



Megaherbivores facilitate large grazing herbivores and suppress small mammals through vegetation structure and cryptic pathways

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ARTICLE INFO

Keywords:

Savanna
Mammalian interactions
Community dynamics
Trophic cascades
Exclusion experiments
Ecosystem engineers
Indirect ecological effects

ABSTRACT

Variability in large mammalian herbivores can reshape smaller animal communities in complex ways. Accordingly, conservation strategies require a deeper understanding of the extent to which mesoherbivores (>20–1000 kg) and megaherbivores (>1000 kg) influence on animal communities are mediated by changes to vegetation structure, and the extent to which the influence of megaherbivores overlap with mesoherbivores. Using an exclusion experiment, we examined how megaherbivores altered mesoherbivore activity and how both groups influenced small mammals. We compared influences that were mediated by broad metrics of vegetation structure (i.e., indirect effects) with all other influences that were not mediated by vegetation structure (e.g., direct effects). We found megaherbivores were linked to increased mesoherbivore activity, particularly grazers, through both vegetation structure-mediated and other pathways. Alternatively, we found small mammals were suppressed where megaherbivores were present, and their population fluctuations were explained by both structure-mediated and other pathways. Small mammal abundance was higher where large herbivores were excluded compared to open plots, with no difference between plots excluding only megaherbivores and those excluding all herbivores. This suggests that these effects were produced by either megaherbivores alone, or by megaherbivores in conjunction with the increased mesoherbivore activity they facilitated. While small mammal abundance was linked to mesoherbivore-induced changes in grass biomass, their non-linear response, did not correspond with the exclusion of mesoherbivores. These findings highlight megaherbivores' capacity to reshape animal communities through interactions beyond broad metrics of vegetation structure, underscoring the importance of considering the varied influences of megaherbivores on mammal communities in conservation strategies.

1. Introduction

The unprecedented loss of species has had widespread ecological consequences that cascade through ecosystems (Barnosky et al., 2011; Ceballos et al., 2015). Large mammalian herbivores (> 5 kg, Flojgaard et al., 2022), including both mesoherbivores (>2–1000 kg; Wells et al., 2021) and megaherbivores (> 1000 kg, Owen-Smith, 1988) are among the most vulnerable mammals to population declines and extinction

(Ripple et al., 2015; Atwood et al., 2020). Anthropogenic, size-dependent extinctions have led to the elimination of megaherbivores in most parts of the planet and have far-reaching ecological consequences (Gill, 2014; Pringle et al., 2023). Conservation actions to restore (Wedel et al., 2024) and reintroduce (Dvorský et al., 2022; Gordon et al., 2021) the ecological functions and massive influences of megaherbivores and mesoherbivores on vegetation (Cook et al., 2023; Tiller et al., 2022; Smit, 2011), have become increasingly urgent (Seddon

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<https://doi.org/10.1016/j.biocon.2025.111378>

Received 25 November 2024; Received in revised form 12 June 2025; Accepted 16 July 2025

Available online 28 July 2025

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et al., 2014; Lundgren et al., 2018). Conversely, in regions with sizable meso- and megaherbivore populations, there are concerns about their potentially deleterious impacts on vegetation structure (Cumming et al., 1997; Herremans, 1995; Kerley and Landman, 2006; Ogada et al., 2008; McCleery et al., 2018).

While it is well-established that both mesoherbivores and megaherbivores can broadly reshape grass biomass and woody cover (Bakker et al., 2016; Cid et al., 1991; Coverdale et al., 2024; Kimuyu et al., 2014), conservation initiatives often give little weight to their influence on other animal communities. This is likely because their impacts on animal communities are often complex and harder to isolate (Kerley and Landman, 2006; Poulsen et al., 2018; Goheen et al., 2018). Nonetheless, research has linked changes in animal communities to megaherbivores' and mesoherbivores' broad and easily measurable changes to the structure (e.g., woody cover and grass biomass) of vegetation (Guiden et al., 2023; Ogada et al., 2008; Pringle, 2008; Valeix et al., 2011), but their potential to influence animal communities beyond these structural measures remain poorly understood (Kerley and Landman, 2006; Svenning et al., 2016; Poulsen et al., 2018). Other more cryptic influences may arise from mammals behavioral response to megaherbivores, such as attraction to avoid predation (Ferry et al., 2016) and to find favorable foraging sites (Schulte and LaDue, 2021), or avoidance of competition and trampling (Fletcher et al., 2023; Landman and Kerley, 2014; Avenant and Cavallini, 2007). Additionally, both megaherbivore and mesoherbivores can alter soils (e.g., compaction and nutrients), and generate subtler changes to vegetation, from trail formation and compositional changes to enhanced palatability and reductions in fruits and seeds (Haynes, 2012; Arsenault and Owen-Smith, 2002; Goheen et al., 2018), all of which may influence other animal communities. Compared with the more obvious broad structural influences of megaherbivores and mesoherbivores, these subtler effects are considerably harder to isolate and replicate via management interventions and have received less attention. Accordingly, effective conservation, restoration, and rewilding strategies require a deeper understanding of the extent to which the impacts of mesoherbivores and megaherbivores overlap (Moe et al., 2009; O'Kane et al., 2014) and are mediated by changes in broad measures of vegetation structure or other ecological interactions (Bakker et al., 2016; Cid et al., 1991; Coverdale et al., 2024; Kimuyu et al., 2014).

To address this knowledge gap and better inform restoration and mitigation efforts, we conducted a six-year exclusion experiment in southern Kruger National Park, South Africa, to understand the relationship between megaherbivores, mesoherbivores, and small mammal communities. Using treatments that selectively excluded only megaherbivores or all mesoherbivores and megaherbivores, we aimed to determine the extent of their indirect influences through broad measures of vegetation structure and distinguish these from the other effects of megaherbivores and mesoherbivores (e.g., behavioral influences, soil compaction, trails, plant composition, plant palatability) on small mammal populations. We predicted three specific outcomes. 1) Small mammals would decline with reductions in grass biomass from mesoherbivores, but excluding megaherbivores would have no influence because megaherbivores should not exert a strong direct influence on grass biomass (Keesing, 2000; Saetnan and Skarpe, 2006; Young et al., 2015). 2) Mesoherbivore activity would increase where megaherbivores were present, as they responded positively to megaherbivore reductions in woody cover that facilitate foraging (Arsenault and Owen-Smith, 2002; Owen-Smith, 1988) and reduce perceived predation risk (Epperly et al., 2021; Le Roux et al., 2018). 3) Mesoherbivores have been shown to aggregate in areas with megaherbivore activity to avoid predation (Ferry et al., 2016), access improved forage quality and palatability (Arsenault and Owen-Smith, 2002), and use megaherbivores' distinct paths (Haynes, 2012). Accordingly, we predicted that a portion of their responses to megaherbivores would not be explained through megaherbivore-induced changes of broad vegetation structure metrics (e.g., cover and biomass), commonly used to explain changes in

mesoherbivore activity (Valeix et al., 2011; de Boer et al., 2015; Le Roux et al., 2018; Wells et al., 2021).

2. Material and methods

2.1. Study area

We established herbivore exclosures in southeastern KNP. The park covers 19,000 km² of savannas and woodlands in northeastern South Africa (Fig. 1). This region of the park has nutrient rich basaltic soil and receives 500–700 mm of rain annually (Smit et al., 2013). Over the last 70 years, this portion of KNP has seen a considerable decrease in woody vegetation (Asner and Levick, 2012) coupled with increased elephant activity (Abraham et al., 2021). The density of elephants in KNP as of 2020 was 1.66 per km² (Ferreira et al., 2024). Because of our study area's productivity, there has been greater elephant activity at our study area compared with other regions of KNP (Abraham et al., 2021). Prior to the implementation of our treatments, overstory (> 5 m) canopy cover was 3.5 %, shrub cover (woody vegetation up to 3 m in height) was 5.5 %, and there was negligible bare ground (McCleery et al., 2018). Ground cover was dominated by the grasses *Themeda triandra* and *Megathyrsus maximum* while the shrub layer was dominated by *Dichrostachys cinerea* and *Gymnosporia senegalensis*. The tree canopy mostly comprised of *Senegalia nigrescens* and *Vachellia gerrardii* (Jones et al., 2022). Our study site was managed with prescribed fires at a mean return interval of 4–5 years (Smit et al., 2013) and a management-related fire occurred on all plots in May 2020.

Our study site was frequented by several herbivores that were common throughout KNP. In addition to elephants (2020 KNP estimate = 31,324; 1.66/ km²), other megaherbivores included southern giraffe (*Giraffa giraffa*, 2021 KNP estimate = 12,270; 0.65/ km²) and white rhino (*Ceratotherium simum*, 2022 KNP estimate = 1849; 0.10/ km²). We detected southern giraffe with 75 % less frequency than elephants, and white rhinos have become extremely uncommon (1 detection). Common mesoherbivores included blue wildebeest (*Connochaetes taurinus*, 2023 KNP estimate = 18,845; 1.00 km²), plains zebra (*Equus quagga burchellii*, 2023 KNP estimate = 51,284; 2.70 km²), and Cape buffalo (*Syncerus caffer*, 2023 KNP estimate = 30,999; 1.63/ km²). While impala has been the most common mesoherbivores in KNP (*Aepyceros melampus*, 2023 estimate = 144,525; 7.61/ km²), they were less common than other mesoherbivores on our sites, possible due to the distance from a permanent water source (Smit et al., 2007). The rodent community at our study site has been dominated by the Natal multimammate mouse (*Mastomys natalensis*) and has included the single-striped mouse (*Lemniscomys rosalia*), fat mouse (*Steatomys pratensis*) and pouched mouse (*Saccostomus campestris*) (McCleery et al., 2018).

2.2. Experimental design

To quantify the influence of megaherbivores on mesoherbivore activity and to understand how both these groups influence small mammal populations we initiated the BROWSE (Biodiversity Research On Wildlife and Savanna Ecosystems) long-term field experiment on three grids with 5 plots each, with each grid >350 m apart (Fig. 1). We randomly assigned the 0.49 ha plots (70 × 70 m) to three different exclosure treatments, Open (open to all herbivores), Mega (excluding megaherbivores but accessible to small mammals and mesoherbivores) and Full (excluding megaherbivores and mesoherbivores but accessible to small mammals). We replicated the Full treatments three times and the Open and Mega treatments six times (Fig. 1). We doubled the samples of the Open and Mega treatments to increase statistical power to isolate megaherbivore effects and because of the potential for these two treatments to show more varied responses (Goheen et al., 2013). Fence posts for the exclosures were made of galvanized steel placed 1.5 m below and 2.5 m above ground. Our Mega exclosures have a large metal cable and three electrified wires starting at 2.5 m above ground. In addition to

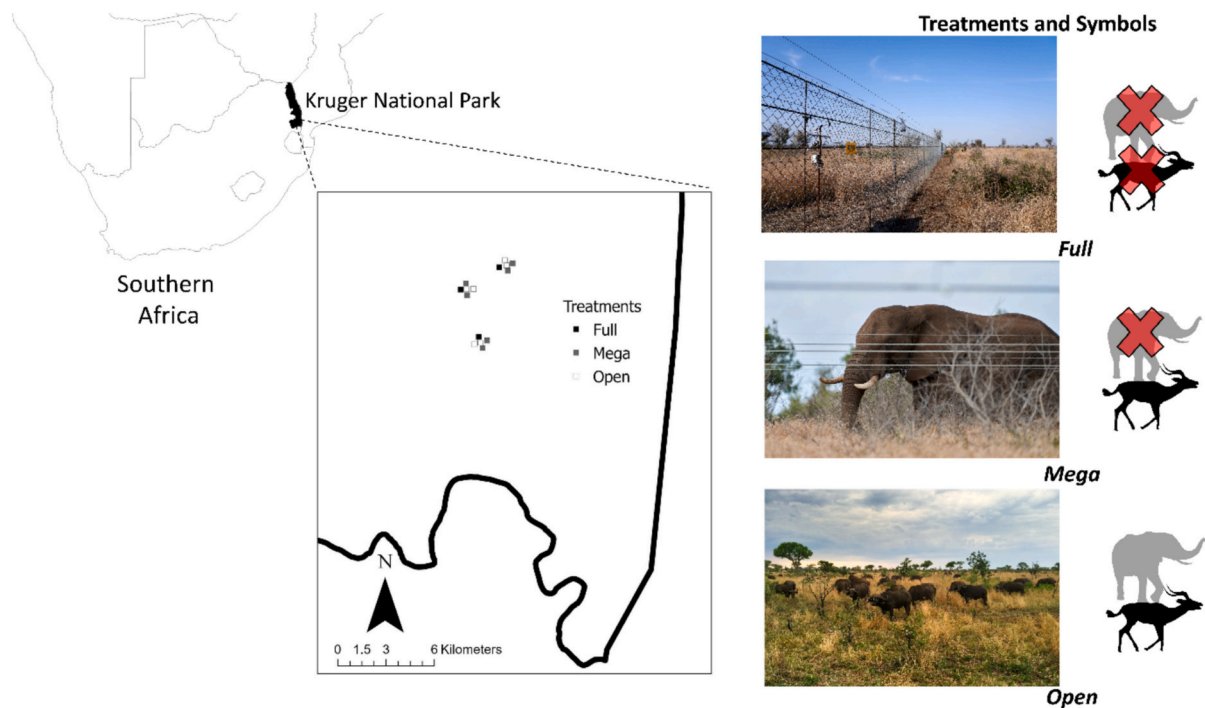


Fig. 1. Study areas in Kruger National Park, South Africa. Our experiments consisted of three grids with 5 plots each (15 plots total). We assigned plots (70 × 70 m) three different treatments, Open (open to all herbivores), Mega (excluding megaherbivores but accessible to small mammals and mesoherbivores) and Full (excluding megaherbivores and mesoherbivores but accessible to rodents).

these features, the Full enclosures have three electrified wires clustered at approximately 20–35 cm above ground and a chain linked fence (Fig. 1). The Open plots were unmodified. From the initiation of treatments in December 2018, we checked fences every month for damage that might influence enclosure integrity; additionally, we used twice annual dung counts and game cameras twice a year for 10–14 days to examine the integrity of our enclosures.

2.3. Vegetation structure and rainfall

To capture changes in vegetation structure on the plots, we established a center line running south to north through the plot, ending 10 m from the plot boundary. Next, we created two parallel 50 m transects placed 10 m on both sides of this line. We measured the three dominant structural layers (grass, shrubs, tree canopy) at the end of each growing season (May–June). We sampled the biomass of grass (and other herbaceous plants) using a disc pasture meter sampling every 5 m ($n = 22$). We converted raw scores to estimates of biomass (t/ha) based on calibrations established for KNP (Zambatis et al., 2006). To estimate shrub cover, (all woody cover up to 2 m) we measured the amount of shrub cover crossing our transects using the line intercept method (Canfield, 1941), sampling every 10 m along the transects. While traversing the transect we also measured overstory canopy cover, taking one reading every 10 m in the direction of transect with a spherical convex densiometer. We converted the measure of reflected cover on densiometer into a measure of percent cover (Lemon, 1956).

We extracted annual rainfall totals from the nearest weather station in Lower Sabie, approximately 10 km away. Using this publicly available data (<https://www.sanparks.org/conservation/scientific-services/data-information-resources/kruger-climate-rainfall>), we summed monthly rainfall totals from June to May to generate a measure of rainfall for 1 year prior to the collection of our measures of vegetation structure.

2.4. Mammal communities

We surveyed small mammals for four nights on each plot using 20

folding-box traps (3 × 3.5 × 9" Sherman traps, Tallahassee, FL, USA; McCleery et al., 2022) in a 4 × 5 formation with 10 m spacing (30 × 40 m), to sample the core of the 50 × 50 m area (0.25 ha) of the plot. We identified all small mammals to species. For each animal, we recorded mass, sex, age (adult or juvenile) and the length of its hindfoot, body, and tail. We administered an ear-tag (1005–1, National band Co., Newport, KY, USA) to each new capture. In accordance with previous work, we trapped small mammals at the end of the growing season (May–June) when rodents are most abundant in this region (Loggins et al., 2019; McCleery et al., 2018; O'Farrell et al., 2008). We estimated rodent abundances on each plot using a minimum number of individuals alive estimator. This provided a standard measure that is commonly used when a paucity of detections from some samples precludes the use of detection-corrected abundance estimates for all samples (McCleery et al., 2022).

To assess interannual change in mesoherbivore activity across the experimental plots, we estimated the density of dung as a proxy for plot-based activity (Goheen et al., 2013). To sample the center 50 × 50 m area (0.25 ha), we established five 50 m transects running south to north and surveyed them using a distance sampling methodology (Buckland et al., 2004) (Appendix A). We measured the perpendicular distance from the transect to the center of each dung pile, identified dung to species, and measured the pile's diameter at the largest point. Based on observations of dung persistence on our plots, we broke large clumps of dung into small pieces to prevent recounting during subsequent seasons. We sampled twice a year during May/June and November/December and combined the measure into annual estimates of activity. To understand variation in response across treatments, we grouped mesoherbivores into two functional groups: grazers (blue wildebeest, plains zebra, common warthog [*Phacochoerus africanus*], and Cape buffalo) and those that eat woody vegetation, including browsers (greater kudu [*Tragelaphus strepsiceros*] and common duiker [*Sylvicapra grimmia*]) and mixed feeders (impala). To evaluate the efficacy of our experiment, we also recorded the presence of megaherbivore dung. All animal surveys were conducted in accordance with scientific permits from South African National Parks (KRUGL1427), the American Society of

Mammalogist (Sikes et al., 2016) and approved by the University of Florida's Institutional Animal Care and Use Committee (#202011155) and the University of Florida's Non-regulatory Animal Review Committee Institutional Animal Review (010-13WEC).

2.5. Analysis

Our general approach was to evaluate the response of small mammals and mesoherbivores over time and then to explain variation in their responses via different drivers and pathways. First, we examined the annual responses of small mammals and large herbivores to our treatments by comparing estimates from the year prior to our manipulations (pre-treatment = 2018) with each of the 5 years after the initiation of the treatments (post-treatment-2019-2023), which included a prescribed fire in May 2020 that burned all the plots in this experiment. Then to understand how vegetation structure and other pathways explained changes in these two communities, we examined the linkages from treatments, fire and rainfall to vegetation structure and animal communities. We detail our approach below.

To understand how both small mammals and mesoherbivores responded annually, we used a generalized linear mixed model (GLMM) framework in the glmmTMB package (Brooks et al., 2017) on the R platform (v4.5.0, R Core Team, 2023). We also constructed annual models for two mesoherbivore functional groups, grazers, which were common on our plots, and browsers and mixed feeders. The latter were not common before or after the initiation of treatments. Pre-treatment data for all mesoherbivores was derived from sampling in May 2018 before construction of fences (October–December 2018) and we did not consider the Full enclosures in our mesoherbivore models because mesoherbivores were excluded from these treatments. To assess variation in the animal responses we parameterized our model with the categorical variables treatment, year and the interaction between year and treatment. We used Poisson distributions and included grid as a random effect to account for unexplained heterogeneity in grids. Distance sampling generates estimates of continuous data; however, the resultant distributions often follow a Poisson distribution (Buckland et al., 2004) and can be modeled as count data (Royle et al., 2004; McNeil et al., 2019) by rounding to the nearest integer (Kowal and Wu, 2023). We considered significant ($P < 0.05$) interactions between the treatment and year to indicate a response to experiments. Consistent with other megaherbivore and mesoherbivore exclusion studies, we interpreted differences between Open and Mega plots as reflecting a megaherbivore effect, and differences between Mega and Full plots as reflecting a mesoherbivore effect. In the absence of a mesoherbivore effect, we also interpreted differences between Open plots and plots that exclude megaherbivores as a megaherbivore effect (Jones et al., 2025; Wells et al., 2021; Goheen et al., 2013). Using the predicted responses and SE from GLMMs, we graphically displayed the response of each animal community to each treatment by year.

To explain how small mammals and mesoherbivore communities varied across time and space we used a mixed model piecewise Structural Equation Modeling approach (PSEM) (Bowen et al., 2017). To untangle the indirect effects of treatments (i.e., via vegetation structure-mediated), from more direct pathways (i.e., those not mediated by vegetation structure) we evaluated PSEMs with and without direct treatment effects. Finding no pre-treatment differences in measures of vegetation and mammal communities across our plots, we combined all pre-treatment data (i.e., animal and vegetation data from all plots) into a single pre-treatment category (Gibb et al., 2021). We populated both PSEMs with four GLMMs, three using vegetation structures (grass biomass, shrub cover and canopy cover) and one using animal communities (mesoherbivore activity and small mammal numbers) as response variables. First, we modeled broad measures of vegetation structure as response variables correlated with fire (yes or no), annual rainfall totals and herbivore treatments (Pre-treatment, Open, Mega, Full). We transformed measures of grass biomass and canopy cover using

a Tukey Ladder of Powers Transformation, which fits different (e.g., square root, logarithm, inverse) transformations to stabilize variance and improve normality, to better meet assumptions of normality (Mangiafico, 2020). Next, we fitted a model with each animal community as the response variable. These models included each measure of vegetation structure, our treatments, fire, and rain. These models also included a quadratic term for grass to capture nonlinear responses. For each model we included we included grid as a random effect. We fit models of vegetation to Gaussian distributions and models with count data (small mammals [minimum number of individuals alive] and mesoherbivores [estimated number of dung piles]) to Poisson distributions using the glmmTMB package (Brooks et al., 2017). Next, we combined these models in PSEMs using the piecewiseSEM package (Lefcheck, 2016). We parameterized the PSEM to allow variables influencing the number of small mammals and the activity of mesoherbivores to covary. This included direct pathways from fire and rainfall to both communities. Fire can cause the direct mortality of individuals in both communities (Swanepoel, 1981; Nieman et al., 2022). Alternatively, mesoherbivores may respond positively to fire because of reductions in parasite and disease (Scasta, 2015). Moreover, the dominant rodent on our site, the Natal multimammate mouse, has been shown to increase density in recently burnt areas, likely capitalizing on different food resources, such as insects (Monadjem and Perrin, 2003; Manyoni et al., 2020). Alternately, increased rainfall can flood rodent burrows (Sheppe and Osborne, 1971) and promote parasites and diseases in mesoherbivores (Cizauskas et al., 2015; Huang et al., 2021). Lastly, elevated rainfall can increase mesoherbivores activity in areas like our study site that are removed from permanent sources of surface water (Ogutu et al., 2008; Harris et al., 2015). To control for collinearity between treatment and rainfall, we used group-mean centering—subtracting the average rainfall per treatment group from each observation—to evaluate within-treatment effects of rain on herbivore activity.

We evaluated the overall fit of the PSEMs with and without direct links of treatments to animal communities using the χ^2 statistic and considered $P > 0.05$ as an adequate fit. Given that our herbivore exclusion treatments were categorical, we used a χ^2 Likelihood ratio tests and post-hoc pairwise comparisons to test pathways (Bowen et al., 2017; Lenth et al., 2019). Direct effects of herbivore treatments were reported as estimated marginal means (EMMs), while indirect and vegetation effects were standardized using model-based estimates incorporating predicted values and R^2 -adjusted standardization (Grace et al., 2018). We also evaluated the response of small mammals and mesoherbivores across the entire study by comparing their predicted responses to treatments using the emmeans package (Lenth et al., 2019). Additionally, by limiting our comparison to two categories, megaherbivore exclusion after initiation of treatments (Post Mega) and full access after the initiation of treatment (Post Open), we were able to apply model-based standardizations to assess the strength of direct and indirect pathways. We estimated direct effects by calculating the difference in regression coefficients (β values) between these two categories. To quantify indirect effects, we multiplied the treatment-associated β values for vegetation structure (grass biomass, shrub cover, and canopy cover) by the respective β values describing vegetation's effects on rodent abundance and mesoherbivore activity. Then we standardized effect sizes using model-predicted values and R^2 -adjusted variance (Grace et al., 2018). This approach follows the principles of causal mediation analysis (Vander Weele, 2015), where megaherbivore exclusion can influence small mammal abundance and mesoherbivore activity through changes in vegetation structure and other pathways.

3. Results

Over the course of this study, there was no observable damage to fences of the Full enclosures. Poles on our Mega enclosures were bent by elephants on three occasions and repaired; however, we only have one

recorded incident (based on a dung pile) of a small elephant on one Mega enclosure before it was repaired. We recorded megaherbivore dung on 14 of 15 plots prior to initiation of treatments and for the subsequent 5 years we recorded megaherbivore dung on every open plot, every year, except for once on one plot during the second-year post treatments.

3.1. Response of small mammals

While we captured nine species of small mammal, >82 % (1280 of 1546) of the captures were Natal multimammate mice. Prior to the initiation of treatments, we estimated 38.0 (SE = 6.02) rodents per plot, during subsequent 5 years we estimated an average of 17.5 (SE = 2.5) on all plots. Small mammal numbers were elevated in areas where megaherbivores and all large herbivores were excluded. This pattern changed over the course of the study, we found smaller but significant differences in the response of small mammals to the treatment during the first three years post-treatment. There were more small mammals on both enclosure treatments relative to open plots, increasing on the Full (year 3 post) and Mega (year 2 post) treatments separately and together (year 1 post) (Table S1). However, during years 4 and 5, this pattern became increasingly clear and more pronounced, with negligible differences between the small mammal response on the Mega and Full treatments (Fig. 2). After the fences were established, with and without the inclusion of the fire year, we found no difference in small mammal numbers between the Full (small mammals = 22.0 SE = 3.1) and Mega treatments (small mammals = 19.4, SE = 2.6) suggesting no mesoherbivore effect, but there were fewer small mammals on the Open treatment (small mammals = 12.9, SE = 1.8) when compared to the Mega and Full treatments (Tables S2, S3) suggesting small mammal abundance was limited on treatments with megaherbivores present (i.e., Open plots).

Our PSEMs with a treatment pathway that was not mediated by vegetation fit the observed data well for small mammals ($X^2 = 1.04$, $P = 0.793$) and the model explained 64 % of the variation in the response of small mammals. The model without direct effects (i.e., treatment pathway) did not fit the data well (goodness of fit $X^2 = 161.42$, $P = 0.00$). As predicted, small mammals responded positively to increases in grass biomass ($\beta = 1.58$), which decreased with fire and exposure to

herbivores (Fig. 3). However, the positive response of small mammals was mediated by an almost equally strong and negative quadratic term ($\beta = 1.22$), with small mammals decreasing at the highest and lowest measures of grass biomass (Fig. 4). Consistent with our predictions, we found differences in small mammal numbers were explained by pathways that were unrelated to vegetation structure (Fig. 3). Moreover, more of the reduction in rodents in the presence of megaherbivores (Post-Open) compared with their exclusion (Post-Mega), was explained by pathways that were not mediated by vegetation structure (Fig. 6). We

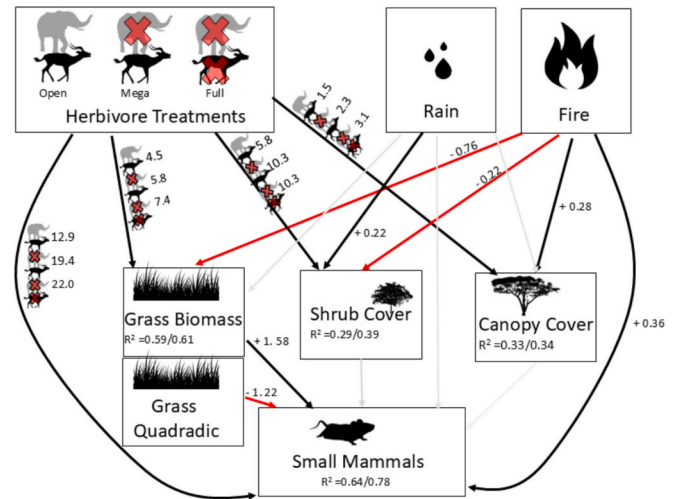


Fig. 3. Piecewise Structural Equation Modeling (PSEM) of herbivore treatments (Open, Mega and Full) fire and on vegetation structure (% shrub cover, % canopy cover, t/ha grass biomass) and small mammal numbers. Gray lines = no significant effect. Black lines = post-treatment differed from pre-treatment conditions. Red lines = post-treatment decreased from pre-treatment conditions. Marginal means are reported for categorical herbivore treatments, other estimates are standardized. R² values are presented as marginal and then conditional values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

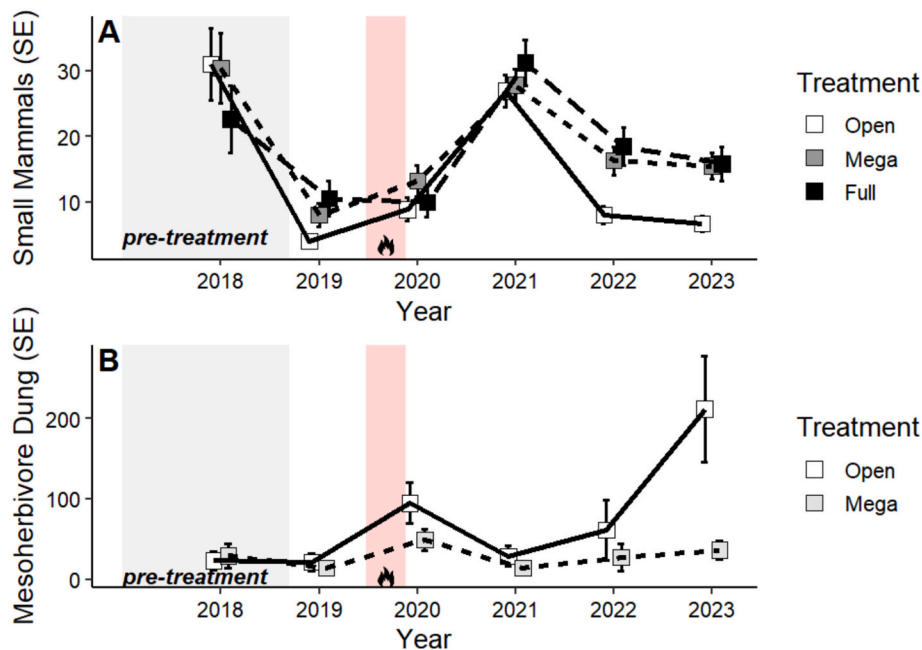


Fig. 2. The predicted annual response and SE (error bars) of A) small mammals (number of individuals) and B) Mesoherbivore activity (dung piles per plot) as a function of three experimental treatments, Open (open to all herbivores), Mega (excluding megaherbivores but accessible to small mammals and mesoherbivores) and Full (excluding megaherbivores and mesoherbivores but accessible to small mammals), across 6 years.

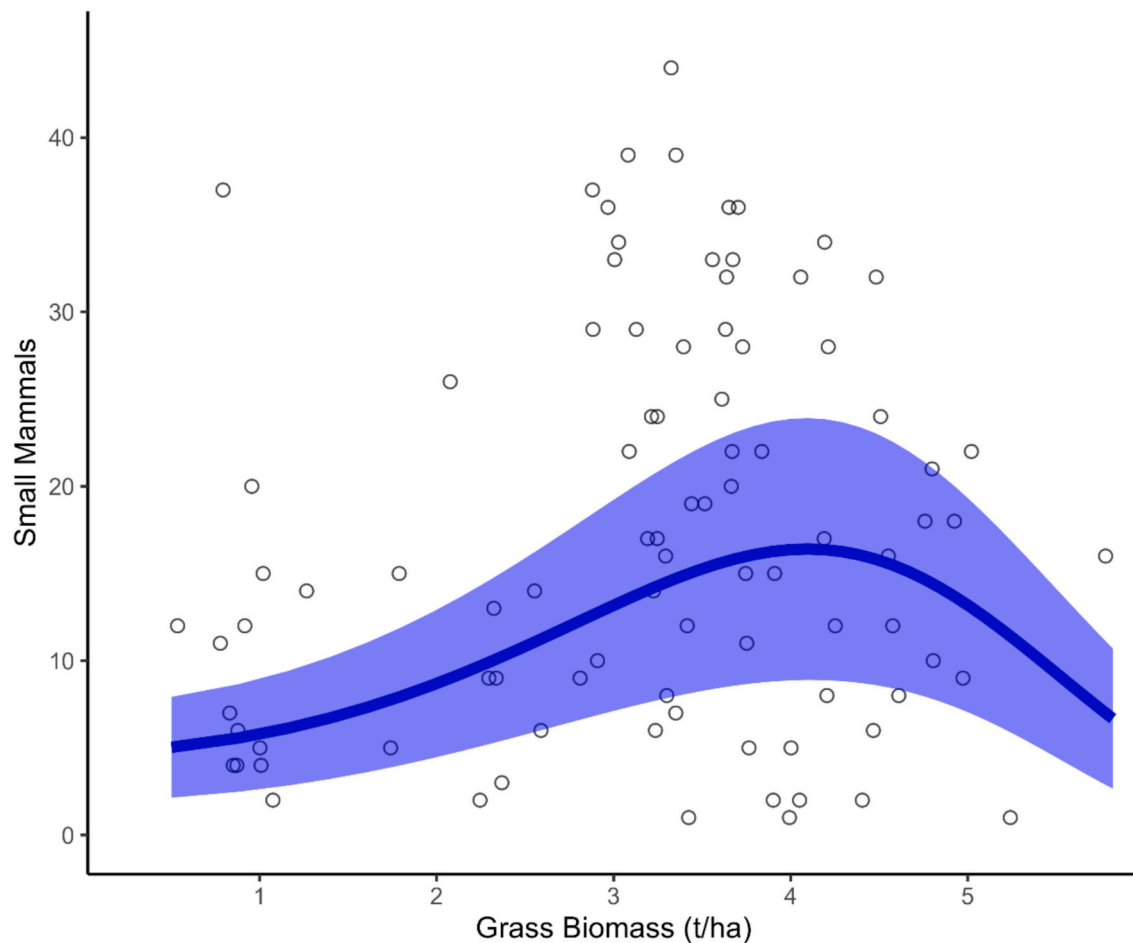


Fig. 4. Predicted small mammal response (number of individuals) to tons (t/ha) of grass biomass on 15 plots in Kruger National Park from 2018 to 2023. The solid line represents the predicted means from model used in PSEM, the shaded area represents predicted 95 % CI and the circles are data points used to generate the model.

also saw a small positive ($\beta = 0.36$) influence of fire on rodent abundance (Fig. 3).

3.2. Response of mesoherbivores

Grazers accounted for 90 % of mesoherbivore dung observed. The most common mesoherbivores we detected were zebra, wildebeest, and cape buffalo. Prior to the initiation of treatments, we estimated 31.8 (SE = 11.3) piles of dung per plot as a metric of activity; however, during subsequent years we estimated an average of 48.3 (SE = 17.0) on all plots open to mesoherbivores. We found significant differences in the activity of mesoherbivores on Open vs. Mega treatments during each of the five years after the treatment (Table S1), with trends of increasing differences between the treatments over time (Fig. 2). After five years of treatments, we found a > 650 % increase of measure of activity (pre-treatment = 28.1, SE = 8.9, 5-years post = 211.0, SE = 65.6) on open plots, but no change on the Mega treatments (pre-treatment = 35.1, SE = 11.1, 5-years post = 36.2, SE = 11.4). Aggregating all five years after the initiation of treatments, we saw a smaller but considerable increase in activity from pre-treatment (Open and Mega treatment across 5-years post = 37.4 SE = 13.2) and a reduction in activity on the Mega treatments (Mega treatment across 5-years post = 21.6 SE = 7.4; Fig. 2; Table S2). The annual differences in grazer activity between Open and Mega plots, was almost identical to the patterns seen when we considered all mesoherbivores together (Fig. S1; Table S1). Browsers and mixed functional groups only differed across treatments during the third-year post-treatment when there was a slight increase in the activity

of browser/mixed feeders on the Open treatments (0.9, SE = 1.0) compared with the Mega treatment (0.07, SE = 0.1) (Fig. S1; Table S1).

The mesoherbivore PSEMs with a treatment pathway that was not mediated by vegetation fit the observed data well ($\chi^2 = 2.09$, $p = 0.553$) and explained 67 % of the variation in the response of mesoherbivores. The model without this pathway did not fit the data well ($\chi^2 = 666.94$, $p = 0.00$). Mesoherbivores responded to changes in vegetation structure, rainfall and exclusion of megaherbivores (Fig. 5). Mesoherbivore activity, measured via dung per plot, increased with shrubs cover and decreased with canopy cover, both of which decreased on open plots with exposure to megaherbivores (Fig. 5; Table S2). Mesoherbivore activity also increased with reductions in grass biomass (Fig. 5). After initiation of our treatments, mesoherbivores increased activity 183 % on open plots (Post Open) compared to megaherbivore (Post Mega) plots (Fig. 5, Table S2). Additionally, the greatest portion of this increase could be attributed to the pathway that did not account for megaherbivore influence on mesoherbivores through broad measures of vegetation structure (Fig. 6).

4. Discussion

There is little doubt that megaherbivores and mesoherbivores can profoundly alter vegetation structure and architecture across ecosystems, with cascading effects on associated animal communities (Bakker et al., 2016; Pringle et al., 2023). We found that where megaherbivores were present mesoherbivore activity increased and small mammals were suppressed. Consistent with prior research, we found that

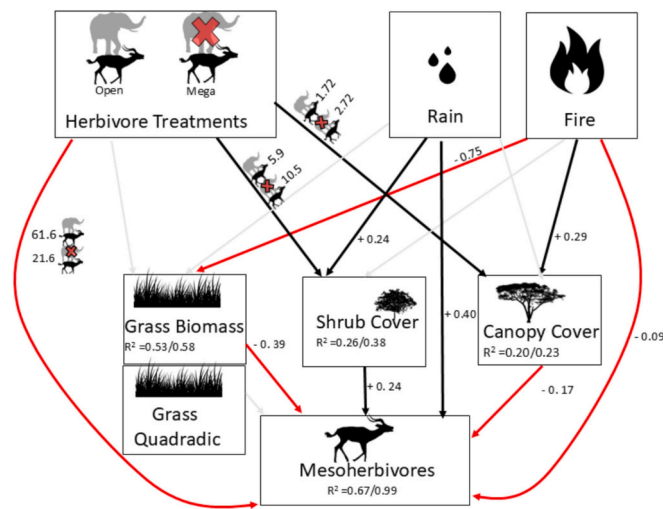


Fig. 5. Piecewise Structural Equation Modeling (PSEM) of herbivore treatments (Open, Mega) fire and on vegetation structure (% shrub cover, % canopy cover, t/ha² grass biomass) and mesoherbivore activity. Gray lines = no significant effect. Black lines = post-treatment increased from pre-treatment conditions. Red lines = post-treatment decreased from pre-treatment conditions. Marginal means are reported for categorical herbivore treatments, other estimates are standardized. R^2 values are presented as marginal and then conditional values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mesoherbivores influence grass biomass which helped explained some of the variation in the response of small mammals, and megaherbivores had an influence on mesoherbivores through their impact on woody vegetation. However, contrary to our small mammal predictions and previous studies on both small mammals (Goheen et al., 2018; Keesing, 2000; Young et al., 2015) and mesoherbivores (Valeix et al., 2011; de Boer et al., 2015; Le Roux et al., 2018; Wells et al., 2021), the responses of small mammals and mesoherbivores to megaherbivores were only partially attributable to megaherbivores influence on vegetation structure. Our results underscore the significant, yet complex, impacts megaherbivores have on mammal communities.

In many grass-dominated systems, declines in small mammal populations in the presence of mesoherbivores have been attributed to reductions in grass resources that small mammals rely on for food and shelter (Bueno et al., 2012; den Herder et al., 2016; Young et al., 2015). In contrast, our findings showing the strength of the pathways that did not represent vegetation-structure, suggest that subtler environmental changes or behavioral responses—such as avoidance of trampling or competition—may play a larger role. This nuance highlights the need for a broader perspective when evaluating herbivore-driven ecosystem changes, extending beyond traditional vegetation structure focused approaches. It is likely that excluding megaherbivores increased the availability of seeds (Goheen et al., 2018), fruits (Bernard et al., 2015), and insects (Ogada et al., 2008), all of which benefit small mammals in this system (Monadjem, 1997). Alternatively, small mammals may have avoided areas with larger herbivores because of competition (e.g., cryptic interference; Ferry et al., 2016), trampling risks (Avenant and Cavallini, 2007), or exposure to mammalian predators along game trails (Cusack et al., 2015).

While mesoherbivores reduced grass biomass (Table S2), the relationship between small mammals and grass was non-linear. Small mammal numbers declined at both the lowest and highest levels of grass biomass (Fig. 4). Thus, mesoherbivores could potentially increase small mammal populations by reducing grass biomass when it is high (> 4.5 t/ha) or decreased small mammal populations by reducing grass biomass to levels that are less than optimal (\approx 3.8 t/ha; Fig. 4). It is also possible that the activity of mesoherbivores was not sufficient to induce the

changes in grass biomass necessary to establish a strong negative relationship between mesoherbivores and small mammals. However, large herbivore biomass in our study area appeared comparable to sites where strong grass-mediated effects on small mammals have been observed (Staver et al., 2021). Moreover, a marked increase in mesoherbivore activity in 2023 (Fig. 2) did not alter the observed response of small mammals to the treatments. In savannas, small mammal densities are often linked to grass and rainfall (Byrom et al., 2014; Loggins et al., 2019; Young et al., 2015). However, with above-average rainfall throughout the study period (792 mm annually), and low small mammal numbers at the highest grass biomass levels, it seems unlikely that rainfall or grass were primary limiting factors under these conditions.

Similar to small mammals, mesoherbivores exhibited responses to our treatments that were only partially mediated by our broad measures of vegetation structure. In fact, the direct pathway accounting for the megaherbivores' influences on mesoherbivores that were not mediated by vegetation structure were more than two times stronger than vegetation-structure mediated pathways (Fig. 6). Three potential explanations for this response include: (1) species interactions, such as behavioral facilitation; (2) environmental changes not captured by our measurements of vegetation structure; or (3) avoidance of fenced plots. Behavioral facilitation may arise when grazers, such as zebra and wildebeest, increase proximity to megaherbivores to reduce predation risk from apex predators like lions (Ferry et al., 2016), or because they are signaling quality foraging (Schulte and LaDue, 2021). Alternatively, megaherbivores could have altered vegetation composition—reducing forbs and benefiting grazers like zebra (Young et al., 2005)—or improved forage quality and palatability by removing moribund grasses (Arsenault and Owen-Smith, 2002). Megaherbivores' distinctive game trails might also enhance accessibility for mesoherbivores (Haynes, 2012). Finally, while temporary avoidance of fences (e.g. 4 days) has been documented (Jakopin et al., 2021), there is no evidence of longer-term fence avoidance from similar studies (Saikkonen et al., 2019; Wells et al., 2021). Moreover, if mesoherbivores responses were a function of fence avoidance, over time we would have expected to see a consistent difference or a decline in the differences between their activity on Mega and Open plots. This is the opposite of what we observed.

Mesoherbivores activity increased after the fire and during the last two years of the study. The notable increase at the end of the study may have been a function of elevated rainfall during these years (>940 mm) that allowed zebra and cape buffalo to expand their foraging away from permanent sources of water (Ogutu et al., 2008; Harris et al., 2015). Mesoherbivore activity also increased with shrub cover in this relatively open system. This response may reflect the behavior of grazers seeking higher-quality forage near woody vegetation (Ludwig et al., 2008). Conversely, mesoherbivores avoided areas with elevated tree canopy cover, a pattern previously observed in wildebeest and zebra that may be related to reductions in grass biomass (Mandlate et al., 2019; Soto-Shoender et al., 2018). Throughout the study we found more mesoherbivore activity in areas with reduced grass biomass, consistent with their preference for greener, lower biomass vegetation (Mandinyanya et al., 2020; Mariotti et al., 2020). In contrast, the density of browsing herbivores is typically associated with woody vegetation (Smit and Prins, 2015), but minimal initial woody vegetation and browsing herbivore numbers likely limited such effects in our study. Over the last 40 years, our study area has experienced marked declines in tree canopy and overstory cover, largely attributed to elephants and fire (Asner and Levick, 2012; Eckhardt et al., 2000). If the observed recovery trends in shrubs and canopy cover on our megaherbivore exclusion plots continue, we might expect increased activity of browsers and mixed feeders (Smit and Prins, 2015).

Like most large-scale field experiments, our study's spatial and temporal scope imposed limitations on the generalizability of our findings. While our results offer strong evidence for the influence of megaherbivores on vegetation structure and faunal abundance, extending these insights across broader landscapes, timeframes and community

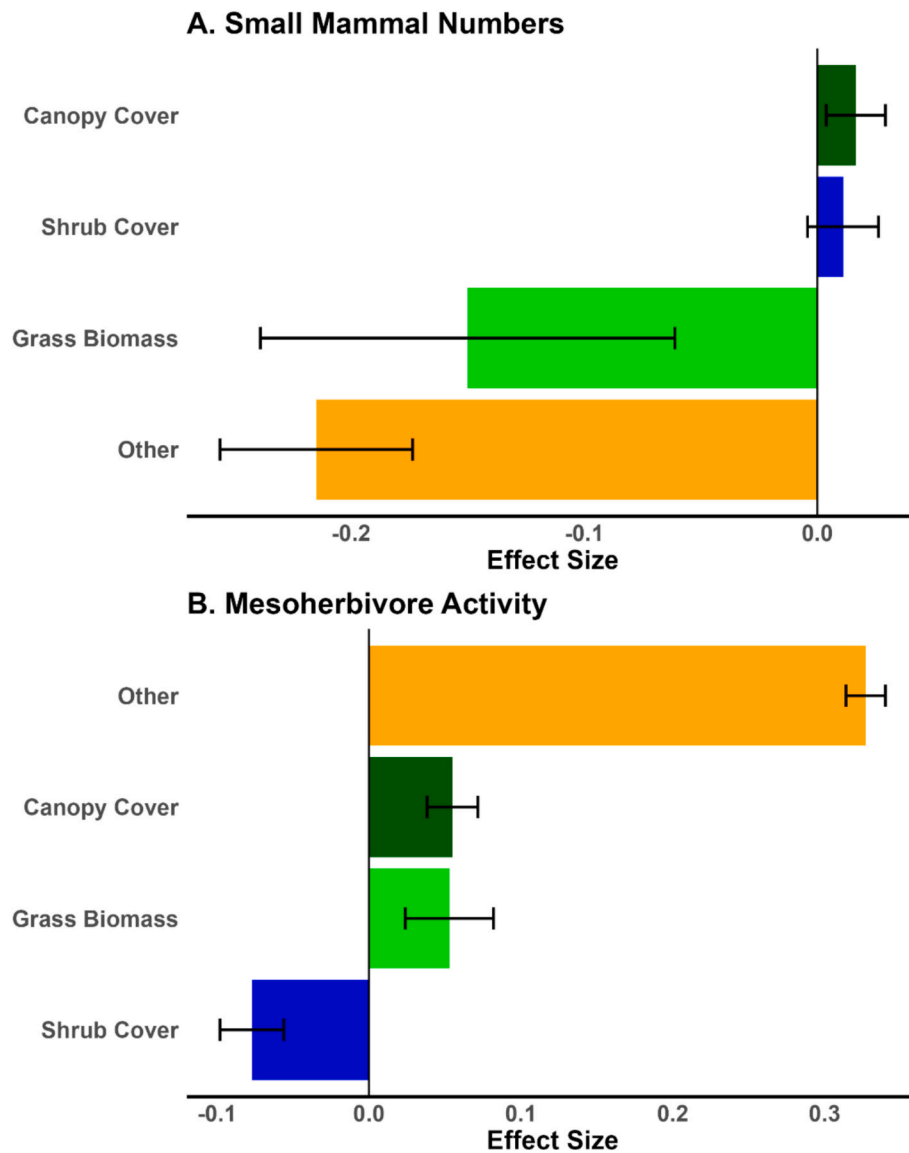


Fig. 6. Comparison of models to predict A) small mammal numbers and B) mesoherbivore activity given the exclusion of megaherbivores (Mega plots after initiation vs. Open plots after initiation) with vegetation mediated pathways (canopy cover, grass biomass, and shrub cover) and a direct pathway that was not mediated by vegetation structure (other). Colored bars represent standardized effect sizes from model-predicted values and R^2 -adjusted variance. Error bars represent standardized standard errors (SE) of effect sizes.

metrics (e.g., diversity and dominance) will require additional work. One promising avenue is the integration of experimental data with broader-scale observational platforms, such as citizen science or remote sensing datasets (McCleery et al., 2023). Furthermore, long-term monitoring of our experimental plots should help us determine if the observed dynamics continue or fluctuate over time. We also acknowledge that the enclosures may concentrate resources, potentially amplifying small mammal responses relative to the surrounding matrix. This scale mismatch highlights the importance of future work that compares localized patterns with broader landscape conditions. Finally, our current analysis uses derived abundance estimates as covariates, a common approach in ecological field studies. However, future work could develop Bayesian or meta-analytical frameworks to more fully account for the uncertainty in these estimates and better integrate diverse data sources.

4.1. Conservation and management applications

As rewilding, restoration, and herbivore impact mitigation efforts

expand, it is essential to consider the complex interplay among megaherbivores, mesoherbivores, vegetation structure, and other animal communities. Our findings emphasize the multifaceted role megaherbivores play in shaping ecosystems, highlighting that their impacts extend well beyond structural changes to vegetation. Megaherbivores likely reshape other animal communities through a host of subtle environmental (Haynes, 2012) and behavioral pathways (Ferry et al., 2016; Valeix et al., 2007; Landman and Kerley, 2014) that are not easily replicated via management or the use of other large herbivores.

The management of abundant megaherbivore and mesoherbivore populations are also likely to present critical tradeoffs. In our study site and other areas with substantial megaherbivores, concerns persist about their cascading impacts on wildlife communities (Cumming et al., 1997; Herremans, 1995; Kerley and Landman, 2006; McCleery et al., 2018). In these contexts, deterrents (Cook et al., 2023; Tiller et al., 2022), fences (Dupuis-Desormeaux et al., 2016), and the removal of artificial surface water (Smit, 2011) have been used to protect sensitive vegetation from megaherbivores (O'Connor et al., 2007). However, such measures may inadvertently prevent megaherbivores from reducing populations of

smaller mammals that prey on seeds and seedlings of the same vegetation (Teman et al., 2021; Goheen et al., 2010). Similarly, managing megaherbivores is likely to generate tradeoffs between their effects on smaller versus larger wildlife communities (Vaccaro and Schulte, 2024). To address these challenges, assessments of megaherbivores' potentially deleterious impacts on wildlife must account for the differing spatial and temporal scales at which populations and communities of varying body sizes operate.

Our findings underscore that some ecological functions of megaherbivores—such as their suppression of small mammals and ability to increase the activities of mesoherbivores—cannot be replicated through vegetation management alone (Gordon et al., 2023; O'Connor and Page, 2014). Nor can these roles be entirely replaced by more common mesoherbivores (Moe et al., 2009; O'Kane et al., 2014) or surrogates like cattle (Pringle et al., 2023; Veblen et al., 2016). Moreover, by increasing the activity of mesoherbivores and suppressing small mammals, megaherbivores are helping address the global loss and replacement of large mammals with smaller ones (Epperly et al., 2021; Estes et al., 2011).

Ultimately, restoring and maintaining the full functionality of savannas and other ecosystems may not be achievable without the challenging yet essential task of establishing (Gordon et al., 2023), protecting (Ripple et al., 2015), and managing megaherbivore populations. This effort will require integration across small conservation areas and larger landscape matrices that include agriculture and other anthropogenic land uses (Garai et al., 2004; Gordon et al., 2023; Svenning et al., 2016). By addressing these complexities, conservation practitioners can better ensure that megaherbivores contribute to biodiversity conservation, ecosystem functionality, and resilience in a rapidly changing world.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111378>.

CRedit authorship contribution statement

Robert A. McCleery: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Laurence Kruger:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Ara Monadjem:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Donovan Tye:** Writing – review & editing, Supervision, Project administration, Investigation, Data curation. **Philip Mhlava:** Writing – review & editing, Supervision, Investigation. **Emanuel Zwane:** Writing – review & editing, Supervision, Investigation. **Alison Bijl:** Writing – review & editing, Supervision, Investigation, Data curation. **Maggie Jones:** Writing – review & editing, Investigation, Data curation. **Jack Hartfelder:** Writing – review & editing, Methodology, Investigation. **Muzi Sibya:** Writing – review & editing, Methodology, Investigation. **Corli Coetsee:** Writing – review & editing, Supervision, Conceptualization. **Robert J. Fletcher:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

All authors declare they have no competing interests.

Acknowledgements

We thank South African National Parks for their support of this project and the interns and students for their efforts collecting field data. This project was funded in part by NSF IRES Grants (No. 1459882 and 1952393) and the Institute of Food and Agricultural Sciences at the University of Florida, Nsasani Trust and the Organization for Tropical Studies. We acknowledge that drawings in figures from Sarah Werning

(elephant, modified to gray []), T. Michael Keesey (impala), Katy Lawler (mouse), Karen Arnold (grass), Kalpa Madhushan (fire), Erik Flowers (rain), openClipart (Acacia = SVG ID: 150774, Shrub = SVG ID: 22423) were used as part under creative commons licenses <https://creativecommons.org/licenses/by/3.0/>. Photo credit to Laurence Kruger for elephant pictures in Fig. 1.

Data availability

Data will be available upon request

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