Long-term effects of an elephant-dominated browser community on the architecture of trees in a fenced reserve

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Submission and Acceptance Dates

Received: _____; Revised: _____; Accepted: _____.

ABSTRACT

African elephants (*Loxodonta africana*), in conjunction with the community of browser species, exert substantial top-down control over the woody vegetation in savannas by utilising large amounts of plant biomass, as well as through non-consumptive effects. However, how much browsers affect the pattern of proportional growth between different tree components remains understudied. Using vegetation data collected in 2000-2001 and 2019 for more than 3,500 trees inside and outside Madikwe Game Reserve, South Africa, we determined the long-term effects of an increasing elephant population, in conjunction with the community of meso-browsers, on structural relationships in 13 tree species. The number of trees utilised by elephants increased between 2000 and 2019, but individual trees were not more intensively utilised. After almost two decades of use by elephants, we observed a reduction in the logged initial growth rate of the structural relationship between tree height and stem diameter, without modification of the asymptotic change in growth rate. Despite species-specific variability, tree height was overall reduced for a given stem diameter. Canopy area, as well as its structural relationship with stem diameter remained mostly stable. We suggest that elephants are responsible for hedging by reducing tree height. Together with impala, the dominant species in this meso-browser community, they could stimulate regrowth by browsing the canopy of the vegetation maintained in the browsing trap. Our study emphasises the necessity of long-term, species-specific studies to improve our understanding of how the browser community, and elephant in particular, affects structural relationships in trees.

Data availability statement: The data that support the findings of this study are openly available in Zenodo Repository at https://doi.org/10.5281/zenodo.14268021.

Keywords: *Aepyceros melampus*, allometry, browsing trap, canopy, *Loxodonta africana*, Madikwe Game Reserve, savanna ecosystem, tree height.

1. INTRODUCTION

Savannas, which cover approximately half of sub-Saharan Africa (du Toit and Cumming, 1999) and a fifth of the earth's land surface (Sankaran et al., 2005), are a dominant biome 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 rainfall, soil dynamics, micro- and macro-herbivory, as well as fire and frost regimes, which contribute to the diversity of plant species and the structure of the vegetation in these landscapes (Scholes and Archer, 1997; Du Toit and Cumming, 1999; Van Langevelde et al., 2003; Sankaran et al., 2005; Sankaran et al., 2008; Holdo et al., 2009; Shannon et al., 2011). Although fire is commonly considered the dominant factor shaping savanna vegetation by reducing canopy cover and maintaining a continuous grass understory competing with trees, the herbivore community also strongly influences both vegetation structure and plant community composition through the consumption of biomass (Bond et al., 2005; Danell et al., 2006; Sankaran et al., 2008; Lagendijk et al., 2015). Herbivory can theoretically lead to a decrease of up to 30 % in tree abundance and 57 % in grass abundance (Staver et al., 2021).

In African savannas, historically characterised by remarkably high large herbivore biomass (Hempson et al., 2015), the woody vegetation is influenced by a rich community of browsers (Sankaran et al., 2013; Staver and Bond, 2014). Among them, the African elephant (*Loxodonta africana*) plays a determinant role as an ecosystem engineer (Jones et al., 1994; Cumming et al., 1997; Valeix et al., 2011). Elephants affect species diversity by reducing the density of palatable tree species (e.g., *Senegalia mellifera*, *Sclerocarya birrea caffra*; Sankaran et al., 2013; Cook et al., 2017), sometimes causing local extirpation of highly selected species (e.g., baobab *Adansonia digitata* and *Commiphora ugogensis*; Barnes, 1983; O'Connor et al., 2007). Although elephants are known for pushing over, uprooting and

80 debarking trees, which can cause mortality, they also consume biomass, topple stems and
81 break branches, leaving the trees alive but modifying their architecture (O'Connor et al.,
82 2007; Boundja and Midgley, 2010; Cook et al., 2017).

83 Tree allometry (i.e., the proportional relationships between different components of
84 an individual through growth; Huxley and Teissier, 1936) is the result of the interaction
85 between abiotic factors such as soil composition, water availability, fire frequency, and
86 browsing pressure (Archibald and Bond, 2003; Moncrieff et al., 2011). To persist despite
87 browsing, tree species have evolved various mechanisms of compensation (e.g., coppicing in
88 *Colophospermum mopane*; Lewis, 1991) or protection (e.g., spinescence or cage effect in
89 *Ziziphus mucronata*; Charles-Dominique et al., 2017). Some of these evolutionary
90 modifications, as well as the phenotypic changes imposed by direct removal of biomass by
91 browsers, and in particular elephants, lead to changes in tree allometric and structural
92 relationships (e.g., ratio between tree height, canopy volume, shoot density and total basal
93 area; Styles and Skinner, 2000; MacGregor and O'Connor, 2004; Makhabu et al., 2006;
94 Mapaure and Moe, 2009; Ferry et al., 2021; O'Connor et al., 2024).

95 The structural modifications generated by elephants in particular, can have cascading
96 impacts on community interactions, such as the modification of forage quality and
97 availability for other browsers (Styles and Skinner, 2000), habitat structure and selection by
98 other mammal and bird species (Valeix et al., 2011; Tripathi et al., 2019), and even
99 biogeochemical processes such as carbon cycle and storage (Sandhage-Hofmann et al., 2021).
100 While earlier studies suggested that elephant activity could transform woodlands and forests
101 into grasslands or open savannas across Africa, a concern known as "the elephant problem"
102 (Laws, 1970; Caughley, 1976), more recent research indicates that elephant effect on savanna
103 vegetation is highly variable. A meta-analysis highlighted that these effects depend on
104 environmental conditions, such as rainfall and geographical constraints (Guldemond and Van

Aarde, 2008). Additionally, the expected changes might be less striking in open systems than in fenced reserves sustaining high population densities, or when measured over longer periods (Skarpe et al., 2004; Guldemond and Van Aarde, 2008; Ferry et al., 2021).

In this study, we determined the effect that elephants, in conjunction with the meso-browser community, have on structural relationships in 13 dominant tree species. We used historical data from woody vegetation monitoring conducted in 2000-2001 and repeated in 2019 in Madikwe Game Reserve (hereafter MGR), which was exposed to an increasing elephant population, and in the adjacent Barokologadi Communal Property (hereafter BCP) in 2019, which did not contain elephants. We examined how the browser community affected the relationship between stem diameter, tree height and canopy area. We expected a decrease in the coefficients of the structural relationship between tree height and stem diameter with increasing elephant density. Because of the ability, and regular habit, of elephants to break main stems of trees, mature individual trees with large stem diameters should be shorter as elephant utilisation increases in MGR through time and comparatively to BCP, the elephant free area. Additionally, we expected a decrease in the coefficients of the structural relationship between canopy area and stem diameter. In MGR, meso-browsers should reduce canopy area as elephants catalyse a browsing trap by reducing tree height (Smallie and O'Connor, 2000; Staver and Bond, 2014). We expected species-specific patterns due to elephant selectivity and tree species life history traits.

2. METHODS

1. Study site and species

MGR (24°49′ S - 26°13′ E, South Africa), is a fenced reserve currently covering 750 km² (Supporting information 1). MGR is situated within the central bushveld bioregion, as part of the broader savanna biome. The dominant soils are dolomites, black clay and red clay loam

(Nel, 2022, unpublished report). The reserve usually experiences a dry season from mid-April to mid-November (Mucina and Rutherford, 2006), with an average annual rainfall of 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; reserve size formerly 650 km^2; North West Parks and Tourism Board, 2024). By 2019, the elephant population increased almost threefold, with an estimated 1,318 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 browser and mixed-feeder herbivores present in the reserve include giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), impala (*Aepyceros melampus*), bushbuck (*Tragelaphus scriptus*) and black rhinoceros (*Diceros bicornis*). Although the meso-herbivore population remained mostly stable, the density of impala increased substantially between 2011 and 2019, from 3.84 individuals/km^2 to 6.30 individuals/km^2 (Fig. 1).

BCP covers 160 km^2 (Supporting information 1) and is separated from MGR by an elephant-proof fence, rendering it an elephant-free zone. The physico-chemical conditions of the area are similar to MGR, and the dominant soils are black clay and red clay loam (Nel, 2022, unpublished report). BCP has been used for cattle, goat, and sheep farming for meat production since 2009, with occasional firewood collection by local communities (Barokologadi Communal Property Association, unpublished report), all of which can affect the structure of the woody vegetation (e.g., Scogings and Macanda, 2005; Tripathi et al., 2019). Bushbuck, greater kudu and impala roam freely in BCP in unknown numbers, but at lower densities than in MGR. Overall, BCP undergoes very little disturbance compared to MGR.

As no fire records were available locally for the study sites, we used the MODIS Burned Area Monthly Global 500 m layer from the NASA website (data retrieved on 2025-03-10 from https://modis.gsfc.nasa.gov; Giglio et al. 2018) to estimate fire occurrence in the study site between 2000 and 2019 (satellite data only available since 2000). Fire should primarily affect tree survival and density (Van Langevelde et al., 2003), but only seldomly tree structure. Indeed, young and small individuals would simply be removed by fires, while mature and tall individuals outside the fire trap should remain mainly unaffected (Morrison et al., 2016). Medium individuals are the most susceptible to fire in terms of structure and can be subjected to reduced canopy volume. Nevertheless, such an effect would be noticeable in a relatively short time scale after the last fire occurring in the area. MGR experienced yearly fires between 2001 and 2012 (except in 2007), but fire has been absent since then. BCP seldom experienced fires between 2000 and 2019 (in 2002, 2003, 2006, 2010 and 2011). We thus expect no major effect of fire on observed tree structure in this study (Schafer and Mack, 2014).

2. 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. Sampling sites were selected randomly to cover the different vegetation types present in the study sites (covering mostly three dominant vegetation types: western sandy bushveld, dwaalboom thornveld and Madikwe dolomite bushveld, Mucina et al., 2008). The minimal distance between sites was approximately 100 m. In each site, a 50-meter long transect was used to record woody plants while adjusting width for tree density. The transect was laid out using a central line as the base from which to measure distances to the sides of sample rectangles. Depending on the local vegetation density, the distance from the central

line to the sides of the sample rectangles was adjusted from two to five meters, in order to minimize sampling time while maximizing the diversity of tree height and tree species. A targeted sampling was performed in some sites to better accommodate low-abundant dead trees, rare species, or to the contrary overabundant species (e.g. *Dichrostachys cinerea*), extending the sample area to a maximum of 50 m on each side of the central line. However, the inconsistencies in transect sizes only marginally influence our analyses as tree abundance was not the object of the present study.

The 35 original sites from 2000-2001 were re-sampled between February and June 2019 (except for two 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 (covering mostly three dominant vegetation types: western sandy bushveld, Madikwe dolomite bushveld and Dwarsberg mountain bushveld, Mucina et al., 2008). The minimum distance between sites in BCP was approximately 240 m.

We defined three spatio-temporal conditions: i) "Old", corresponding to MGR data from 2000-2001 and exposed to a relatively low elephant density (n = 2,318 trees, 0.60 elephants/km^2), ii) "New", corresponding to MGR data from 2019 and exposed to a higher elephant density (n = 1,582 trees, 1.76 elephants/km^2) and iii) "Out", corresponding to BCP data from 2019 and excluding elephants (n = 1,006 trees, 0.00 elephants/km^2). Although not completely untouched by meso-browsers (as well as occasional firewood collection), the "Out" condition provides a good control condition in the absence of any elephant pressure in a similar landscape.

For each tree sampled, we recorded the number of live stems and measured stem diameters. Diameters were measured with callipers to the nearest 0.10 cm, at 0.50 - 0.75 m above the ground for tall trees (approx. > 2.00 m tall), at 0.10 - 0.50 m above the ground for

small trees (approx. between 0.10 and 2.00 m tall), and at ground level for very small trees (approx. < 0.10 m tall). To prevent lengthy measurements in the field in the case of multi-stem trees (mean ± sd number of stems per tree = 4 ± 5 stems, range = 1 - 68 stems), all the stems coppicing the same year were identified as a clump and one of these stem diameters was measured as a reference. All the stems of the same clump were then allocated to the same diameter value. Regular checks on randomly selected stems of the same clump were done to insure the consistency and validity of the grouping. For the analyses, we 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", mean ± sd diameter = 2.60 ± 4.83 cm, range = 0.10 to 75.00 cm).

For trees < 2.00 m tall (more than 80 % of the individuals), we measured tree height to the nearest 0.01 m as the vertical distance from the ground to the tree's highest point, and height of the bottom of the canopy (HBC) as the vertical distance from the ground to the height where the main canopy starts, using a measuring tape. For trees taller than 2.00 m in height, tree height and HBC were estimated to the nearest 0.50 m using an object of known height as a reference (e.g. measuring pole or one of the field technicians) to facilitate estimation of the height of the tree, as described in Shannon et al. (2008).

From these field measurements, we then calculated the total stem diameter as the diameter of a disk of area equal to the sum of all the stem areas, each stem being modelled as a perfect cylinder, as explained in equation (1):

$$stem\ diameter = \sqrt{\sum_{i=1}^{n} nb\ stem_i \times d_i^2} \qquad \text{equation (1),}$$

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 vertical area of the canopy, a proxy of the canopy volume taking advantage of the measurements available in the historical data collection protocol, using the formula of the surface of an oval as explained in equation (2):

$$canopy\ area = \pi \times \frac{max\ horizontal\ diameter}{2} \times \frac{canopy\ height}{2} \qquad \text{equation (2),}$$

where *max horizontal diameter* corresponds to the widest horizontal diameter of the oval formed by the canopy, and *canopy height* corresponds to the difference between tree height and HBC and represents the vertical diameter of the oval formed by the canopy. A Spearman correlation test confirmed the existence of a high rank correlation between max horizontal diameter and canopy height (all $P < 0.05$ except one, see Supporting information 2 for details).

To disentangle the influence of meso- (i.e., mostly eland, greater kudu, springbok, impala and bushbuck) and mega- (i.e., mostly elephant and giraffe) browsers in this landscape, we defined three tree height classes following common thresholds used in the current literature (Makhabu, 2005; Sankaran et al., 2013; Staver and Bond, 2014; Lagendijk et al., 2015; Ferry et al., 2021; Thompson et al., 2022): i) small trees, < 0.50 m tall (mainly seedlings and saplings) mostly utilised by meso-browsers, ii) medium trees, between 0.50 m and 2.00 m potentially utilised by both meso- and mega-browsers, iii) tall trees, > 2.00 m (mainly mature trees) mainly utilised by mega-browsers.

For each individual tree, we estimated an elephant utilisation index as the percentage of biomass (i.e., branches, leaves, stems, bark and/or roots) removed by elephants, 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 %, Walker, 1976). Contrary to meso-browsers, elephant utilisation is easy to discriminate accurately and rapidly in the field due to the characteristic marks left on the trees browsed (Thompson et al., 2022), explaining why only elephant utilisation was recorded in the historical protocol.

3. Statistical analyses

All statistical analyses were conducted using R (version 4.4.2, R Core Development Team 2024). We first identified the species that were present in all three spatio-temporal conditions with sufficient sample size (i.e., ≥ 15 trees in each spatio-temporal condition) and included only these species in all our analyses to ensure comparability between spatio-temporal conditions and statistical robustness (n = 13 species; n_{Old} = 1,689 trees, n_{New} = 1,391 trees, n_{Out} = 712 trees; Supporting information 3). In other words, this study focussed on the dominant tree species in this landscape.

We first studied the change in elephant utilisation frequency as the amount of utilised versus non-utilised trees, between "Old" and "New" conditions using a Fisher exact test. We then compared the distribution of elephant utilisation index (i.e., ranging between 1 and 7) between "Old" and "New" conditions for each tree height class using a Kolmogorov-Smornov test.

We investigated the changes in tree height and canopy area between spatio-temporal conditions. We conducted a one-way ANOVA on the log-transformed (natural log to meet assumptions of normality and homoscedasticity) tree height and canopy area of all species pooled together. We subsequently conducted a post-hoc pairwise comparison test using a Tukey test to identify significant differences between spatio-temporal conditions. We conducted the same analysis for each species individually to check for the presence of species-specific patterns (Supporting information 4). We also tested the correlation between tree height and canopy area using a Spearman's correlation for each species in each condition, as these two variables are known to be correlated (e.g., Archibald and Bond, 2003; Arzai and Aliyu, 2010). We subsequently conducted a two-way ANOVA on the log-transformed (natural log to meet assumptions of normality and homoscedasticity) canopy area and stem diameter of all species pooled together according to the tree height classes, and

spatio-temporal conditions, followed by post-hoc pairwise comparison tests using a Tukey test.

To study the structural relationships in trees, we used the dataset with all trees pooled together to determine the species-specific coefficients of the structural relationships between tree height and stem diameter, and between canopy area and stem diameter (as well as between max horizontal diameter of the canopy and stem diameter, see Supporting information 5), in each spatio-temporal condition. We used stem diameter as a reference in the structural relationships as browsers are expected to have no effect on this parameter (following Moncrieff et al., 2011; Schafer and Mack, 2014). One commonly expected relationship in general tree allometry (Chave et al., 2005) can be written as equation (3):

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

where X and Y are two tree measurements (X is stem diameter and Y is either tree height or canopy area here), A corresponds to the mathematical term "initial growth rate" of the relationship between Y and X, B corresponds to the "asymptotic change in growth rate" of the relationship, and C is a constant close to 0. C is 0 in nature as a tree with no stem cannot have a measurable height or canopy. If C is significantly different from 0, it suggests poor fit of the model. Mathematically, the initial growth rate A illustrates the intrinsic growth of the structural relationship linking the two parameters X and Y, namely the growth potential that can be reached. The asymptotic change in growth rate B corresponds to the speed of the increase in growth, namely how fast the curve increases. If $B < 1$ the growth rate in tree height (resp. canopy area) decreases as the stem diameter increases; if $B > 1$ the growth rate increases with increasing stem diameter.

However, in our study, visual inspection revealed non-normality and heteroscedasticity associated with an important variance in tree height and canopy area, creating a poor fit of the data with equation (3). Therefore, we used the log-transformed

formula (under the assumption of C = 0), and we fitted the corresponding linear regression instead, as described in equation (4):

$$log(Y) = I + B \times log(X) \qquad \text{equation (4)},$$

where X and Y are the same two tree measurements, B remains the asymptotic change in growth rate described in equation (3), and I corresponds to the logged initial growth rate A described in equation (3). In each spatio-temporal condition, we fitted such a relationship for each species separately. We tested the effect of sampling site as a random intercept with the "ranef" function of the "lme4" package (Bates et al., 2015), and removed it when it had no effect. We extracted the coefficients B and I for each species in each spatio-temporal condition, and we assessed the effect of the spatio-temporal condition on the variability of these coefficients using a one-way ANOVA followed by Tukey post-hoc pairwise comparison tests.

We then reconstructed the initial structural relationships between tree height (resp. canopy area) and stem diameter as described in equation (3), for each spatio-temporal condition. We used the average of the coefficients B and I estimated for each species with equation (4). We weighted these averages using species frequencies in each spatio-temporal condition to account for the relative importance of each species in the overall relationship. To assess the quality of the fit, we calculated the residuals of this fit, namely the difference between the observed and the predicted values, for each tree height class (Supporting information 6).

3. RESULTS

We identified 13 species represented by more than 15 individuals in all three spatio-temporal conditions: *Combretum hereroense*, *Dichrostachys cinerea*, *Euclea undulata*, *Flueggea virosa*, *Grewia flava*, *Grewia monticola*, *Gymnosporia buxifolia*, *Senegalia erubescens*,

328 *Senegalia mellifera*, *Vachellia karroo*, *Vachellia tortilis*, *Ximenia americana* and *Ziziphus*
329 *mucronata* (Supporting information 3). The most abundant species within all three spatio-
330 temporal conditions was *Dichrostachys cinerea* (n_{old} = 327, n_{new} = 482, n_{out} = 193), and the
331 least abundant species was *Senegalia mellifera* in the "Old" and "New" condition (n_{old} = 23,
332 n_{new} = 15, n_{out} = 67), as well as *Vachellia karroo* in the "Out" condition (n_{old} = 108, n_{new} = 54,
333 n_{out} = 16). Both MGR and BCP were characterised by shrub-dominated vegetation, with more
334 than 80 % of the trees < 2.00 m tall (1.24 ± 1.29 m tall on average, Fig. 2a) and an average
335 canopy area of approx. 1.80 ± 4.46 m^2 (Fig. 2b).

336 Elephant utilisation varied between 0 and 7 in all tree height classes (Supporting
337 information 7), both in "Old" and "New" conditions (except for the fact that none of the
338 shortest and tallest trees in "Old" were completely utilised, Table 1). Most of the trees in our
339 dataset were not utilised at all by elephants (90 and 60 % of non-utilised trees in "Old" and
340 "New", respectively), but there was a significant increase in the amount of trees utilised
341 between "Old" and "New" (Fisher exact test: X-squared = 343.99, df = 1, P < 0.01). When
342 excluding the non-utilised trees, there was no significant difference in the intensity of
343 elephant utilisation index between "Old" and "New" for any of the tree height classes
344 (Kolmogorov-Smirnov test: all P > 0.05). *Gymnosporia buxifolia*, *Senegalia erubescens* and
345 *Vachellia tortilis* were the most utilised species in "Old" (between 20 and 30 % of the trees
346 utilised), while *Ximenia americana* was not utilised at all. More than 20 % of the trees of all
347 13 species, except from *Ximenia americana* and *Euclea undulata*, were utilised at various
348 degrees in "New". At least 50 % of the trees of *Senegalia erubescens* and *Grewia flava* were
349 utilised to various degrees.

350 Overall, tree height was significantly lower in "New" than in "Old" (P < 0.01) and in
351 "New" than in "Out" (P < 0.01, Fig. 2a) conditions. The canopy area was similar in "New"
352 and "Old" conditions (P = 0.40), but it was significantly larger in "Out" than in "New"

353 conditions ($P < 0.01$, Fig. 2b). Although these results were mostly consistent among six
354 species (*Dichrostachys cinerea*, *Grewia flava*, *Grewia monticola*, *Vachellia karroo*,
355 *Vachellia tortillis* and *Ziziphus mucronata*), there were species-specific patterns (see
356 Supporting information 4 for details). Notably, *Flueggea virosa* increased in tree height and
357 canopy area between "Old" and "New" conditions, and the differences in tree height and
358 canopy area were less pronounced between "New" and "Out" for *Gymnosporia buxifolia*. No
359 significant differences were detected between spatio-temporal conditions for *Senegalia*
360 *mellifera*. We found a significant and very high rank correlation between tree height and
361 canopy area in all species in all three spatio-temporal conditions (Spearman test: all $\rho > 0.6$,
362 all $P < 0.01$, Supporting information 2). Overall, stem diameters were all significantly
363 different from each other across spatio-temporal conditions and tree height classes, except
364 from the tallest trees that were all similar regardless of the condition, and the shortest trees
365 that were similar between "New" and "Out" conditions (Fig. 3a, see details in Supporting
366 information 8). Canopy areas from the shortest trees that were all similar regardless of the
367 condition, and the tallest trees that were also similar between "Old" and "New", as well as
368 "New" and "Out" conditions, but all other canopy areas were all significantly different from
369 each other across spatio-temporal conditions and tree height classes (Fig. 3b, see details in
370 Supporting information 8).
371 Regarding the structural relationships, we found similar positive trends between stem
372 diameter and tree height (canopy area, resp.) for all 13 species in all three spatio-temporal
373 conditions (note species-specific variability related to the spatio-temporal condition such as
374 in *Grewia monticola*, and a negative relationship for *Senegalia mellifera* in the "New"
375 condition, Supporting information 5). Regarding the coefficients of the structural
376 relationships, *I* was significantly lower in "New" than in "Old" conditions in the tree height -
377 stem diameter relationship (Tukey test: $P = 0.02$, Fig. 4b). Although not significant

(ANOVA: P = 0.12), we found a similar trend for *I* in the canopy area - stem diameter relationship (Fig. 4d). *B* was significantly different according to the condition in the tree height - stem diameter relationship (ANOVA: P = 0.04, Fig. 4a), although no pairwise difference was significant (Tukey: all P > 0.05). *B* was not significantly different between "New" and "Old" (Tukey: P = 0.88), but was close to be between "New" and "Out" (Tukey: P = 0.06) conditions for the canopy area - stem diameter relationship (Fig. 4c). The reconstructions of the structural relationships (equation (3)) based on the averaged coefficients extracted from equation (4) showed a good fit in "Out" condition for both tree height and canopy area (Fig. 5a and 5b, Supporting information 6). The predictions slightly under-estimated tree height and to a lower extent, canopy area for tall trees in "Old" condition (Fig. 5a and 5b, Supporting information 6). A similar but stronger pattern was visible in "New" condition, also affecting medium trees (Fig. 5a and 5b, Supporting information 6).

4. DISCUSSION

In this study, we highlighted the effects of an increasing elephant population on the structure of the woody vegetation at the tree community scale. Overall, the number of trees utilised by elephants increased in MGR over time, but most of the trees sampled were not utilised by elephants and the intensity of utilisation remained stable across height classes. More than 80 % of the trees were below 2.00 m tall and thus within the browsing trap (Smallie and O'Connor, 2000; Staver and Bond, 2014). We suggest that the effect of elephants is exacerbated by persistent browsing by meso-browsers. By reducing tree height (known as "hedging", Styles and Skinner, 2000), elephants create conditions for the woody vegetation to become even more subjected to intense browsing by both elephants and meso-herbivores in a browsing trap, which in turn affect the canopy area. Their combined effect generates

403 heterogeneity in tree height and canopy area for a given stem diameter, modifying the
404 structural relationships in trees.

405 Tree height was smaller in MGR in 2019 compared to 2000 (the low elephant density
406 condition) and BCP in 2019 (the elephant-free area). There was a reduction in the logged
407 initial growth rate (*I*) of the structural relationship between tree height and stem diameter,
408 without modification of the asymptotic change in growth rate (*B*) in MGR in 2019 compared
409 to the other conditions, further confirmed by the deceleration of the tree height-stem diameter
410 structural relationship at large diameters in MGR versus BCP. These results denote a
411 reduction of the overall growth potential of trees in MGR, but not of the speed at which the
412 growth potential is reached, and suggests that elephants might participate in the maintenance
413 of small trees in the landscape (e.g., Kalwij et al., 2010) by keeping older tree shorter than
414 expected for their stem diameter. Even at moderate density, elephants are known to reduce
415 the abundance of very large trees in African savannas (e.g., Mapaure and Moe, 2009;
416 Gandiwa et al., 2011; Cook et al., 2017; Watson et al., 2019). Although giraffes can also
417 participate in reducing tree height by consuming the top buds (Makhabu, 2005; Cameron and
418 du Toit, 2007), they are present in very limited numbers in MGR and probably contribute
419 only marginally to the observed effects.

420 During the study period, impala, which was the dominant species among the meso-
421 browsers, more than doubled in MGR (from 2,879 individuals in 2011 to 6,110 individuals in
422 2021). Impala, a mixed feeder (Hofmann, 1989), is known to inhibit recruitment of the
423 recruitment of trees in both the seedling and sapling classes, but also reducing recruitment
424 into taller height classes as they restrain tree growth within the browsing trap (O'Kane et al.,
425 2012; Sankaran et al., 2013). However, we did not find a significant difference in terms of
426 canopy area in MGR between 2000 and 2019, the canopy area remaining stable or even
427 increasing in small and medium height classes. Although the projection of the structural

428 relationship illustrated a decrease in the canopy area for large diameter trees, the coefficients
429 of the structural relationship remained mostly stable across the three conditions, and there
430 was even a tendency towards an increase in the asymptotic change in growth rate (*B*) in MGR
431 in 2019 versus 2000. These findings, consistent with another study finding no reduction in
432 shrub canopy volume with increasing elephant density (O'Connor et al., 2024), suggest
433 potential compensatory mechanisms in response to browsing.

434 When exposed to herbivory, trees can develop compensatory mechanisms to balance
435 the loss of biomass (McNaughton, 1983; Paige, 1992; Johnson and Ebersole, 2017), although
436 species-specific patterns are common (*Vachellia tortilis* and *Ziziphus mucronata* showed a
437 significant decrease in canopy area between 2000 and 2019; see also Focardi and Tinelli,
438 2005). More shoots appear following heavy meso-herbivore browsing (Fornara and du Toit,
439 2007), and trees broken and toppled by elephant coppice (Lewis, 1991). Alternatively,
440 elephant presence is usually associated with a decrease in tree density (Watson et al., 2019),
441 which might also have reduced competition for light in a dense bushy landscape such as
442 MGR, leading to increased growth of individual tree canopy, in a similar way that herbivores
443 increase species diversity by reducing light competition in grassland systems (Borer et al.,
444 2014).

445 The predictions of the structural relationship between tree height (and to a lesser
446 extent, canopy area) and stem diameter were slightly under-estimated in MGR in 2000, and
447 even more so in 2019. To the contrary, they were very accurate in BCP, the relatively
448 undisturbed condition, providing empirical support for the suitability of our approach. The
449 presence of browsers in the system disturbs the expected structural relationship by creating
450 variance in tree height and canopy area for a given stem diameter, and so among every tree
451 height class. The changes observed in the structural relationships in MGR thus originate from
452 a cumulative effect of the heterogeneity generated in small stem diameter trees by all

453 browsers, as well as in large stem diameters utilised only by mega-browsers. Under-
454 estimation in MGR also illustrates the possibility for more complex effects of the browser
455 community on these structural relationships. Moncrieff et al. (2011) found threshold models
456 best described the effect of elephants and giraffes on the same relationship. Here, we adjusted
457 a single regression to describe the structural relationship across all tree height classes, but
458 each browser species acts at its own height (Makhabu, 2005). The effect of a given species
459 might reverberate on different portions of the relationship, even where its effect is not
460 predominant. For instance, impalas affect the smaller trees, such as seedlings and saplings,
461 and thus the mathematical initial growth rate in the relationship, whose fluctuations
462 reverberate on the adjustment at larger stem diameters. Additionally, elephants demonstrate a
463 wide browsing range in terms of tree height (Supporting information 7; Smallie and
464 O'Connor, 2000; Makhabu, 2005), implying that the medium- and small-sized trees are
465 probably affected both by them and the meso-herbivore community.
466 Each tree species has its own allometry, and reacts differently to browsing, creating a
467 high dispersion in the overall relationship. Some species characterised by higher abundance
468 or palatability can be preferentially selected by herbivores (elephants preferentially select e.g.
469 *Combretum elaeagnoides*, Makhabu, 2005, *Colophospermum mopane*, Smallie and O'Connor
470 2000, while giraffes select *Acacia* species, Mahenya et al., 2016). In MGR in 2019, *Senegalia*
471 *erubescens* was the most frequently targeted species by elephants with more than 65 % of the
472 trees utilised, whereas *Euclea undulata* remained mostly untouched (only 6 % of the trees
473 utilised). Depending on the tree and herbivore species, different parts of the tree can be
474 preferentially selected and exposed to various types of modifications. Elephants can topple,
475 strip and break stems, such as in *Vachellia tortilis* (Boundja and Midgley, 2010), utilised in
476 almost 40 % of the cases and with a significantly reduced tree height in MGR in 2019, while
477 giraffes browse exclusively on soft nutritious material such as leaves and shoots (e.g. in

Acacia species; Mahenya et al., 2016). Such preferences generate the potential for species-specific responses in structural relationships in trees (MacGregor and O'Connor, 2004).

Structural, and more generally, allometric relationships in trees have important evolutionary consequences for their maintenance and reproduction (Styles and Skinner, 2000; Archibald and Bond, 2003). These relationships arise from a complex interplay between tree species traits (e.g. regeneration by regrowth in *Senegalia nigrescens*, Fornara and du Toit, 2007), abiotic factors (e.g. fire regimes; Schafer and Mack, 2014) and herbivore preferences (e.g. different herbivores browse different plant parts depending on their size and diet; Cameron and du Toit, 2007). Understanding the profound effects of these interacting factors on tree structure should be taken to the next step by using technologies such as LiDAR (light detection and ranging) instruments, which can provide a more integrative overview of the three-dimensional structure of trees (e.g., Davies et al., 2018; McNeil et al., 2023).

TABLES

Table 1: Number of trees per elephant utilisation index for each tree height class in Madikwe Game Reserve (MGR) spatio-temporal conditions: "Old", data collected in MGR in 2000 and 2001 at relatively low elephant use (n_{old} trees = 1689); "New", data collected in MGR in 2019 at relatively high elephant use (n_{new} trees = 1391).

Tree height class	**< 0.5 m**		**0.5 to 2 m**		**> 2 m**	
Elephant utilisation index	**old**	**new**	**old**	**new**	**old**	**new**
0	496	426	808	356	199	56
1	3	21	5	61	9	34
2	3	17	32	55	34	29
3	4	18	17	80	38	41
4	8	23	6	67	11	11
5	3	35	6	23	2	7
6	1	10	2	9	1	1
7	0	1	1	6	0	4

FIGURE LEGENDS

Figure 1: Changes in population density of browser and mixed-feeder species in Madikwe Game Reserve between 2011 and 2019.

Figure 2: Variation of a) tree height and b) canopy area, between the three spatio-temporal conditions 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. White dots correspond to the median, red dots correspond to the mean, black boxes correspond to the interquartile range (IQR) of the distribution, whiskers extend to the minimum and maximum values within 1.5 times the IQR and shaded areas correspond to the kernel density estimation of the distribution.

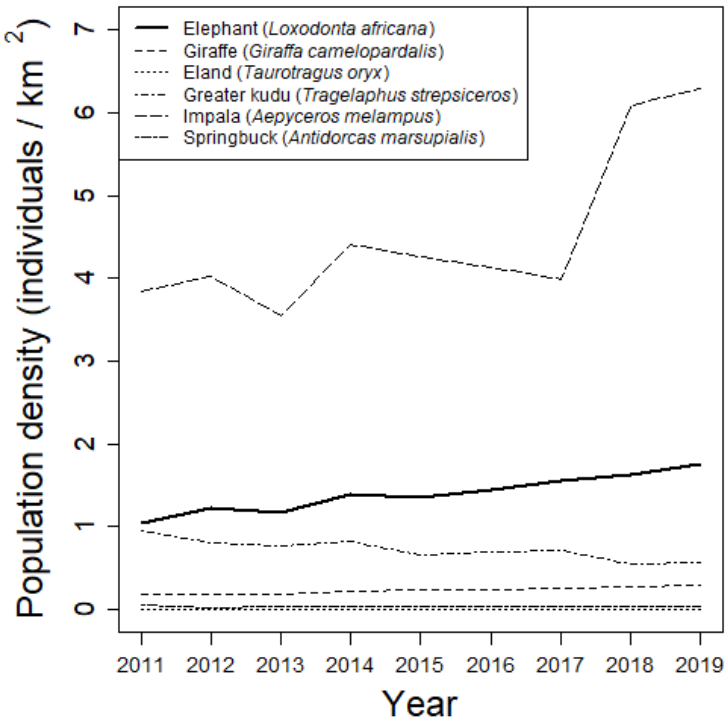
Figure 3: Distribution of: a) stem diameters and b) canopy areas, according to tree height classes (< 0.5 m, from 0.5 to 2 m, > 2 m) in the three spatio-temporal conditions: "Old", data collected in Madike Game Reserve (MGR) in 2000 and 2001 at relatively low elephant use; "New", data collected in MGR in 2019 at relatively high elephant use; "Out", data collected in Barokologadi Communal Property (BCP) in 2019 in the absence of elephants. White dots correspond to the median, red dots correspond to the mean, black boxes correspond to the interquartile range (IQR) of the distribution, whiskers extend to the minimum and maximum values within 1.5 times the IQR and shaded areas correspond to the kernel density estimation of the distribution.

Figure 4: Asymptotic change in growth rate (*B*) and logged initial growth rate (*I*) according to the spatio-temporal condition in Madikwe Game Reserve (MGR) and Barokologadi Communal Property (BCP), South Africa for the tree height - stem diameter and the canopy area - stem diameter relationships: a) *B* for the tree height - stem diameter relationship; b) *I* for the tree height - stem diameter relationship; c) *B* for the canopy area - stem diameter relationship; d) *I* for the canopy area - stem 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 spatio-temporal conditions. White dots correspond to the median, red dots correspond to the mean, black boxes correspond to the interquartile range (IQR) of the distribution, whiskers extend to the minimum and maximum values within 1.5 times the IQR and shaded areas correspond to the kernel density estimation of the distribution.

Figure 5: Structural relationship: a) between tree height and stem diameter, b) between canopy area and stem diameter, in the three spatio-temporal conditions ("Old", data collected in Madikwe Game Reserve 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 Barokologadi Communal Property in 2019 in the absence of elephants). Dots represent the observed data, lines represent the predictions of the model (see text for details).

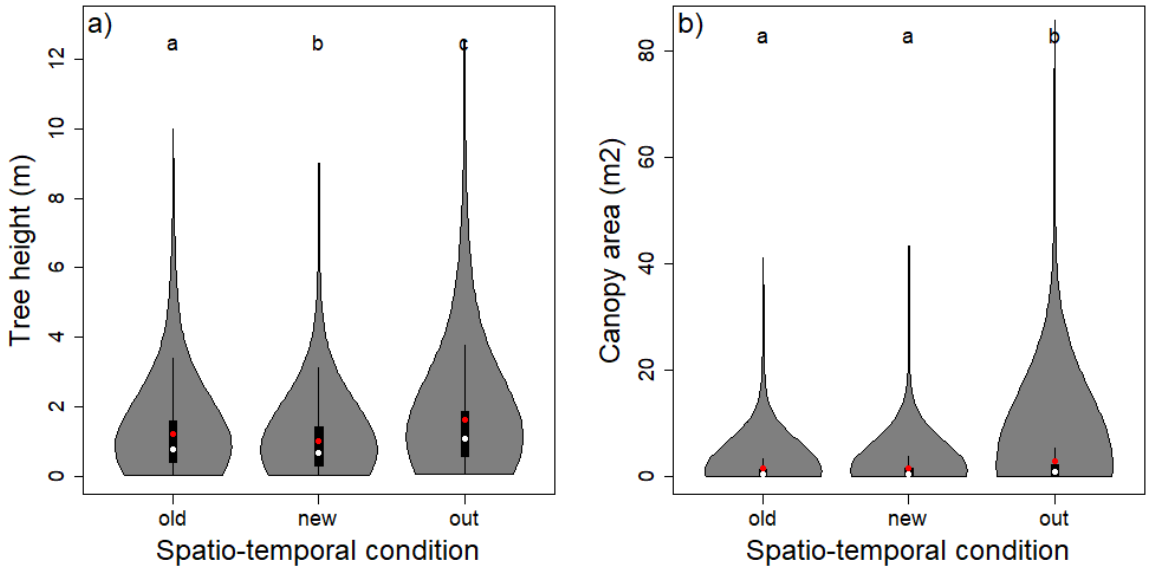
540 **FIGURES**

541 **Figure 1**



542

543 **Figure 2**



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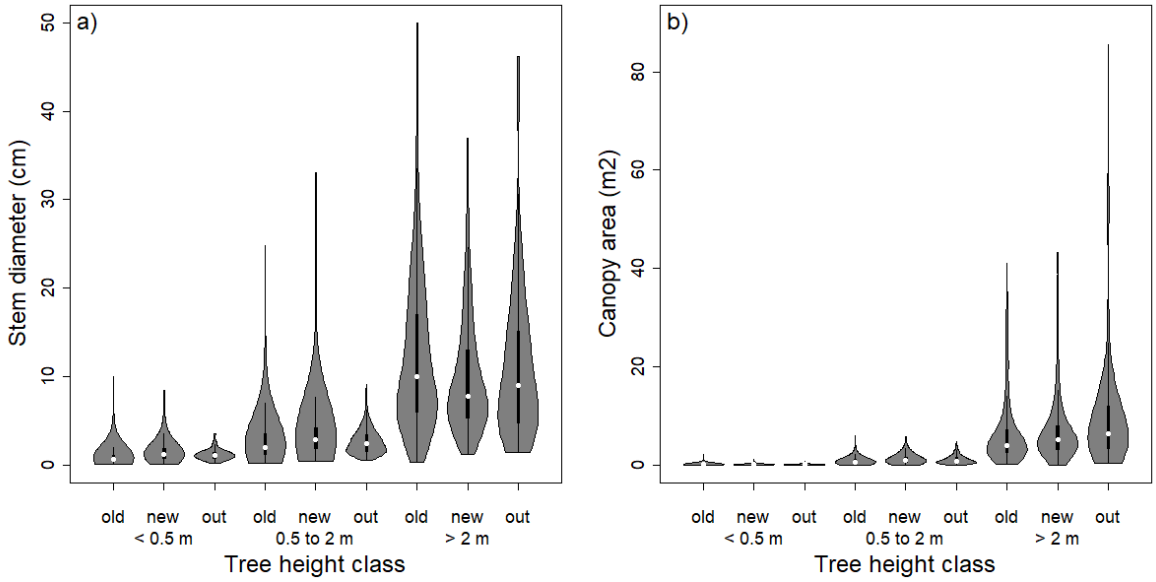
545 **Figure 3**



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547 **Figure 4**

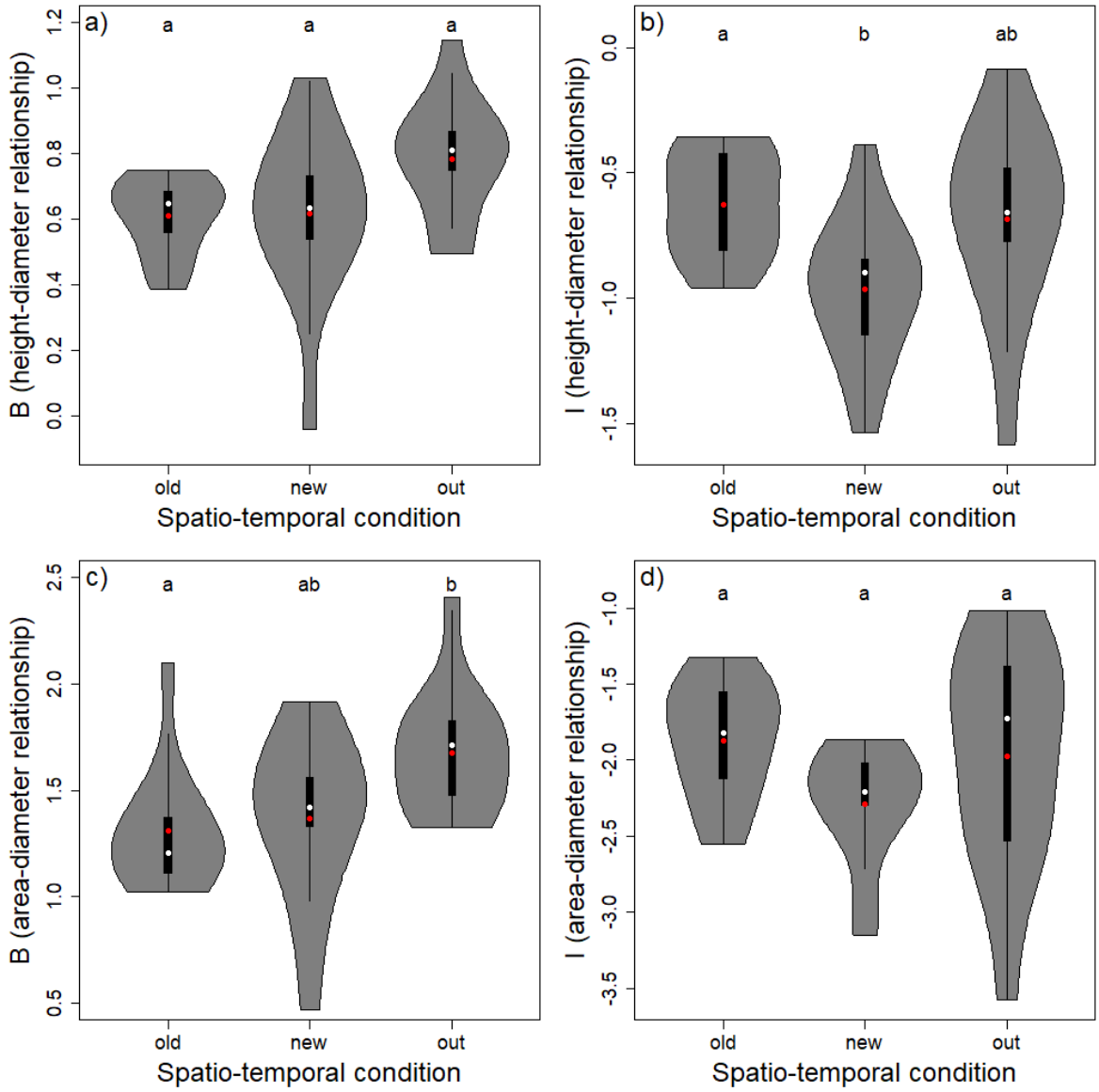

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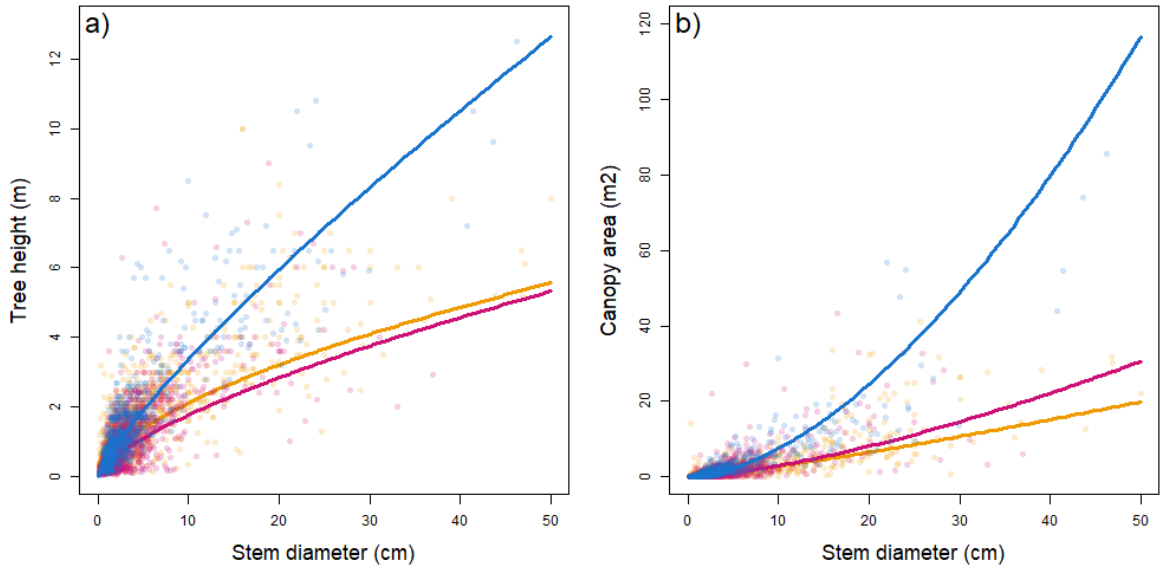
Figure 5


a)
Tree height (m)
0
2
4
6
8
10
12
0
10
20
30
40
50
Stem diameter (cm)
b)
Canopy area (m2)
0
20
40
60
80
100
120
0
10
20
30
40
50
Stem diameter (cm)

ACKNOWLEDGMENTS

We acknowledge and thank Bruce Page, who designed the sampling protocol, and supervised the sampling in 2000-2001. We thank all University of Kwazulu-Natal students and volunteers involved in the 2000-2001 sampling. We thank the fieldworkers who collected the data in 2019 and managed the data for this study: Yentl Swartz, Chris Brooke, Adriaan Venter, Michelle Marais, Jandre Vermaak, Terry-Lee Honiball. We also thank the North-West Parks and Tourism Board for their logistical support for the study.

The 2000-2001 sampling was funded by the Amarula Elephant Research Programme through a donation by Distell (PTY) Ltd, and the University of Kwazulu-Natal, with in-kind support from North West Parks and Tourism Board. Postgraduate Research Scholarship funding from Nelson Mandela University and REHABS funding to DS.

AUTHORS CONTRIBUTION STATEMENT

Conceptualization: LT, DS, JV, HF; **Methodology**: LT, DS, HF; **Formal analysis**: LT; **Investigation**: LT, DS; **Data Curation**: LT, DS, SO, GL, RS, JV; **Writing: Original Draft**: LT, DS, SO; **Writing: Review & Editing**: LT, DS, SO, GL, RS, JV, HF; **Visualisation**: LT; **Resources**: DS; **Funding acquisition**: RS, JV, HF; **Validation**: LT, DS, SO, GL, RS, JV, HF; **Supervision**: JV, HF; **Project administration**: JV, HF.

DISCLOSURE STATEMENTS

Conflict of interest: The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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