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RESEARCH ARTICLE

Repeated clearing as a mechanism for savanna recovery following bush encroachment

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Abstract

1. Many savannas are experiencing increased cover of trees and shrubs, resulting in reduced herbaceous productivity, shifts in savanna functional structure and potential reductions in ecotourism. Clearing woody plants has been suggested as an effective management strategy to mitigate these effects and restore these systems to an open state with higher rates of grass production and herbivory. This study investigated the effectiveness of repeated shrub clearing as a tool to mitigate bush encroachment in a semi-arid savanna in southern Africa.
2. We present data from a 7-year experiment in the Mthimkhulu Game Reserve bordering Kruger National Park, South Africa. *Colophospermum mopane* stems and resprouting shoots were basally cut 2–3 times per year (2015–2022) in three pairs of treatment and control plots of 60 × 60 m. We monitored changes in soil moisture, grass biomass and herbivore activity via dung counts. We assessed *C. mopane* physiological responses to repeated cutting using non-structural carbohydrates and stable water isotopes to infer changes to energy storage and functional rooting depth, respectively.
3. The cleared treatment had higher soil moisture and grass biomass than the control treatment. Dung counts showed impala and buffalo visited the cleared treatment more frequently than the control treatment.
4. Repeated cutting had limited effects on *C. mopane* survival in the first 2–3 years after initial clearing, but 80% of individuals were dead after 7 years. Repeatedly cut *C. mopane* had lower belowground starch concentrations and used water from shallower soil depths than *C. mopane* in control plots.
5. *Synthesis and applications*. Repeated cutting increased soil moisture availability and grass biomass, and attracted charismatic grazing herbivores. While more costly than once-off clearing methods, this practice created more employment opportunities for a neighbouring rural community. Transforming portions of the ecosystem to a grass-dominated state may increase ecotourism potential through improved game viewing in open systems.

KEYWORDS
Colophospermum mopane, grass, herbivore, non-structural carbohydrates, resprout, South Africa, stable isotopes, woody thickening

1 | INTRODUCTION

Woody plants in African savannas provide beneficial services for human livelihoods including timber and fuelwood, food sources for domestic and wild browsers and carbon storage (Makhado et al., 2014). While woody plants are integral components of savanna ecosystems, tree and shrub cover has increased over the past century in savannas worldwide, a process known as bush encroachment (Venter et al., 2018). Bush encroachment often results in negative economic and ecological shifts including decreased grass biomass used for livestock production (Archer & Predick, 2014), decreased biodiversity (Ratajczak et al., 2012) and depleted soil moisture via increased rainfall interception and transpiration (Honda & Durigan, 2016). In southern African savannas, bush encroachment is associated with a shift from tall trees to short-statured shrubs (Zhou et al., 2021), which can make it difficult to see the charismatic animals that attract tourists, possibly resulting in a loss of tourism revenue for protected areas (Gray & Bond, 2013; Luvuno et al., 2022).

Frequent or high-intensity fire is often proposed as the most effective way to prevent large-scale bush encroachment (Scholtz et al., 2022), but the benefits of high-intensity fire to reduce woody cover are short-lived (Strydom et al., 2023). Additionally, in semi-arid and bush encroached savannas, grass biomass is often too low to carry regular fires that are intense enough to limit woody cover (Scholtz et al., 2022; Smit et al., 2013). More intensive management approaches are needed in these systems to control woody plants, open the canopy and increase grass biomass. Bush clearing has become a common management technique to mitigate the negative effects of bush encroachment (Eldridge & Ding, 2021; Smit, 2005), particularly in small game reserves where fire is a risk to infrastructure (Smit et al., 2022). This strategy typically involves the removal of small-statured trees and shrubs while maintaining large trees to preserve habitat heterogeneity, shade for livestock and wildlife, and the gradients of nutrient and water availability associated with large trees (Schmitt et al., 2022). Bush clearing is labour-intensive and expensive (Luvuno et al., 2022), but may be a viable and necessary alternative in areas where fire is infrequent and herbicide application is undesirable.

Long-term reductions in tree and shrub cover require either the use of herbicide or repeated clearing efforts, as most savanna woody species are well-adapted to disturbance and resprout following the loss of their above-ground parts (Bond & Midgley, 2001). These species use non-structural carbohydrates (NSC) stored in their trunks and belowground organs to regrow above-ground tissues following disturbance (Wigley et al., 2019). Single or infrequent disturbances only have short-term effects on tree size and cover because these species typically have sufficient NSC stores to recover. In addition, resprouting often results in the transformation of tall, single-stemmed trees into short, multi-stemmed shrubs which can make game viewing more difficult and contradict the initial goals of bush clearing efforts (Fisher et al., 2014). Repeated cutting has the potential to deplete NSC reserves in woody species to the point of mortality—especially in conjunction with other pressures like browsing or fire—leading to long-term reductions in woody plant cover (Smit, 2004).

Our focus was on *Colophospermum mopane* (Kirk ex Benth.) J. Léonard (hereafter 'mopane') a dominant tall tree or short multi-stemmed shrub (<4 m) that occurs over ~35% of southern African savannas (Stevens, 2021). The short-statured shrubs have increased in abundance over the past several decades (Zhou et al., 2021) resulting in encroachment (O'Connor et al., 2014; Stevens, 2021). Given the widespread dominance of mopane across southern Africa, it is necessary to assess the potential costs and benefits of clearing this species, particularly in protected areas as most research on the effects of bush clearing have been conducted in rangelands (Fisher et al., 2014; Smit, 2004).

Here, we used repeated bush clearing to ascertain if this treatment resulted in widespread shrub mortality, and describe any long-term changes in ecosystem structure including changes in grass biomass, herbivore presence and woody plant physiology. In this experiment, mopane shrubs <4 m tall were cut repeatedly from 2015 to 2022 to explore if repeated bush clearing is a viable alternative to herbicide and fire. We assessed the effects of cutting on grass biomass and monitored herbivore presence via dung counts. We predicted that repeated clearing would increase grass biomass, due to reduced competition between mopane and grasses, and increase grazer abundances, due to increased forage and a preference for more open areas by certain herbivore species (Burkepile et al., 2013). We also examined the effects of cutting on mopane belowground NSC storage and functional rooting depth, to assess the mechanisms by which repeated cutting eventually leads to mortality and long-term alteration of woody plant abundance. We predicted that repeated bush clearing would deplete belowground NSC storage, reducing the energy available for resprouting and shift mopane water uptake to shallower soils due to potentially reduced carbon allocation in deeper roots (Landhäusser & Lieffers, 2012).

2 | MATERIALS AND METHODS

2.1 | Study site

Mthimkhulu Game Reserve is a rural 7500-ha community-owned reserve that shares an open border with Kruger National Park, South Africa (23°31′46″ S; 31°06′12″ E) and is managed by the Mthimkhulu Tribal Authority. Since 2016, the South African Environmental

Observation Network has been working with this authority on long-term, socio-ecological research that can both improve ecosystem services and create employment for rural people living adjacent to the reserve. The tribal authority identified ecotourism as the most desirable land use for the reserve, and bush clearing was suggested to enhance tourism, as has typically been done in privately owned game reserves in the region. Access to the site was permitted by the Mthimkhulu Tribal Authority.

The site receives 467 mm mean annual rainfall, most of which falls between November and April (Mahlangeni Ranger station, 14 km south of the site, 1968–2010). Summers are hot and humid, with maximum temperatures typically above 30°C, while minimum temperatures in winter rarely fall below 10°C. The region has granite-derived, nutrient poor soils but the experimental plots were located on an old alluvial terrace of the Klein Letaba River with soils at least 1 m deep. Soil texture is approximately 62% sand, 20% clay and 17% silt (see Table S1). The site falls within the Lowveld Mopaneveld vegetation type of Mucina and Rutherford (2006), a semi-arid savanna characterized by a dense cover of mopane shrubs, sparsely scattered trees and low grass cover. The plots contained dense monotypic mopane stands with occasional *Combretum imberbe* Wawra and *Vachellia tortilis* (Forssk.) Gallaso & Banfi trees and *Grewia bicolor* Juss. shrubs. The grass layer was sparse and consisted mostly of annual *Aristida* species, with scattered tufts of perennial grasses *Urochloa mosambicensis* (Hack.) Dandy and *Panicum maximum* Jacq. Most of the ground cover consisted of bare soil and mopane leaf litter. Fire is infrequent in the region (~10 years; Smit et al., 2013), but the site burned in 2014, the year before the study began, resulting in top-kill of most mopane shrubs <2 m (*personal observation*).

2.2 | Experimental design and community sampling

In 2015, we established six 60 × 60 m plots divided into three blocks (two plots per block). The blocks were spread equidistant across an alluvial terrace, with specific locations selected to ensure that tree and shrub cover was similar within each block. One plot within each block was randomly assigned to a repeated mopane clearing treatment and the other plot assigned as a control ($n = 3$ cleared and 3 control plots). From 2015 to 2022, mopane shrubs <4 m tall were cut at the base 2–3 times during each growing season with a panga and cut material was removed from the plots (Figure 1). The timing of each clearing was determined by the height of resprouting stems, with clearing taking place shortly after the start of each growing season (October–December) and then again once resprouting stems reached 30–50 cm tall. For most response variables, sampling began in 2017 at the end of the growing season. In every plot, volumetric soil water content (VWC) was measured every hour (18 October 2017–13 June 2022) using CS655 time-domain reflectometry probes (Campbell Scientific Inc., Logan, UT, USA) at 10, 30 and 80 cm depths. To assess the effects of mopane clearing on the plant and animal community, we randomly established two 50 m transects within each plot. Transects were nonoverlapping and at least 20 m apart and 10 m from the nearest plot boundary. Grass and shrub cover were estimated using the point-step method (Evans & Love, 1957). At each 1 m point along each transect we measured the distance to the nearest perennial grass tuft, the width of the tuft and the presence of mopane cover directly above each 1 m point. Mopane individuals were categorized into four height classes: <0.5, 0.5–2, 2–5 and >5 m. The number of mopane in each height class was summed across the two transects in each plot. Frequency of each height class was calculated as the percentage of points with tree or shrub cover directly overhead. At the end of each growing season, herbaceous biomass ($\mathrm{g\,m^{-2}}$) was clipped in four to six 0.5 × 0.5 m quadrats randomly located per plot. Biomass samples were dried at 80°C for 2 days, sorted into current and past season material and weighed. We used each transect line as a 4 m wide belt transect to estimate animal visitation by counting species dung piles approximately every 1–2 months from April 2016 to August 2022.

2.3 | Mopane physiology

At the end of each growing season, mopane mortality was surveyed in each cleared plot by walking from a random cut mopane to its

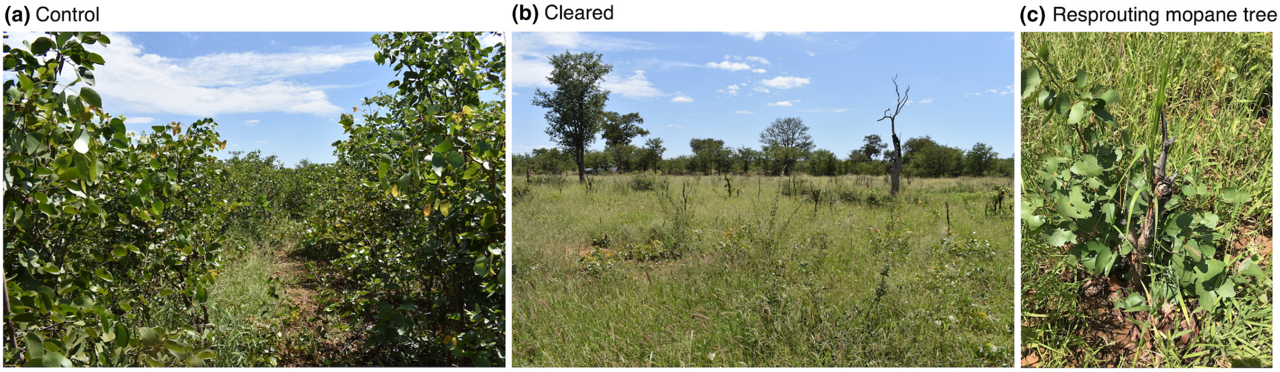

FIGURE 1 (a) Control plots at Mthimkhulu Game Reserve. *Colophospermum mopane* forms thick, monodominant stands. (b) Plots cleared of all mopane trees and shrubs <4 m tall. (c) resprouting mopane shrub. Photos taken in March 2020.

nearest dead or alive neighbour until 100–250 individuals were recorded. Individuals were considered dead if no green resprouting tissue was present. As the stumps of dead individuals persisted for many years, this provided a viable means of estimating mortality over time. We did not measure mortality in the control plots, but background mortality rates in mopane-dominated savannas are typically below 5% (Swemmer, 2020).

We used established protocols to measure functional rooting depth of mopane and adjacent grasses using the stable isotopic signature of xylem- and soil water (Dawson et al., 2002). In March of 2015, 2017 and 2018, we collected non-photosynthetic tissue from mopane (stem tissue) and grasses (crown tissue) within each plot to collect xylem water. We collected soil samples from 10, 30 and 50 cm depths from soil pits. All samples were placed in exetainer vials on ice and frozen until processing. We used cryogenic vacuum distillation to extract water for isotopic analysis. Samples were analysed on the Picarro L1102-I CRDS analyser (Picarro, Inc., Santa Clara, CA) at Kansas State University. Samples were referenced to V-SMOW and converted to delta notation using:

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where R is the ratio of the heavy to light isotope. ChemCorrect software was used to flag samples that had organic contamination, which were removed from any subsequent analyses.

We measured NSC concentrations of mopane belowground stems to assess changes in carbon storage. Sections of mopane stems/boles were collected 10–20 cm below the soil surface concurrent with collection for isotope samples. Samples were washed to remove soil, microwaved for 90 s to stop enzymatic activity, dried for 72 h, and ground to a fine powder. NSC extraction and analysis followed the procedure outlined in O'Connor et al. (2020).

2.4 | Statistical analysis

We used R V4.2.1 (R Core Team, 2022) for all statistical analyses. Repeated measures ANOVAs using the *lme4* and *car* packages (Bates et al., 2015; Fox & Weisberg, 2019) were used to test the effects of mopane clearing on soil VWC, mopane and grass responses and mopane NSC concentrations. We used Tukey's HSD for pairwise comparisons using the package *emmeans* (Lenth, 2022). For soil VWC, distance to perennial grass tuft, width of grass tuft and mopane NSC analyses we included an interaction between treatment and year as fixed effects and block as a random effect. For soil VWC, we only included data during the growing season (November–April). We ran the same model for grass biomass, but included quadrat nested within block as a random effect to account for variability due to multiple quadrats taken within each plot ($n = 4–6$ quadrats per plot). For the frequency of mopane size classes, we included an interaction between treatment and size class as fixed effects, with block nested within year as random effects. To meet the assumptions of normality and homogeneity of variance, we transformed grass biomass (square root) and mopane frequency, distance to the nearest perennial grass tuft and the width of the grass tuft (log+1).

Dung counts were analysed following Voysey et al. (2021). Since the length of transects used for dung counts varied from 50 to 100 m, we standardized dung counts by transect length and summed the number of dung piles per species across the two transects within each plot. We then divided the number of dung piles by the number of days between sampling dates to estimate dung deposition per day. To assess if this dung metric significantly differed for each species between cleared and control plots, we used a generalized mixed effects model with a Tweedie distribution using the *glmmTMB* function with a log link function and date nested within block as a random effect (Brooks et al., 2017). The Tweedie distribution was used to account for zero-inflated data common in herbivore dung surveys (Voysey et al., 2021). We calculated herbivore preference for cleared versus control plots by dividing the number of dung piles in cleared plots by the total number of dung piles in cleared and control plots for each sampling date, where 1 is complete preference for cleared plots and 0 is complete preference for control plots (Donaldson et al., 2018; Voysey et al., 2021).

To assess differences in functional rooting depth among grasses and mopane in the cleared and control treatments, we analysed each year (2015, 2017 and 2018) separately. Since δD and δ^{18}O were collinear and varied similarly with soil depth (Figures S1 and S2), we collapsed δD and δ^{18}O into a single axis using PCA to analyse both water isotopes in a single analysis (sensu Case et al., 2020; Holdo et al., 2018). The PCA approach is an alternative to isotope mixing models when plant signatures fall outside of the range of sampled soil signatures, indicating plants are using deeper soil water than sampled. We then used PC1 as the response variable in a linear mixed effects model with an interaction between vegetation type (mopane or grass) and treatment and included block as a random effect.

3 | RESULTS

3.1 | Soil moisture

VWC was higher in cleared than control plots at all depths ($p < 0.001$; Figure 2a; Table S2), but these differences were first evident at 10 cm soil depth. Across all growing seasons, mean daily VWC was 39% higher at 10 cm, 10% at 30 cm and 18% at 80 cm. From 2020 to 2021, when rainfall was above-average (Figure 2b), the difference at 10 cm was nearly 60%.

3.2 | Vegetation responses

Mopane mortality was low in the first few years of clearing, then increased steadily to 80% cumulative mortality after 7 years (Table 1).

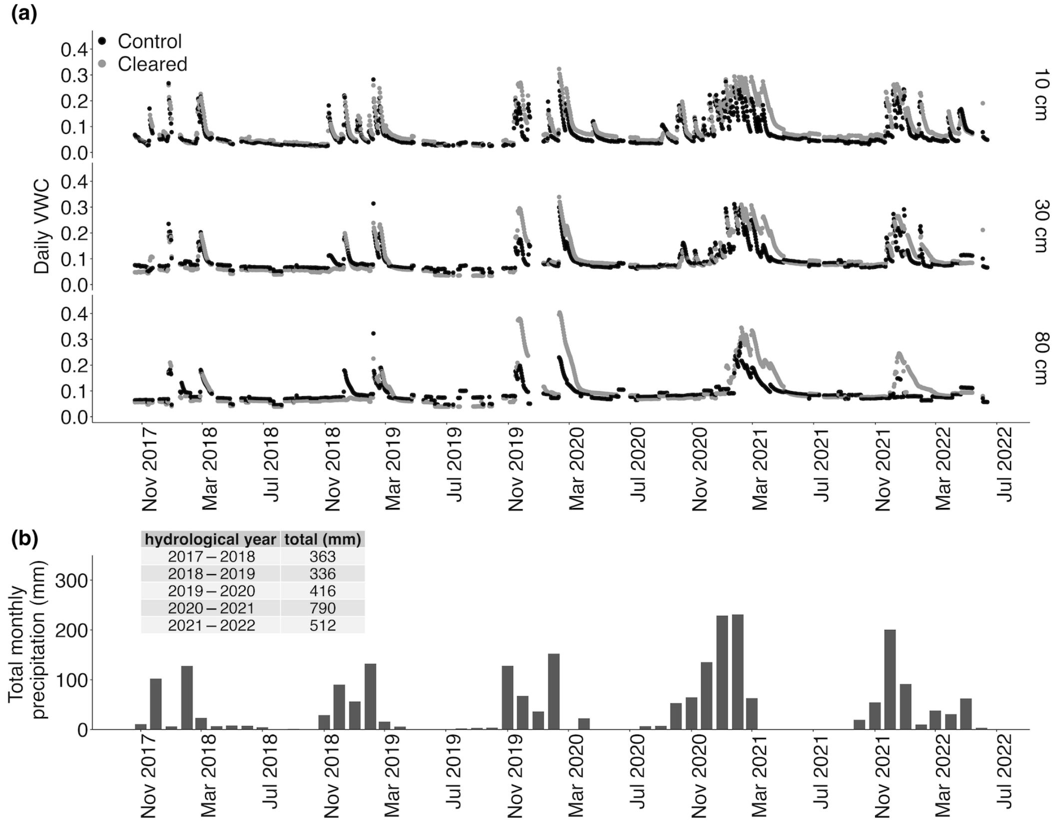

FIGURE 2 (a) Mean daily volumetric water content for cleared and control treatments at 10, 30 and 80 cm soil depths for November 2017–July 2022. Growing season spans November–April. (b) Total monthly precipitation (mm) from November 2017 to July 2022. Inset shows total precipitation (mm) for each hydrological year (1 July–30 June).

TABLE 1 Average percent mortality (±1 SE) of mopane shrubs in cleared plots ($n=3$).

Year	Cumulative % mortality	Total shrubs surveyed
February 2018	4 ± 2	442
July 2019	18 ± 5	631
May 2020	45 ± 5	537
May 2021	50 ± 5	411
March 2022	80 ± 8	449

Note: Bush clearing began in 2015. In each cleared plot, we recorded whether the nearest neighbour of a randomly selected mopane was dead or alive until 100–250 shrubs were recorded.

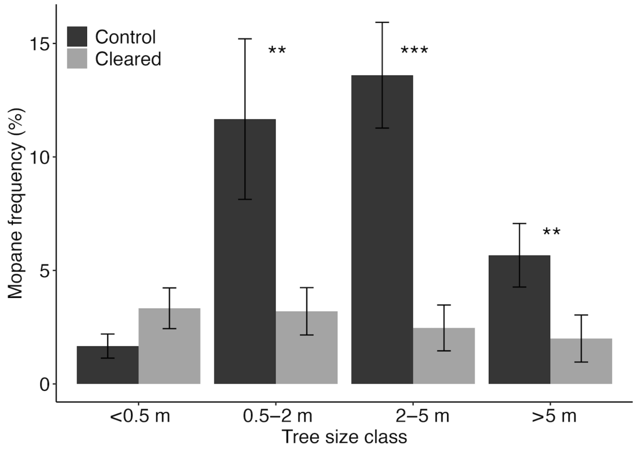

FIGURE 3 Mean (±1 SE) frequency (%) of mopane tree size classes averaged across years (2017–2022). Bush clearing began in 2015. The height of every mopane tree at each meter along two 50 m long transects was measured and categorized into one of four size classes: <0.5, 0.5–2, 2–5 or >5 m. Frequency was calculated as the percentage of points with mopane cover directly overhead. $^{**}p<0.01$, $^{***}p<0.001$.

The frequency of mopane taller than 0.5 m was significantly lower in cleared than control plots (Figure 3; Table S3). In cleared plots, most mopane were less than 0.5 m tall, while most mopane in control plots were between 2 and 5 m tall with few small trees.

Grass biomass was higher in cleared than control plots in 2018 and 2020–2022 (Figure 4a; Table S4). For these years, average grass biomass was 1.7, 2.1, 2.2 and 1.4 times higher in the cleared than control plots, respectively. The mean distance to the nearest perennial grass tuft was shorter in the cleared treatment in 2021, suggesting higher average grass density in cleared plots (Figure 4b). The widths of perennial grass tufts did not differ among treatments, except in 2017, where tufts in the cleared plots were larger than those in the control plots (Figure 4c).

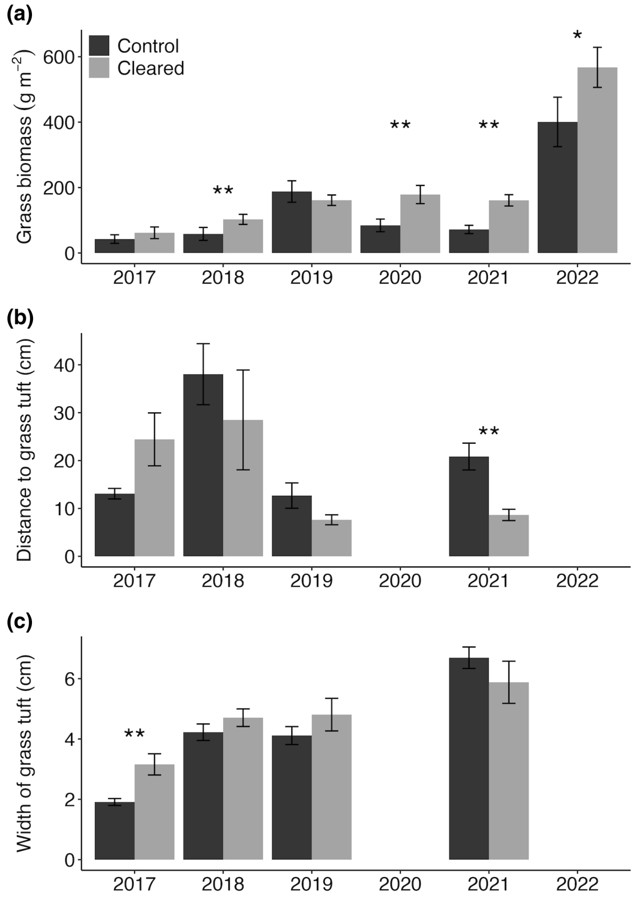

FIGURE 4 Mean (±1 SE) (a) grass biomass (g m^{-2}), (b) distance from transect to nearest perennial grass tuft (cm) and (c) width of nearest perennial grass tuft (cm) in cleared and control plots. $^{*}p < 0.05$, $^{**}p < 0.01$. Grass data from 2020 and 2022 are missing due to sampling constraints.

3.3 | Animal dung counts

Between April 2016 and August 2022, dung from 11 herbivore species were recorded (Table S5). Dung of impala (*Aepyceros melampus*), buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*) were the most common and present in all years, while many herbivores had low dung counts and were not present in all years (Figure S3). Total dung counts across years were higher in cleared than control plots, mostly driven by buffalo and impala (Table S5; Figure S4). These species had significantly higher dung deposition per day in the cleared plots (Figure 5; Table S6) and preferred cleared plots to control plots (Figure 6).

3.4 | Mopane physiology

Glucose and sucrose concentrations were unaffected by cutting in most years except for 2017 (Figure 7a,b). In contrast, stem starch concentrations were significantly lower in cut than control mopane in 2016–2018 (Figure 7c; Table S7). This difference increased with repeated cutting, with average starch concentrations 1.8, 2.6 and 7.8 times greater in control than cut shrubs in 2016, 2017 and 2018, respectively.

Soil water isotopic composition represented by PC1 declined with soil depth in all years where shallow soil layers had isotopically enriched signatures (Figure S5). Mopane used deeper soil water than grasses in cleared and control plots (Figure 8; Table S8). In 2017 and 2018, cleared mopane shrubs tended to use shallower soil water than control shrubs, but these differences were only significant in 2017 (Figure 8).

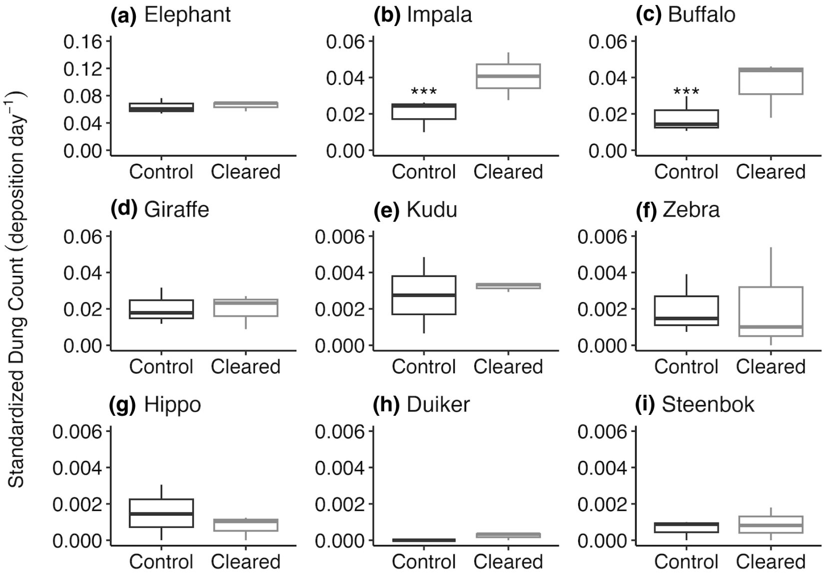

FIGURE 5 Boxplot of estimated dung deposition per day for various herbivore species (a–h). Species are ordered from the highest total dung counts recorded to the lowest. Standardized dung counts were averaged for each species in each plot across all sampling dates ($n = 3$). Note panels (b–d) are an order of magnitude higher than panels (e–i). Panel (a) has a unique scale. $^{***}p < 0.001$.

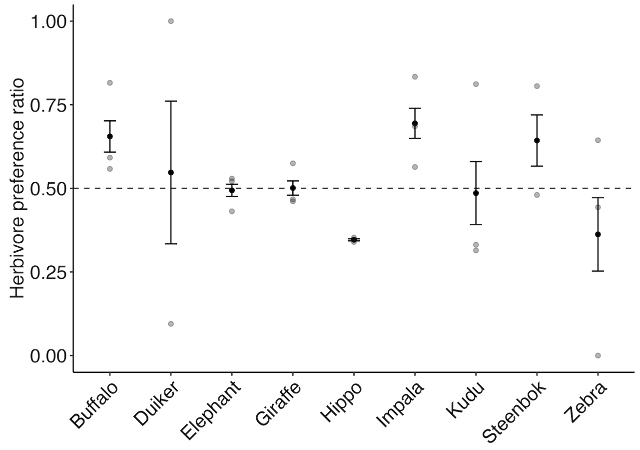

FIGURE 6 Habitat preference ratio of various herbivores (mean ± 1 SE). Preference ratio was calculated from the total standardized dung counts for each species in each plot across all sampling dates. Preference ratio ranges between 0 and 1, where 1 is complete preference for cleared plots and 0 is complete preference for control plots. Grey points are the preference ratio for each plot ($n = 3$).

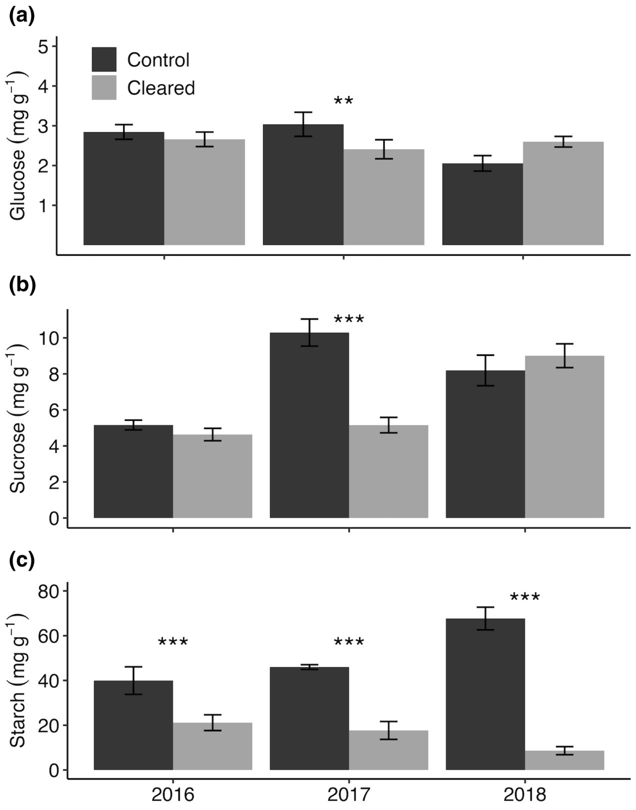

FIGURE 7 Mean (±1 SE) (a) glucose, (b) sucrose and (c) starch concentrations (mg g^{-1}) of mopane trees in cleared and control plots. $^{**}p < 0.01$, $^{***}p < 0.001$.

4 | DISCUSSION

Repeated clearing of a dominant woody species initially appeared to have only minor effects on mortality (5% after 2–3 years of clearing). However, repeated clearing eventually resulted in high shrub mortality (cumulatively 80% after 6–7 years), with increased soil water availability, greater grass biomass and altered herbivore activity. This experiment demonstrates that repeated cutting can be an effective management tool for opening the canopy after bush encroachment, at least in mopane-dominated, semi-arid savannas. While some ecological responses occurred rapidly (after only a few cuts), multiple cuttings over many years were required to induce significant mortality and long-term reductions in woody cover.

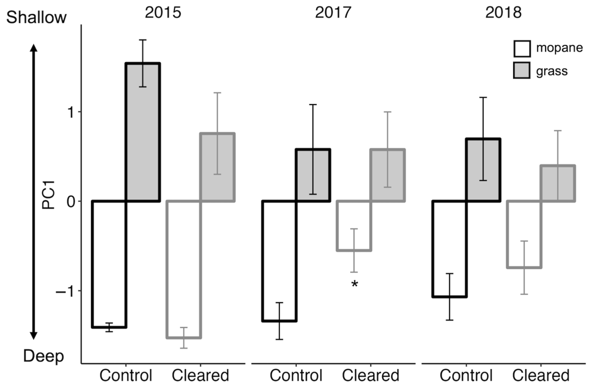

FIGURE 8 Mean PC1 isotope scores (±1 SE) in cleared and control plots in 2015, 2017 and 2018. The PC1 axis represents both δD and δ^{18}O values. Lower PC1 values correspond with deeper soil water. Asterisk represents significant differences between cleared and control mopane trees in 2017 ($p < 0.05$).

4.1 | Grass responses

Woody plants in semi-arid savannas have been hypothesized to have facilitative effects on grass growth and biodiversity through amelioration of heat and water stress and nutrient enrichment under canopies (Dohn et al., 2013; Moustakas et al., 2013). However, woody plants in high densities can reduce grass biomass and diversity through shading (Pilon et al., 2021). Our results indicate that mopane trees have strong competitive effect on the grass layer and that reducing water in the upper soil layers is likely to be a mechanism of competition. Higher woody cover can lead to decreased moisture at surface and deep soil layers through increased transpiration, canopy interception of rainfall and reduced infiltration (Aldworth et al., 2022; Smit & Rethman, 2000). There appeared to be a lagged response of 5 years after initial clearing before grass biomass consistently increased in the cleared plots, although this was confounded with differences in annual rainfall (the first 3 years of the study period had below-average rainfall and the last 3 years above-average). Changes in perennial grass tuft size and 'point-to-tuft' distance over time suggest that while perennial tufts in the cleared treatment were able to increase in size after the initial cuts, increased density occurred after 2 years of cutting. This increase in density presumably created substantial increases in biomass over the entire sward. The large interannual fluctuations in 'point-to-tuft' distances suggest that the dominant perennial species (i.e. *Urochloa mossambicensis*) had population fluctuations in response to changes in annual rainfall, but with greater recruitment in the cleared plots. This is consistent with the results of Wilcox et al. (2020) who found a rapid recolonization by this species following a severe drought at a nearby site.

4.2 | Herbivore responses

The opening of the canopy that facilitated increased grass biomass also created areas of preferred habitat for impala and buffalo. We lack the required data to mechanistically explain habitat selection, but results could be due to a combination of increased forage quantity, grass species palatability and predator visibility (Burkepile et al., 2013). Our data suggest the 60×60m plot size was meaningful for impala and buffalo abundance, but other megaherbivores, such as elephants, are unlikely to show preferences at this scale due to their movement across large areas. For other species, low dung counts limited our ability to draw general conclusions on herbivore feeding guilds (Table S5). Further research is needed to test whether these patterns would hold if clearing were implemented over larger scales. At the landscape scale, it is likely that the grazer density would either be unaffected or increase, given the greater supply of forage and shade availability provided by sporadic woody cover. Browser density could decline if vast areas of woody cover were cleared. Ideally, reserve management would aim to create a mosaic of cleared and uncleared landscapes, similar to Schmitt et al. (2022), who found herbivore species richness and abundance were highest in areas of intermediate woody cover and lowest in areas of low habitat heterogeneity (similar to the monodominant mopane stands in the control plots of this study).

4.3 | Mopane physiology

Despite repeated loss of all above-ground parts, most mopane individuals persisted for many years. This demonstrates the remarkable resprouting ability of mopane and highlights the difficulty of creating long-term reductions in shrub density. However, reduced starch reserves weaken the ability of mopane shrubs to recover following disturbance and the combination of multiple disturbances (e.g. cutting with drought, fire or herbivory) may increase shrub mortality and long-term, large-scale reductions of woody cover (O'Connor et al., 2020; Staver et al., 2009). Repeated defoliation can reduce carbon investment in roots (Landhäusser & Lieffers, 2012), which may have driven the shift in water uptake to shallower soil layers in cut mopane shrubs. However, cleared mopane still used deeper soil water than grasses, suggesting that deeper soil water is critical for their survival and hydrological niche partitioning exists even when shrubs have been depleted of belowground reserves. Mopane invests most of its fine roots in in the top 40cm of soil while coarse roots are common between 40 and 60cm of soil (Smit & Rethman, 1998). This shallow and sprawling root system suggests differences in water uptake depth between trees and grasses may be small when water is available in the surface layers (Kulmatiski et al., 2020).

4.4 | Large-scale and long-term changes

Transition of a savanna ecosystem from a bush encroached to a stable open state requires internal reinforcing feedbacks after ceasing shrub removal treatments (Ratajczak et al., 2018). Scholes (1990) found that mopane stands cut and treated with herbicide returned to their pre-cleared density within 14years, suggesting that one-time bush clearing is unlikely to reduce mopane cover over decadal time scales, and clearing is required about every 10years. However, in that study, the application of herbicide was estimated to cause only 40% mortality. We found 80% mortality after 7years of repeated cutting and return to original densities may, therefore, take much longer. While the method used for this study is labour-intensive and requires greater short-term investment, it may prove to be more cost-effective in the long term. Rates of seedling recruitment will play a key role in determining effective control, as seed sources from uncleared areas could facilitate large recruitment events in years with ideal environmental conditions. Clearing larger areas, with lower perimeter: area ratios could be beneficial in reducing seed establishment from surrounding areas. Additionally, recruitment events may be limited by increases in grass biomass that limits woody plant establishment and growth rates and supports more intense fire, particularly in wet years when grass biomass is high (February et al., 2013; Riginos, 2009).

The economic value of bush clearing encroached savannas in South Africa has been estimated to be US $2.1 billion (Stafford et al., 2017). This estimate included the potential benefits of restoring soil water recharge and grazing capacity and using harvested wood for electricity, fuel and wood composite products. This presents potential industrial economic benefits of clearing bush encroached areas on a large scale. Additionally, bush clearing may benefit local individuals at smaller scales by using targeted woody biomass for firewood and fencing (Makhado et al., 2014). However, we recognize bush clearing has variable effects dependent on climate and the woody species to be removed (Eldridge & Ding, 2021), and proper ecosystem management will vary depending on the goals of local communities, ecologists and economists. The method used in this study was notably more expensive (~US $22,000 ha^{-1} for 7years of repeat cutting or ~US $3100 $\text{ha}^{-1}\,\text{year}^{-1}$) than the widely used method of a one-off cut followed by herbicide application (~US $4300 ha^{-1} for 1year). However, the use of herbicides may be undesirable due to the toxicity of the chemicals to humans and wildlife and the potential effects on non-target plant species. Furthermore, our method created regular employment in an area where poverty and unemployment are high. While repeated clearing provides a limited amount of temporary and unskilled labour, similar interventions at large scales and the resulting transformation of dense savanna to open savanna could increase ecotourism potential.

Increased ecotourism is a primary goal of the game reserve used in this study and could create long-term, skilled and higher paid employment opportunities in areas where few economic opportunities exist. The social benefits may outweigh financial costs, particularly if donor funding can be used to support management objectives. Finally, more intensive clearing methods may be necessary in the future, if the drivers of encroachment, such as elevated atmospheric CO_2, continue to increase. Targeted and frequent management practices are increasingly necessary in a changing climate and fragmented landscapes where the return of disturbance (fire or browsers) to the system is insufficient to limit bush encroachment (Case & Staver, 2017; Collins et al., 2021).

In summary, our results highlight that repeated, targeted bush clearing can increase soil moisture, grass biomass and ungulate habitat in semi-arid savannas. Crucially, repeated clearing was necessary to reduce starch reserves to levels that prevent resprouting and induce tree mortality. While this approach was more expensive than conventional methods, it had positive ecological effects, created social benefits in the form of temporary employment and may produce longer-lasting reductions in shrub densities. We recommend decadal-scale management plans for bush-clearing projects that include repeated clearing to increase the return on investment and successfully mitigate the negative impacts of bush encroachment in the long term. More research is required to determine the exact thresholds of shrub mortality and understand how less intensive bush clearing in combination with other disturbances, such as fire, may achieve similar management goals dependent on the site.

AUTHOR CONTRIBUTIONS

Emily R. Wedel led the data analysis and writing the manuscript. Anthony M. Swemmer and Jesse B. Nippert designed the experiment and aided in writing the manuscript. Anthony M. Swemmer, Jesse B. Nippert and Peace Nkuna led data collection. Rory C. O'Connor led the processing of non-structural carbohydrate samples. All authors contributed to each draft and approved of the final manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.tht76hf6j (Wedel et al., 2024).

STATEMENT OF INCLUSION

Our study took place on Mthimkhulu Game Reserve, a community-owned game reserve in Limpopo, South Africa. Residents from Phalaubeni village, adjacent to the reserve, were employed as labourers for bush clearing and assisted with data collection. Community members were involved in the planning and execution of this experiment.

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REFERENCES

Aldworth, T. A., Toucher, M. L. W., Clulow, A. D., & Swemmer, A. M. (2022). The effect of Woody encroachment on evapotranspiration in a semi-arid savanna. *Hydrology*, *10*(1), 9. https://doi.org/10.3390/hydrology10010009

Archer, S. R., & Predick, K. I. (2014). An ecosystem services perspective on brush management: Research priorities for competing land-use objectives. *Journal of Ecology*, *102*(6), 1394–1407. https://doi.org/10.1111/1365-2745.12314

Bates, B., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution*, *16*(1), 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Burkepile, D. E., Burns, C. E., Tambling, C. J., Amendola, E., Buis, G. M., Govender, N., Nelson, V., Thompson, D. I., Zinn, A. D., & Smith, M. D. (2013). Habitat selection by large herbivores in a southern African savanna: The relative roles of bottom-up and top-down forces. *Ecosphere*, *4*(11), art139. https://doi.org/10.1890/ES13-00078.1

Case, M. F., Nippert, J. B., Holdo, R. M., & Staver, A. C. (2020). Root-niche separation between savanna trees and grasses is greater on sandier soils. *Journal of Ecology*, *108*(6), 2298–2308. https://doi.org/10.1111/1365-2745.13475

Case, M. F., & Staver, A. C. (2017). Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna. *Journal of Applied Ecology*, *54*(3), 955–962. https://doi.org/10.1111/1365-2664.12805

Collins, S. L., Nippert, J. B., Blair, J. M., Briggs, J. M., Blackmore, P., & Ratajczak, Z. (2021). Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters*, *24*, 636–647. https://doi.org/10.1111/ele.13676

Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*, *33*(1), 507–559. https://doi.org/10.1146/annurev.ecolsys.33.020602.095451

Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K. A., & Hanan, N. P. (2013). Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis.

Journal of Ecology, *101*(1), 202–209. https://doi.org/10.1111/1365-2745.12010

Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., & Parr, C. L. (2018). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, *55*(1), 225–235. https://doi.org/10.1111/1365-2664.12956

Eldridge, D. J., & Ding, J. (2021). Remove or retain: Ecosystem effects of woody encroachment and removal are linked to plant structural and functional traits. *New Phytologist*, *229*(5), 2637–2646. https://doi.org/10.1111/nph.17045

Evans, R. A., & Love, R. M. (1957). The step-point method of sampling: A practical tool in range research. *Journal of Range Management*, *10*(5), 208. https://doi.org/10.2307/3894015

February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, *94*(5), 1155–1164. https://doi.org/10.1890/12-0540.1

Fisher, J. T., Erasmus, B. F. N., Witkowski, E. T. F., Van Aardt, J., Asner, G. P., Wessels, K. J., & Mathieu, R. (2014). Management approaches of conservation areas: Differences in woody vegetation structure in a private and a national reserve. *South African Journal of Botany*, *90*, 146–152. https://doi.org/10.1016/j.sajb.2013.10.016

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage Publications. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gray, E. F., & Bond, W. J. (2013). Will woody plant encroachment impact the visitor experience and economy of conservation areas? *Koedoe*, *55*(1), 1–9. https://doi.org/10.4102/koedoe.v55i1.1106

Holdo, R. M., Nippert, J. B., & Mack, M. C. (2018). Rooting depth varies differentially in trees and grasses as a function of mean annual rainfall in an African savanna. *Oecologia*, *186*(1), 269–280. https://doi.org/10.1007/s00442-017-4011-4

Honda, E. A., & Durigan, G. (2016). Woody encroachment and its consequences on hydrological processes in the savannah. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *371*(1703), 20150313. https://doi.org/10.1098/rstb.2015.0313

Kulmatiski, A., Beard, K. H., Holdrege, M. C., & February, E. C. (2020). Small differences in root distributions allow resource niche partitioning. *Ecology and Evolution*, *10*(18), 9776–9787. https://doi.org/10.1002/ece3.6612

Landhäusser, S. M., & Lieffers, V. J. (2012). Defoliation increases risk of carbon starvation in root systems of mature aspen. *Trees*, *26*(2), 653–661. https://doi.org/10.1007/s00468-011-0633-z

Lenth, R. (2022). emmenas: Estimated marginal means, aka least-squares means. https://CRAN.R-project.org/package=emmeans

Luvuno, L., Biggs, R., Stevens, N., & Esler, K. (2022). Perceived impacts of woody encroachment on ecosystem services in Hluhluwe, South Africa. *Ecology and Society*, *27*(1), art4. https://doi.org/10.5751/ES-12767-270104

Makhado, R., Potgieter, M., Timberlake, J., & Gumbo, D. (2014). A review of the significance of mopane products to rur'l people's livelihoods in southern Africa. *Transactions of the Royal Society of South Africa*, *69*(2), 117–122. https://doi.org/10.1080/0035919X.2014.922512

Moustakas, A., Kunin, W. E., Cameron, T. C., & Sankaran, M. (2013). Facilitation or competition? Tree effects on grass biomass across a precipitation gradient. *PLoS One*, *8*(2), e57025. https://doi.org/10.1371/journal.pone.0057025

Mucina, L., & Rutherford, M. C. (Eds.). (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.

O'Connor, R. C., Taylor, J. H., & Nippert, J. B. (2020). Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. *Ecology*, *101*(2), e02935. https://doi.org/10.1002/ecy.2935

O'Connor, T. G., Puttick, J. R., & Hoffman, M. T. (2014). Bush encroachment in southern Africa: Changes and causes. *African Journal of Range & Forage Science*, *31*(2), 67–88. https://doi.org/10.2989/10220119.2014.939996

Pilon, N. A. L., Durigan, G., Rickenback, J., Pennington, R. T., Dexter, K. G., Hoffmann, W. A., Abreu, R. C. R., & Lehmann, C. E. R. (2021). Shade alters savanna grass layer structure and function along a gradient of canopy cover. *Journal of Vegetation Science*, *32*(1), e12959. https://doi.org/10.1111/jvs.12959

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ratajczak, Z., Carpenter, S. R., Ives, A. R., Kucharik, C. J., Ramiadantsoa, T., Stegner, M. A., Williams, J. W., Zhang, J., & Turner, M. G. (2018). Abrupt change in ecological systems: Inference and diagnosis. *Trends in Ecology & Evolution*, *33*(7), 513–526. https://doi.org/10.1016/j.tree.2018.04.013

Ratajczak, Z., Nippert, J. B., & Collins, S. L. (2012). Woody encroachment decreases diversity across north American grasslands and savannas. *Ecology*, *93*(4), 697–703. https://doi.org/10.1890/11-1199.1

Riginos, C. (2009). Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology*, *90*(2), 335–340. https://doi.org/10.1890/08-0462.1

Schmitt, M. H., Stears, K., Donovan, M. K., Burkepile, D. E., & Thompson, D. I. (2022). Integrating herbivore assemblages and woody plant cover in an African savanna to reveal how herbivores respond to ecosystem management. *PLoS One*, *17*(8), e0273917. https://doi.org/10.1371/journal.pone.0273917

Scholes, R. J. (1990). The regrowth of *Colophospermum mopane* following clearing. *Journal of the Grassland Society of Southern Africa*, *7*(3), 147–151. https://doi.org/10.1080/02566702.1990.9648223

Scholtz, R., Donovan, V. M., Strydom, T., Wonkka, C., Kreuter, U. P., Rogers, W. E., Tayler, C., Smit, I. P. J., Govender, N., Trollope, W., Fogarty, D. T., & Twidwell, D. (2022). High-intensity fire experiments to manage shrub encroachment: Lessons learned in South Africa and the United States. *African Journal of Range & Forage Science*, *39*(1), 148–159. https://doi.org/10.2989/10220119.2021.2008004

Smit, G. N. (2004). An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *Journal of Environmental Management*, *71*(2), 179–191. https://doi.org/10.1016/j.jenvman.2004.02.005

Smit, G. N. (2005). Tree thinning as an option to increase herbaceous yield of an encroached semi-arid savanna in South Africa. *BMC Ecology*, *5*(1), 4. https://doi.org/10.1186/1472-6785-5-4

Smit, G. N., & Rethman, N. F. G. (1998). Root biomass, depth distribution and relations with leaf biomass of Colophospermum mopane. *South African Journal of Botany*, *64*(1), 38–43. https://doi.org/10.1016/S0254-6299(15)30825-5

Smit, G. N., & Rethman, N. F. G. (2000). The influence of tree thinning on the soil water in a semi-arid savanna of southern Africa. *Journal of Arid Environments*, *44*(1), 41–59. https://doi.org/10.1006/jare.1999.0576

Smit, I. P., Joubert, M., Smith, K., Van Wilgen, N., Strydom, T., Baard, J., & Herbst, M. (2022). Fire as friend or foe: The role of scientists in balancing media coverage of fires in National Parks. *African Journal of Range & Forage Science*, *39*(1), 136–147. https://doi.org/10.2989/10220119.2021.1991473

Smit, I. P., Smit, C. F., Govender, N., Linde, M. V. D., & MacFadyen, S. (2013). Rainfall, geology and landscape position generate large-scale spatiotemporal fire pattern heterogeneity in an African savanna. *Ecography*, *36*(4), 447–459. https://doi.org/10.1111/j.1600-0587.2012.07555.x

Stafford, W., Birch, C., Etter, H., Blanchard, R., Mudavanhu, S., Angelstam, P., Blignaut, J., Ferreira, L., & Marais, C. (2017). The economics of landscape restoration: Benefits of controlling bush encroachment and invasive plant species in South Africa and Namibia. *Ecosystem Services*, *27*, 193–202. https://doi.org/10.1016/j.ecoser.2016.11.021

Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J., & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an

African savanna. *Ecological Applications*, *19*(7), 1909–1919. https://doi.org/10.1890/08-1907.1

Stevens, N. (2021). What shapes the range edge of a dominant African savanna tree, *Colophospermum mopane*? A demographic approach. *Ecology and Evolution*, *11*(9), 3726–3736. https://doi.org/10.1002/ece3.7377

Strydom, T., Smit, I. P. J., Govender, N., Coetsee, C., Singh, J., Davies, A. B., & Van Wilgen, B. W. (2023). High-intensity fires may have limited medium-term effectiveness for reversing woody plant encroachment in an African savanna. *Journal of Applied Ecology*, *60*(4), 661–672. https://doi.org/10.1111/1365-2664.14362

Swemmer, A. M. (2020). Locally high, but regionally low: The impact of the 2014–2016 drought on the trees of semi-arid savannas, South Africa. *African Journal of Range & Forage Science*, *37*(1), 31–42. https://doi.org/10.2989/10220119.2020.1723696

Venter, Z. S., Cramer, M. D., & Hawkins, H. J. (2018). Drivers of woody plant encroachment over Africa. *Nature Communications*, *9*(1), 2272. https://doi.org/10.1038/s41467-018-04616-8

Voysey, M. D., Archibald, S., Bond, W. J., Donaldson, J. E., Staver, A. C., & Greve, M. (2021). The role of browsers in maintaining the openness of savanna grazing lawns. *Journal of Ecology*, *109*(2), 913–926. https://doi.org/10.1111/1365-2745.13518

Wedel, E. R., Nippert, J. B., Nkuna, P., O'Connor, R. C., & Swemmer, A. T. (2024). Data from: Repeated clearing as a mechanism for savanna recovery following bush encroachment. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.tht76hf6j

Wigley, B. J., Staver, A. C., Zytkowiak, R., Jagodzinski, A. M., & Wigley-Coetsee, C. (2019). Root trait variation in African savannas. *Plant and Soil*, *441*(1–2), 555–565. https://doi.org/10.1007/s11104-019-04145-3

Wilcox, K. R., Koerner, S. E., Hoover, D. L., Borkenhagen, A. K., Burkepile, D. E., Collins, S. L., Hoffman, A. M., Kirkman, K. P., Knapp, A. K., Strydom, T., & Thompson, D. I. (2020). Rapid recovery of ecosystem function following extreme drought in a south African savanna grassland. *Ecology*, *101*(4), e02983. https://doi.org/10.1002/ecy.2983

Zhou, Y., Tingley, M. W., Case, M. F., Coetsee, C., Kiker, G. A., Scholtz, R., Venter, F. J., & Staver, A. C. (2021). Woody encroachment happens via intensification, not extensification, of species ranges in an African savanna. *Ecological Applications*, *31*(8), e02437. https://doi.org/10.1002/eap.2437

SUPPORTING INFORMATION

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

Table S1: Average percent of sand, silt, clay, total inorganic nitrogen, and total organic carbon in cleared and control plots at 10, 30, 50, and 100 cm soil depths.

Table S2: ANOVA output for soil volumetric water content at 10, 30, and 80 cm soil depths.

Table S3: ANOVA output for frequency of mopane tree size classes.

Table S4: ANOVA output for grass biomass, distance to nearest perennial grass tufts, and width of perennial grass tuft.

Table S5: Total standardized dung counts of herbivore species.

Table S6: Generalized linear mixed effects model for herbivore dung counts.

Table S7: ANOVA output for mopane stem/bole non-structural carbohydrate concentration, including glucose, sucrose, and starch.

Table S8: ANOVA output for functional rooting depth of mopane trees and grasses.

Figure S1: δD and δ^{18}O values for C_4 grasses (open circles), mopane trees (closed squares), and soil (plus symbols) in 2015, 2017, and 2018.

Figure S2: (a) δD and (b) δ^{18}O values for C_4 grasses (open circles), mopane trees (closed squares), and soil (closed circles) by depth in 2015, 2017, and 2018.

Figure S3: Habitat preference of various herbivores from 2016 to 2022.

Figure S4: Total standardized dung counts over time for all herbivore species (elephant, impala, buffalo, giraffe, kudu, zebra, hippo, duiker, steenbok, waterbuck, and wildebeest).

Figure S5: Average PC1 values ±1 SE for C_4 grasses (open circles), mopane trees (closed squares) and soil samples (closed circles) in cleared and control plots in 2015, 2017, and 2018.

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