



RESEARCH ARTICLE

The hard lives of trees in African savanna—Even without elephants

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Abstract

The ongoing loss of large trees and densification of shrubs are two prevalent processes that take place in African savannas, with profound consequences for their structure and function. We evaluated herbivore impacts on savanna woody communities using a long-term exclosure experiment in the Kruger National Park, South Africa, with three treatments: the exclusion of large mammals only (i.e. elephant and giraffe), exclusion of all herbivores larger than a hare, and areas open to all herbivores. We asked three questions: (1) How did variable exclusion of herbivores affect woody density and structure across the catena (i.e. riparian, sodic and crest vegetation)? (2) Did the exclusion of herbivores result in unique woody species composition? (3) Did herbivore exclusion result in a higher proportion of palatable species? After 17 years, we found that herbivores mainly affected the heights and densities of existing species, rather than leading to turnover of woody species assemblages. Although densities of individuals increased in the full exclosure (350 ha^{-1}), the change was more moderate than expected. By contrast, mixed mega-and meso-herbivores decreased the number of trees and shrubs (decreases of 780 ha^{-1}) via a variety of physical impacts. Meso-herbivores alone, on the other hand, had less impact on individual density (i.e. no change), but limited average height growth and canopy dimensions in certain habitat types. Where elephants are present, they are effective at reducing the density of woody stems to the point of counteracting woody encroachment, but at the same time are actively preventing the persistence of large trees ($>5 \text{ m}$) as well as preventing trees from recruiting to larger size classes. However, the lack of massive recruitment and woody cover increases with elephant exclusion, especially for more preferred species, suggests that factors beyond elephants, such as dispersal limitation, seed predation, and drought, are also acting upon species.

KEY WORDS

exclosure, herbivory, meso-herbivores, tree recruitment, woody species assemblage

INTRODUCTION

Trees are integral to ecosystem functioning in savannas as they provide food and habitat for animals (Dean et al., 1999; Rushworth et al., 2018) and play an important role in increasing local nutrient pools

(Belsky et al., 1993; Ludwig et al., 2001, 2003; Treydte et al., 2009). The continued loss of tall trees in African savannas, especially those taller than 5 m, is a topic that receives much attention (Davies et al., 2018; Levick & Asner, 2013; O'Connor & Goodall, 2017; Shannon et al., 2008, 2011; Smit et al., 2010; Vanak

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et al., 2012). At the same time, however, savannas are also gaining woody cover through thickening or densification of shrubs (Buitenwerf et al., 2012; Stevens et al., 2016, 2017; Zhou et al., 2021). The loss of tall trees in protected areas is mostly the result of increased mortality from local drivers such as elephants, fires, and the interaction of these. The causes of woody thickening of the shrub layer are not always clear and depend on both local context and global processes. Local drivers include fire suppression and lack of megaherbivores and wildlife browsers (Rohde & Hoffman, 2012; Venter et al., 2018). For instance, areas in southern Africa with the lowest recorded woody thickening rates are more arid with elephants (*Loxodonta africana*) present (Stevens et al., 2016). Global drivers include increasing CO₂ and climate change (Buitenwerf et al., 2012; O'Connor et al., 2014; Stevens et al., 2017).

Elephants are major ecosystem engineers and physically alter woody cover and structure with consequences that reverberate through savanna ecosystems (Pringle, 2008; Pringle et al., 2015, 2016). Treefall rates in savannas are significantly higher and canopy cover 15%–95% lower in areas with elephants (Asner et al., 2009; Asner & Levick, 2012; Sankaran et al., 2013; Wigley, Coetsee, Augustine, et al., 2019). Elephants, more than any other herbivore, are responsible for mortality of trees and shrubs through impacts which include debarking, pollarding, and pushing over (Cook et al., 2017; Shannon et al., 2008), although chronic low browsing also results in mortality (Morrison et al., 2016). Previous elephant damage also aggravates fire damage such that existing elephant damage increases future mortality rates significantly in fire-prone systems (Das et al., 2022; Shannon et al., 2008, 2011; Vanak et al., 2012). High elephant impacts have in some cases been associated with a conversion of woodland to grassland (Childes & Walker, 1987; Laws, 1970), but southern African wooded savannas most often converted to a shrub-dominated state (Ferry et al., 2021; Holdo, 2006; Skarpe et al., 2014).

Although elephants keep trees from recruiting through their pruning of seedlings and saplings, meso-herbivores can be just as important in regulating woody recruitment. Analyses of historical data including pollen analyses and dendrochronology suggest that trees recruit when herbivore populations are low, resulting in cohorts of even aged trees with distinct missing size classes (Holdo et al., 2009; Prins & Van der Jeugd, 1993; Staver et al., 2011). Browsers such as impala (*Aepyceros melampus*) are known to intensely predate seedlings (Moe et al., 2009; Prins & Van der Jeugd, 1993; Skarpe et al., 2004). Apart from recruitment, meso-herbivores may also have pronounced effects on adult shrubs and smaller trees. Skarpe et al. (2004) showed that impala and kudu browsed on species that elephants do not favour, such as *Capparis tomentosa* and *Combretum mossambicense*, in riparian woodlands in Botswana. However, there is also substantial overlap between elephant and meso-browsers in niches of species browsed and browsing heights (O'Kane et al., 2011, 2014) and competition with elephant can displace meso-herbivores (Fritz et al., 2002; Lagendijk et al., 2015; Valeix et al., 2008).

Herbivore effects on woody cover are not always detrimental; for instance, elephants may contribute to the dispersal and propagation of certain large savanna tree species, transporting seeds up to 65 km away from the source (Bunney et al., 2017). For some species, seeds not dispersed from the parent suffer high mortality and low germination rates (Chapman et al., 1992; Cochrane, 2003; Midgley et al., 2012; Helm et al., 2009). Herbivores may potentially alter woody community composition through variable impacts on mortality and recruitment. However, previous work on herbivore impacts indicates that herbivores more often change abundances of existing woody species and decrease structural diversity, rather



than create unique woody communities that are dissimilar in species composition (Levick & Rogers, 2008; Scogings et al., 2012; Trollope et al., 1998; Wigley et al., 2014).

Herbivore exclosure experiments offer a unique opportunity to quantify herbivore impacts on savanna woody plants, especially when they are maintained long enough to observe slow, decadal-scale responses. During 2002, two large exclosures, one excluding any animal larger than a hare, and another that excludes only elephant and giraffe, were erected along the Sabie River in Kruger National Park, South Africa. We aim to quantify the impacts of about 17 years of full and partial protection from herbivores on the structural, compositional, and functional characteristics of woody communities, spanning riverine to upland vegetation. We ask three main questions: (1) How did the exclusion of herbivores affect woody density and structure across the catena? We predicted that after being released from browsing, trees would increase in size but that density-dependent factors would limit massive increases in individual counts. We were unsure whether protection against elephant would result in an increase in woody density because previous work has suggested displacement of meso-herbivores into the partial exclosure possibly due to competition with mega-fauna (Case et al., 2019). (2) Did the exclusion of herbivores result in unique woody species composition? We predicted that some species would increase or decrease in abundance but that no unique communities in terms of species would establish (Wigley et al., 2014). Lastly (3) Did herbivore exclusion result in a higher proportion of palatable species? We expected the abundance of palatable species to decrease with herbivore presence and especially so in the presence of elephants and giraffe.

METHODS

Study site

The study was undertaken in the south-central region of the Kruger National Park (KNP), which is situated in the north-east corner of South Africa. The Nkuhlu exclosures, named after the picnic site across the river, are situated on the banks of the Sabie River (corners of the site are: S –24.982218, E 31.770729; S –24.982800, E 31.778353; S –24.989403, E 31.776630; S –24.994300, E 31.771321). Rain falls mainly between October and April and the mean annual rainfall (over 105 years) for the area is ~541 mm (Van Wilgen & Herbst, 2017), although the worst drought on record occurred during 2015/2016 with 2016–2019 receiving below-average rainfall (Malherbe et al., 2020). Average long-term daily minimum and maximum temperatures are 20.6°C and 32.6°C in January and 5.7°C and 25.9°C in July (Scholes et al., 2001). However, average temperatures have increased by 0.85°C between 1960 and 2009 and by 1.7°C between 2013 and 2016 (Van Wilgen & Herbst, 2017). Additionally, the number of days that the Extreme Climate Index exceeded the 90th percentile reached record highs in the period between 2015 and 2018 (Malherbe et al., 2020). The soils of the region are derived from the underlying Nelspruit granite suite consisting of migmatite, gneiss, and granite, which give rise to nutrient-poor sands (Barton et al., 1986). Paterson and Steenekamp (2003) described soils and produced a soil map for the Nkuhlu long-term exclosure site that shows that soils are generally consistent with catena topography (Siebert & Eckhardt, 2008). Soils are mostly shallower on the crests (Eutric Leptosols and Regosols), apart from one area on the crest of the partial exclosure, which is underlain by deeper Arenosols. The sodic duplex soils have sandy loam topsoil over sandy clay loam subsoil (Calcisols and Luvisols) which



are high in sodium with an effective depth to 1200 mm. The strip of alluvial (Arenic Fluvisol) soils closer to the river are deeper, in some places >1500 mm.

The Nkuhlu exclosure site falls within the Granite Lowveld vegetation type (SVI 3), within the Lowveld Bioregion of the vegetation map of South Africa (Rutherford et al., 2006). Siebert and Eckhardt (2008) divided the vegetation of the site further into five plant communities and 10 sub-communities, of which the wetland types (i.e. seasonal pans and reedbeds) have no relevance to this study. The remaining three plant communities represent distinct communities along the catena which are closely related to hydrology and soil type: from the riverbank woodland on alluvial soil (hereafter, riparian), through the sodic bushveld on duplex, sodium-enriched soil (hereafter, sodic), to the crest savanna on coarse sands overlying granitic rock (hereafter, crest; see Figure 1 for plant communities). The moderately closed riparian woodland along the banks of the Sabie River is characterized by large jackal berry (*Diospyros mespiliformis*), *Kigelia africana* and *Trichilia emetica* trees, *Grewia flavescens* in the shrub layer and *Panicum maximum* dominating the herbaceous layer among ~30 different forb species. In the northern section of the riverbank (i.e. stretching along the central control area and partial exclosure), the riparian woodland changes in structure from a closed woodland to a dry, sandy riverbank scrub where large, evergreen trees are less prominent and shrubs, such as *Gymnosporia senegalensis* and *Flueggea virosa* dominate the woody layer.

Situated on the bottomlands of the granitic catena where it borders the riparian woodland and -scrub communities, the *Sporobolus nitens-Euclea divinorum* dry sodic savanna community covers ~25% of the Nkuhlu exclosure site. The sodic community is dominated by woody species, such as *Acacia grandicornuta*, *Pappea capensis*, *Rhigozum zambesiacum*, *Spirostachys africana*, *Euclea divinorum*, and the iconic succulent shrubs, *Adenium multiflorum* and *Ad. swazicum*. The upland dry, mixed savanna crest vegetation covers large parts of the study area (~43%) and is distinctly different from the other communities. Most of the dominant woody species are broad-leaved, deciduous trees and shrubs of which *Combretum apiculatum*, *Combretum zeyheri*, *Terminalia sericea*, *Grewia bicolor* and *Cissus cornifolia* are most common. Fine-leaved species include *Acacia nigrescens*, *Ac. exuvialis* and an abundance of *Dichrostachys cinerea*.

As the Nkuhlu sites is situated on a large perennial river, the area is favoured by animals. To get an indication of animal presence in the different treatments, camera traps were erected in January 2020 and removed in March 2022. From preliminary observations, it is clear that the full exclosure was really efficient in keeping animals out as over the period, there were only a couple of kudu (*Tragelaphus strepsiceros*) and bushbuck (*Tragelaphus scriptus*) detected, which were then removed from the exclosure as soon as possible. Both control areas had many animal observations which included frequent visits from elephant herds. Long-term elephant densities for the study area are 39–40 km⁻² (Louw et al., 2021). Other species often observed on the camera traps were hippo (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), impala, zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), kudu and giraffe (*Giraffa camelopardalis*) who were passing through, but also spent large amounts of time feeding in the area. A similar pattern was observed in the partial exclosure, but differed in that no elephants or giraffe were seen and on a few occasions, a lone black rhino (*Diceros bicornis*) was observed in the evenings. As in the control many of the animals spent large amounts of time in this area, feeding and preliminary observations suggest that impala preferred the partial exclosure to the open areas.

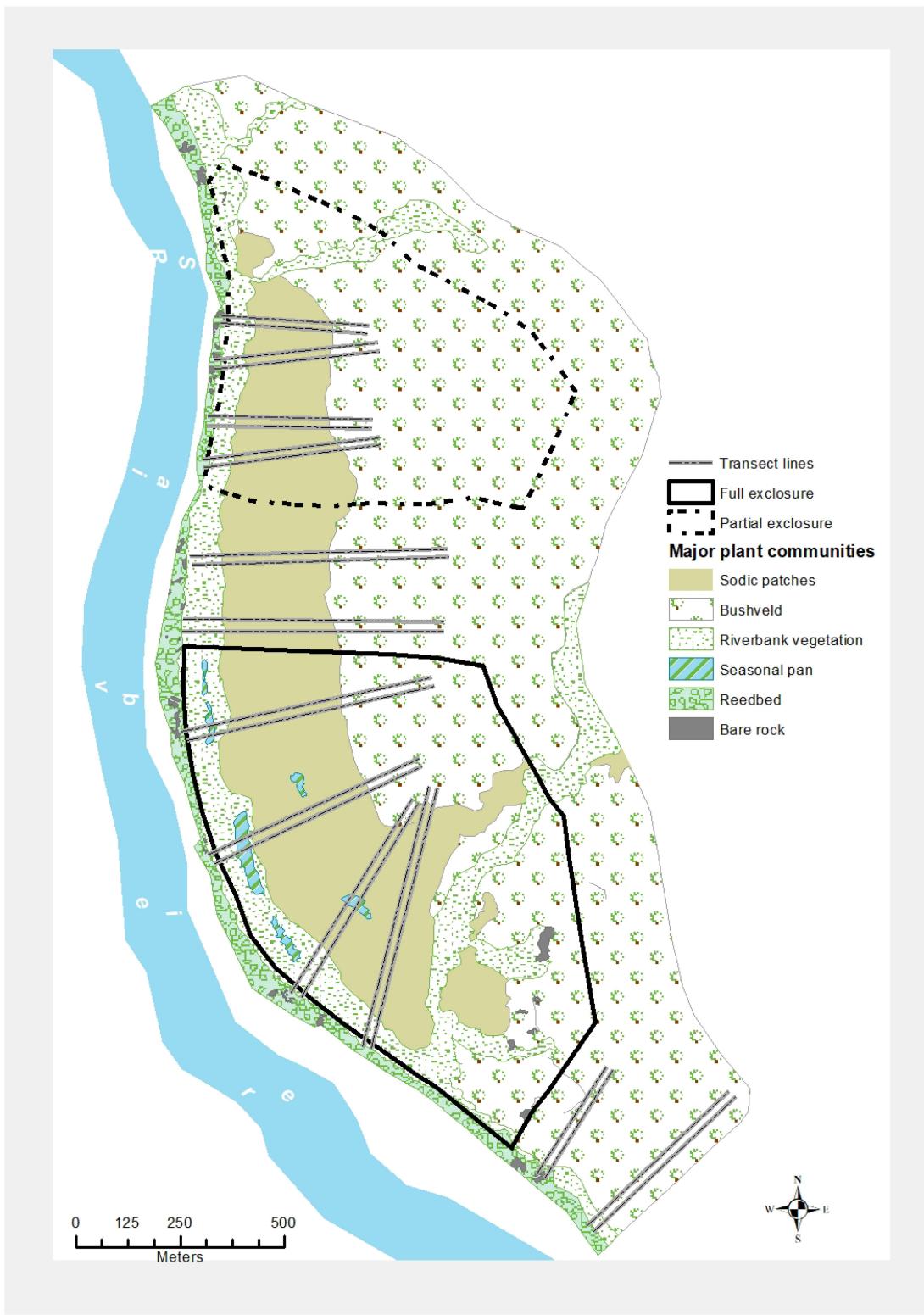


FIGURE 1 Map of study site with vegetation communities from Siebert and Eckhardt (2008) with experimental layout and transects overlaid onto these. For the purposes of this study, riparian plots were placed in “riverbank vegetation” and crest plots in “bushveld”

Surveys

One of the initial objectives of the experiment was to document post-flood recovery of vegetation; a large flood removed much of the vegetation in the channel of the Sabie River in 2000. However, it is impossible to maintain



exclosures in the footprint of flooding because subsequent floods will keep on damaging the infrastructure. As a result, most of the experimental vegetation effects are away from the river, spanning riparian vegetation (on the levee away from the channel) to the crest. The study site is divided into three main treatment levels; a fully electrified 70 ha "full" exclosure that excluded any animal larger than the size of a hare (hereafter F), a 45 ha "partial" exclosure with two cables and electric wiring at 1.8 and 2.2 m above ground (hereafter P), and two areas open to herbivores (one between the two exclosures and another east of the full exclosure, hereafter O). Even though the full exclosure is in theory supposed to exclude every animal larger than a hare for most of the time, access is gained by porcupines (*Hystrix africaeaustralis*) who dig under the fence, and Chacma baboon (*Papio ursinus*) and vervet monkey (*Chlorocebus pygerythrus*) who find a way over the fence, as well as the occasional antelope as mentioned above. Within each treatment, four permanently marked transects span across the catenal gradient (Figure 1). The number of 10 × 20 m plots in each catenal position varied due to the area of the community and the length of the transect; for example, the narrow riparian strip could only accommodate 5–6 plots per transect, while 3–14 plots were fitted on the crests.

The sampling protocol is described in detail by O'Keefe and Alard (2002) and Scogings et al. (2012). Each transect was originally laid out using a differential GPS geo-referenced to a nearby base station and permanent 25 × 25 × 50 cm concrete markers built at the ends of each transect. Along each transect, steel rods (12 × 500 mm) every 20 m, 5 m south of the transect, mark the location of sampling plots, with the short side parallel to the transect. All four corners of each plot are also permanently marked. There is a total of 82, 59 and 77 sampling plots marked, in the open, partial and full exclusion treatments, respectively. Within each 200 m² plot, all woody plants rooted inside a plot were recorded in terms of species name, height, and canopy dimensions (width and breadth) per individual. The first sampling was done shortly after fences were erected, that is, in 2002, and repeated in 2019. For multi-stemmed species, stems <50 cm apart were considered as one plant. We considered woody vegetation (i.e. trees/shrubs) to be all species that have a woody stem and an upright growth-form as the dominant form (although some of the shrubs may creep on occasion). However, if a creeping or liana form was the dominant form, the species was omitted from the analyses.

Species were sorted into two categories of palatability (low/moderate and high) based on what is available in the literature (O'Connor et al., 2007; Owen-Smith & Cooper, 1987; Scogings et al., 2012; Wigley et al., 2014, 2018; Wiseman et al., 2004), augmented with our own observations of whether the species is a preferred browse species at the study site and elsewhere in the Kruger National Park (Appendix S1).

Half of the exclosures are burned (i.e. 2 of 4 transects) with a managed fire every 5 years. Should a fire event occur in the area surrounding the exclosure site, it is allowed to enter the open control area east of the full exclosure; however, fire is excluded from the control area between the two exclosures. Both exclosures burned at the start of the experiment, the full exclosure burned again in 2007, 2012, and 2017, the partial exclosure burned in 2012 and 2017 but not in 2007 due to a lack of flammable material.

Statistical analyses

Initially, fire was included in analyses, but fire was omitted as treatment because (i) the two open areas have different intensities of animal utilization which makes it impossible to distil the fire vs herbivory intensity effects,



and (ii) as also shown by Combrink (2016), initial analyses indicated negligible effects of fire on woody abundances and heights (see Figure S1). We acknowledge that fire may have effects on individual species and that fire effects may interact with catenal position to affect some species responses. Thus the decision to focus rather on changes between 2019 and the initial surveys. The study is a manipulative experiment with no replicates per “treatment”; hence, the study is inherently pseudoreplicated (Hurlbert, 1984).

All analyses were performed using R (version 3.5.1, R Core Team, 2020). To analyse the count data, we used mixed effects models on data from the two sampling periods with year, treatment, and catenal position (i.e. riparian, sodic, crest) as fixed factors and their interactions in the full model, and with plot nested in transect as random factor. As the count data had a non-normal distribution, generalized linear mixed modelling was used (GLMM) following Brandvain (2022). Numerous families (including negative binomial and Poisson) and link functions were evaluated and optimal parameters were selected based on the Akaike information criterion (AIC). A negative binomial family was selected for the overdispersed count data of individuals (non-zero-inflated) (glmmTMB, Brooks et al., 2017). As the glmmTMB did not converge with a three-way interaction included as fixed effect, we reran the model using the three pairs of two-way interactions (treatment \times year, treatment \times catenal position, and catenal position \times year) as fixed effects.

To compare heights across treatments, stem diameters, and canopy area, as well proportions of palatable to less palatable species (the sum of palatable counts divided by less palatable species counts) and heights of palatable species, we used linear mixed effects models on change data (Δ 2019-2002) with treatment and catenal position (e.g. riparian, sodic, crest) and interaction as fixed factors in the full model, and with transect as random factor (as data were summarized at level of the plot, using lmer [lme4 package, Bates et al., 2015]). The significance of fixed factors and interactions were based on the model output (F-ratio and p values) and the inclusion of the random factor was based on ranova results (function in the lmerTest package, ranova produces an anova-like table of random effects via likelihood ratio tests, Kuznetsova et al., 2017). Tukey post-hoc tests were then performed for pair-wise comparisons using the least square means (lsmeans using lmerTest, Lenth, 2016) or estimated marginal means (emmeans, Lenth, 2021), which depended on the number of observations. Standardized residuals were evaluated graphically using predicted vs level plots.

Species composition among the treatments in 2002 and 2019 were visually compared for each catenal position using non-metric multidimensional scaling (NMDS) in R (vegan) (Oksanen et al., 2017). NMDS is an effective method for multivariate data reduction and visualization of ecological community data sets and is considered to be one of the most powerful ordination techniques available (McCune et al., 2002), well suited to data that are non-normal or are on arbitrary or discontinuous scales (McCune et al., 2002). To compare communities across treatments and years, we conducted a permutational multivariate analysis of variance (PERMANOVA) using the adonis2() function in the vegan package. PERMANOVA is a geometric partitioning of multivariate variation in the space of a chosen dissimilarity measure according to a given ANOVA design, with p -values obtained using appropriate distribution-free permutation techniques (Anderson, 2014). This non-parametric multivariate statistical permutation test is used to compare groups of objects and test the null hypothesis that the centroids and dispersion of the groups are equivalent. We initially ran the PERMANOVA analysis for all community data, with catenal position, treatment, year,



and an interaction between treatment and year as independent variables. Because catenal position was by far the greatest determinant of differences between groups, we then conducted the same PERMANOVA analysis on subsets by catenal position (with treatment, year, and a treatment by year interaction as independent variables) to examine compositional differences within habitats.

RESULTS

How did the exclusion of herbivores affect woody density and structure across the catena?

Treatment and catenal position as well as the interaction between treatment and year and treatment and catenal position contributed significantly to variability in counts (Figure 2, both interactions $p < 0.0001$). Averaged across all treatments (across catenal positions), there were no differences in individual counts per plot across years; however, treatment determined whether plots gained or lost woody individuals. Comparing the years 2002 and 2019, counts increased in the full enclosure (from 52.6 ± 4.61 to 59.7 ± 5.12 per plot or 355 ha^{-1}) and decreased in the open treatments (from 55.4 ± 4.54 to 39.8 ± 3.43 per plot or 780 ha^{-1}), with little change observed in the partial enclosure. As a result of these changes, in 2019, the full enclosure (59.7 ± 5.12 , $p = 0.01$) had more individuals per plot than the open treatment (39.8 ± 3.43). Averaged across years, the most pronounced differences were seen on the sodic sites where both the full enclosure (57.8 ± 5.14 , $p < 0.0001$) and partial enclosures (41.3 ± 4.28 , $p < 0.0001$) had higher counts than the open areas (18.9 ± 2.80) and the full enclosure sodic areas also had higher counts than inside the partial enclosure ($p = 0.03$).

For changes in height; treatment, catenal position, and their interaction ($p < 0.0001$ for main effects and $p = 0.0002$ for interaction) all contributed significantly to the variability in height change. In general, trees gained the most height when fully protected from larger herbivores (riparian = $+0.68 \text{ m} \pm 0.14$, sodic = $+0.47 \text{ m} \pm 0.13$, crest = $+0.51 \text{ m} \pm 0.14$), although the increase in heights overall was highest in riparian trees in the partial

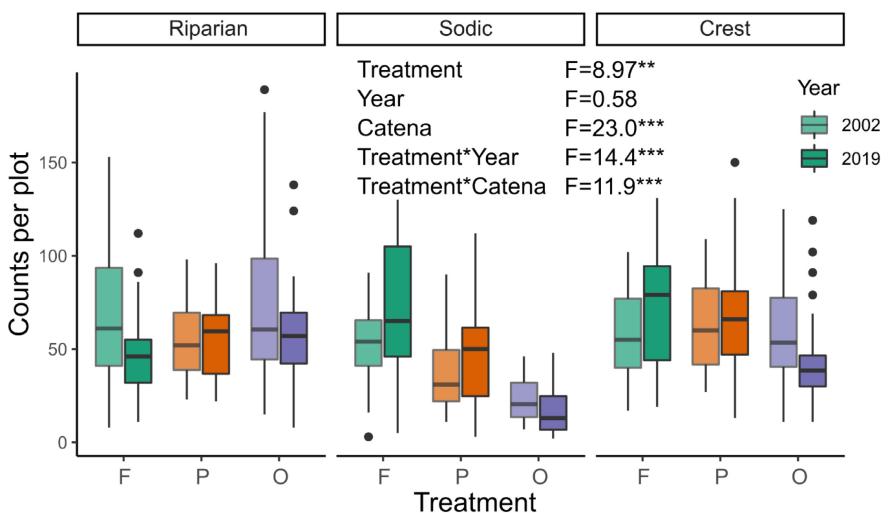


FIGURE 2 Counts of individual live trees (which included shrubs but not lianes) per plot for the two sampling periods for each treatment, shown here for each catenal position separately (F = full enclosure, P = partial enclosure, O = open areas). The solid line in each box denotes the median, the top and bottom of the boxes depict the third and first quartiles, respectively, ends of vertical lines denote the maximum and minimum values, or 1.5-fold the interquartile range (whichever is smaller), and dots represent outliers. In 2019, the full enclosure (59.7 ± 5.12) had more individuals per plot than the open treatment (39.8 ± 3.43 , $p = 0.01$).

exclosure ($+0.88 \text{ m} \pm 0.14$) (Figures 3a). Apart from the riparian areas, heights in the partial exclosure did not change on the crests and sodic sites and changes in mean height were negligible when open to herbivores (Figure 3a). These changes resulted in heights significantly increasing in both the exclosures when compared to the open in riparian areas ($F - O, p = 0.0009$ and $P - O, p < 0.0001$). On the sodic areas, the increase was significant in the full exclosure when compared to the other two treatments ($F - P, p = 0.005$ and $F - O, p = 0.006$). Similarly, crest vegetation had taller individuals in both exclosures compared to the herbivore exposed area, although the difference between the partial exclosure and the open areas was marginal ($F - O, p < 0.0001$ and $P - O, p = 0.06$).

For stem diameter changes, the interaction between treatment and catena was significant ($p = 0.01$) but not the main effect of treatment ($p = 0.14$), with no significant changes in stem diameters when comparing treatments

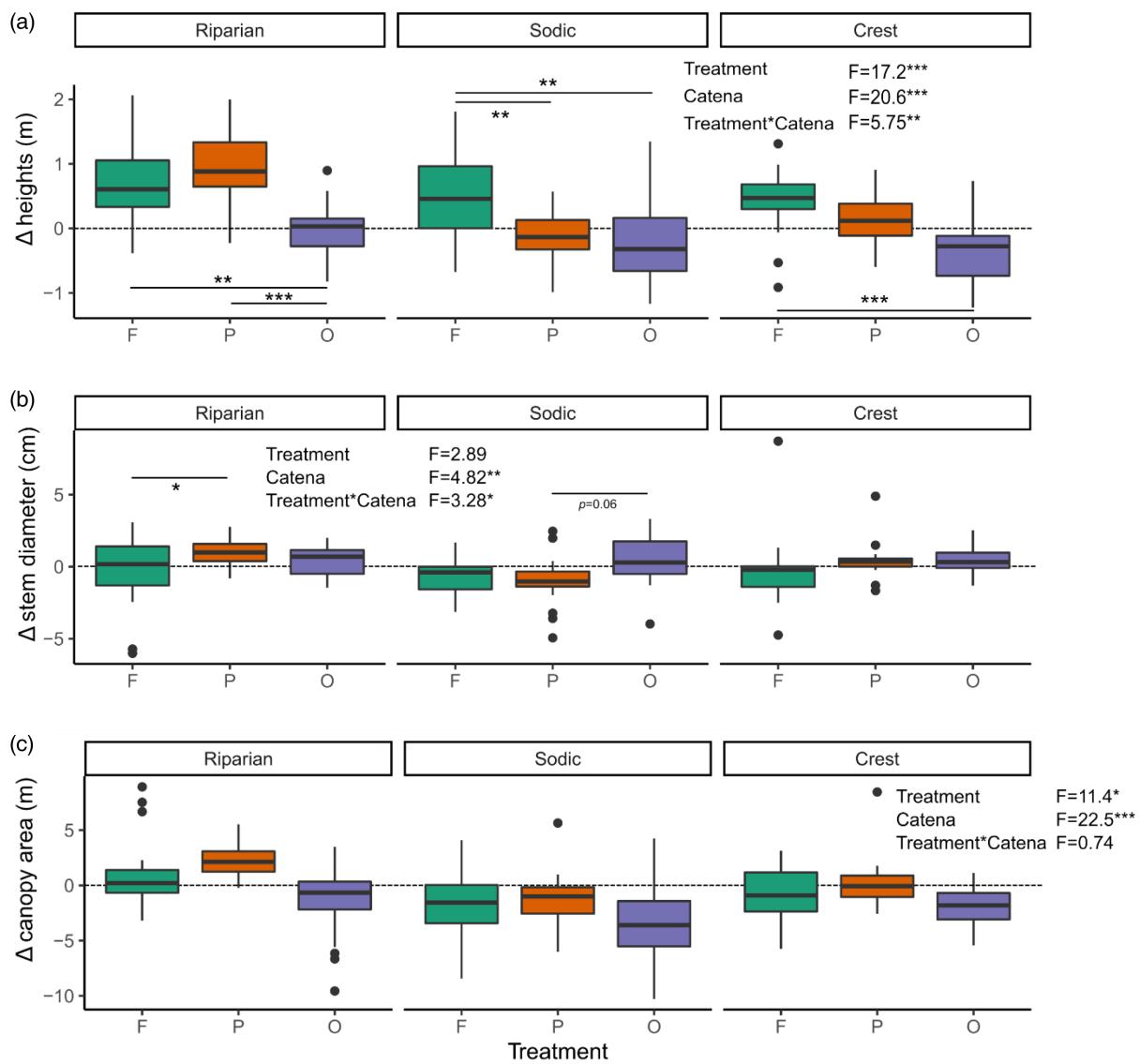


FIGURE 3 Changes in (a) height (m), (b) stem diameter (cm), and (c) canopy area (m²) over 17 years at the Nkuhlu exclosure site for three catena positions; riparian, sodic, and crest (F = full exclosure, P = partial exclosure, O = open areas). For canopy area, canopies were larger on average in exclosures compared to areas where herbivores are present ($F - O, p = 0.01$ and $P - O, p = 0.001$). The solid line in each box denotes the median, the top and bottom of the boxes depict the third and first quartiles, respectively, ends of vertical lines denote the maximum and minimum values, or 1.5-fold the interquartile range (whichever is smaller), and dots represent outliers. The black dotted line represents no change. p -Values marked with an * significant at a level of $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$



overall. For instance, in the partial exclosure, stems widened by 1.05 cm in the riparian but decreased on average by 1.37 cm on sodic sites ([Figure 3b](#)). The result of these changes were marginally wider diameters in partial exclosure stems when compared to stem diameters in the full exclosure ($p = 0.05$). For canopy area changes across catenal positions (there was no significant interaction between catenal position and treatment), individuals in the exclosures changed very little (e.g. partial exclosure gained on average 0.28 m^2 , while the change in canopies of trees in the full exclosure were not meaningfully different from 0, [Figure 3c](#)). However, individuals open to herbivores lost on average 2.23 m^2 of canopy area. The large loss in canopy area when herbivores are present resulted in canopies being significantly larger on average in both exclosures compared to areas where all herbivores are present ($F - O, p = 0.01$ and $P - O, p = 0.001$).

Did the exclusion of herbivores result in unique woody species composition?

The PERMANOVA results showed that vegetation composition at the different catenal positions explained most of the variation among communities, with treatment and year (and the interaction) together contributing less ($R^2 = 0.14$ for catenal position, vs. $R^2 < 0.06$ for each other variable). PERMANOVA analyses within catenal habitats indicated that communities differed between treatments for both surveys and changed over time ([Table 1](#), [Figure 4](#)). However, there was no significant interaction between year and treatment within catenal habitats, indicating that herbivore treatment did not systematically mediate compositional change.

Examining the variety of responses of common species across time illustrates why there was little systematic pattern detected in the direction of community turnover in response to herbivore exclusion treatments. Seven common species decreased regardless of protection from herbivores; six did respond clearly to herbivore protection (increasing in numbers with both full and partial protection, but decreasing when fully accessible to herbivores); while, 10 others showed variable or idiosyncratic responses to herbivory ([Figure S2](#)).

Are palatable species increasing with full protection?

There were no significant differences among treatments in the change of the proportion of palatable species counts (over all species counts) over

TABLE 1 PERMANOVA results by habitat type

Habitat	Predictor	R ²	F	p
Riparian	Treatment	0.12	9.48	0.001*
	Year	0.05	8.61	0.001*
	Treatment*Year	0.02	1.46	0.09
Sodic	Treatment	0.17	12.3	0.001*
	Year	0.02	2.22	0.015*
	Treatment*Year	0.02	1.35	0.13
Crest	Treatment	0.12	11.5	0.001*
	Year	0.03	6.54	0.001*
	Treatment*Year	0.01	1.24	0.21

Note: "Treatment*year" indicates an interaction between herbivore treatment and year. p-Values marked with an asterisk were significant at a level of $p < 0.05$.

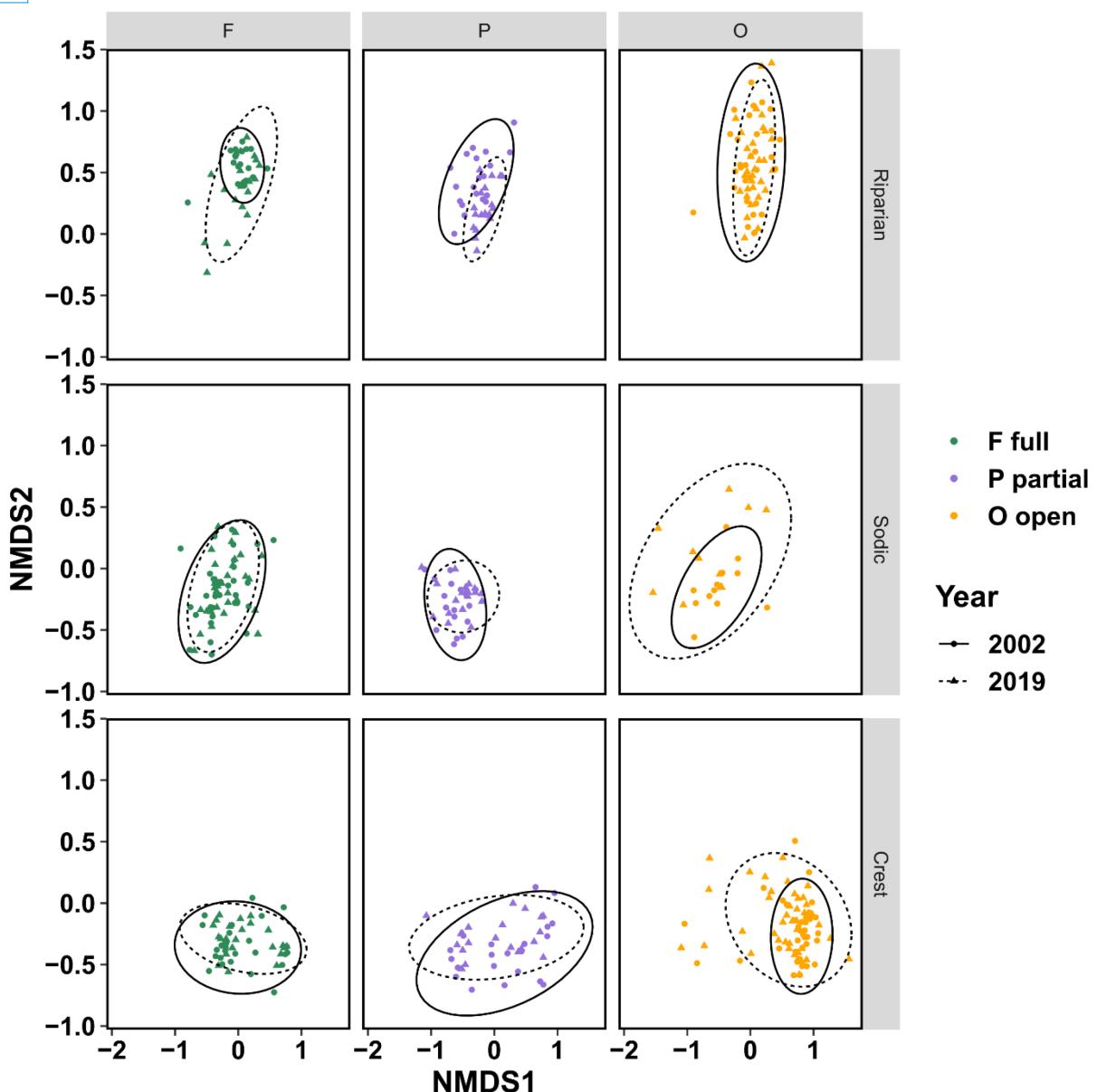


FIGURE 4 Non-metric multidimensional scale plot of abundance data per plot at each catena position, for the three treatments for both survey years. An initial run was made using a three-dimensional space, Bray-Curtis distance measure and 100 iterations. To find the lowest number of axes at which the reduction in stress gained by adding another axis was small, we examined a plot of stress versus iteration. A final run of 50 iterations was made using three axes with a randomly selected starting configuration. The stress obtained from the data was compared to the stress from 50 runs of randomized versions of data. For the NMDS ordination, the greatest reduction in “stress” was achieved with a three-dimensional solution. The final NMDS solution had a stress value of 0.17.

time ($p > 0.05$), with the only significant change being an increase in the proportion of palatable species in the riparian when fully protected compared to plots open to all herbivores ($p = 0.04$, Figure 5a). Regardless of statistical significance, some plots on the sodic sites open to herbivores lost over 25% of their palatable individuals. Palatable species heights on the other hand were significantly impacted by herbivores; fully protected palatable species grew taller across the catena ($\Delta + 0.39$ m to 0.82 m depending on position on catena), while excluding elephant and giraffe resulted in palatable species growing taller in riparian areas ($\Delta + 0.84$ m \pm 0.13). These changes resulted in individuals in open plots in riparian areas being on average shorter than those in the exclosures (Figure 5b, $p < 0.001$). On sodic sites, the full exclosure individuals were

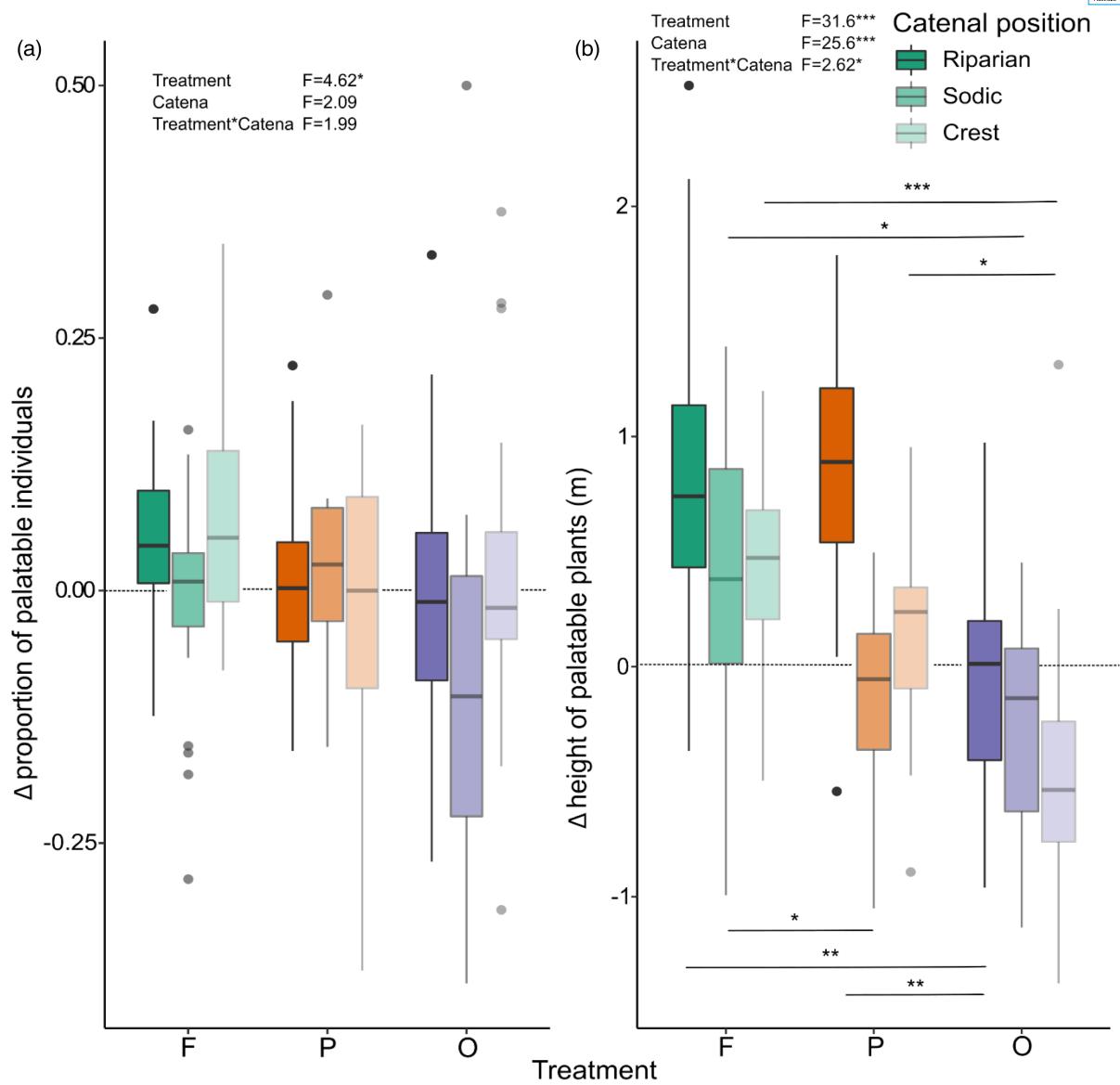


FIGURE 5 (a) Changes in the proportion of palatable individuals to less palatable individuals with treatment across the catena, (b) the changes in height (m) of individuals belonging to palatable species (F = full exclosure, P = partial exclosure, O = open areas). For A, the only significant change was an increase in the proportion of palatable species in the riparian when fully protected compared to plots open to all herbivores ($p = 0.04$). The solid line in each box denotes the median, the top and bottom of the boxes depict the third and first quartiles, respectively, ends of vertical lines denote the maximum and minimum values, or 1.5-fold the interquartile range (whichever is smaller), and dots represent outliers. The black dotted line represents no change. p -Values marked with an * significant at a level of $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$

on average taller than those of partial and open areas (F-P, $p = 0.009$ and F-O, $p = 0.002$). On crests, palatable individuals open to all herbivores were shorter than those in exclosures (F-O, $p < 0.0001$ and P-O, $p = 0.002$).

Additionally, we also looked at patterns of individual key palatable species, such as *Sclerocarya birrea*, *Lannea schweinfurthii*, and *Dalbergia melanoxylon* because of concerns related to their numbers in areas exposed to elephants (Helm & Witkowski, 2013; Wigley et al., 2014). For these three species, full protection had variable outcomes; *L. schweinfurthii* increased with 17 individuals (35 ha^{-1}), *D. melanoxylon* did not change much (increased with 1 individual) and *S. birrea* decreased from 5 to 2 individuals.

DISCUSSION

Variable protection against herbivores resulted in the following main trends over almost 18 years with respect to tree density and size: woody density (i.e. individuals) generally increased in the full enclosure, and trees and shrubs grew taller, while when open to all herbivores, individuals decreased (by 780ha^{-1}), trees were also shorter, and mean canopy area decreased. We were unsure how partial exclusion would affect woody vegetation; protection against mega-fauna resulted in no significant changes in density of individuals over time, but individuals gained height in the riparian areas and on the crests. As expected for species patterns, although most species decreased in abundance when fully accessible to all herbivores (apart from *F. virosa* and *G. maranguensis*), no unique changes to woody community composition occurred with and without protection against herbivores. Lastly, and counter to what we predicted was that the ratio of very palatable to less palatable species did not differ much with herbivore treatment. However, heights of palatable species increased when fully protected, decreased when accessible to all herbivores, and had variable responses when partially protected.

Woody densities in savannas generally decrease when exposed to intense browsing (Bakker et al., 2016; Goheen et al., 2018; Mosugelo et al., 2002; Sankaran et al., 2013; Wigley et al., 2014). Despite this general trend, there are places in the Kruger National Park where woody thickening proceeds even though a full suite of extant herbivore species is present (Case & Staver, 2017; Zhou et al., 2021). However, herbivory, including browsing by elephants, was sufficiently intense to counter woody thickening in the present study as the treatments open to all herbivores lost individuals. Although not quite to the extent that expected (Bakker et al., 2016), woody individuals increased in the full enclosure. Species that were responsible for these increases in woody densities included a thickening of common species such as *A. grandicornuta* and *D. cinerea* (Figure S2). *D. cinerea* is one of the main encroacher species across southern African savannas and also in KNP (Zhou et al., 2021). Although previous work has suggested that *D. cinerea* is stimulated by disturbance and decrease in exclosures or grow slower (Wigley et al., 2014), this was not observed at the Nkuhlu enclosure site. *D. cinerea* increased quite significantly when protected, either fully against all herbivores or partly against elephant and giraffe. Wigley et al. (2014) reported large decreases of *D. cinerea* in older exclosures (~50 years) in the KNP. It is possible that this species may increase initially when protected from browsers and then be regulated by density-dependent processes and self-thinning as time without disturbance progresses (Roques et al., 2001; Sea & Hanan, 2012). Roques et al. (2001) showed that in mono-dominant stands of *D. cinerea*, once 40% cover is reached (i.e. $2400\text{ individuals ha}^{-1}$), mortality, not thickening, is the prevalent process over time.

Rainfall was below-average for the last 5 years of the study and the most extreme drought on record took place during 2015/2016 (Malherbe et al., 2020; Swemmer et al., 2018). Together with below-average rainfall, the highest temperatures on record were also logged during the drought period. For instance, the number of heat wave days ($>35^\circ\text{C}$) increased between 50% and $>100\%$ when compared with the long-term average heat wave days per annum (Malherbe et al., 2020). The dry conditions may have contributed to changes in density of drought-sensitive species such as *D. cinerea* between the start and end points of this study. *D. cinerea* and to a lesser extent, *A. grandicornuta* (48 in the full enclosure, 108ha^{-1} and 19 in the partial enclosure, 43ha^{-1}), had mortalities that could not be attributed to herbivore damage (i.e. standing dead without obvious damage) in the



2019 survey. In the full exclosure where *D. cinerea* occurred in the greatest numbers, mortality was more than double (366 in full exclosure, 830 ha^{-1}) compared to areas open to herbivores (146 in the open areas, 330 ha^{-1}). Previous work has shown this species to be vulnerable to drought, i.e. Case et al. (2019, 2020) found high mortality after the 2015/2016 drought in KNP and low growth rates during the drought. Even though *D. cinerea* was the species most obviously impacted by drought, it is not impossible that smaller individuals of other species that died during the drought, may have been overlooked or have already disappeared due to decomposition or termite activity by 2019.

The drought could not explain, however, why woody density increases were low with full protection and recruitment of new trees appeared quite limited. Other studies have shown slow recovery on bare soils after herbivore exclusion, although woody density increased in general (Augustine et al., 2019). This is the result of limited and slow colonization on patches that were initially without cover, because of low water infiltration caused by sealed surface soils (Augustine et al., 2019; Goheen et al., 2018). Also, high competition from grass is particularly limiting to savanna tree seedling growth (February et al., 2013; Goheen et al., 2004; Sea & Hanan, 2012) and although we do not have data for grass biomass, herbivore exclusion has strong effects on grass biomass and cover at other savanna exclosures in the region (Staver & Bond, 2014; Wigley et al., 2020).

Work from elsewhere in southern African savanna suggests that the presence of herbivores, and specifically the presence of impala, constrain tree height and hinder small trees from “escaping” the browse trap and growing into larger trees (Staver & Bond, 2014; Voysey et al., 2020). This may result in a landscape that appears to have low woody cover but should result in fast tree growth and much increased canopy cover once released from browsing (Staver & Bond, 2014; Voysey et al., 2020). Previously, there was no general increase in mean heights after 5 years of full exclusion at Nkuhlu, and Scogings et al. (2012) predicted correctly at the time that 5 years may be too short a period to observe changes. After 17 years, we found there were pronounced increases in heights of trees with full exclusion and also with partial exclusion in the riparian area. These results were also mirrored by very palatable species in general where heights increased with full protection. Regardless of some increases in heights and canopy dimensions of certain individuals (in the riparian) when protected from mega-fauna but accessible to meso-herbivores, meso-herbivores seemed able to counter any increases in woody densities (of individual counts). This may support Case et al. (2019) when they suggested high usage of the partial exclosure by smaller herbivores in order to avoid competition with mega-fauna.

Previous work on herbivore impacts suggest that herbivores more often change abundances of existing woody species and decrease structural diversity, rather than create unique woody communities that are dissimilar in species composition (Levick & Rogers, 2008; Scogings et al., 2012; Trollope et al., 1998; Wigley et al., 2014). Our results support these findings. Differences in plant communities depended most strongly on catenal position and were present at the onset of the experiment. Over time, community composition was dynamic, but according to permutational analyses did not change in any systematic, directional way with respect to herbivore protection. This was a result of species decreasing over time regardless of herbivore treatment (Figure S2a), or responding idiosyncratically to protection from herbivores (e.g. no predictable pattern, Figure S2c).

Certain species, however, are clearly much preferred by herbivores, and some to the extent that they are a major conservation concern in areas with high herbivore densities. Marula (*Sclerocarya birrea*) is one such species,



and a key question for conservation is whether this species was able to recruit once herbivores were excluded. Marula bark is much favoured by elephants and although marula has high capacity for bark recovery (Wigley, Coetsee, Kruger, et al., 2019), bark damage renders the tree sensitive to subsequent fire damage (Das et al., 2022; Levick et al., 2015; Shannon et al., 2011). So although elephant is perhaps not such an important factor in adult marula mortality when compared to fire (Levick et al., 2015), a lack of individuals in the lower height classes in KNP has been attributed to elephant impact (Helm et al., 2009; Helm, Scott, & Witkowski, 2011; Helm, Wilson, et al., 2011). However, regardless whether elephants and fire were excluded, marula did not increase over the study period in the full and partial exclosures. Previous work from KNP has shown that seed predation by rodents and other small mammals is highest in areas with low disturbance, including inside exclosures (Helm, Scott, & Witkowski, 2011; Helm, Wilson, et al., 2011). The low density of adult trees, combined with high predation of seed and limited seed dispersal opportunities may be responsible for poor recruitment of marula in the exclosure. False marula (*L. schweinfurthii*) on the other hand, recruited with full protection. False marula fruit does not have the same hard casing protecting a nutritious nut that makes marula so popular with rodents and we assume that it is not predated to the same extent.

CONCLUSIONS

In summary, herbivores impact the density and size structure of woody communities in savannas, but perhaps to a lesser extent than anticipated. Given the long lives and slow establishment of trees, some of these responses can take decades to manifest (see, for example, the difference between this work and earlier work in the same experimental exclosures that found no height responses after 5 years; Scogings et al., 2012), emphasizing the importance of maintaining and monitoring herbivore exclusion experiments such as this one for as long as possible. After 17 years, we found that herbivore exclusion mainly acted upon the heights and densities of existing species, even the most palatable ones, rather than leading to turnover to a new woody species assemblage. Furthermore, the lack of a massive recruitment pulse suggests that factors beyond elephants, such as dispersal limitation, seed predation, and drought, are also acting upon species.

Notably, while much attention has been paid to the role of elephants as ecosystem engineers in this system (Asner et al., 2009; Asner & Levick, 2012; Sankaran et al., 2013; Wigley et al., 2014), the multiple levels of herbivore exclusion in this experiment reveal that meso-herbivores play a major role even in the absence of mega-herbivores. However, meso-herbivores alone have less of a direct impact on stem density, limiting average height growth rather than outright killing trees. By contrast, the increase in density in the full exclosure means that mega-herbivores play the unique role of actually limiting the number of trees and shrubs—suppressing establishment of new individuals, or killing existing individuals, via a variety of physical impacts (Cook et al., 2017; Morrison et al., 2016; Shannon et al., 2008). In a future where managers of savanna landscapes are simultaneously concerned about the loss of iconic large trees (Davies et al., 2018; Levick & Asner, 2013; O'Connor & Goodall, 2017; Shannon et al., 2008, 2011; Smit et al., 2010; Vanak et al., 2012) and the densification or encroachment of smaller trees and shrubs (Buitenhof et al., 2012; Stevens et al., 2017, 2016; Zhou et al., 2021), this does present a conundrum. Where elephants are present, they are clearly the most



effective at reducing the density of woody stems to the point of counter-acting woody encroachment, but at the same time are actively preventing the recruitment and persistence of desired trees in larger size classes. Even without elephants, however, this experiment makes clear that meso-herbivore populations play a major role in shaping the height demography of woody populations even if not directly limiting densities, and likely will into the future (Staver et al., 2021).

AUTHOR CONTRIBUTIONS

Corli Coetsee: Conceptualization (lead); formal analysis (lead); visualization (lead); writing – original draft (lead). **Judith Botha:** Conceptualization (supporting); data curation (equal); formal analysis (supporting); writing – original draft (supporting). **Madelon Case:** Conceptualization (supporting); formal analysis (supporting); visualization (supporting); writing – original draft (supporting). **Adolf Manganyi:** Investigation (lead); project administration (lead). **Frances Siebert:** Conceptualization (supporting); data curation (supporting); investigation (supporting); writing – original draft (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

NOMENCLATURE

Plant nomenclature follows Coates-Palgrave (2002).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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