



# Contrasting Effects of Grazing vs Browsing Herbivores Determine Changes in Soil Fertility in an East African Savanna

C. Coetsee,<sup>1,2\*</sup> B. J. Wigley,<sup>2,3,4</sup> M. Sankaran,<sup>4,5</sup> J. Ratnam,<sup>4</sup> and D. J. Augustine<sup>6</sup>

*Scientific Services, South African National Parks, Skukuza, South Africa; School of Natural Resource Management, Nelson Mandela University, Madiba Rd, George 6529, South Africa; Department of Environmental Biology, Sapienza University of Rome, P. le A. Moro 5, Rome, Italy; National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bellary Rd, Bangalore 560065, India; Faculty of Biological Sciences, School of Biology, University of Leeds, Leeds, UK; U.S. Department of Agriculture, Rangeland Resources Research Unit, Agricultural Research Service, Fort Collins, Colorado, USA*

## ABSTRACT

We used a long-term herbivore removal experiment where paired enclosure–open treatments were established at the Mpala Research Centre, Laikipia, Kenya, in 1999 to examine changes in soil nitrogen (N) at nutrient-rich glades and adjacent nutrient-poor bushland sites after almost two decades of herbivore removal. Glades in this landscape are created by large inputs of dung and urine from previous long-term corralling of cattle in an otherwise nutrient-poor matrix of woodland (bushland). We predicted (1) a net gain of soil nutrients at bushland sites (that is, inputs of nutrients > losses) and (2) a net loss of soil nutrients at glade sites (that is, inputs of nutrients < losses) following herbivore exclusion. As expected, soil N increased (by 28% after 17 years) with herbivore removal, but remained largely unchanged in the presence of herbivores at low-nutrient bush-

land sites. However, contrary to our expectations, soil total N in nutrient-rich glades also increased (+18%) when herbivores were removed, but declined when grazed (–11%). Although the underlying mechanisms are unclear, we suggest that increased N fixation by *Acacia* spp., combined with increased canopy cover and associated tree leaf litter, resulted in elevated soil N following browser removal in low-nutrient bushland sites, while grazer-induced increases in the rate of N transformations between organic and mineral forms resulted in a more “open” N cycle (as evidenced by higher N mineralization rates and foliar N), with increased potential for N loss in gaseous forms, in grazed nutrient-rich glade sites. Grazers and browsers thus appear to affect the N cycle and create and reinforce heterogeneity in unique ways.

**Key words:** browsers; glades; grazers; herbivore exclusion; nitrogen; soil dynamics.

Received 26 March 2021; accepted 5 February 2022

MS, DA and JR initially envisioned the experiment (that is, enclosure set-up). DA, MS, BW and JR gathered data and performed research. CC conceived the particular research questions and developed it further with the help of DA and BW. CC analysed data and wrote the paper with the help and inputs of the other authors.

\*Corresponding author; e-mail: Corli.wigley-coetsee@sanparks.org

Published online: 11 March 2022

## HIGHLIGHTS

- Variable effects of herbivores on N dynamics at nutrient-rich vs. nutrient-poor sites
- Increases in cover of woody N fixers increases soil N on nutrient-poor patches
- Nutrient-rich patches with herbivores lose N over time, but not P

## INTRODUCTION

Rangelands are characterized by substantial spatial heterogeneity in plant communities and soil nutrients arising not only from edaphic and topographic variability across space, but also from feedback effects generated by herbivores, both domestic and wild (Pastor and others 1999; Augustine and Frank 2001; Yoshihara and others 2010; Lilleeng and others 2016; Liu and others 2016; Limb and others 2018; Bubnicki and others 2019). These feedbacks are varied; herbivores directly affect spatial patterns in nutrient availability and vegetation by redistributing nutrients across the landscape in dung and urine, by changing the physical characteristics of soil (for example, trampling), and by affecting plant physiological processes (Frank and others 1994, 2000; Knapp and others 1999; Bardgett and Wardle 2003; Van der Waal and others 2011; Schrama and others 2013; Liu and others 2016; Andriuzzi and Wall 2017; Veldhuis and others 2018). Herbivores also exert indirect effects; selective feeding impacts both plant species composition and the quantity and quality of litter inputs to soils (via associated stoichiometric differences), while physical disturbances have the potential to change soil fauna and associated decomposition dynamics, both of which can have variable outcomes for whether herbivores accelerate or decelerate nutrient cycling (Ritchie and others 1998; Singer and Schoenecker 2003; Persson and others 2005; Pastor and others 2006; Andriuzzi and Wall 2017; Sitters and others 2017; Penner and Frank 2019).

The net effect of herbivores on nutrient pools, nutrient availability and plant production is hypothesized to be contingent on soil fertility. In the short term, herbivore effects may be positive in fertile ecosystems because rhizosphere processes and microbial biomass are stimulated by N-rich detritus with positive outcomes for net primary productivity and nutrient cycling rates, while the opposite may be expected in unproductive ecosystems (classical theory of Hobbie 1992; Ritchie and

others 1998; Bardgett and Wardle 2003). On the other hand, the presence of herbivores can result in microbes being C-limited on more fertile soils, which will decrease N availability as a result of increased N immobilization by microbes (stoichiometric approach of Cherif and Loreau 2013; Sitters and Venterink 2015). Based on the classical theory, modelling efforts suggest that herbivore-related enhancement of nutrient cycling rates and stimulation of plant production can only be sustained in the long term if faster nutrient cycling rates are not associated with greater nutrient loss rates, and if nutrient input rates are greater than a threshold value dependent on the sensitivity of plant uptake to increases in the nutrient (de Mazancourt and others 1998). At present, while there is ample evidence from savanna ecosystems to indicate that herbivores are capable of enhancing nutrient cycling rates and stimulating plant production in the short term (McNaughton 1985; Verweij and others 2006; Waldram and others 2008; Bonnet and others 2010), the degree to which herbivores affect the long-term balance of soil N in savanna ecosystems remains unclear.

Here, we leverage an herbivore removal experiment established at the Mpala Research Centre, Laikipia, Kenya, in 1999 to examine how large ungulate herbivores influence N-budgets over the long term in nutrient-rich 'glades' and nutrient-poor 'bushland' sites. In central Kenya where this work took place, and elsewhere in Africa, indigenous pastoralists corral cattle at night in "bomas" (Augustine 2003; Scholes and Walker 2004). These sites are initially identical to the background matrix of bushland in terms of geomorphology, soil and vegetation (Western and Dunne 1979; Blackmore and others 1990; Augustine 2003). Historically, sites were cleared of trees in order to construct bomas and the labour involved resulted in these being used for extended periods (Western and Dunne 1979; Veblen and Porensky 2019). Cattle forage during the day in the surrounding landscape and concentrate nutrients into bomas during the night through dung and urine deposition (Augustine 2003; Porensky and Veblen 2015). After abandonment, the concentrated layer of dung and urine develops over time into nutrient-enriched glades dominated by grazing-tolerant grasses, where woody vegetation may either remain absent for decades to centuries (Young and others 1995; Augustine and others 2003; Veblen 2012) or differ in composition from the surrounding matrix (Scholes and Walker 2004). More recently, bomas have been constructed from movable gates and are moved frequently; however, bomas that have been

in place for about a month still result in glades with glade-like nutrient-rich vegetation, that attract herbivores and initiate “ecosystem hotspots” (Porensky and Veblen 2015; Veblen and Porensky 2019).

Depending on time since boma abandonment, N can be more than 7 times higher and phosphorus (P) 27 times higher in central Kenyan glade soils, compared to bushland soils (Young and others 1995; Augustine and others 2011). Glades are heavily utilized by both domestic and native herbivores as glade forage is high in nutrients and the open areas provide high visibility in terms of predators (Young and others 1995; Augustine 2003; Treydte and others 2006; Augustine and others 2019). This then becomes a self-perpetuating system that may persist for millennia (Marshall and others 2018), as animals utilize lawns often and contribute high inputs of N and P through dung and urine, which in turn contributes to high productivity on glades (Augustine and others 2003).

We hypothesized that on nutrient-rich glade sites, (1) N will have remained stable or increased in the presence of herbivores because previous work has shown that net imports of nutrients (N, P) are generally higher or equal to net exports (Augustine and others 2003), and (2) herbivore exclusion will have reduced soil N because of a lack of inputs. Additionally, we hypothesized that on adjacent, less nutrient-rich bushland, (3) total soil N would have either decreased in the presence of herbivores, as these sites are mostly grazed by cattle that are corralled elsewhere at night, with a net export of nutrients (Augustine and others 2003) or remain unchanged as herbivore utilization is typically low, while (4) herbivore exclusion would have enhanced total soil N as a result of increased canopy cover of N-fixing woody plants (Sankaran and others 2013; Wigley and others 2020), as well as a lack of grass nutrient redistribution from the bushland to glades.

## METHODS

### Study Area

Our study was carried out in a semiarid savanna with an Acacia-dominated tree and shrub layer and a discontinuous layer of perennial grasses at the Mpala Research Centre (MRC) and Mpala Ranch in the Laikipia district of central Kenya (37°53'E, 0°17' N; Augustine 2003). Soils at the study sites consist of sandy red loams (74% sand, 15% clay), which originate from basement metamorphic parent

materials (Ahn and Geiger 1987). Inherent soil properties such as texture, pH (Augustine 2003; Augustine and others 2003) and bulk density (1.51 g cm<sup>-3</sup> for bushland vs. 1.52 g cm<sup>-3</sup> for glades) are similar between glades and bushland soils.

Mean annual rainfall between 1972 and 2009 was 514 mm (Sankaran and others 2013) and 633 mm between 2003 and 2016 (Augustine and others 2019). MRC is managed for cattle production using traditional Maasai methods where cattle are actively herded and corralled at night in bomas; 1,400–3,100 cattle are kept at Mpala (averaging 10–20 cattle km<sup>-2</sup>) (Odadi and others 2018; Augustine and others 2019). The property supports a diverse suite of native browsers and mixed feeders, which include impala (*Aepyceros melampus* c. 20 km<sup>-2</sup>), Günther's dik-dik (*Madoqua guentheri* c. ~100 km<sup>-2</sup>), eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis reticulata*) and elephant (*Loxodonta africana* (c. 1.7 km<sup>-2</sup>) (Augustine 2010; Ford and others 2015). Native grazers are found in low densities (< 1.5 km<sup>-2</sup>) and include waterbuck (*Kobus ellipsiprymnus*), zebra (*Equus burchellii*) and buffalo (*Syncerus caffer*). Predators at MRC include spotted hyena (*Crocuta crocuta*), wild dog (*Lycan pictus*), lion (*Panthera leo*) and leopard (*Panthera pardus*).

Young and others (1995) previously described a two-phase mosaic at MRC which consists of relatively small (0.5–1 ha in size) long-term glades (ca. 1% of the landscape) and Acacia-dominated bushland (ca. 99% of the landscape). Vegetation on the glades is typically dominated by the grazing-tolerant, perennial stoloniferous grass *Cynodon plectostachyus* (Georgiadis and McNaughton 1988), while the bushland areas support a heterogeneous mosaic of bare soil patches, perennial grass-dominated patches and woody plant-dominated patches (illustrated in Augustine and others 2019). The woody layer in the bushland areas is dominated by *Acacia brevispica*, *Acacia mellifera*, *Acacia etbaica*, *Balanites pedicellaris* and *Grewia tenax* (Young and others 1995; Wigley and others 2019). Tree species nomenclature follows Birnie and Noad (2011), and grass nomenclature follows Fish and others (2015).

### Long-term Herbivore Exclusion Experiment

At each of three sites in central and southern MRC, two paired 70×70 m plots were demarcated in glade and bushland areas in 1999 (Augustine and McNaughton 2006). For each pair, one plot was retained as a control open to herbivores and the other was fenced off using a 3-m-tall, electrified

fence (see Sankaran and Augustine 2004 for details). All herbivores larger than 2 kg were excluded from the enclosure plots for the duration of the experiment. The inner 50 × 50 m of the enclosure and paired control sites were demarcated using a 10 × 10 m grid marked with metal pegs driven into the ground, leaving 10 cm protruding above the ground, which were painted white to help with relocating them. The metal pegs were numbered from 1 to 36 and recorded in a standard fashion across all plots.

## Sample Collection and Laboratory Analyses

### *Soil Carbon, Nitrogen, $\delta^{15}\text{N}$ and Phosphorus*

Ten of the 36 metal pegs in each paired plot were randomly selected in 1999 and soils adjacent to pegs sampled to a depth of 15 cm using a soil corer. Soils were sieved and air-dried and then analysed for carbon (C) and nitrogen (N) by Dumas combustion with a Carlo-Erba CN Analyser (Milan, Italy). Soils at the same ten metal pegs in each plot were resampled at 0–5 and 10–15 cm (with a third depth of 25–30 cm at bushland sites) in 2016 using a soil corer. The 2016 soil samples were also air-dried, sieved and subsampled before nutrient and isotope (bushland sites only) analyses. In addition to C and N that were determined by combustion using a LECO TruSpec CN analyser (LECO Corporation), soil phosphorus (P) was determined in 2016 from acid-digested samples (treated with 70%  $\text{HNO}_3$  and 30%  $\text{H}_2\text{O}_2$ ), using inductively coupled plasma (ICP) spectrophotometry (ICP 6300, Thermo Fisher Scientific). As soils were sampled to 15 cm in 1999 and 0–5 cm and 10–15 cm in 2016, we used the average of these two depths to compare the change in C and N values between 1999 and 2016 (2 years × 3 sites × 2 types (bushland and glade) × 2 treatment levels × 10 replicates = 240 samples). At bushland sites, soils from all three depths were analysed for  $\delta^{15}\text{N}$  values at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria (South Africa) (3 sites × 2 treatment levels × 3 depths × 10 replicates = 180 samples). A detailed description of the soil sampling methods and laboratory analyses can be found in Wigley and others (2020).

As the dominant vegetation (for example, tree vs. grass) at the sampling point could have affected the soil independently of herbivore effects (or interacted with herbivore effects), we took additional measurements of soil N and C values below bare patches, grass patches and woody vegetation at

three different depths in 2019 at bushland sites. Soils were more intensely sampled at bushland sites with a primary focus on obtaining  $^{13}\text{C}$  values, which were used by Wigley and others (2020) to quantify C storage. Glade sites were fully covered by grass, that is, no bare patches and no influence of trees. These samples were dried, milled and analysed for C and N according to the same methods outlined above (3 sites × 2 treatment levels × 3 vegetation types × 3 depths × 5 replicates = 270 samples).

### *Soil Nitrogen Mineralization*

Potential N mineralization rates were quantified following laboratory incubations of soils under anaerobic conditions. Five-gram soil samples, collected from 0–5 cm (3 sites × 2 types × 2 treatment levels × 10 replicates = 120 samples), were immersed in water-filled scintillation vials (1:4 weight/volume) for 7 days and then extracted with 25 ml 0.01 M  $\text{CaCl}_2$ . Extracts were then analysed for  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  using colorimetry-based reactions in microtiter plates. The reactions are modified versions of the Berthelot reaction for ammonium estimation (Krom 1980) and the Griess-Ilosvay reaction for nitrate estimation (after reducing to nitrite; Oms and others 1995). Potential N mineralization rates over seven days ( $\mu\text{g} \times \text{g soil}^{-1} \times 7 \text{ days}^{-1}$ ) were determined as the difference in inorganic N between incubated and control soils (Sankaran and others 2008) and converted to obtain rate per day for statistical analyses.

### *Foliar Nitrogen, $\delta^{15}\text{N}$ and Phosphorus*

During the peak of the 2017 growing season, we collected fully expanded, sun-exposed leaf material from the five dominant tree species (which included *Acacia brevispica*, *Acacia etbaica*, *Acacia mellifera*, *Balanites pedicellaris* and *Grewia tenax*), growing both inside and outside of the enclosures at bushland sites (not all species were found at all sites, 150 samples). Leaves from seven dominant grass species (*Bothriochloa insculpta*, *Cynodon dactylon*, *Digitaria milanjiana*, *Enteropogon macrostachyus*, *Eragrostis tenuifolia*, *Setaria incrassata* and *Themeda triandra*) were also sampled at bushland sites. The abundances of these varied across sites, and a maximum of four species were sampled per site. We also sampled the monodominant grass species (*Cynodon plectostachyus*) growing both inside and outside of the enclosures at glade sites (total for both bushland and glade of 120 samples). All plant samples were air-dried at Mpala Research Station and then milled using a MF10 basic IKA grinder fitted with a 1-mm

sieve. As for soils, plant  $\delta^{15}\text{N}$  values on bushlands were analysed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria (South Africa). Tree and grass foliar C and N were determined by combustion, using a LECO TruSpec CN analyser (LECO Corporation), and foliar P was determined from acid-digested samples (treated with 70%  $\text{HNO}_3$  and 30%  $\text{H}_2\text{O}_2$ ) using inductively coupled plasma (ICP) spectrophotometry (ICP 6300, Thermo Fisher Scientific).

The fraction of N derived from atmospheric  $\text{N}_2$  was estimated by the following mixing model (taken from Craine and others 2015):

$$fN_{\text{atm}} = \frac{\delta^{15}N_{\text{ref}} - \delta^{15}N_{\text{target}}}{\delta^{15}N_{\text{ref}} - \delta^{15}N_{\text{fix}}}$$

where  $\delta^{15}N_{\text{ref}}$  is the  $\delta^{15}\text{N}$  for a reference plant that does not depend on  $\text{N}_2$  fixation,  $\delta^{15}N_{\text{fix}}$  is the  $\delta^{15}\text{N}$  of a plant relying only on  $\text{N}_2$  fixation (assumed to be 0‰) and  $\delta^{15}N_{\text{target}}$  is the  $\delta^{15}\text{N}$  of the species for which dependence is being calculated (Shearer and Kohl 1986). We used *Balanites pedicellaris* as a reference species that does not fix N (Raddad and others 2005; Githae and others 2013). We do acknowledge that this is only a rough estimate that depends on the assumption that foliar N is representative of whole plant  $\delta^{15}\text{N}$  and also varies widely depending on the choice of reference plant (Craine and others 2015).

## Statistical Analyses

All analyses were performed using R version 3.4.2 (R Development Core Team 2020). We used the Fligner–Killeen test of homogeneity of variance (fligner.test in the stats package for R) to determine whether data used for treatment comparisons (herbivores absent [h–] vs. herbivores present [h+]) had equal variance. Soil phosphorus values were approximately log-normally distributed and were therefore log-transformed to attain approximate normality and homogeneity of residuals. We used linear mixed effects models to test for the effect of treatment on soil parameters, focussing on nitrogen, using the lmer function available in the lme4 (Bates and others 2015) package in R.

Depending on sample set-up, treatment, type (if both bushland and glade sites sampled) and their interactions, when appropriate, were treated as fixed effects, and random effects varied. The minimum full models used were as follow: soil [N]/[C]  $\sim$  Year:Treatment:Type + (1|Site:Type) + (1|Plot),  $\log(\text{soil}[P]) \sim$  Treatment:Type + (1|Site:Type), bushland soil  $\delta^{15}\text{N} \sim$  Treatment:Depth + (1|Site) + (1|PegID), soil [N]/[C] under different vegetation

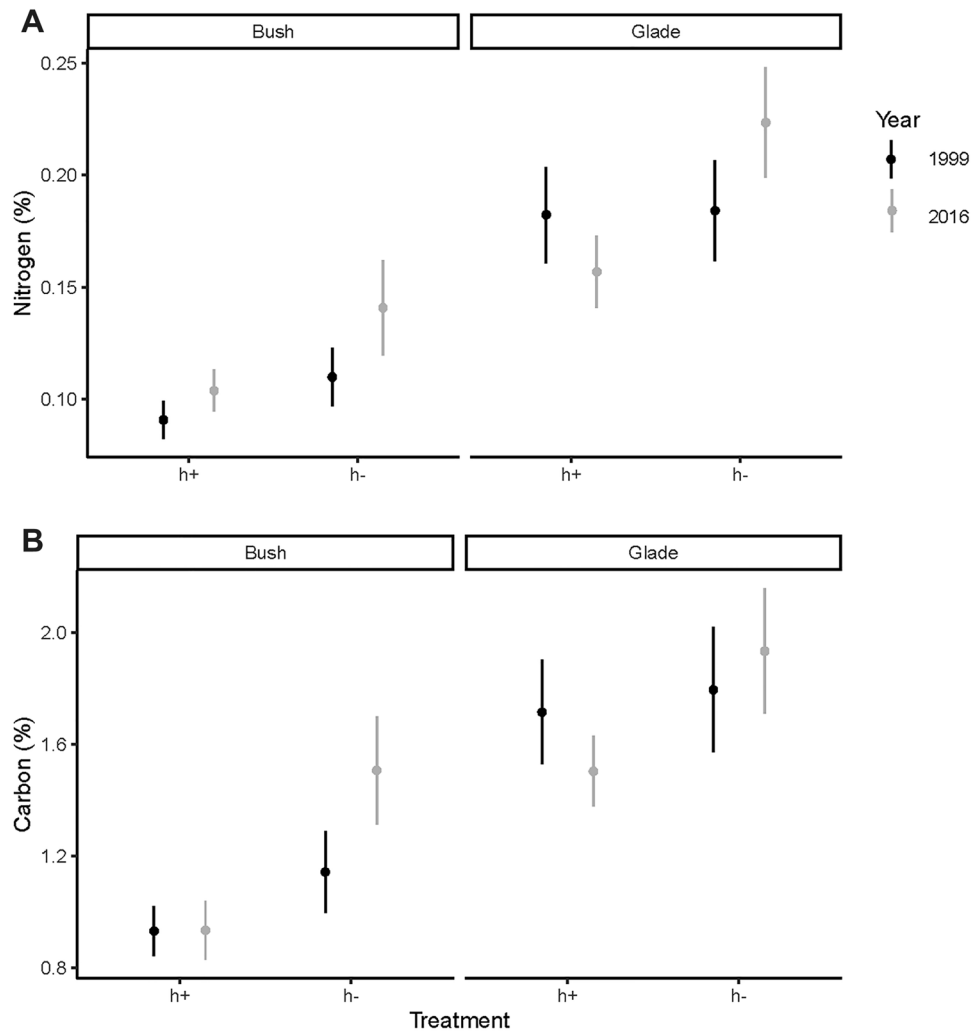
patches  $\sim$  Vegetation:Treatment + Treatment:Depth + (1|Site) + (1|PegID), mineralizable N  $\sim$  Treatment:Type + (1|Site:Type). For bushland tree and grass values, we included grazing treatment as a fixed effect and species nested in site as a random effect. Paired with lmer, we used lmerTest (Kuznetsova and others 2017); the lmerTest package provides p-values in type I, II or III ANOVA and summary tables for linear mixed models via Satterthwaite's degrees of freedom method. We also compared the minimum "full" model with treatment as an effect, with a model where we omitted treatment, using likelihood ratio tests.

We then used the ranova function in lmerTest to test removal of random-effect terms via likelihood ratio tests on the best minimum model. We used the function lsmeans in the lsmeans package (V.2.30–0, Lenth 2016) to perform post hoc contrasts of effects in these models using the Tukey adjustment for multiple comparisons. Residual plots were visually inspected for obvious deviations from homoscedasticity and normality.

## RESULTS

### Soil Nitrogen, Carbon, $\delta^{15}\text{N}$ and Phosphorus

At the initiation of the experiment in 1999, there were no differences in soil nitrogen concentration [N] between control and enclosure areas (Figure 1a,  $0.09\% \pm 0.02$  (mean  $\pm$  SE) for control and  $0.10\% \pm 0.03$  for enclosure at bushland sites,  $P > 0.05$ , and  $0.18\% \pm 0.05$  for control and  $0.18\% \pm 0.06$  for enclosure at glade sites,  $P > 0.05$ ). Between 1999 and 2016, soil N increased with herbivore exclusion at both glades ( $+0.04\%$ ,  $P=0.0004$ ) and bushland sites ( $+0.05\%$ ,  $P=0.005$ ). At the same time, glades open to herbivores lost some N ( $-0.02\%$ ,  $P=0.02$ ), but N in open bushland sites stayed stable ( $P > 0.05$ ). The net effect of changes over time resulted in soil N being significantly higher in both glades ( $0.22\% \pm 0.06$ ,  $P < 0.0001$ ) and bushland ( $0.14\% \pm 0.06$ ,  $P=0.02$ ) with herbivores excluded, than with herbivores present, in 2016. Soil carbon mirrored soil N closely; initially, there were little differences between treatments (Figure 1b,  $0.93\% \pm 0.24$  for control and  $1.14\% \pm 0.39$  for enclosure at bushland sites,  $P > 0.05$ , and  $1.71\% \pm 0.50$  and  $1.79\% \pm 0.60$  for glade sites,  $P > 0.05$ ), but differences became apparent over time with herbivore exclusion, with increases to  $1.51\% \pm 0.52$  at bushland and an increase to  $1.93\% \pm 0.60$  at glades ( $P < 0.0001$  for both the difference be-



**Figure 1.** Plots of **a** bushland and glade total soil nitrogen to 15 cm in 1999 and 2016 inside (h-) and outside (h+) of exclosures at Mpala Research Centre, and **b** soil carbon (%) between 1999 and 2016 inside and outside of exclosures (means  $\pm$  95% CIs).

tween initial and 2016 values, as well as difference between where herbivores absent and present).

Because bushland vegetation cover is heterogeneous at the scale of our 0.25-ha plots, consisting of discrete patches of bare soil, grass cover and woody plant cover, we examined the magnitude of heterogeneity in soil N and C across these patch types (Figure 2a, b). For bushland sites, the overall effect of herbivore exclusion resulted in higher soil [N] (Figure 2a,  $\chi^2(1)=25.0$ ,  $P < 0.0001$ ). However, herbivore exclusion enhanced soil [N] to a much greater degree in woody patches ( $0.24\% \pm 0.01$  in exclosures vs.  $0.17\% \pm 0.01$  with herbivores) than in bare soil patches ( $0.14\% \pm 0.005$  in exclosures vs.  $0.13\% \pm 0.006$  with herbivores). Finally, the exclusion of herbivores resulted in increased soil [P] (Figure 3c,  $\chi^2(1)=19.1$ ,  $P < 0.0001$ ) at bushland

sites, at both depths, but no differences were detected in and out of exclosures at glade sites ( $P > 0.05$ ).

### Soil nitrogen mineralization

Herbivore exclusion did not affect net potential N mineralization rates in bushland soils (Figure 3a,  $2.54 \mu\text{g g}^{-1} \text{d}^{-1} \pm 0.07$  vs.  $2.72 \mu\text{g g}^{-1} \text{d}^{-1} \pm 0.07$ ,  $P = 0.19$ ), and herbivore exclusion reduced net potential N mineralization rate in glade soils ( $2.56 \mu\text{g g}^{-1} \text{d}^{-1} \pm 0.07$  vs.  $2.31 \mu\text{g g}^{-1} \text{d}^{-1} \pm 0.05$ ,  $P = 0.03$ ). Herbivore presence enriched soil  $\delta^{15}\text{N}$  ( $\chi^2(1)=10.8$ ,  $P = 0.0005$ , Figure 3b) in bushland soils (data were not available for glades); however, the difference was only significant to a depth of 5 cm ( $7.25\% \pm 0.18$  vs.  $6.45\% \pm 0.18$ ,  $P = 0.0002$ ) with no differences at

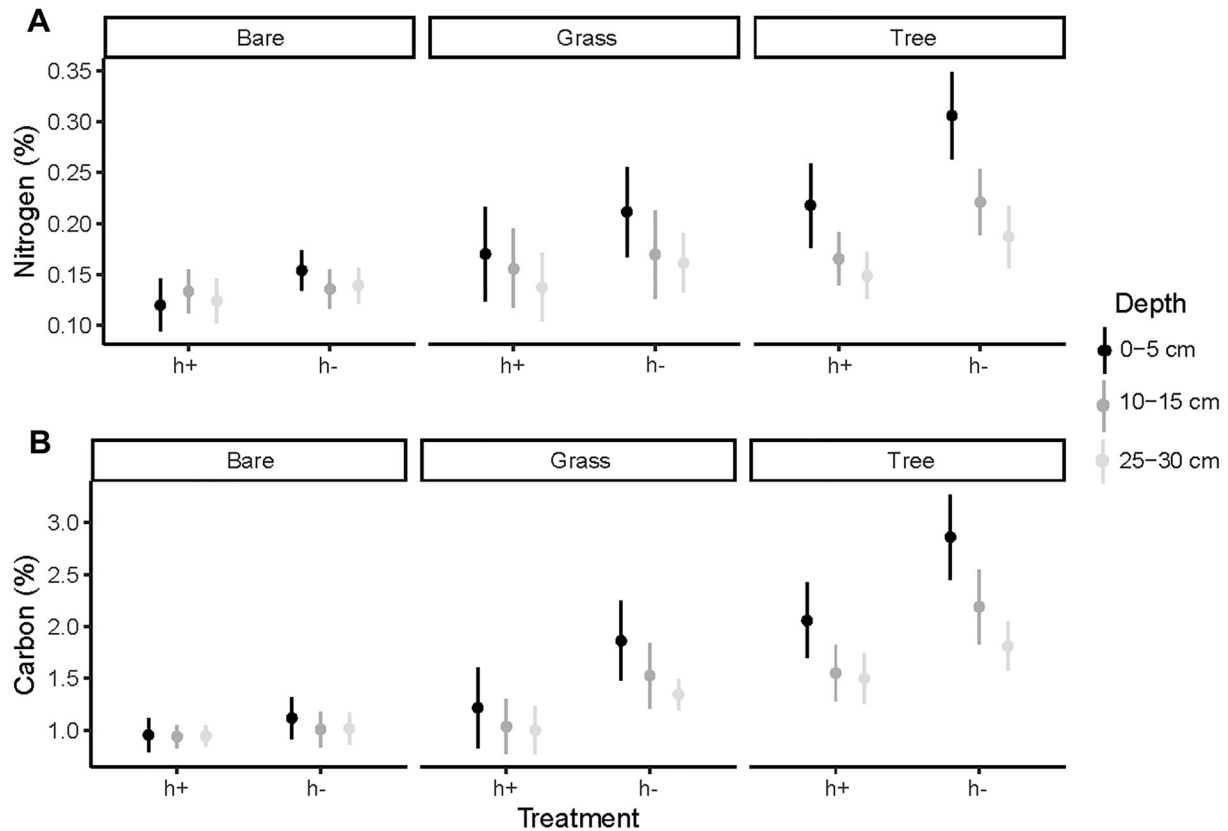


Figure 2. Bushland soil **a** nitrogen and **b** carbon inside (h<sup>-</sup>) and outside (h<sup>+</sup>) of exclosures at three depths and three cover types; bare ground, grass and tree cover (means $\pm$ 95% CIs).

deeper depths ( $7.23\text{‰}\pm 0.17$  vs.  $6.82\text{‰}\pm 0.15$ ,  $P=0.19$ , Figure 3b).

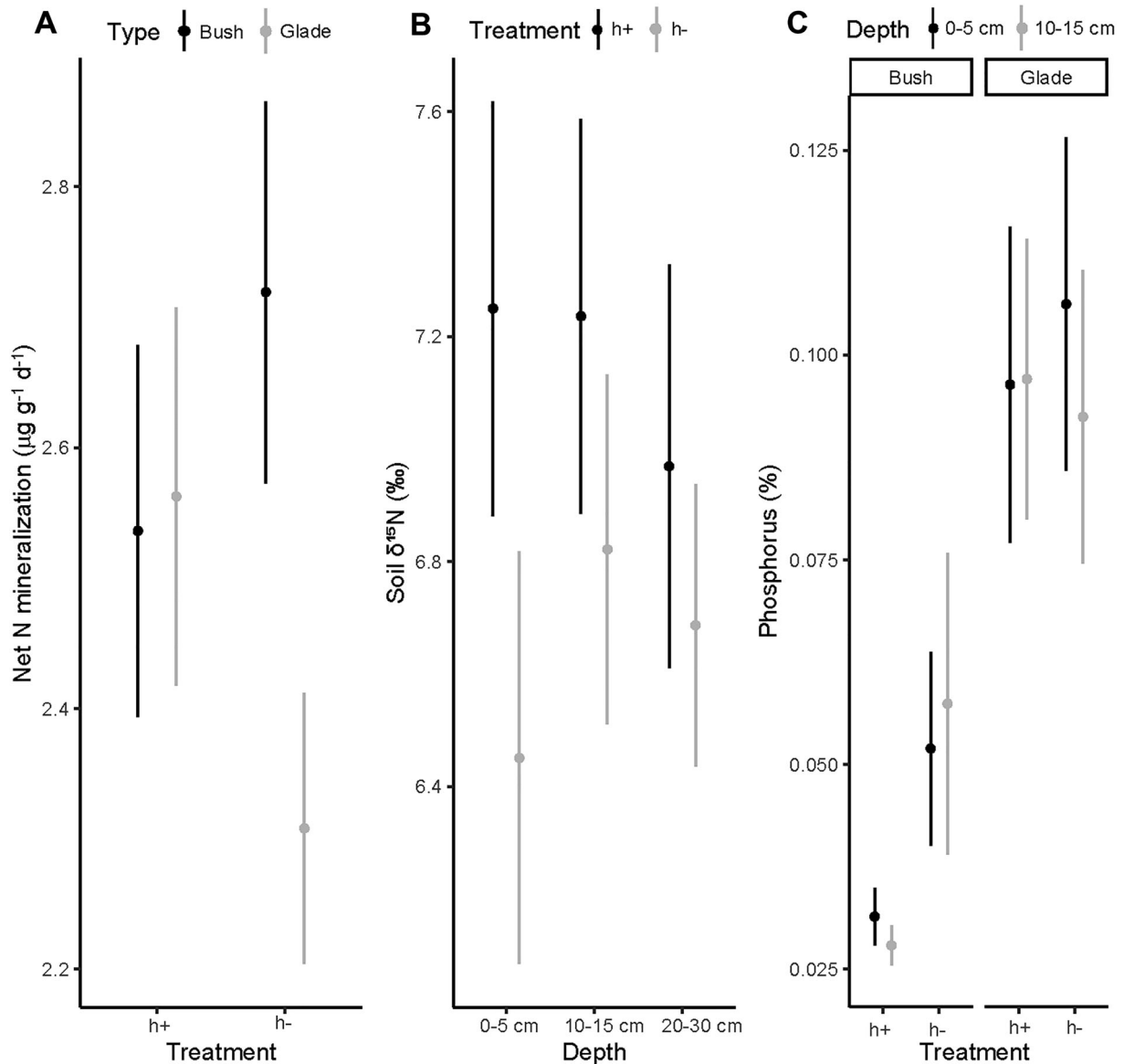
### Foliar Nitrogen, $\delta^{15}\text{N}$ and Phosphorus

Herbivore exclusion at bushland sites had little consistent effect on tree foliar N across species ( $\chi^2(1)=10.0$ ,  $P=0.12$ ) with effects depending on species. On the other hand, herbivore exclusion substantially depleted tree foliar  $\delta^{15}\text{N}$  ( $\chi^2(1)=100$ ,  $P<0.0001$ ), especially for the Acacias (Table 1). With herbivore exclusion, *Acacia brevispica* increased  $\text{N}_2$  fixed by about 0.08 (or 8%), *A. etbaica* almost doubled N from fixation (0.57–0.89%) and *A. mellifera* more than doubled N from fixation (0.23–0.88%) to obtain most N from atmospheric  $\text{N}_2$ . Across grass species (Table 2), herbivore exclusion reduced grass foliar N at bushland sites ( $\chi^2(1)=23.7$ ,  $P=0.001$ ) and N in *C. plectostachyus* at glade sites ( $\chi^2(1)=22.7$ ,  $P<0.0001$ ), while grass foliar P was not affected by herbivore exclusion ( $\chi^2(1)=7.33$ ,  $P=0.40$ ). In general across grass species, herbivore exclusion resulted in depleted grass foliar  $\delta^{15}\text{N}$  at bushland sites ( $\chi^2(1)=28.1$ ,  $P<0.0001$ ).

### DISCUSSION

Our work shows herbivores have substantial long-term effects on soil [N], but that these effects operate through different mechanisms and pathways in bushland versus glades. As predicted, at the bushland, soil nitrogen [N] did not decline over time in the presence of herbivores, but increased substantially (by 28%) with herbivore removal over 17 years. Analyses of soil [N] variation among patches of bare soil vs. grass and woody-dominated vegetation patches revealed that the large increases in soil N occurred mostly in woody-dominated patches, which was only present in bushland. Counter to what was predicted, [N] in glade soils decreased with herbivore presence, although these were relative minor, such that soils still remained enriched relative to bushland soils, while soil N increased on protected glades.

At our bushland sites, woody vegetation was stable over time in the face of intense browsing and doubled in cover when protected from herbivores (Augustine and others 2019; Wigley and others 2020). At the same time, bare patches contracted and grass patches also expanded with herbivore



**Figure 3.** **a** Net soil N mineralization to a depth of 5 cm at bushland and glade sites inside (h-) and outside (h+) of exclosures, **b** soil  $\delta^{15}\text{N}$  (‰) at bushland sites for three depths inside and outside of exclosures, and **c** phosphorus (%) for bushland and glades at two depths (means  $\pm$  95% CIs).

removal (Augustine and others 2019). These increases in vegetation cover result in higher above- and below-ground litter inputs, which result in increased soil N (and carbon) (Belsky and others 1989; Treydte and others 2009; Wigley and others 2014). Apart from increased inputs of litter when herbivores are excluded, an additional factor appears to be the input of N via fixation within the woody patches. Our analysis of  $\delta^{15}\text{N}$  in leaves of two of the *Acacia* species, both of which are capable of fixing atmospheric N (Assefa and Kleiner 1998; Kambatuku and others 2013), indicates that herbivore exclusion enabled these species to dramati-

cally increase N fixation rates. Whether this is an effect of more P available inside exclosures, lower browsing pressure (and more resources available) or competition from grass (Cramer and others 2007; Kambatuku and others 2013) is a subject for further study. Increased N fixation by plants with herbivore exclusion has also been shown to profoundly affect ecosystem N in temperate savannas (Ritchie and others 1998; Knops and others 2000). This could also be a mechanism for increased soil [N] in glade exclosures, where leguminous forbs have greatly increased over time (see Figure 4).



**Table 1.** Foliar Nitrogen ( $\text{mg g}^{-1}$ ) and Foliar  $\delta^{15}\text{N}$  (‰) for Dominant Tree Species at Bushland Sites Inside (h-) and Outside of Exclosures (h+)

Species	Treatment	Foliar N ( $\text{mg g}^{-1}$ )	95% CIs	Foliar $\delta^{15}\text{N}$ (‰)	95% CIs
<i>Acacia brevispica</i>	h+	35.5	32.9–37.9 <sup>‡</sup>	4.94	4.68–5.20*
	h-	33.3	31.7–34.9 <sup>‡</sup>	3.73	3.05–4.39*
<i>Acacia etbaica</i>	h+	30.2	29.5–31.0*	3.20	1.99–4.41*
	h-	32.9	31.5–34.2*	0.73	0.17–1.29*
<i>Acacia mellifera</i>	h+	33.8	33.1–34.5	5.70	4.65–6.75*
	h-	32.9	31.6–34.3	0.76	0.16–1.37*
<i>Balanites pedicellaris</i>	h+	29.7	27.2–31.2	7.43	6.84–8.02*
	h-	29.2	25.5–32.9	6.46	6.02–6.91*
<i>Grewia tenax</i>	h+	29.5	27.3–31.6	3.74	2.68–4.81
	h-	31.5	29.6–33.4	4.03	3.48–4.58

\*significant differences at  $P \leq 0.01$  with treatment, <sup>‡</sup>marginal differences ( $P \sim 0.05$ ) (following Hector 2015).

**Table 2.** Foliar Nitrogen ( $\text{mg g}^{-1}$ ), Foliar Phosphorus (%) and Foliar  $\delta^{15}\text{N}$  Values Inside (h-) and Outside of Exclosures (h+)

Species	Treatment	Foliar N ( $\text{mg g}^{-1}$ )	95% CIs	Foliar P ( $\text{mg g}^{-1}$ )	95% CIs	Foliar $\delta^{15}\text{N}$ (‰)	95% CIs
<i>Glades</i>							
<i>Cynodon plectostachyus</i>	h+	31.0	27.6–34.4*	7.90	7.10–8.70 <sup>‡</sup>		
	h-	21.7	19.0–24.2*	9.17	8.00–10.4 <sup>‡</sup>		
<i>Bushland</i>							
<i>Digitaria milanijana</i>	h+	16.1	9.80–22.4	0.57	0.10–1.30	3.67	3.35–3.99*
	h-	14.9	10.6–19.2	0.90	0.60–1.20	1.77	1.08–2.46*
<i>Cynodon dactylon</i>	h+	28.4	25.4–31.4*	1.80	1.30–2.30	6.92	5.21–8.63*
	h-	22.9	20.4–25.4*	1.47	0.90–2.00	3.43	2.46–4.42*
<i>Enteropogon macrostachyus</i>	h+	20.6	14.6–20.7	1.36	1.00–1.80	4.42	3.40–5.45
	h-	18.3	15.7–20.9	1.31	1.10–1.50	4.08	2.67–5.49
<i>Eragrostis tenuifolia</i>	h+	17.6	14.6–20.7	0.66	0.30–1.00 <sup>‡</sup>	3.98	2.57–5.39
	h-	18.5	15.7–20.9	1.16	0.80–1.50 <sup>‡</sup>	2.53	1.87–3.20
<i>Themeda triandra</i>	h+	13.3	11.9–14.8	0.72	0.30–1.10	2.81	2.46–3.17*
	h-	13.5	11.2–15.9	1.03	0.90–1.20	1.03	0.44–1.63*
<i>Bothriochloa insculpta</i>	h+	14.0	13.1–15.0 <sup>‡</sup>	1.25	0.90–1.60	3.98	2.81–5.15*
	h-	15.4	13.8–17.0 <sup>‡</sup>	1.22	0.80–1.70	1.72	0.97–2.47*
<i>Setaria incrassata</i>	h+	21.1	18.6–23.5	1.20	0.80–1.60	5.01	3.68–6.35
	h-	20.6	17.5–15.9	1.20	0.80–1.50	4.19	3.27–5.12

\*significant differences at  $P \leq 0.01$ , <sup>‡</sup>marginal differences ( $P \sim 0.05$ ) (following Hector 2015)  
 Bushland grasses are in order of dominance. Foliar  $\delta^{15}\text{N}$  was not measured at glades.

At glade sites on the other hand, soil [N] seems to have declined slightly in the presence of herbivores (from 0.18 to 0.16% which equates to a decline of 11% relative to the initial value). If soil N in grazed glades were to continue to decline at this rate, another half-century would be required for glade soil to decline to the surrounding bushland level. All of our study glades were present as glades in aerial photographs from 1961 and hence were more than 60 years old. To the extent that our results from grazed glades are robust for the con-

ditions occurring during the 1900s, they suggest bomas abandoned prior to 1960, which often involved occupancy by livestock for many months to years, could persist as N-enriched glades for over a century. The loss of N over time from ex-boma sites has been documented before. Newly abandoned bomas have high soil [N] ( $\sim 1.7\%$ ), which decreases to less than 1.0% by 24 years and further to around 0.2% after 30–40 years (Augustine 2003). More recently, experimental studies of short-term bomas that only accumulated livestock dung and



**Figure 4.** Fence-line contrast of enclosure (right) and area open to herbivores (left) with substantial forb and sub-shrub layer inside of the enclosure. Photograph taken by Benjamin Wigley.

urine for 14–28 days showed they can still develop into glades (Porensky and Veblen 2015; Veblen and Porensky 2019), but their longevity remains unknown.

At the same time, we found that herbivore removal from glades increased total soil N by 18% over the 17-year period. We suggest herbivore removal primarily altered soil N stocks by reducing the rate of N losses, via two potential mechanisms. First, many studies have shown that grazers affect N cycling by increasing rates of N transformations between organic and mineral forms in grasslands worldwide (Ruess and McNaughton 1987; Holland and Detling 1990; Frank and Evans 1997; Coetsee and others 2011). Previous work at our site showed that the pool of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ -N in the surface soil layer (0–15 cm) is 2–3 times greater in grazed compared to ungrazed glades during dry seasons and periods of low plant growth rates (Augustine and McNaughton 2006). We also found that herbivores increased leaf [N] content for the dominant stoloniferous grass (*Cynodon plectostachyus*) on glades, which enhances the quality of litter inputs to decomposers. Increases in mineral N pools and in nitrification rates (Figure 3a) are well known to provide the substrates and opportunity for N loss via  $\text{N}_2\text{O}$ , NO,  $\text{N}_2$  and  $\text{NH}_3$ , although these rates have not been measured at our study site. Long-term N loss from herbivore-induced increases in mineral N pools is less likely to affect bushland compared to N glade stocks, given that bushland mineral N pools are much lower than in glades and are not as strongly affected by herbivore removal (Augustine and McNaughton 2004, 2006). Additionally, urine deposition represents a substantial proportion of

the N cycle in glades, estimated to be equivalent to approximately 50% of the N contained in above-ground net primary production by grasses during average-precipitation years, but comprises a much smaller component of the N cycle in bushland. Herbivore removal from glades could therefore substantially reduce long-term N losses to ammonia volatilization. Reduction of these losses in ungrazed glades, combined with inputs from leguminous forbs, provides another potential explanation for the long-term increase in soil N in ungrazed glades.

Second, herbivores can spatially redistribute N between glades and the surrounding landscape via differential rates of consumption vs. excretion in glades, at rates that could affect total N stocks over many years (Augustine and others 2003). During our study, annual rainfall increased compared to prior decades, from 546 mm during the past 44 years to 613 mm annually during 2003–2016 (Augustine and others 2019). In particular, the site experienced four consecutive years of above-average rainfall during 2010–2013. Under these conditions, extended and more productive growing seasons enable cattle to increase consumption in glades and redistribute more N from glades to bomas. Quantitative estimates of the magnitude of this N flux done previously at the study site suggest that the long-term N balance depends on the balance between good growing seasons (when net export of N by cattle dominates) vs. dormant seasons (when net N inputs from impala occur; Augustine and others 2003). Herbivore exclusion prevents this pathway of N loss from glades, again contributing to soil N accumulation from other sources of inputs, such as litter, N deposition and N fixation.

Overall, we found that the way large herbivores influence soil N balance in the bushland landscape differs notably from the way they affect soil C storage. Using C isotopes, Wigley and others (2020) showed that herbivore exclusion primarily enhances soil C via inputs of C from grasses to the soil, which occur both in the grass-dominated patches, and via grass in the understory of woody patches. This result implicates large grazers (here, primarily cattle and impala, and to a lesser extent plains zebra, Grevy's zebra, and waterbuck) as the primary herbivore influence on soil C storage (Wigley and others 2020). In contrast, herbivore effects on soil N in the bushland landscape are affected primarily by browsers, through their influence on N fixation rates of the Acacia species that dominate the woody community. The dramatic increase in soil C storage driven largely by the removal of grazer effects on grasses reported by Wigley and others (2020) at

bushland sites may therefore be facilitated by increased soil N availability associated with browser removal and associated increases in N inputs to the soil from the woody layer.

A key question for rangeland managers who seek to manipulate boma and glade density to influence landscape-level forage quality and wildlife habitat is how the length of boma occupancy is related to the time period over which soils remain enriched in N, support nutrient-rich lawn grasses such as *Cynodon plectostachyus*, and serve as a focal grazing location for large herbivores (Veblen and Porensky 2019). Herbivores increased leaf N content for the three most abundant stoloniferous grasses (*Cynodon plectostachyus* on glades; *Cynodon dactylon* and *Digitaria milanjiiana* on bushland soils) and for a wide-spread, palatable bunchgrass (*Enteropogon macrostachyus*), while foliar P and soil P were not affected. Our results suggest that large herbivore effects on glade N stocks are influenced by spatial movements of nutrients in and out of glades (which would influence both N and P balance), but also by the degree to which herbivores accelerate gaseous losses of N (which does not affect P balance). In conclusion, the movement of cattle and native ungulates creates strong gradients of use in these African savannas that in turn creates and reinforces spatially heterogeneous landscapes. The increased heterogeneity benefit wildlife and biodiversity by providing diverse habitats and create feeding opportunities that allow much more productive herbivore systems (Sankaran and others 2013; McCleery and others 2018; Augustine and others 2019; Otieno and others 2019).

## ACKNOWLEDGEMENTS

This work was funded by the National Centre for Biological Sciences, TIFR, India, National Geographic (grant 982815) and NERC (grant NE-E017436-1). We are grateful to MRC for logistical support and the Office of the President of the Republic of Kenya for permission to conduct the research. We thank Junior Parsare for his assistance in the field and Chengappa S.K. and Balavignesh B. for their assistance with laboratory analyses.

## REFERENCES

Ahn PM, Geiger LC. 1987. Kenya soil survey - soils of Laikipia District. Kabete, Kenya: Ministry of Agriculture, National Agricultural Laboratories.

Andriuzzi WS, Wall DH. 2017. Responses of belowground communities to large aboveground herbivores: Meta-analysis reveals biome-dependent patterns and critical research gaps. *Global Change Biology* 23:3857–3868.

Assefa F, Kleiner D. 1998. Nodulation pattern and acetylene reduction (nitrogen fixation) activity of some highland and lowland *Acacia* species of Ethiopia. *Biology and Fertility of Soils* 27:60–64.

Augustine DJ. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* 40:137–149.

Augustine DJ. 2010. Response of native ungulates to drought in semi-arid Kenyan rangeland. *African Journal of Ecology* 48:1009–1020.

Augustine DJ, Frank DA. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* 82:3149–3162.

Augustine DJ, McNaughton SJ. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41:45–58.

Augustine DJ, McNaughton SJ. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9:1242–1256.

Augustine DJ, McNaughton SJ, Frank DA. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications* 13:1325–1337.

Augustine DJ, Veblen KE, Goheen JR, Riginos C, Young TP. 2011. Pathways for positive cattle–wildlife interactions in semiarid rangelands. *Smithsonian Contributions to Zoology* 632:55–71.

Augustine DJ, Wigley BJ, Ratnam J, Kibet S, Nyangito M, Sankaran M. 2019. Large herbivores maintain a two-phase herbaceous vegetation mosaic in a semi-arid savanna. *Ecology and Evolution* 9:12779–12788.

Bardgett RD, Wardle DA. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258–2268.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of applied ecology*:1005–24.

Birnie A, Noad T. 2011. *Trees of Kenya: An illustrated field guide*. Nairobi: Kenway Publications Ltd.

Blackmore AC, Mentis MT, Scholes RJ. 1990. The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South Africa. *Journal of biogeography* 17:463–70.

Bonnet O, Fritz H, Gignoux J, Meuret M. 2010. Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. *Journal of Ecology* 98:908–916.

Bubnicki JW, Churski M, Schmidt K, Diserens TA, Kuijper DP. 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *ELife* 8:e44937.

Cherif M, Loreau M. 2013. Plant–herbivore–decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proceedings of the Royal Society b: Biological Sciences* 280:20122453.

Coetsee C, Stock WD, Craine JM. 2011. Do grazers alter nitrogen dynamics on grazing lawns in a South African savannah? *African Journal of Ecology* 49:62–69.

Craine JM, Brookshire ENJ, Cramer MD, Hasselquist NJ, Koba K, Marin-Spiotta E, Wang L. 2015. Ecological interpretations

- of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil* 396:1–26.
- Cramer MD, Chimphango SB, Van Cauter A, Waldram MS, Bond WJ. 2007. Grass competition induces N<sub>2</sub> fixation in some species of African Acacia. *Journal of Ecology* 95:1123–1133.
- De Mazancourt C, Loreau M, Abbadie L. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology* 79:2242–2252.
- Fish L, Mashau AC, Moeaha MJ, Nembudani MT. 2015. Identification guide to southern African grasses: an identification manual with keys, descriptions and distributions. South African National Biodiversity Institute
- Ford AT, Goheen JR, Augustine DJ, Kinnaird MF, O'Brien TG, Palmer TM, Pringle RM, Woodroffe R. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology* 96:2705–2714.
- Frank DA, Evans RD. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 78:2238–2248.
- Frank DA, Inouye RS, Huntly N, Minshall GW, Anderson JE. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* 26:163–188.
- Frank DA, Groffman PM, Evans RD, Tracy BF. 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia* 123:116–121.
- Georgiadis NJ, McNaughton SJ. 1988. Interactions between grazers and a cyanogenic grass, *Cynodon plectostachyus*. *Oikos* 51:343–350.
- Githae EW, Gachene CK, Njoka JT, Omondi SF. 2013. Nitrogen fixation by natural populations of *Acacia senegal* in the drylands of Kenya using <sup>15</sup>N natural abundance. *Arid Land Research and Management* 27:327–336.
- Hector A. 2015. *The New Statistics with R: An introduction for biologists*. New York, USA: Oxford University Press.
- Hobbie SE. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* 7:336–339.
- Holland EA, Detling JK. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71:1040–1049.
- Kambatuku JR, Cramer MD, Ward D. 2013. Nitrogen fertilisation reduces grass-induced N<sub>2</sub> fixation of tree seedlings from semi-arid savannas. *Plant and Soil* 365:307–320.
- Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience* 49:39–50.
- Knops JM, Ritchie ME, Tilman D. 2000. Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*) influences productivity and ecosystem nitrogen pools in an oak savanna. *Ecoscience* 7:166–174.
- Krom MD. 1980. Spectrophotometric determination of ammonia: a study of a modified Berthelot reaction using salicylate and dichloroisocyanurate. *Analyst* 105:305–316.
- Kuznetsova A, Brockhoff PB, Christensen RH. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82:1–26.
- Lenth RV. 2016. Least-Square Means: The R Package lsmeans. *Journal of Statistical Software* 69:1–33.
- Lilleeng MS, Hegland SJ, Rydgren K, Moe SR. 2016. Red deer mediate spatial and temporal plant heterogeneity in boreal forests. *Ecological Research* 31:777–784.
- Limb RF, Hovick TJ, Norland JE, Volk JM. 2018. Grassland plant community spatial patterns driven by herbivory intensity. *Agriculture, Ecosystems & Environment* 257:113–119.
- Liu C, Song X, Wang L, Wang D, Zhou X, Liu J, Zhao X, Li J, Lin H. 2016. Effects of grazing on soil nitrogen spatial heterogeneity depend on herbivore assemblage and pre-grazing plant diversity. *Journal of Applied Ecology* 53:242–250.
- Marshall F, Reid RE, Goldstein S, Storzum M, Wreschnig A, Hu L, Kiura P, Shahack-Gross R, Ambrose SH. 2018. Ancient herders enriched and restructured African grasslands. *Nature* 561:387–390.
- McCleery R, Monadjem A, Baiser B, Fletcher R Jr, Vickers K, Kruger L. 2018. Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. *Biological Conservation* 226:54–62.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294.
- Odadi WO, Riginos C, Rubenstein DI. 2018. Tightly bunched herding improves cattle performance in African savanna rangeland. *Rangeland Ecology & Management* 71:481–491.
- Oms MT, Cerda A, Cerda V. 1995. Sequential injection analysis of nitrites and nitrates. *Analytica Chimica Acta* 315:321–330.
- Otieno TO, Goheen JR, Webala PW, Mwangi A, Osuga IM, Ford AT. 2019. Human-and risk-mediated browsing pressure by sympatric antelope in an African savanna. *Biological Conservation* 232:59–65.
- Pastor J, Cohen Y, Moen R. 1999. Generation of spatial patterns in boreal forest landscapes. *Ecosystems* 2:439–450.
- Pastor J, Cohen Y, Hobbs NT. 2006. The roles of large herbivores in ecosystem nutrient cycles. *Conservation Biology Series-Cambridge* 11:289.
- Penner JF, Frank DA. 2019. Litter decomposition in Yellowstone grasslands: the roles of large herbivores, litter quality, and climate. *Ecosystems* 22:929–937.
- Persson I-L, Pastor J, Danell K, Bergström R. 2005. Impact of moose population density on the production and composition of litter in boreal forests. *Oikos* 108:297–306.
- Porensky LM, Veblen KE. 2015. Generation of ecosystem hot-spots using short-term cattle corrals in an African savanna. *Rangeland Ecology & Management* 68:131–141.
- R Development Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing [Computer software]. <https://www.R-project.org/>
- Raddad EAY, Salih AA, El Fadl MA, Kaarakka V, Luukkanen O. 2005. Symbiotic nitrogen fixation in eight *Acacia senegal* provenances in dryland clays of the Blue Nile Sudan estimated by the <sup>15</sup>N natural abundance method. *Plant and Soil* 275:261–269.
- Ritchie ME, Tilman D, Knops JM. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177.
- Ruess RW, McNaughton SJ. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos* 49:101–10.
- Sankaran M, Augustine DJ. 2004. Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. *Ecology* 85:1052–1061.

- Sankaran M, Ratnam J, Hanan N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17:236–245.
- Sankaran M, Augustine DJ, Ratnam J. 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. *Journal of Ecology* 101:1389–1399.
- Scholes RJ, Walker BH. 2004. An African savanna: synthesis of the Nylsvley study. Cambridge University Press <https://books.google.co.za/books?hl=en&lr=&id=FtXeA8IxMwQC&oi=fnd&pg=PP1&dq=scholes+an+african+savanna&ots=TyYIqXMf8B&sig=-fnDOFtZYQtqm-Md0t7aKuyJsHY>
- Schrama M, Heijning P, Bakker JP, van Wijnen HJ, Berg MP, Olf H. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia* 172:231–243.
- Shearer G, Kohl DH. 1986. N<sub>2</sub>-fixation in field settings: estimations based on natural <sup>15</sup>N abundance. *Functional Plant Biology* 13:699–756.
- Singer FJ, Schoenacker KA. 2003. Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management* 181:189–204.
- Sitters J, Venterink HO. 2015. The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling. *Plant and Soil* 396:421–426.
- Sitters J, Bakker ES, Veldhuis MP, Veen GF, Olde Venterink H, Vanni MJ. 2017. The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences. *Frontiers in Earth Science* 5:32.
- Treydte AC, Bernasconi SM, Kreuzer M, Edwards PJ. 2006. Diet of the common warthog (*Phacochoerus africanus*) on former cattle grounds in a Tanzanian savanna. *Journal of Mammalogy* 87:889–898.
- Treydte AC, Grant CC, Jeltsch F. 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. *Biodiversity and Conservation* 18:3989.
- Van der Waal C, Kool A, Meijer SS, Kohi E, Heitkönig IM, de Boer WF, van Langevelde F, Grant RC, Peel MJ, Slotow R, et al. 2011. Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia* 165:1095–1107.
- Veblen KE. 2012. Savanna glade hotspots: plant community development and synergy with large herbivores. *Journal of Arid Environments* 78:119–127.
- Veblen KE, Porensky LM. 2019. Thresholds are in the eye of the beholder: plants and wildlife respond differently to short-term cattle corrals. *Ecological Applications* 29:e01982.
- Veldhuis MP, Gommers MI, Olf H, Berg MP. 2018. Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem. *Journal of Ecology* 106:422–433.
- Verweij R, Verrelst J, Loth PE, Heitkönig I MA, Brunsting A MH. 2006. Grazing lawns contribute to the subsistence of meso-herbivores on dystrophic savannas. *Oikos* 114:108–116.
- Waldram MS, Bond WJ, Stock WD. 2008. Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* 11:101–112.
- Western D, Dunne T. 1979. Environmental aspects of settlement site decisions among pastoral Maasai. *Human Ecology* 7:75–98.
- Wigley BJ, Fritz H, Coetsee C, Bond WJ. 2014. Herbivores shape woody plant communities in the Kruger National Park: Lessons from three long-term exclosures. *Koedoe* 56:1–12.
- Wigley BJ, Coetsee C, Augustine DJ, Ratnam J, Hattas D, Sankaran M. 2019. A thorny issue: Woody plant defence and growth in an East African savanna. *Journal of Ecology* 107:1839–1851.
- Wigley BJ, Augustine DJ, Coetsee C, Ratnam J, Sankaran M. 2020. Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. *Ecology* 101:e03008.
- Yoshihara Y, Ohkuro T, Buuveibaatar B, Jamsran U, Takeuchi K. 2010. Spatial pattern of grazing affects influence of herbivores on spatial heterogeneity of plants and soils. *Oecologia* 162:427–434.
- Young TP, Patridge N, Macrae A. 1995. Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. *Ecological Applications* 5:97–108.