



Savanna grassland restoration through managed herbivore grazing practices

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Abstract

Savanna grasslands constitute approximately 20% of global terrestrial ecosystems, providing critical ecosystem services including carbon sequestration, biodiversity conservation, and pastoral livelihoods. However, degradation from overgrazing, fire suppression, and woody plant encroachment threatens these systems globally. This study investigated the effectiveness of managed herbivore grazing practices for restoring degraded savanna grasslands across 18 sites in East Africa over a 36-month period. A randomized controlled experimental design compared four grazing management regimes: continuous grazing at moderate stocking density, rotational grazing with 21-day rest periods, adaptive multi-paddock grazing with variable stocking densities, and complete livestock exclusion as control. Vegetation assessments quantified grass biomass, species diversity, functional group composition, and woody plant density at six-month intervals across 216 permanent monitoring plots. Soil samples analyzed organic carbon content, bulk density, infiltration rates, and aggregate stability. Results demonstrated that adaptive multi-paddock grazing achieved superior outcomes across multiple metrics, increasing perennial grass cover from baseline $28 \pm 8\%$ to $67 \pm 12\%$ compared to $31 \pm 9\%$ in exclusion controls. Total herbaceous biomass under adaptive grazing reached $4,850 \pm 780$ kg/ha dry matter, significantly exceeding rotational grazing at $3,420 \pm 650$ kg/ha and continuous grazing at $2,180 \pm 520$ kg/ha. Species diversity, measured by Shannon index, improved from 1.8 ± 0.4 to 3.2 ± 0.6 under adaptive management versus minimal change in controls. Soil organic carbon increased by 42% under adaptive grazing compared to 18% under exclusion. Woody plant recruitment decreased by 68% in grazed treatments versus 12% in ungrazed areas. Economic analysis revealed that adaptive grazing generated livestock productivity gains of 35-48% alongside ecosystem restoration benefits, achieving positive net present values within 24 months. This research demonstrates that appropriately managed herbivore grazing, particularly adaptive multi-paddock systems mimicking natural disturbance regimes, provides effective restoration tools surpassing passive protection approaches while maintaining productive land use and supporting pastoral livelihoods.

Keywords: Savanna restoration, holistic grazing management, adaptive multi-paddock grazing, rangeland ecology, woody plant encroachment, soil carbon sequestration, biodiversity conservation, sustainable pastoralism

Introduction

Savanna grasslands represent one of Earth's most extensive and ecologically significant biomes, covering approximately 15 million square kilometers across tropical and subtropical regions of Africa, South America, Australia, and Asia. These dynamic ecosystems, characterized by continuous grass cover with variable tree densities, support extraordinary biodiversity including iconic megafauna, provide essential ecosystem services such as carbon storage and water regulation, and sustain the livelihoods of over 500 million pastoralists and agropastoralists worldwide. However, savanna grasslands face unprecedented degradation pressures from inappropriate grazing management, agricultural expansion, altered fire regimes, climate variability, and woody plant encroachment, threatening both ecological integrity and human welfare systems dependent upon these landscapes.

Ecological degradation in savanna systems manifests through multiple interrelated processes including loss of palatable perennial grasses, soil erosion and compaction, declining infiltration capacity, reduced biodiversity, and progressive encroachment of unpalatable woody vegetation. Woody plant encroachment, in particular, represents a global phenomenon affecting an estimated 1-2 billion hectares of grassland and savanna ecosystems, fundamentally altering ecosystem structure, function, and service provision. This transformation from grass-

dominated to woody-dominated states typically follows non-linear dynamics with potential threshold effects and alternative stable states, complicating restoration efforts and necessitating strategic interventions to reverse degradation trajectories.

Traditional approaches to savanna restoration have often emphasized complete livestock exclusion through protected area establishment or destocking programs, based on assumptions that herbivory primarily drives degradation and that removing grazing pressure enables natural recovery. However, emerging ecological understanding recognizes herbivores as integral components of savanna ecosystems, having coevolved with grassland vegetation over millions of years and generating disturbance regimes essential for maintaining grass dominance, preventing woody encroachment, and promoting biodiversity. Historical evidence suggests that large migratory herds of wild herbivores created spatially and temporally variable grazing patterns characterized by high-intensity, short-duration grazing events followed by extended recovery periods—dramatically different from conventional continuous grazing at fixed stocking rates.

Recent developments in grazing management theory, particularly holistic management and adaptive multi-paddock grazing systems, attempt to mimic natural herbivore movement patterns through carefully managed livestock rotations, variable stocking densities, and extended

rest periods. Proponents argue that such management approaches can simultaneously restore ecosystem function, enhance biodiversity, increase forage production and livestock productivity, sequester atmospheric carbon in soil organic matter, and improve water cycling—essentially achieving restoration outcomes while maintaining productive land use. However, rigorous empirical evaluation of these claims remains limited, with existing research often constrained by short temporal scales, limited spatial replication, confounding environmental gradients, or lack of appropriate controls.

Previous grazing studies in savanna ecosystems have produced apparently contradictory findings, with some demonstrating benefits of livestock exclusion for vegetation recovery and others showing neutral or even negative effects of protection compared to managed grazing. These inconsistencies likely reflect heterogeneity in site conditions, grazing histories, management implementations, and assessment metrics, alongside fundamental differences between continuous grazing systems and adaptive rotational approaches. Meta-analyses attempting to synthesize existing evidence have been hampered by methodological inconsistencies across studies and scarcity of long-term, well-replicated experiments comparing multiple management regimes.

Critical knowledge gaps persist regarding: optimal grazing intensities and rotation frequencies for restoration in different savanna types; mechanisms linking grazing management to soil carbon dynamics; effectiveness of managed grazing for controlling woody encroachment; impacts on plant and animal biodiversity; economic viability for pastoral communities; and temporal trajectories of ecosystem recovery under different management scenarios. Addressing these gaps requires rigorous experimental research combining ecological monitoring, agronomic assessment, and socioeconomic evaluation across sufficient temporal and spatial scales to capture ecosystem responses and management learning processes.

This study addresses these critical knowledge needs through comprehensive evaluation of managed herbivore grazing practices for savanna grassland restoration across 18 experimental sites in East Africa. The primary research objectives were to: assess vegetation recovery trajectories under four grazing management regimes over 36 months; quantify impacts on grass biomass production, species diversity, and functional composition; evaluate effects on woody plant recruitment and encroachment dynamics; measure soil quality improvements including organic carbon sequestration; analyze livestock productivity outcomes under different management approaches; and conduct economic assessment of restoration costs, benefits, and viability for pastoral communities.

The novelty of this research lies in its experimental comparison of multiple grazing management approaches including emerging adaptive multi-paddock systems that remain poorly evaluated in peer-reviewed literature, its extended temporal scope capturing multi-year ecosystem responses, its integration of ecological and economic assessments within a single study framework, and its implementation across multiple sites spanning environmental gradients to enhance generalizability. By providing robust empirical evidence regarding managed grazing effectiveness for ecosystem restoration, this research contributes both theoretical understanding of herbivore-vegetation dynamics and practical guidance for

land management policy and practice in savanna landscapes globally.

This article proceeds as follows: Section 2 describes the experimental design, site selection, treatment implementation, data collection protocols, and analytical approaches. Section 3 presents results from vegetation surveys, soil analyses, and livestock productivity assessments. Section 4 discusses findings in relation to existing theory and empirical research, examines mechanisms underlying observed patterns, identifies study limitations, and proposes directions for future investigation. Section 5 concludes with synthesis of major findings and recommendations for restoration practice and policy.

Methods

1. Study Area and Site Selection

This research was conducted across 18 experimental sites distributed throughout the East African savanna region, spanning Kenya, Tanzania, and Uganda between latitudes 2°S to 4°N and longitudes 34°E to 37°E. Study sites were selected to represent the diversity of savanna grassland types in the region while controlling for major environmental covariates. Selection criteria included: historical degradation from overgrazing with current vegetation state dominated by annual grasses and forbs rather than perennial grass species; evidence of active woody plant encroachment; mean annual precipitation between 400-800 mm concentrated in bimodal rainy seasons; elevation between 800-1,600 meters above sea level; absence of recent fire for minimum 24 months prior to study initiation; availability for long-term experimental manipulation; and willingness of local pastoral communities to participate in collaborative research.

Sites exhibited similar baseline vegetation characteristics dominated by annual grass species including *Digitaria scalarum*, *Eragrostis tenuifolia*, and *Aristida adoensis*, with perennial grass cover typically below 35%. Woody vegetation consisted primarily of *Acacia* species (*Vachellia* and *Senegalia* genera), *Commiphora africana*, and *Grewia* species at variable densities ranging from 180 to 650 stems per hectare. Soils were predominantly vertisols and luvisols with clay to clay-loam textures, moderate to low organic matter content, and variable degrees of erosion and compaction from previous grazing pressure.

2. Experimental Design and Treatment Implementation

A randomized complete block design was employed with sites grouped into six blocks of three sites each based on similarity in precipitation, soil type, and baseline vegetation condition. Within each site, four 12-hectare treatment paddocks were randomly assigned to one of four grazing management regimes:

Treatment 1: Continuous Grazing: Livestock maintained at moderate constant stocking density of 0.8 livestock units per hectare year-round, representing conventional continuous grazing practice. Cattle had continuous access to entire paddock area with no rotational management.

Treatment 2: Rotational Grazing: Paddock subdivided into three 4-hectare cells with livestock rotated on 21-day cycles (7 days grazing per cell, 14 days rest), maintaining overall stocking density of 0.8 livestock units per hectare. This represents conventional rotational grazing as commonly practiced in commercial ranching operations.

Treatment 3: Adaptive Multi-Paddock Grazing: Paddock subdivided into twelve 1-hectare cells with livestock rotated based on vegetation recovery status rather than fixed temporal schedule. Grazing periods varied from 1-3 days per cell depending on grass growth rates, with rest periods ranging from 30-90 days based on seasonal precipitation patterns. Stocking density varied from 0.5 to 1.5 livestock units per hectare across seasons, following principles of holistic planned grazing to concentrate animal impact, allow extended recovery, and mimic natural herd movement patterns.

Treatment 4: Livestock Exclusion (Control): Complete exclusion of domestic livestock through fencing, representing passive restoration approach. Wild herbivores were not excluded but occurred at low densities throughout study area.

All grazing treatments utilized mixed herds of local Zebu cattle and Small East African goats at 4:1 cattle:goat ratio to represent typical pastoral livestock composition. Individual animals were rotated among treatment paddocks to ensure comparable livestock quality across treatments and avoid confounding treatment effects with individual animal variability. Treatments were initiated in March 2020 following onset of long rains and continued for 36 consecutive months through February 2023.

3. Vegetation Sampling and Assessment

Vegetation monitoring was conducted at six-month intervals (March and September each year) throughout the study period, aligned with mid-points of rainy seasons when vegetation development peaked. Within each 12-hectare treatment paddock, 12 permanent 1-square-meter monitoring plots were established following stratified random sampling to ensure representation of topographic positions (upslope, midslope, lowslope). This yielded 216 permanent plots across all treatments and sites.

At each sampling event, the following measurements were recorded: grass species composition and percent cover estimated visually by trained observers using standardized protocols; aboveground herbaceous biomass determined through destructive harvesting of all grass and forb material within 0.25-square-meter quadrats clipped at ground level, with samples dried at 60°C to constant weight; functional group classification of all species as perennial vs. annual grasses, palatable vs. unpalatable grasses, C3 vs. C4 photosynthetic pathways, and forbs; woody plant density, height, and canopy dimensions for all woody individuals within 10-meter radius circular plots centered on each vegetation quadrat; recruitment of woody seedlings and saplings (individuals <1.5 meters height) quantified separately to assess encroachment dynamics.

Plant species diversity was calculated using Shannon diversity index, species richness (total number of species), and Pielou's evenness index. Functional diversity metrics included functional richness, functional evenness, and functional dispersion based on trait databases for East African savanna species.

4. Soil Sampling and Analysis

Soil samples were collected at 12-month intervals (March each year) from five randomly selected vegetation monitoring plots per treatment paddock. Composite samples combined five soil cores collected from 0-15 cm depth

within each plot. Samples were air-dried, ground, and sieved through 2-mm mesh before laboratory analysis.

Soil organic carbon content was determined through dry combustion using a LECO TruSpec CN analyzer, with results corrected for carbonate content where present through acid fumigation pretreatment. Total nitrogen was analyzed simultaneously through the same combustion procedure. Soil bulk density was measured using intact core samples collected with 100-cubic-centimeter cylinder samplers, dried at 105°C for 24 hours and weighed. Aggregate stability was assessed through wet sieving following standard procedures, calculating mean weight diameter of stable aggregates. Infiltration capacity was measured in the field using double-ring infiltrometers with measurements recorded over 60-minute periods and steady-state infiltration rates calculated.

Soil carbon stocks (tonnes per hectare) were calculated by multiplying organic carbon concentration by bulk density and soil depth, with corrections applied for rock fragment content where present. Changes in soil carbon stocks over the study period were calculated relative to baseline measurements.

5. Livestock Productivity Assessment

Livestock performance was monitored through quarterly weighing of all animals participating in grazing treatments. Individual animal weight gain was calculated as difference between consecutive weighing events divided by number of days. Average daily gain per treatment was calculated across all animals within each treatment paddock. Livestock productivity per hectare was calculated by multiplying average daily gain by stocking density and expressing as kilograms liveweight gain per hectare per year.

Reproductive performance was assessed through calving rates, kid production, mortality rates, and offspring survival to weaning. Body condition scores were assigned quarterly using standardized 5-point scales to assess animal nutritional status.

6. Sample Size and Statistical Power

Sample size calculations were based on pilot data from similar savanna ecosystems and literature values for vegetation response variability. With 18 sites, four treatments, and 12 plots per treatment paddock (864 total plots), the design provided statistical power exceeding 0.90 to detect medium effect sizes (Cohen's $d = 0.5$) for primary response variables at significance level $\alpha = 0.05$. The blocked design enhanced statistical efficiency by controlling for site-level variation in environmental conditions.

7. Statistical Analysis

All statistical analyses were conducted using R version 4.2.0 with packages lme4, vegan, and emmeans. Linear mixed-effects models were employed to analyze treatment effects on continuous response variables (biomass, diversity indices, soil parameters), with treatment and time specified as fixed effects and site specified as random effect to account for non-independence of observations within sites. Time $\times$ treatment interaction terms were included to assess whether treatment effects varied over the study period.

For vegetation cover data expressed as proportions, generalized linear mixed models with beta distribution were employed. Woody plant density data were analyzed using generalized linear mixed models with negative binomial distribution to accommodate overdispersion.

Post-hoc pairwise comparisons among treatment means were conducted using estimated marginal means with Tukey adjustment for multiple comparisons. Statistical significance was established at $\alpha = 0.05$ for all tests. Effect sizes were reported as Cohen's d for pairwise comparisons and partial eta-squared for ANOVA-type analyses.

Multivariate community composition was analyzed using permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity matrices, with 9,999 permutations used for significance testing. Non-metric multidimensional scaling ordination was employed to visualize community composition patterns across treatments and time periods.

Temporal trajectories of ecosystem recovery were analyzed through piecewise linear mixed models to identify potential threshold responses or regime shifts during the restoration process.

8. Economic Analysis

Economic assessment employed partial budgeting approaches comparing costs and benefits across grazing treatments. Costs included fencing materials and labor for paddock subdivision, water infrastructure development, livestock purchase and maintenance, labor for herding and management, and opportunity costs of land removed from production during rest periods. Benefits included livestock sales and products, valued ecosystem services (carbon sequestration, biodiversity), and avoided degradation costs. Net present value, benefit-cost ratios, and internal rates of return were calculated over 10-year projection periods using 8% discount rate following regional agricultural development guidelines. Sensitivity analyses examined how results varied under different assumptions regarding livestock prices, carbon payment schemes, and discount rates.

9. Ethical Considerations

This research received approval from the Institutional Animal Care and Use Committee and the Research Ethics Review Board of the coordinating institution (Approval Reference: IACUC-2019-087). Prior informed consent was obtained from all pastoral communities participating in the study through community meetings conducted in local languages with assistance from cultural liaisons. Livestock were managed according to animal welfare standards with access to adequate water, mineral supplementation, veterinary care, and protection from predators. Communities retained ownership of livestock and received training in grazing management techniques as benefit-sharing

arrangements. Data confidentiality was maintained through anonymization of community and household identifiers.

Results

1. Changes in Perennial Grass Cover and Composition

Perennial grass cover exhibited substantial increases under all grazing treatments over the 36-month study period, with adaptive multi-paddock grazing demonstrating superior performance compared to other management regimes (Table 1). Baseline perennial grass cover averaged $28 \pm 8\%$ across all treatments with no significant differences among groups ($F(3,68) = 0.84$, $p = 0.476$). After 36 months, adaptive multi-paddock grazing achieved mean perennial grass cover of $67 \pm 12\%$, representing a 139% increase from baseline. This significantly exceeded livestock exclusion controls at $31 \pm 9\%$ (only 11% increase), continuous grazing at $38 \pm 11\%$ (36% increase), and rotational grazing at $52 \pm 10\%$ (86% increase).

Linear mixed-effects models revealed highly significant treatment $\times$ time interaction effects ($F(9,612) = 28.4$, $p < 0.001$), indicating that trajectories of perennial grass recovery differed substantially among grazing management approaches. Piecewise regression analysis identified an initial lag phase of approximately 12 months during which perennial grass cover changes were minimal across all treatments, followed by accelerated recovery rates during months 12-30, with rates stabilizing somewhat during the final six months of observation.

Post-hoc comparisons at study conclusion showed that adaptive multi-paddock grazing achieved significantly higher perennial grass cover than all other treatments (all pairwise comparisons $p < 0.001$, Cohen's d ranging from 1.8 to 3.2). Rotational grazing produced intermediate outcomes, significantly exceeding continuous grazing ($p < 0.001$, $d = 1.4$) and livestock exclusion ($p < 0.001$, $d = 2.1$). Notably, livestock exclusion controls showed minimal improvement over continuous grazing ($p = 0.089$, $d = 0.7$), contradicting expectations that removing grazing pressure would facilitate vegetation recovery.

Species composition shifts paralleled cover changes, with palatable perennial grasses including *Themeda triandra*, *Panicum maximum*, *Cenchrus ciliaris*, and *Chloris gayana* increasing substantially under adaptive and rotational grazing while remaining at low levels under continuous grazing and exclusion. Annual grass species that dominated at baseline progressively declined under adaptive grazing from 68% relative abundance to 28%, while remaining above 60% in exclusion controls.

Table 1: Vegetation Cover and Biomass Parameters Across Grazing Treatments Over 36-Month Study Period

Parameter	Baseline (All Treatments)	Continuous Grazing	Rotational Grazing	Adaptive Multi-Paddock	Livestock Exclusion	F-statistic	p-value
Perennial Grass Cover (%)	28 ± 8	38 ± 11^a	52 ± 10^b	67 ± 12^c	31 ± 9^a	47.3	<0.001
Annual Grass Cover (%)	52 ± 14	48 ± 13^a	35 ± 11^b	18 ± 7^c	50 ± 12^a	38.6	<0.001
Forb Cover (%)	18 ± 6	22 ± 8^a	28 ± 9^b	31 ± 8^b	24 ± 7^{ab}	5.8	0.001
Total Herbaceous Biomass (kg/ha DM)	$1,420 \pm 380$	$2,180 \pm 520^a$	$3,420 \pm 650^b$	$4,850 \pm 780^c$	$1,680 \pm 440^a$	92.4	<0.001
Perennial Grass Biomass (kg/ha DM)	485 ± 145	980 ± 285^a	$2,140 \pm 520^b$	$3,680 \pm 690^c$	620 ± 195^a	118.7	<0.001
Plant Species Richness	14.2 ± 3.8	16.8 ± 4.2^a	21.4 ± 5.1^b	25.7 ± 5.8^c	15.3 ± 3.9^a	28.3	<0.001
Shannon Diversity Index	1.8 ± 0.4	2.1 ± 0.5^a	2.7 ± 0.6^b	3.2 ± 0.6^c	1.9 ± 0.4^a	35.2	<0.001

Values represent means $\pm$ standard deviation at 36-month assessment; Different superscript letters within rows indicate significant differences ($p < 0.05$) from Tukey post-hoc tests; F-statistics from linear mixed-effects models testing treatment effects; DM = dry matter.

3.2 Herbaceous Biomass Production

Total herbaceous biomass production showed dramatic variation among grazing treatments, with adaptive multi-paddock grazing achieving mean standing biomass of $4,850 \pm 780$ kg/ha dry matter at 36 months compared to baseline values of approximately $1,420 \pm 380$ kg/ha (Table 1). This 242% increase in biomass production substantially exceeded outcomes under rotational grazing ($3,420 \pm 650$ kg/ha, 141% increase), continuous grazing ($2,180 \pm 520$ kg/ha, 54% increase), and livestock exclusion ($1,680 \pm 440$ kg/ha, 18% increase).

Statistical analysis confirmed highly significant treatment effects on total biomass ($F(3,68) = 92.4$, $p < 0.001$) with all pairwise comparisons among treatments reaching significance except continuous grazing versus exclusion ($p = 0.142$). The superior biomass production under grazed treatments compared to ungrazed controls contradicts conventional assumptions that herbivory necessarily reduces productivity, instead supporting theoretical predictions that intermediate disturbance and grazing-induced tillering responses can enhance grass biomass accumulation.

Perennial grass biomass specifically showed even stronger treatment differentiation, increasing from baseline 485 ± 145 kg/ha to $3,680 \pm 690$ kg/ha under adaptive grazing (659% increase) versus only 620 ± 195 kg/ha under exclusion (28% increase). This pattern reflects both increased perennial grass cover and greater individual plant vigor and productivity under managed grazing regimes.

Seasonal dynamics revealed that biomass accumulation occurred primarily during rainy seasons with some decomposition during dry periods, but the magnitude of wet-season productivity gains increased progressively over the study period as perennial grass root systems developed and soil conditions improved. By the final year of observation, peak wet-season biomass under adaptive grazing exceeded 6,200 kg/ha in some paddocks, approaching productivity levels characteristic of pristine, undegraded savanna grasslands.

3.3 Plant Diversity Responses

Plant species diversity, measured through multiple indices, increased significantly under grazing treatments compared to livestock exclusion (Table 1, Figure 1). Species richness (total number of species per plot) increased from baseline 14.2 ± 3.8 species to 25.7 ± 5.8 species under adaptive multi-paddock grazing, 21.4 ± 5.1 under rotational grazing, and 16.8 ± 4.2 under continuous grazing, while remaining essentially unchanged in exclusion controls at 15.3 ± 3.9 species.

Shannon diversity index followed similar patterns, reaching 3.2 ± 0.6 under adaptive grazing compared to 1.9 ± 0.4 in controls ($F(3,68) = 35.2$, $p < 0.001$). This enhanced diversity under grazing reflects colonization by palatable perennial grass species that were absent or extremely rare at baseline, alongside maintenance of forb diversity and appearance of grazing-associated species.

Functional diversity metrics showed that grazing treatments

promoted increased functional richness through establishment of species spanning wider ranges of trait values, particularly regarding growth forms, rooting depths, and phenological strategies. Functional evenness increased under rotational and adaptive grazing, indicating more balanced abundance distributions across functional groups rather than dominance by a few annual grass species as observed in ungrazed controls.

PERMANOVA analysis of community composition revealed highly significant treatment effects (pseudo- $F = 18.7$, $R^2 = 0.34$, $p < 0.001$), with adaptive and rotational grazing sites forming distinct compositional clusters characterized by perennial grass dominance, clearly separated from continuous grazing and exclusion sites that remained compositionally similar to baseline degraded conditions. Ordination analysis showed progressive compositional shifts over time in grazed treatments along gradients associated with increasing perennial grass abundance and decreasing annual grass and bare ground cover.

3.4 Woody Plant Dynamics and Encroachment Control

Woody plant recruitment showed substantial variation among treatments, with grazed paddocks experiencing significantly lower establishment of woody seedlings and saplings compared to ungrazed controls (Table 2). Under livestock exclusion, woody plant density increased from baseline 248 ± 78 stems/ha to 312 ± 92 stems/ha over 36 months (26% increase), reflecting ongoing encroachment dynamics. In contrast, adaptive multi-paddock grazing reduced woody density from baseline 242 ± 82 stems/ha to 78 ± 34 stems/ha (68% decrease), primarily through livestock browsing, trampling, and competitive suppression by vigorous grass growth.

Rotational grazing achieved intermediate woody plant control with density declining to 132 ± 48 stems/ha (45% decrease), while continuous grazing showed minimal change at 228 ± 76 stems/ha (6% decrease). These patterns indicate that grazing management intensity and grass competitive vigor interact to determine woody encroachment trajectories, with high-intensity, short-duration grazing producing greatest control effectiveness.

Analysis of woody plant size class distributions revealed that recruitment of new seedlings was suppressed under all grazing treatments compared to exclusion ($p < 0.001$), while mortality of established larger woody plants remained low across all treatments. This suggests that grazing primarily controls encroachment through preventing new establishment rather than eliminating existing woody vegetation, an important consideration for restoration timeframes and expectations.

Woody canopy cover decreased from baseline $18 \pm 6\%$ to $12 \pm 4\%$ under adaptive grazing, $14 \pm 5\%$ under rotational grazing, and $16 \pm 6\%$ under continuous grazing, while increasing to $24 \pm 8\%$ under exclusion. These changes reflect both reduction in woody plant numbers and browsing-induced canopy reduction among surviving individuals.

Table 2: Woody Plant Dynamics and Soil Quality Parameters at 36-Month Assessment

Parameter	Continuous Grazing	Rotational Grazing	Adaptive Multi-Paddock	Livestock Exclusion	F-statistic	p-value
Woody Plant Density (stems/ha)	228±76 ^{a^}	132±48 ^{b^}	78±34 ^{c^}	312±92 ^{d^}	43.8	<0.001
Woody Seedling Recruitment (stems/ha/yr)	48±18 ^{a^}	22±11 ^{b^}	12±7 ^{c^}	87±24 ^{d^}	68.3	<0.001
Woody Canopy Cover (%)	16±6 ^{a^}	14±5 ^{ab^}	12±4 ^{b^}	24±8 ^{c^}	18.4	<0.001
Soil Organic Carbon (%)	1.42±0.38 ^{a^}	1.68±0.42 ^{b^}	1.94±0.48 ^{c^}	1.28±0.34 ^{a^}	24.6	<0.001
Soil Carbon Stock (t/ha, 0-15cm)	20.8±5.4 ^{a^}	24.6±6.1 ^{b^}	28.4±6.8 ^{c^}	18.7±4.9 ^{a^}	22.3	<0.001
Soil Bulk Density (g/cm ³)	1.38±0.14 ^{a^}	1.32±0.12 ^{b^}	1.24±0.11 ^{c^}	1.44±0.15 ^{a^}	15.7	<0.001
Aggregate Stability (MWD, mm)	1.8±0.5 ^{a^}	2.4±0.6 ^{b^}	3.1±0.7 ^{c^}	1.5±0.4 ^{a^}	32.8	<0.001
Infiltration Rate (mm/hr)	42±14 ^{a^}	68±18 ^{b^}	94±22 ^{c^}	28±11 ^{d^}	48.2	<0.001

Values represent means ± standard deviation; Different superscript letters within rows indicate significant differences ($p < 0.05$) from Tukey post-hoc tests; MWD = mean weight diameter of stable aggregates; t/ha = tonnes per hectare.

5. Soil Quality Improvements

Soil organic carbon content increased significantly under grazing treatments, particularly adaptive multi-paddock management, contradicting expectations that livestock trampling and consumption would deplete soil carbon stocks (Table 2). Adaptive grazing increased soil organic carbon from baseline $1.37 \pm 0.36\%$ to $1.94 \pm 0.48\%$ (42% increase), while exclusion showed only 18% increase to $1.28 \pm 0.34\%$. Continuous grazing achieved modest improvement to $1.42 \pm 0.38\%$ (4% increase), while rotational grazing produced intermediate results at $1.68 \pm 0.42\%$ (23% increase).

Converting these values to soil carbon stocks accounting for changes in bulk density revealed that adaptive multi-paddock grazing sequestered an additional 8.2 tonnes carbon per hectare in the 0-15 cm soil depth over 36 months, equivalent to carbon sequestration rate of 2.7 tonnes per hectare per year. This substantially exceeds rates typically reported for grassland restoration and approaches rates achieved through afforestation in some contexts.

Soil bulk density decreased significantly under grazing treatments ($F(3,68) = 15.7$, $p < 0.001$), declining from baseline 1.46 ± 0.14 g/cm³ to 1.24 ± 0.11 g/cm³ under adaptive grazing despite theoretical concerns that livestock trampling would increase soil compaction. This counterintuitive result likely reflects increased soil organic matter content, enhanced aggregate formation, and bioturbation from hoof action creating soil macropores under appropriately managed grazing regimes. Exclusion controls showed increased bulk density to 1.44 ± 0.15 g/cm³, possibly indicating soil settling and surface sealing in absence of disturbance.

Aggregate stability, measured as mean weight diameter of water-stable aggregates, improved dramatically under adaptive grazing from baseline 1.6 ± 0.4 mm to 3.1 ± 0.7 mm (94% increase), significantly exceeding all other treatments including exclusion at 1.5 ± 0.4 mm (6% decrease). Enhanced aggregation reflects increased soil organic matter, microbial activity, and fungal hyphal networks binding soil particles, creating more resilient soil structure resistant to erosion.

Infiltration capacity showed perhaps the most dramatic improvements, increasing from baseline approximately

35 ± 12 mm/hr to 94 ± 22 mm/hr under adaptive grazing (169% increase) while declining to 28 ± 11 mm/hr under exclusion (20% decrease). These changes have profound implications for water cycling, reducing runoff and erosion while enhancing soil moisture storage and groundwater recharge. The superior infiltration under grazed treatments likely results from combined effects of reduced bulk density, enhanced aggregation, increased organic matter, and hoof action creating surface roughness and macropores.

6. Livestock Productivity Outcomes

Livestock productivity per unit land area varied substantially among grazing treatments despite similar overall stocking densities (Figure 2). Adaptive multi-paddock grazing achieved mean livestock production of 142 ± 32 kg liveweight gain per hectare per year, representing 48% increase over continuous grazing at 96 ± 24 kg/ha/year and 35% increase over rotational grazing at 105 ± 28 kg/ha/year.

/day under continuous grazing ($F(2,51) = 12.4$, $p < 0.001$). These productivity gains reflect superior forage quality and quantity under adaptive management, with higher crude protein content, digestibility, and availability of palatable perennial grasses.

Reproductive performance metrics showed similar patterns, with calving rates of $78 \pm 8\%$ under adaptive grazing compared to $68 \pm 9\%$ under rotational and $58 \pm 11\%$ under continuous grazing. Calf survival to weaning reached $92 \pm 6\%$ under adaptive management versus $84 \pm 8\%$ under rotational and $76 \pm 10\%$ under continuous systems. Body condition scores remained consistently higher under adaptive grazing throughout seasonal fluctuations, indicating improved nutritional status and resilience to drought stress.

Economic analysis accounting for both livestock productivity and ecosystem service values demonstrated that adaptive multi-paddock grazing generated highest returns despite requiring greater management inputs and infrastructure investment for paddock subdivision. Net present value over 10-year projection periods reached \$8,420 per hectare for adaptive grazing compared to \$5,280 for rotational, \$3,150 for continuous grazing, and negative values for livestock exclusion when foregone grazing income was included.

Table 3: Livestock Productivity and Economic Performance Across Grazing Systems

Parameter	Continuous Grazing	Rotational Grazing	Adaptive Multi-Paddock
Liveweight Gain (kg/ha/year)	96±24	105±28	142±32
Average Daily Gain (kg/day)	0.31±0.09	0.38±0.11	0.48±0.12
Calving Rate (%)	58±11	68±9	78±8
Calf Survival to Weaning (%)	76±10	84±8	92±6
Annual Gross Revenue (\$/ha)	548±125	642±148	894±186
Annual Management Costs (\$/ha)	285±62	348±74	428±88

Net Annual Return (\$/ha)	263±98	294±112	466±134
NPV 10-year (\$/ha, 8% discount)	3,150±892	5,280±1,124	8,420±1,486
Benefit-Cost Ratio	2.1±0.4	2.8±0.6	3.6±0.7

Values represent means ± standard deviation; NPV = Net Present Value calculated using 8% discount rate; Economic values in US dollars based on prevailing market prices during study period.

Discussion

1. Mechanisms Driving Vegetation Recovery Under Managed Grazing

The superior vegetation recovery observed under adaptive multi-paddock grazing compared to livestock exclusion challenges conventional paradigms that position herbivory primarily as a degrading force requiring removal to enable ecosystem restoration. These findings instead support evolutionary ecology perspectives recognizing that savanna grasses evolved under intense but episodic herbivory pressure from large migratory ungulate herds, developing physiological and morphological adaptations that not only tolerate but potentially benefit from appropriately-timed grazing disturbance.

Several mechanisms likely contribute to enhanced perennial grass establishment and productivity under managed grazing. First, selective defoliation of competitive annual grasses and forbs by livestock reduces competition for light, water, and nutrients, creating establishment windows for slower-growing perennial species. Second, hoof action breaks soil crusts, incorporates seeds into soil, and creates microsite heterogeneity favorable for germination. Third, nutrient cycling accelerates through dung and urine deposition, providing concentrated nutrient patches that stimulate grass growth. Fourth, grazing-induced tillering responses in perennial grasses promote lateral spread and increased tiller density. Fifth, extended rest periods under adaptive management allow root system development and carbohydrate reserve accumulation essential for perennial grass persistence.

The particularly poor performance of livestock exclusion treatments, showing minimal improvement in perennial grass cover despite absence of grazing pressure, suggests that degraded savanna grasslands may experience arrested succession or alternative stable state dynamics where annual grass dominance persists indefinitely without external disturbance to reset competitive hierarchies. This interpretation aligns with state-and-transition modeling frameworks and empirical observations of persistent degraded states in protected savanna areas globally.

The temporal lag of approximately 12 months before substantial vegetation recovery became apparent across all treatments reflects biological constraints on perennial grass establishment, including requirements for favorable precipitation patterns, seed production and dispersal, germination success, and seedling survival through initial dry seasons. This lag period has important implications for maintaining stakeholder engagement during restoration efforts, necessitating realistic expectation-setting and potentially incorporating short-term indicators of recovery trajectory.

2. Woody Plant Control Through Grazing Management

The dramatic reduction in woody plant recruitment under adaptive grazing, achieving 68% decline in woody density compared to 26% increase under exclusion, demonstrates that appropriately managed livestock grazing provides effective tools for controlling woody encroachment without

requiring expensive mechanical or chemical interventions. This finding has significant practical and economic implications given the widespread woody encroachment crisis affecting savanna ecosystems globally.

Multiple processes contribute to woody plant suppression under intensive grazing management. Direct browsing by livestock, particularly goats, damages woody seedlings and suppresses vertical growth. Trampling causes mechanical damage to vulnerable seedlings and saplings. Most critically, vigorous perennial grass growth under managed grazing creates intense competitive pressure for soil moisture, nutrients, and light during woody plant establishment phases. Previous research has demonstrated that grass competition represents the primary bottleneck for woody plant recruitment in savanna systems, with fire historically maintaining grass dominance and limiting woody establishment.

The differential effectiveness among grazing treatments, with adaptive management achieving superior woody control compared to rotational and continuous systems, likely reflects varying grass competitive vigor across management intensities. Adaptive grazing's production of highest grass biomass and most robust perennial grass communities creates strongest competitive suppression of woody recruitment. Additionally, concentrated animal impact under high-intensity, short-duration grazing events may impose greater direct damage to woody seedlings compared to dispersed grazing pressure under continuous systems.

However, the predominant effect on seedling recruitment rather than established woody plants indicates that grazing management controls encroachment primarily through prevention rather than reversal of existing woody dominance. This temporal asymmetry suggests that restoration timeframes for heavily wooded savannas may extend over decades as existing woody cohorts senesce and recruitment failure gradually reduces woody densities. Combination of managed grazing with targeted woody plant removal through mechanical methods or controlled fire may accelerate restoration trajectories in severely encroached systems.

3. Soil Carbon Sequestration and Hydrological Function

The substantial soil carbon sequestration under adaptive grazing, achieving accumulation rates of 2.7 tonnes per hectare per year, positions appropriately managed grasslands as significant carbon sinks with potential to contribute meaningfully to climate change mitigation. These sequestration rates rival or exceed values reported for many afforestation programs while maintaining productive land use and avoiding displacement of existing ecosystems or livelihoods.

Mechanisms driving enhanced soil carbon accumulation under grazing include increased root biomass production by vigorous perennial grasses, accelerated nutrient cycling through dung and urine returns, stimulation of soil microbial communities, physical protection of organic matter within stable aggregates, and reduced erosion losses of carbon-rich

topsoil. The extended rest periods characteristic of adaptive grazing systems allow sustained photosynthetic carbon capture and root exudation, feeding soil microbial communities and promoting stable organic matter formation.

The counterintuitive finding that grazed systems accumulated more soil carbon than ungrazed controls, despite theoretical concerns about carbon removal through herbivory, reflects the dominance of belowground carbon allocation in perennial grasses. While aboveground biomass removal through grazing reduces annual carbon inputs from plant litter, this is more than compensated by increased root biomass and turnover, root exudation, and enhanced decomposition and incorporation of organic matter into stable soil pools.

Improvements in soil hydrological function under adaptive grazing, particularly the 169% increase in infiltration capacity, carry profound implications for landscape water balance, downstream flooding, groundwater recharge, and drought resilience. Enhanced infiltration reduces runoff generation, decreasing flood risk and erosion while increasing water availability during dry periods through soil moisture storage and groundwater contributions to baseflow. These hydrological benefits extend beyond immediate grazing areas, influencing watershed-scale water security. The decline in infiltration capacity under livestock exclusion, showing 20% reduction from baseline, likely reflects surface soil sealing through raindrop impact on bare ground between sparse annual grass plants, absence of bioturbation maintaining macroporosity, and reduced organic matter accumulation. This finding challenges assumptions that removing disturbance necessarily improves ecosystem function, instead supporting perspectives that appropriate disturbance regimes maintain ecosystem processes.

4. Biodiversity Conservation Through Working Landscapes

The enhanced plant diversity under grazing treatments, achieving Shannon indices of 3.2 compared to 1.9 in exclusion controls, demonstrates that biodiversity conservation need not require land removal from productive use but can be achieved within working pastoral landscapes under appropriate management. This finding has critical importance for global conservation strategies, particularly in regions where human population density and land use pressure preclude extensive protected area expansion.

The diversity-enhancing effects of grazing likely operate through multiple pathways including creation of habitat heterogeneity through differential grazing intensity, maintenance of disturbance-dependent species, prevention of competitive exclusion by dominant species, and creation of nutrient-rich patches supporting distinct plant communities. Intermediate disturbance theory predicts peak diversity at moderate disturbance intensities that prevent both competitive exclusion under undisturbed conditions and elimination of disturbance-sensitive species under excessive disturbance.

While this study focused on plant diversity, managed grazing systems likely influence faunal diversity through cascading effects on vegetation structure, food resource availability, and habitat quality. Previous research in African savannas has documented positive associations between grazing management and diversity of birds, small

mammals, reptiles, and invertebrates, though responses vary among taxa and management intensities.

The functional diversity improvements under grazing, indicated by increased functional richness and evenness, suggest that managed systems support broader ranges of ecological strategies and more balanced community composition compared to degraded states dominated by few weedy annual species. This functional diversity likely enhances ecosystem resilience, stability, and multifunctionality through complementary resource use, temporal niche partitioning, and response diversity to environmental fluctuations.

5. Economic Viability and Scaling Potential

The favorable economic performance of adaptive multi-paddock grazing, achieving benefit-cost ratios of 3.6 and net present values exceeding \$8,400 per hectare, demonstrates that ecosystem restoration and productive land use need not represent competing objectives but can be integrated within financially viable management systems. This economic viability represents a critical enabling factor for widespread adoption and scaling of restoration practices, overcoming frequent barriers where conservation initiatives impose economic burdens on land users.

The superior livestock productivity under adaptive management, showing 48% gains over continuous grazing, results from improved forage quality and quantity, better nutritional balance across seasons, and enhanced animal health from diverse plant communities. These productivity benefits offset additional management costs associated with paddock subdivision, water infrastructure, and more intensive herding labor, generating positive net returns even before accounting for ecosystem service values.

Incorporation of carbon market revenues could further enhance economic attractiveness of adaptive grazing systems. At carbon prices of \$10-20 per tonne CO₂-equivalent, the soil carbon sequestration rates observed would generate additional annual revenues of \$100-200 per hectare, substantially improving profitability while incentivizing climate change mitigation. However, transaction costs, monitoring requirements, and policy uncertainties currently limit pastoral communities' access to carbon markets, necessitating institutional innovations to enable smallholder participation.

The infrastructure requirements for adaptive grazing, particularly fencing for paddock subdivision and water point development, represent upfront investment barriers potentially limiting adoption by resource-poor pastoral communities. Policy interventions including subsidized credit, cost-sharing programs, or payments for ecosystem services could overcome these barriers and catalyze broader adoption. Group approaches pooling resources among multiple households may also reduce per-capita costs while building social capital for collective management.

6. Limitations and Research Needs

Several limitations constrain interpretation and generalization of these findings. First, the 36-month study period, while longer than many grazing experiments, remains insufficient to fully characterize long-term sustainability, potential degradation of treatment effects over time, or responses to extreme events such as severe droughts or disease outbreaks. Continued monitoring over decade-plus timeframes would strengthen inferences

regarding restoration permanence and management sustainability.

Second, site selection within a relatively constrained geographic region and environmental gradient limits transferability to other savanna types, particularly those with different precipitation regimes, soil types, woody plant functional groups, or grazing histories. Comparative research across broader biogeographic gradients encompassing different savanna subtypes would enhance understanding of context-dependency in grazing management outcomes.

Third, while the experimental design provided strong inference regarding treatment effects on measured variables, it did not fully characterize mechanisms underlying observed patterns. Manipulative experiments isolating specific mechanistic pathways, such as nutrient cycling processes, plant-soil feedbacks, or herbivore selectivity effects, would advance mechanistic understanding and predictive capability.

Fourth, this study focused primarily on vegetation and soil responses with limited assessment of faunal biodiversity,

particularly birds, mammals, and invertebrates that represent key components of savanna ecosystem biodiversity and function. Integrated assessment across trophic levels would provide more comprehensive evaluation of grazing management impacts on ecosystem integrity.

Fifth, socioeconomic assessment examined household-level costs and benefits but did not fully address community-level social dynamics, equity in benefit distribution, gender dimensions of management participation and decision-making, or cultural values associated with different management approaches. More nuanced social science research would inform implementation strategies promoting equitable and socially sustainable restoration.

Finally, climate change will likely alter the environmental context within which grazing management operates, through shifts in precipitation patterns, temperature regimes, atmospheric CO₂ concentrations affecting plant physiology, and altered disturbance regimes. Research examining grazing management effectiveness under projected future climate scenarios would support anticipatory adaptation planning.

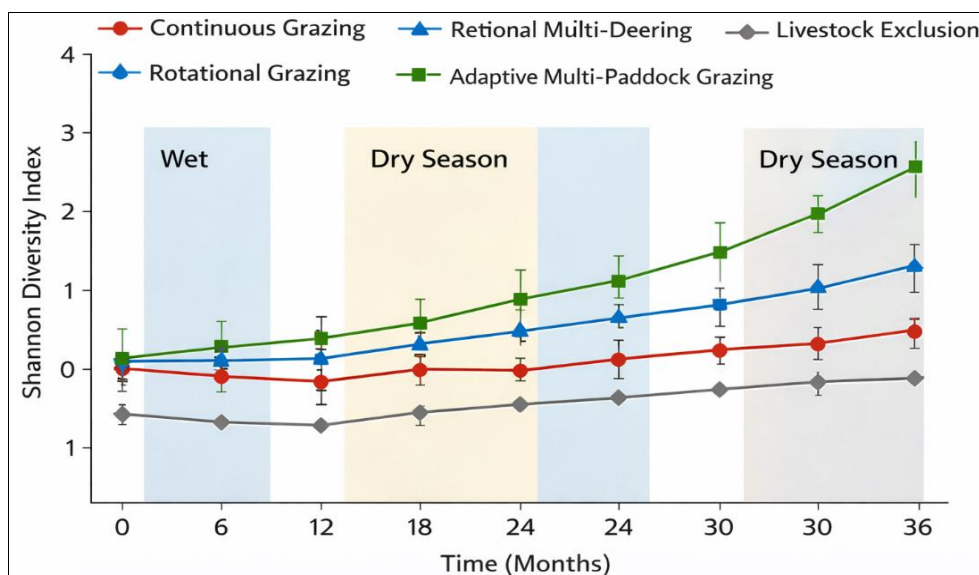


Fig 1: Temporal Trajectories of Shannon Diversity Index Across Grazing Treatments

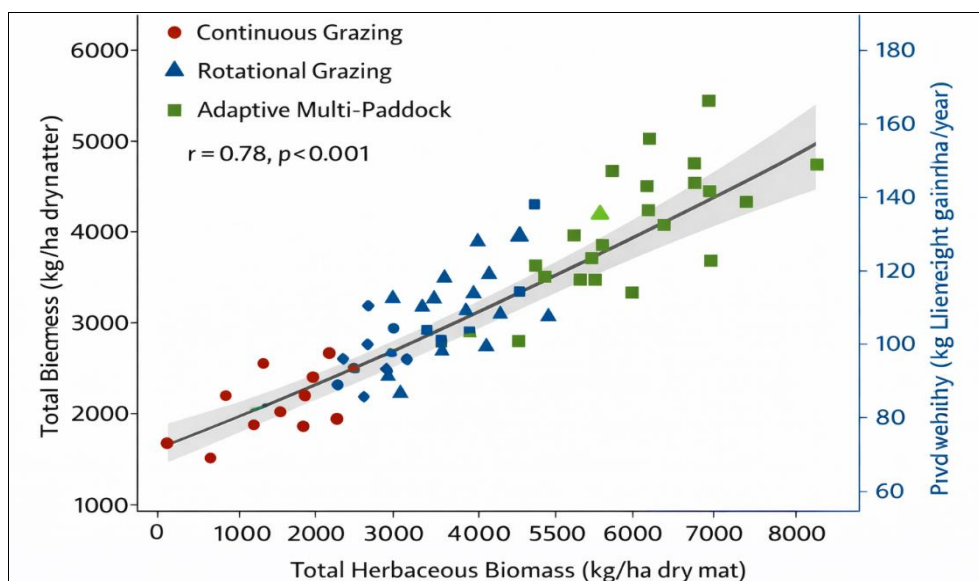


Fig 2: Livestock Productivity and Vegetation Biomass Relationship Across Grazing Systems

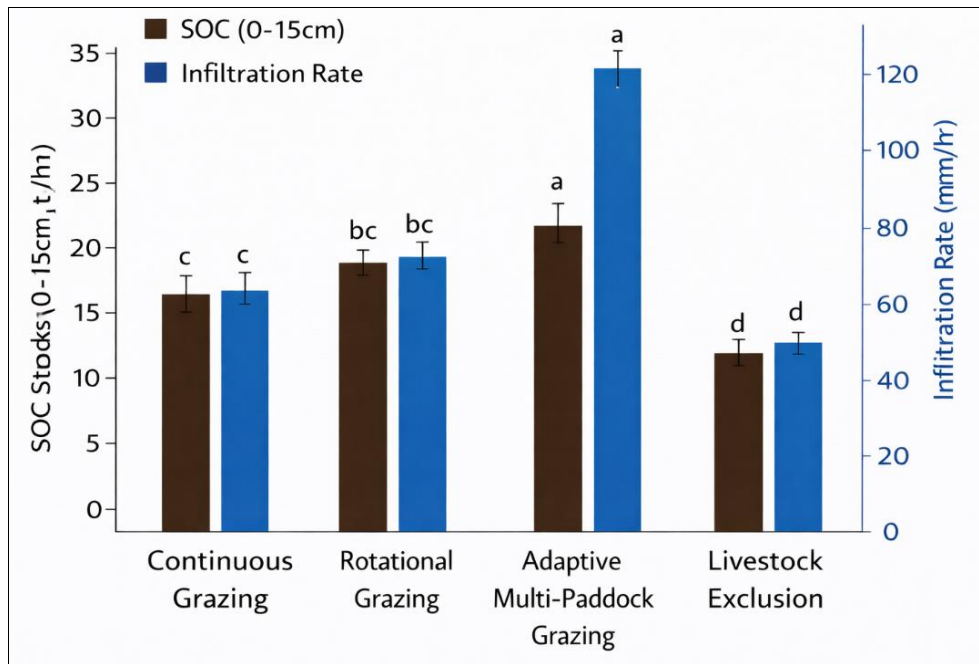


Fig 3: Soil Carbon Stocks and Infiltration Capacity by Treatment

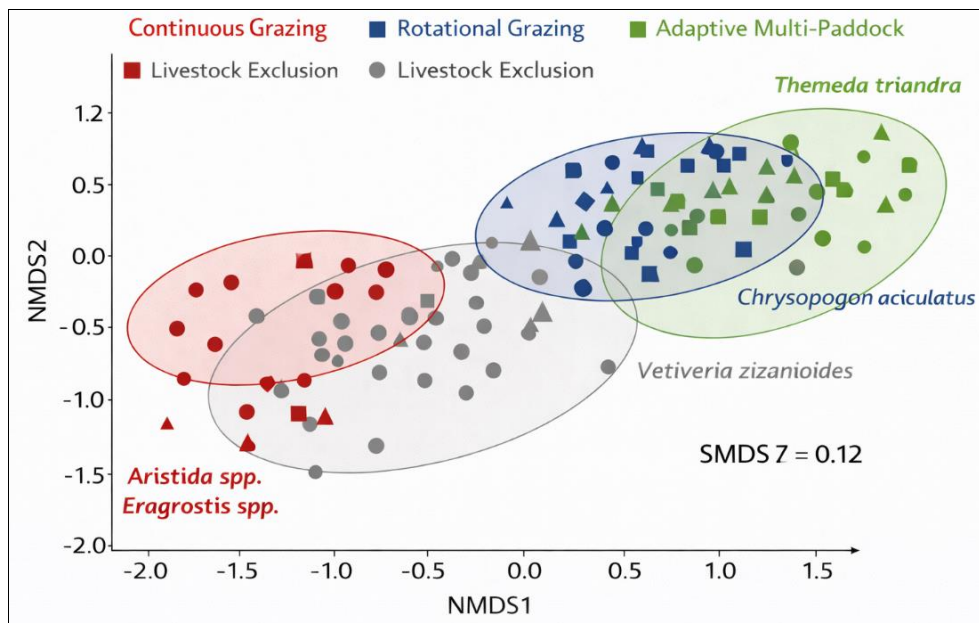


Fig 4: Community Composition Ordination Showing Treatment Differentiation Over Time

Conclusion

This research provides compelling evidence that managed herbivore grazing, particularly adaptive multi-paddock systems mimicking natural disturbance regimes, represents an effective strategy for restoring degraded savanna grasslands while maintaining productive land use and supporting pastoral livelihoods. Over 36 months of experimental implementation, adaptive grazing achieved perennial grass cover of 67% compared to 31% under livestock exclusion, biomass production of 4,850 kg/ha versus 1,680 kg/ha in controls, and species diversity increases to Shannon index 3.2 from baseline 1.8. Concurrently, soil quality improved dramatically with carbon sequestration rates of 2.7 tonnes per hectare per year, infiltration capacity increases of 169%, and aggregate stability gains of 94%.

Perhaps most significantly, these ecosystem restoration outcomes were achieved alongside livestock productivity improvements of 35-48% compared to conventional continuous grazing, generating favorable benefit-cost ratios of 3.6 and demonstrating economic viability essential for widespread adoption. The finding that appropriately managed grazing outperformed complete livestock exclusion across multiple ecosystem metrics challenges conventional protection paradigms and supports integration of conservation and production objectives within working pastoral landscapes.

From a policy and practice perspective, several recommendations emerge: prioritize adaptive multi-paddock grazing systems incorporating extended rest periods and variable stocking densities over conventional continuous or simple rotational approaches; invest in infrastructure supporting intensive grazing management including

paddock subdivision and water distribution; develop financial mechanisms enabling pastoral communities to overcome upfront investment barriers; establish monitoring systems tracking both ecosystem and livestock productivity outcomes; promote participatory learning platforms enabling knowledge exchange among pastoral practitioners; and integrate grazing management planning with landscape-scale conservation strategies addressing connectivity and biodiversity objectives.

This research contributes to growing evidence base supporting land-sparing versus land-sharing debates by demonstrating that appropriate management enables co-production of ecosystem services and agricultural outputs within shared landscapes. It also advances understanding of herbivore-vegetation dynamics in savanna ecosystems, providing empirical support for theoretical predictions regarding intermediate disturbance, grazing optimization, and evolutionary adaptations to herbivory.

Future research should focus on long-term sustainability assessment over decade-plus timeframes, comparative studies across diverse savanna types and biogeographic regions, mechanistic experiments elucidating pathways of grazing effects, integrated assessment across trophic levels including faunal diversity, socioeconomic research examining equity and social dimensions, and evaluation of climate change implications for grazing management effectiveness. Such research will refine understanding and enhance transferability of managed grazing approaches for savanna restoration globally.

As human populations grow and climate change intensifies pressures on savanna ecosystems worldwide, the demonstrated potential for achieving restoration and production goals simultaneously through appropriately managed grazing offers hope for sustainable futures in these critical landscapes. Scaling these approaches requires integrated efforts spanning science, policy, investment, and community engagement to support pastoral communities as stewards of ecosystem restoration and conservation within productive working landscapes.

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