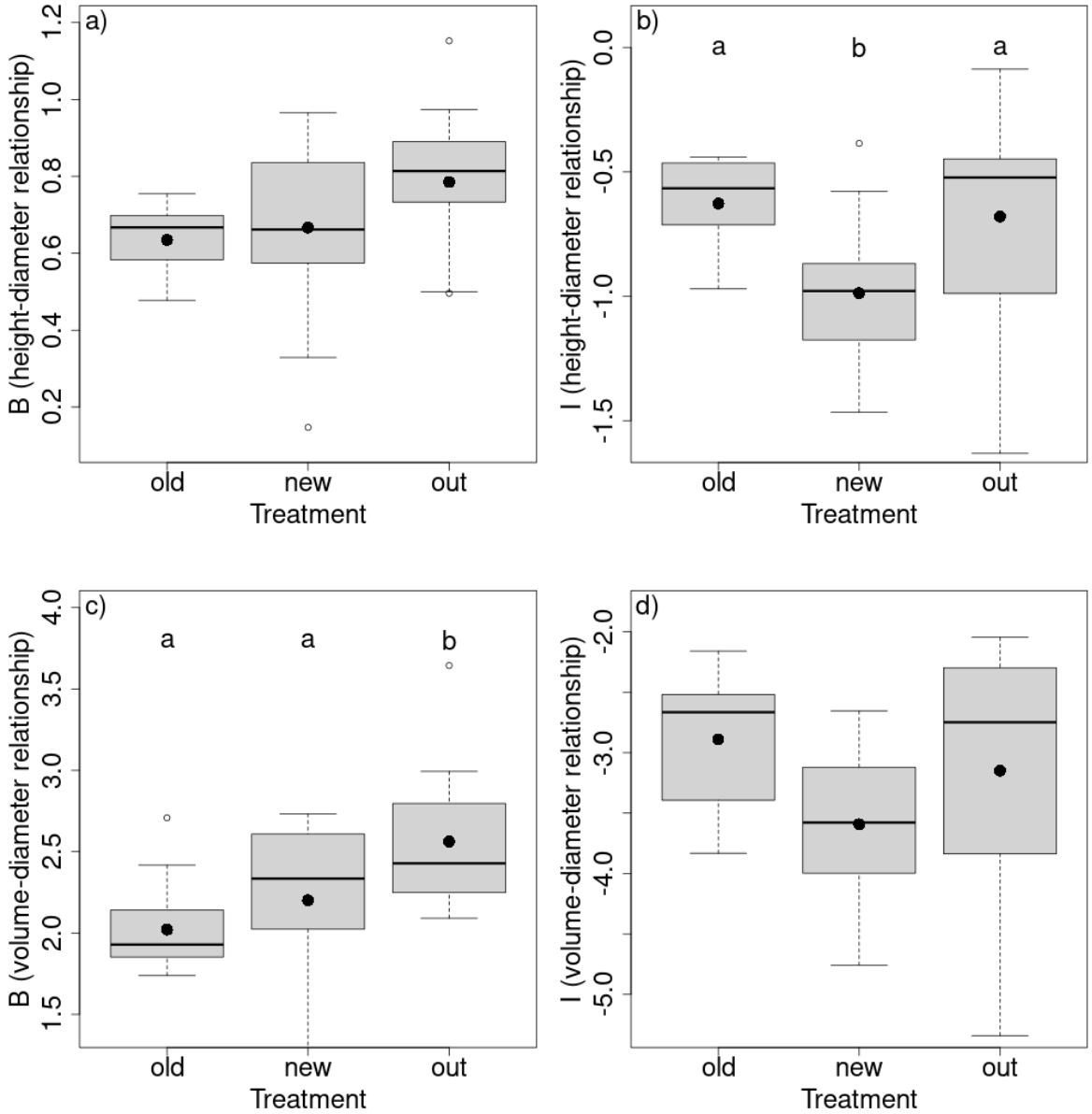

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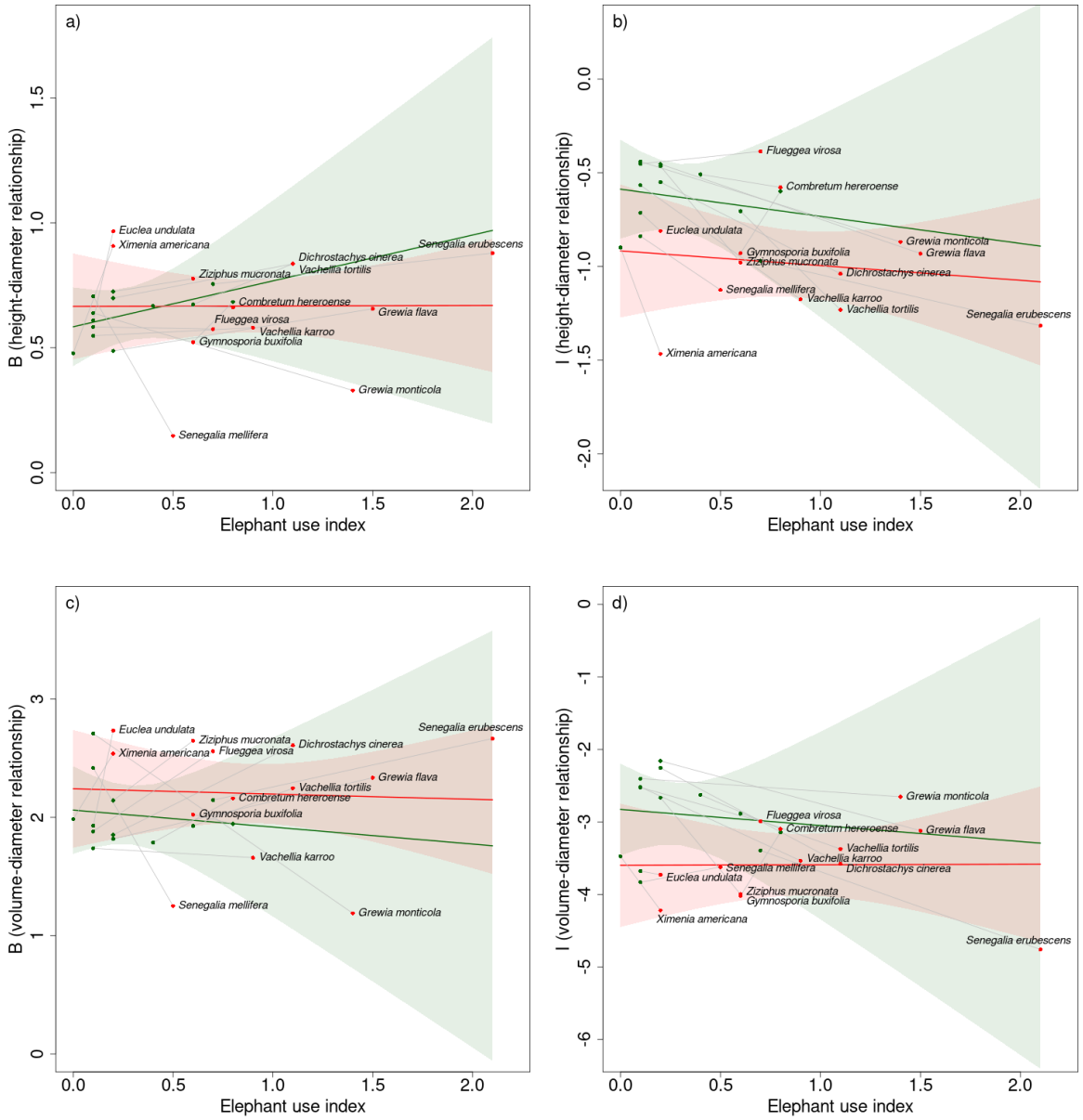
Figure 3


a)
B (height-diameter relationship)
Elephant use index
Euclea undulata
Ximenia americana
Dichrostachys cinerea
Vachellia tortilis
Senegalia erubescens
Ziziphus mucronata
Combretum hereroense
Grewia flava
Flueggea virosa
Vachellia karroo
Gymnosporia buxifolia
Grewia monticola
Senegalia mellifera
b)
l (height-diameter relationship)
Elephant use index
Flueggea virosa
Combretum hereroense
Euclea undulata
Grewia monticola
Gymnosporia buxifolia
Grewia flava
Ziziphus mucronata
Dichrostachys cinerea
Senegalia mellifera
Vachellia karroo
Vachellia tortilis
Senegalia erubescens
Ximenia americana
c)
B (volume-diameter relationship)
Elephant use index
Euclea undulata
Ziziphus mucronata
Dichrostachys cinerea
Senegalia erubescens
Ximenia americana
Flueggea virosa
Grewia flava
Vachellia tortilis
Combretum hereroense
Gymnosporia buxifolia
Vachellia karroo
Senegalia mellifera
Grewia monticola
d)
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Elephant use index
Grewia monticola
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Grewia flava
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