Ecosystems
https://doi.org/10.1007/s10021-024-00944-7

ECOSYSTEMS

Labile Soil Carbon Heterogeneity Driven by Consumer Engineering of Aboveground Structure in a Kenyan Savanna

Elizabeth S. Forbes,[1,5,6]* Dana D. Moore,[1,3] John Naisikie Mantas,[2]
Joshua Schimel,[1] Truman P. Young,[4] and Hillary S. Young[1]

[1]Department of Ecology Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, California 93106, USA; [2]Mpala Research Centre and Conservancy, P.O. Box 555, Nanyuki 10400, Kenya; [3]Oregon Department of Fish and Wildlife, Salem, Oregon 97302, USA; [4]Department of Plant Sciences, University of California Davis, Davis, California 95616, USA; [5]Yale School of the Environment, New Haven, Connecticut 06511, USA; [6]Hudson Carbon, Hudson, New York 12534, USA

ABSTRACT

Aboveground ecosystem structure moderates and even confers essential ecosystem functions. This includes an ecosystem's carbon dynamics, which are strongly influenced by its structure: for example, tropical savannas like those in central Kenya store substantial amounts of carbon in soil. Savannas' belowground allocation of carbon makes them important for global carbon sequestration, but difficult to monitor. However, the labile soil carbon pool is responsive to changes in ecosystem structure and is thus a good indicator of overall soil organic carbon dynamics. Kenya's savanna structure is controlled by belowground ecosystem engineers (termites), ambient weather conditions, and the aboveground engineering influences of large-bodied, mammalian consumers. As a result, climate change and biodiversity loss are likely to change savannas' aboveground structure. To predict likely outcomes of these threats on savanna soil carbon, it is critical to explore the relationships between labile soil carbon and ecosystem structure, local climate, and mammalian consumer community composition. In a large-scale, long-term herbivore exclosure experiment in central Kenya, we sampled labile carbon from surface soils at three distinct savanna structural elements: termite mounds, beneath tree canopies, and the grassland matrix. In one sampling year, we measured total extractable organic carbon (TEOC), total extractable nitrogen (TEN), and extractable microbial biomass for each sample. Across three sampling years with varying weather conditions, we measured rate of labile soil carbon mineralization. We quantified areal coverage of each structural element across herbivore community treatments to estimate pool sizes and mineralization dynamics at the plot scale. Concentrations and stocks of soil TEOC, TEN, and microbial biomass were driven by the structural element from which they were sampled (soils collected under tree canopies gen-

---

Received 13 March 2024; accepted 24 November 2024

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-024-00944-7.

Authors Contribution ESF conceived the study design, carried out fieldwork, lab work, and led dataanalyses/interpretation and manuscript writing. DDM conducted lab work by leading sampleextraction and associated data collection, as well as contributing to data interpretation. JNMshared fieldwork responsibilities with lead author ESF and contributed to data interpretation. JScontributed significantly to lab work as well as study design and data analysis and interpretation.TPY was PI of the KLEE at the start of the study and contributed significantly to overall studydesign. HSY contributed significantly to study design and data interpretation. All authorscontributed critically to the drafts and gave final approval for publication. JS, TPY, and HSYcontributed substantially to manuscript writing.

*Corresponding author; e-mail: forbeselizabeth.s@gmail.com

erally had the highest of each). Large-bodied herbivore community composition interacted variably with concentrations, stocks, and carbon mineralization, resulting in apparently compensatory effects of herbivore treatment and structural element with no net effects of large herbivore community composition on plot-scale labile carbon dynamics. We confirmed engineering of structural heterogeneity by consumers and identified distinct labile carbon dynamics in each structural element. However, carbon and nitrogen were also influenced by consumer community composition, indicating potentially compensatory interacting effects of herbivore treatment and structural element. These results suggest that one pathway by which consumers influence savanna carbon is by altering its structural heterogeneity and thus the heterogeneity of its plot-scale labile carbon.

Key words: Biogeochemistry; Carbon cycle; Exclosure experiment; Large herbivores; Savanna; Zoogeochemistry.

HIGHLIGHTS

- East African savanna structure is controlled by the presence or absence of large-bodied consumer species and by below ground engineers like termites.
- We show that labile soil carbon dynamics are determined by the identity of the structural element at which they are found (e.g., beneath tree canopy, on termite mounds).
- What is more, the effects of structural element on labile soil carbon dynamics interact with the experimental presence or absence, and identity, of mammalian consumers like elephants and domestic cattle.
- As a result, we demonstrate that heterogeneity in aboveground savanna structure, and therefore heterogeneity in labile soil carbon cycling and stocks, is modulated by large-bodied mammalian consumer community composition.

INTRODUCTION

An ecosystem's aboveground structure has long been understood to result in predictable functional outcomes (Lamont 1995). Studies modeling or observing changes to characteristic structures reveal critical ecosystem functionality: for instance, subalpine forests' ribbon structure that confers resistance to wind disturbance, freezing, and desiccation (Bekker and Malanson 2008; de Jager and others 2020; Hessburg and others 2019; Liu and others 2014); similarly, the grass tussocks and crab burrows of tidal saltmarshes contribute to habitat formation and stability, as well as nutrient cycling and storage. One of the many functions mediated by such aboveground ecosystem structure is carbon cycling (Holdo and Mack 2014; Maestre and others 2016; Migliavacca and others 2021): ecosystem structure's effects on carbon cycling are critical, given that terrestrial ecosystems take up and store almost a third of anthropogenic carbon emissions globally (Luo and others 2015).

In Laikipia, Kenya, savannas have a uniform overdispersion of subterranean termite mounds (*Odontotermes* spp.; Pringle and Tarnita 2017) which confers resilience to the plant community during droughts (Bonachela and others 2015). These treeless mounds also localize nutrients, positively influencing the productivity, density, and size of the vegetation immediately surrounding them (Fox-Dobbs and others 2010). This vegetation includes the monodominant, leguminous tree *Acacia drepanolobium* (Porensky and others 2013; Young and others 1998), or whistling thorn Acacia, which is itself fairly predictably distributed (Staver and others 2019) and whose mutualism with a root-associated nitrogen-fixing bacterium creates hotspots of N-availability in otherwise N-poor soils (Gichangi and others 2016). Given the prevalence of both mounds and trees, one can visualize the savanna as a mosaic of three structural elements: area covered by termite mounds, tree canopy, and grassland matrix (without either). Despite evidence of each structural element's importance to general ecosystem functioning, their combined effects on savanna carbon dynamics are relatively understudied.

Critically, the savanna's animal community is also influential to both its structure and carbon cycle. Large-bodied, wild vertebrate consumers are well-documented to mediate carbon cycling and storage generally (Forbes and others 2019; Schmitz and others 2018), and wild consumers often coexist with (or are replaced by) domestic cattle, which may (Veblen and others 2016) or may not (Ratajczak and others 2022; Wells and others 2022b) have functional effects similar to their wild analogs. Large consumers in the savanna engineer its structure. For example, traditional cattle grazing can cause establishment of new, small termite mounds due to increased dietary resources, like stimulated grass productivity and episodic deposits of dung (Charles and others 2021). Elephants knock over savanna trees while browsing, even preferentially selecting tall trees with wide canopies (Asner and Levick 2012; Charles and others 2021; Pringle 2008; Young and others 2018). Tree removal itself is negatively correlated with termite mound abundance, demonstrating one of myriad interactions between engineering fauna (Charles and others 2021). Ambient weather conditions in this seasonally dry savanna are also likely to influence carbon dynamics, with effects that may themselves interact with ecosystem structure and animal community (Munjonji and others 2020). However, despite Kenya's relatively abundant wildlife, its wild herbivore density is threatened by more frequent drought and longer dry seasons, which interact with increases in (economically critical) livestock grazing to produce negative effects on wildlife occurrence (Crego and others 2020) and abundance (Ogutu and others 2016).

By utilizing the longstanding Kenya Long-term Exclosure Experiment (KLEE) we asked: do the savanna's structural elements have distinct soil carbon dynamics? Does experimental manipulation of large herbivore ''loss'' (including herbivore group presence, absence, and identity) and its consequential engineering of the savanna's structural mosaic influence soil carbon dynamics? If so, at what scales? Lastly, does ambient weather (here, drought) interact with carbon dynamics within each structural element, within vertebrate community composition treatments, or at the landscape scale?

We characterized the savanna's surface labile soil carbon stocks and cycling at each structural element—termite mounds, *A. drepanolobium* trees, and the grassland matrix. Given the rapid responses of labile soil carbon (a rapid-turnover subset of the organic carbon pool) to changes in ecosystem structure or use, we determined that labile soil carbon metrics were most likely to demonstrate differences across structural elements and herbivore treatments (Bünemann and others 2018; De Brito and others 2019). Sitters and others (2020) determined that cattle presence decreases, while elephant presence increases, *total* soil carbon in the KLEE. However, while assessing total carbon successfully integrates and measures cumulative treatment effects, it is not possible to parse finer-scale soil carbon dynamics. By monitoring the labile carbon pool, particularly over multiple years, we can infer changes in soil quality and the organic carbon pool over time in response to complex environmental change (Biederbeck and others 1994; Tobiašová and others 2016).

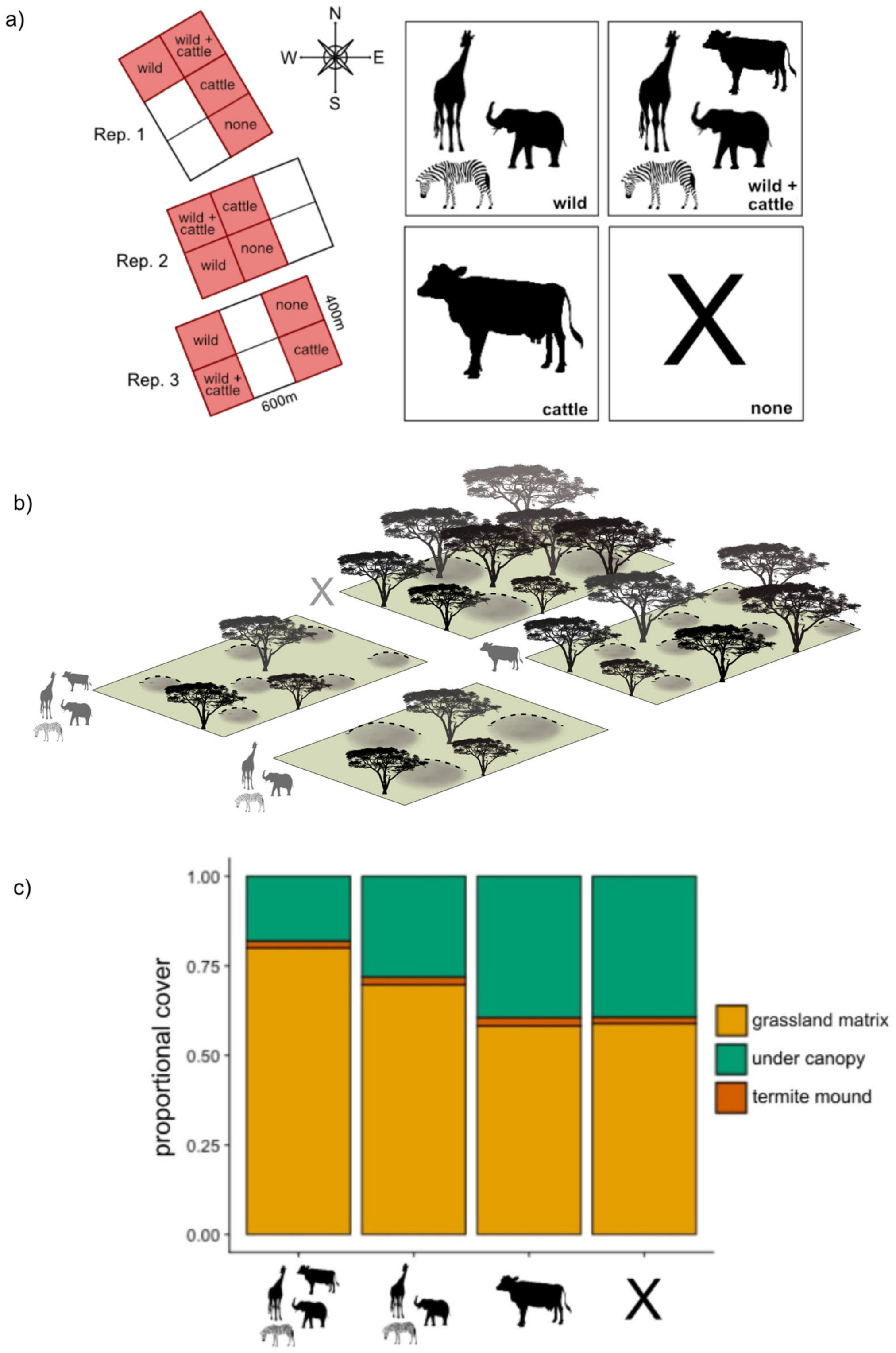
We sampled soils three times across four years, with two wet sampling years bookending an historic drought year. For each year, we measured soil respiration as a proxy for rate of microbial soil carbon mineralization. For one of the years, we also measured concentrations and pool sizes of 1) total extractable organic carbon (TEOC), 2) total (organic and inorganic) extractable nitrogen (TEN), and 3) microbial biomass carbon (MBC) and nitrogen (MBN). (Nitrogen availability regulates plant productivity, and thus drawdown of atmospheric carbon dioxide (CO_2) and inputs of soil organic matter (Soussana and Lemaire 2014). Nitrogen and carbon are also both essential to soil microbial function. Characterizing soil carbon thus requires characterizing carbon, nitrogen, and soil microbial biomass (Zaehle 2013).)

We predicted we would observe greater concentrations of TEOC and microbial biomass per unit area, and larger total pool sizes, at termite mounds and under tree canopies compared to the grassland matrix because of elevated organic matter inputs at mounds (via termite importation) and under trees (via litterfall). For the same reason, as well as nitrogen-fixation at both termite mounds and trees, we predicted we would observe greater TEN concentrations and larger pool sizes at these structural elements. We expected that these elevated pools of nutrients would be associated with faster rates of microbial carbon mineralization under tree canopies and on mounds. We predicted that the presence of large herbivores (wild, domestic, or both) would result in smaller overall pools of TEOC, TEN, and microbial biomass, and slower rates of soil carbon mineralization at all three structural elements, due to lower overall inputs of litter. Given the drought tolerance of the system, we predicted that drought would lower rates of carbon mineralization, but that the effects of structural element and treatment would remain the same relative to each other.

MATERIALS AND METHODS

Study Site

KLEE (0° 17′ N, 36° 52′ E) is a large-scale herbivore exclosure experiment established in 1995 at the Mpala Research Centre and Conservancy in Laikipia County, Kenya, a working cattle ranch (stocking density of 0.10–0.14 cattle/ha) (Odadi and others 2007; Young and others 2005). Mpala retains a largely intact large-bodied (> 15 kg) wild herbivore community, totaling $\sim 1/3$ the density of the cattle population by biomass (Veblen and oth-


a)
wild + cattle
wild
cattle
none
Rep. 1
wild + cattle
cattle
none
wild
Rep. 2
none
wild
cattle
wild + cattle
Rep. 3
400m
600m
N
W
E
S
wild
wild + cattle
cattle
X
none
b)
X
c)
proportional cover
1.00
0.75
0.50
0.25
0.00
X
grassland matrix
under canopy
termite mound

◀**Figure 1.** **a** Schematic diagram of KLEE, with the four treatments used in this study highlighted in red. **b** Representation of the effect of each experimental herbivore community on aboveground savanna structure, including on the size, abundance, and areal coverage of tree canopies (greater in ''cattle,'' ''none'' treatments) and coverage and abundance of termite mounds (more abundant, smaller mounds in plots with cattle grazing). **c** Proportional cover of each landscape feature within each treatment, with decreasing herbivore group presence from left to right. Data from Sitters and others (2020) (under canopy) and Charles and others (2021) (termite mound), with grassland matrix the remaining proportional area.

ers 2016), including ruminants like Grant's gazelle, buffalo, oryx, hartebeest, eland, and giraffe and non-ruminants like zebra and elephant. KLEE uses semi-permeable barriers to experimentally explore interactions between large-bodied (> 15 kg) mammalian herbivores and savanna structure and function. It is located on clay-rich, volcanic vertisol soils (''black cotton'') and experiences a weakly trimodal seasonal rainfall pattern with ~ 600 mm annual precipitation.

We utilized four of KLEE's herbivore treatments: ''Wild'' is a non-fenced treatment where all wild large herbivores are present, but cattle grazing is excluded (with monitoring and visual markers to indicate plot boundaries to herders). ''Wild and cattle'' is also non-fenced and allows for all wild large herbivores and intentional grazing of cattle 3–4 times per year. ''Cattle'' is a fenced exclosure treatment where wild large herbivores are absent, but domestic cattle graze on the same 3–4 × yearly schedule as in ''Wild and cattle.'' This controlled grazing regime results in stocking density and grazing intensity similar to Mpala Ranch and nearby properties, and its episodic nature is consistent with traditional East African pastoralism practices; the cattle do not receive supplementary feeding (see supplement for details). Lastly, ''None'' is also fenced, where all large herbivores (both wild and cattle) are excluded. Each treatment consists of a 4 ha (200 m x 200 m) plot and is replicated in three experimental blocks across the landscape (Young and others 1998) (Figure 1a). Herbivore biomass and total herbivory pressure are not additive across KLEE treatments; cattle herbivory reduces mesoherbivore (> 15 kg, smaller than elephants and giraffes) use of ''wild and cattle'' plots by approximately 9% (Kimuyu and others 2017; Young and others 2018) and elephant use by up to 35% (only in the dry season) (Wells and others 2022a; Young and others 2005) (Figure S1). However, cattle forage efficiency is also lower in ''wild and cattle'' versus ''cattle only'' plots due to competition with elephants (Young and others 2018). Total herbivory pressure therefore varies by herbivore type and covaries with environmental variables like season.

To quantify consumer influence on aboveground savanna structure, we estimated average coverage (m^2) of the three structural elements within each treatment, first the area of termite mounds (Charles and others 2021) and tree canopy cover (Sitters and others 2020) per treatment using published data. By subtracting their combined average area per treatment from the size of one plot (4 ha), we estimated average area of the grassland matrix per treatment (Figure 1c).

Soil Sample Collection

We collected soil samples over three dry seasons (between Jun-Aug) in 2015, 2016, and 2018. While we anticipated that sampling over multiple years' dry seasons would capture strong interannual signals of structural element and treatment impacts, annual rainfall was extremely variable. In 2016 (second year of sampling), an historic, multiyear drought began. In 2018 (third year of sampling), the drought had ended, and it was unusually wet. Because drought impacts soil organic carbon inputs as well as soil microbial growth and carbon mineralization (Deng and others 2021), we assumed year of collection was an important driver of carbon dynamics.

To capture spatial variability, we conducted stratified soil sampling at each structural element, within each treatment plot: beneath the canopy of living *A. drepanolobium* trees (''Under Tree''), from the surface of active termite mounds (''Termite Mound''), and from open soil in the surrounding grassland matrix (''Grassland Matrix''). We sampled the 0–5 cm layer, as the top layer of rangeland soils is most likely to be influenced by exogenous changes like grazing regime (Rotich and others 2018) and because the cracking morphology of vertisol results in thorough mixing of organic matter at the surface and a lack of stratification (Somasundaram and others 2018). We sampled from locations > 50 m from the boundary of each plot to minimize edge effects.

In 2015, sampling intensity was more limited than 2016 and 2018: we collected three samples per structural element, within each of the four treatments across the three experimental replicates, randomly pre-selecting sites at least 75 m apart (totaling 108 samples in 2015). We increased sampling intensity in 2016 and 2018 to address variation observed in 2015. In these years, we placed a 100 m transect down the center of each plot's inner hectare (SE to NW). For grassland matrix samples, we collected one sample every 10 m, from 0 to 90 m, ensuring each was > 10 m from a termite mound or tree canopy. For under canopy soils, at every 10 m we walked perpendicularly away to the nearest live *A. drepanolobium* tree to sample beneath its canopy (alternating left or right to maximize distance between samples). For termite mound soils, we used a preexisting map of active termite mounds (Charles and others 2021) to randomly select up to ten mounds in each plot, sampling every active mound if fewer than ten (totaling up to 360 samples in each 2016 and in 2018). Across all years, samples were at least 10 m apart to ensure spatial independence (Folorunso and others 1988). Soils were air-dried upon returning to the lab, passed through a 2 mm sieve to eliminate non-soil matter within 1–3 days, and isolated from moisture, light, and air until their use within 0.5–5 months.

Soil Incubations: Microbial Soil Carbon Mineralization

In 2015, we assessed the soils' water holding capacities (WHC) by saturating 36 subsamples (three from each structural element, within each of the four herbivore treatments) and measuring their gravimetric water content. While there was no difference in WHC across herbivore treatments, there was a significant difference across structural elements (higher WHC on termite mounds compared to under trees and the grassland matrix). We calculated average WHC for each element. As WHC is not expected to change without significant changes to soil texture, we used the same WHCs for all three years' incubations (Lowery and others 1996).

To conduct incubations of each year's soil samples, we rehydrated each sample to 50% WHC before sealing them in jars for 144 h (six days). Every 24 h, we took gas samples from the jar headspaces via a rubber septum with a non-coring needle and syringe. We measured CO_2 concentration of each gas sample with a flow-through LI-COR infrared gas analyzer (Li-6252) (see supplement for details). We calculated total µg CO_2–C produced per gram of soil using ideal gas laws, jar volume, and dry mass of each sample, and the rate of mineralized C at the end of the incubation in µg CO_2–C per gram of soil per day.

Total Extractible Organic Carbon, Total Extractible Nitrogen, Microbial Biomass Concentrations

We selected the 2016 soils to assess non-microbially associated TEOC, TEN, and soil microbial biomass C and N. To do so we conducted a second incubation of 2016 samples, allowing the soils (which had been archived for one year) to equilibrate to ''field moist'' conditions prior to chemical extraction. We expected a large pulse of microbial activity (thus soil carbon mineralization) upon rehydration due to the Birch effect and microbial breakdown of osmoregulatory compounds produced during the year (Fierer and Schimel 2003; Unger and others 2010). Pre-incubation allowed for this pulse to pass and the microbial community to equilibrate before extraction (Blazewicz and others 2014; Slessarev and others 2020). (While field-moist soils are preferable, due to restrictions on export it was necessary to use dried soils. As the soils are clay-rich (Jones and others 2019; Kaiser and others 2015), collected from a semi-arid region in a dry season (Fierer and others 2003; Zornoza and others 2009, 2007), and from the soil's surface (Blazewicz and others 2014; Slessarev and others 2020), we assumed a negligible impact of drying and re-wetting. See ''Methods'' in supplement for more details on this determination.) At the pre-incubation's conclusion, we extracted each sample for TEOC, TEN, and the TEOC and TEN associated with microbial biomass using chloroform-fumigation extraction (Vance and others 1987) with a 0.05 M K_2SO_4 solution (Haney and others 2001) (see ''Methods'' in supplement for solution selection process). We analyzed each liquid extract with a Shimadzu Total Organic Carbon analyzer and standardized outputs of TEOC, TEN, and microbial biomass extractable C and N to concentration in mg/kg dry soil.

By multiplying these values by soil bulk density at each structural element, then by 5 cm sampling depth, we calculated concentration *per unit area* (kg/m^2). We used data on surface soil bulk density in KLEE collected in 2011 (by Brody and Petipas) using metal rings to a fixed depth of 3 cm (Petipas and Brody 2014). We compared average bulk density between the grassland matrix and termite mounds. Two additional datasets (Sitters and others 2020; unpublished historical KLEE data 2015) allowed us to extrapolate bulk density for the grassland matrix and under *A. drepanolobium* tree canopies and compare across herbivore treatments. (See ''Bulk Density'' in supplement for sampling details and extrapolation.)

Table 1. Full Summary Results, Linear Mixed Effects Model of Microbial Respiration Rate (lg CO2–C/g soil/day) with Fixed Effects of Herbivore Treatment, Structural Element, Sampling Year, and Their Interactions

	Treatment, landscape element across sampling years	
Predictors	**Estimates**	***p***
Intercept	– 3.62 *** (– 3.77–– 3.46)	< **0.001**
Wild	– 0.15 (– 0.33–0.03)	0.113
Cattle	0.07 (– 0.11–0.25)	0.422
None (no herbivores)	0.05 (– 0.13–0.23)	0.595
Tree canopy	0.20 * (0.04–0.37)	**0.015**
Termite mound	0.12 (– 0.05–0.28)	0.155
2016	– 0.17 *(– 0.33–– 0.01)	**0.034**
2018	– 0.05 (– 0.22–0.11)	0.508
Wild * tree canopy	– 0.04 (– 0.19–0.10)	0.556
Cattle * tree canopy	0.03 (– 0.11–0.17)	0.672
None * tree canopy	– 0.07 (– 0.21–0.07)	0.331
Wild * termite mound	– 0.20 ** (– 0.34–– 0.05)	**0.007**
Cattle * termite mound	– 0.02 (– 0.16–0.12)	0.773
None * terminate mound	– 0.07 (– 0.22–0.07)	0.329
Wild * 2016	0.24** (0.06–0.43)	**0.010**
Cattel * 2016	0.02 (– 0.17–0.20)	0.855
None * 2016	0.09 (– 0.10–0.27)	0.362

All models conducted on log-transformed data. Bolded p values are significant to the p = 0.05 level.

Pool Sizes of Extractable Organic Carbon, Total Extractable Nitrogen, Microbial Biomass

To calculate pool sizes of TEOC, TEN, and microbial biomass (kg/ha) associated with each structural element within each treatment, we used our calculated estimates of the proportional area of each structural element per treatment (Charles and others 2021; Sitters and others 2020). We multiplied TEOC, TEN, and microbial biomass concentration (kg/m^2) by the average area (m^2) of the structural element it was sampled from within each treatment. To estimate total average stocks of TEOC, TEN, and microbial biomass per herbivore treatment (kg), we summed the pools for each structural element within each treatment and divided by plot size (4 ha).

Statistical Analysis

We did all analyses using R (version 4.0.4, R Core Team 2021) in RStudio. We deployed linear mixed effects models (lmerTest package; Kuznetsova and others 2017) to ask how the experimental manipulation of the large herbivore community, identity of structural element, and (when relevant or significant) their interactions affected each response variable. Reference level for fixed effect of treatment was ''wild and cattle''; for structural element, ''grassland matrix.'' For all models, we included KLEE replicate (three levels) as a random intercept to account for unmeasured environmental variance across blocks. We assessed residual diagnostics using the DHARMa package (Hartig 2022). We assessed the final models' null hypotheses with omnibus F-tests to identify systemic effects of fixed factors and conducted a priori-identified pairwise comparisons (Tukey adjustment for multiple comparisons) (emmeans package; Lenth 2022) (see supplement for model selection and reporting).

Soil Microbial Carbon Mineralization

To assess differences in microbial soil carbon mineralization, we used the fixed factors of year, herbivore treatment, and structural element on log-transformed CO_2-C production rate, with treatment (four levels), feature (three), year of sample collection (three), and the interaction effects of all three. We also modeled each year's incubation separately, with treatment and structural element as fixed effects.

TEOC, TEN, Microbial Biomass Concentration; Within-Treatment and Treatment-Level Pools

We compared log-transformed soil TEOC, TEN, and microbial biomass concentration per unit area

Table 2. Full Summary Results of Three Linear Mixed Effects Models of Microbial Respiration Rate (lg CO2-C/g soil/day) with Fixed Effects of Herbivore Treatment, Structural Element, and Their Interaction (if significant to the $p = 0.05$ level)

Predictors	2015		2016		2018	
	Estimates	p	Estimates	p	Estimates	p
Intercept	− 3.60 *** (− 3.80–− 3.39)	< **0.001**	− 3.76 *** (− 3.83–− 3.69)	< **0.001**	− 3.70 ***(− 3.81–− 3.59)	< **0.001**
Wild	− 0.23 * (− 0.44–− 0.01)	**0.040**	0.02 (− 0.06–0.10)	0.613	0.25 **(0.10–0.41)	**0.001**
Cattle	0.08(− 0.14–0.29)	0.480	0.09 *(0.02–0.17)	**0.014**	0.04(− 0.12–0.19)	0.636
None (no herbivores)	0.00(− 0.21–0.22)	0.989	0.09 * (0.01–0.16)	**0.026**	0.27 *** (0.11–0.42)	**0.001**
Tree canopy	0.18(− 0.00–0.37)	0.054	0.13 ***(0.07–0.20)	< **0.001**	0.48 ***(0.32–0.64)	< **0.001**
Termite mound	0.05 (− 0.14–0.23)	0.622	− 0.11 ***(− 0.18–− 0.05)	**0.001**	0.26 **(0.10–0.41)	**0.001**
Wild * tree canopy					− 0.18 (− 0.40–0.04)	0.116
Cattle * tree canopy					0.03(− 0.19–0.25)	0.772
None * tree canopy					− 0.07 (− 0.29–0.15)	0.556
Wild * termite mound					− 0.43 ***(− 0.65–− 0.21)	< **0.001**
Cattle * termite mound					− 0.02(− 0.24–0.20)	0.848
None * termite mound					− 0.13 (− 0.35–0.09)	0.238
Random effects						
σ^2	0.16		0.07		0.09	
τ00	0.00 $_{\text{replicate}}$		0.00 $_{\text{replicate}}$		0.00 $_{\text{replicate}}$	
ICC	0.03		0.02		0.01	
N	3 $_{\text{replicate}}$		10 $_{\text{replicate}}$		10 $_{\text{replicate}}$	
Observations	108		353		354	
Marginal R^2 / Conditional R^2	0.105 / 0.131		0.145 / 0.166		0.322 / 0.326	

$^{*}p < 0.05$, $^{**}p < 0\ 01$, $^{***}p < 0.001$

One model per year to disentangle effects of ambient weather from effects of herbivore treatment and structure. All models conducted on log-transformed data. Bolded p values are significant to the p = 0.05 level.

across structural element and treatment, with element and treatment as fixed effects. We compared pool sizes (log-transformed) for each structural element, within each treatment, with treatment and structural element as fixed effects; we also compared *total* plot-level stocks/pool sizes (log-transformed) across treatments with treatment as the sole fixed effect.

Microbial C:N at Sampling Locations

As a proxy for microbial community composition, we compared the ratio of microbial carbon to nitrogen (microbial biomass C:N); higher C:N indicates a relatively higher proportion of fungi (Wang and others 2019). We removed biologically infeasible outliers (Cleveland and Liptzin, 2007) and modeled log-transformed C:N with structural element and treatment as fixed effects.

RESULTS

Structural element had the strongest and most consistent effects on carbon cycling dynamics, frequently interacting with sampling year (for example, drought conditions) and herbivore treatment. While sampling year and herbivore treatment also drove effects on carbon cycling dynamics, the effects of herbivore treatment on plot-scale *pools* of extractable, labile carbon and nitrogen were faint, if undetectable, due to its interaction with structural element.

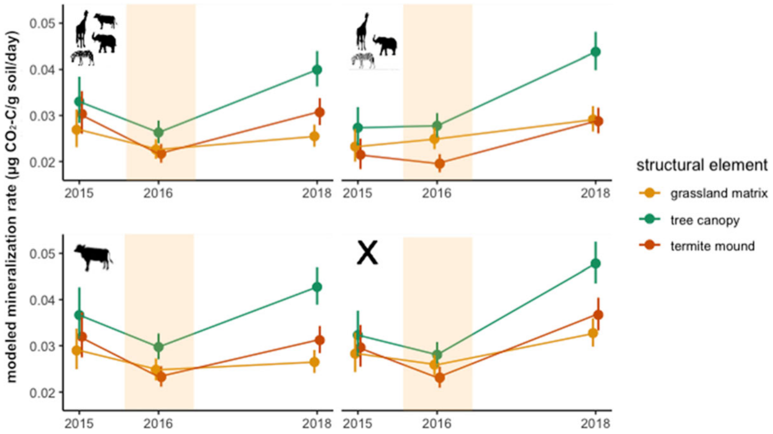


Figure 2. Predicted rates of soil microbial respiration rate (a proxy for carbon mineralization) for each structural element, within each herbivore treatment, across the three sampling years. 2016, the drought year, is shaded in yellow for each treatment. Herbivore treatments are (left to right, top row) ''wild + cattle,'' ''wild,'' and (left to right, bottom row) ''cattle,'' ''none.'' Interactions between sampling year and structural element are evident by crossed lines, and inconsistency of these interactions indicate interactions with herbivore treatment (for example, ''wild'' treatment). Whiskers indicate the 95% confidence interval on model-predicted means. Model conducted on log-transformed data, but visualized untransformed.

Microbial Soil Carbon Mineralization Rate

Microbial soil carbon mineralization varied significantly by year ($F_{2,515} = 99.62$, $p < 0.001$), herbivore treatment ($F_{3,782} = 7.65$, $p < 0.001$), and structural element ($F_{2,782} = 42.88$, $p < 0.001$). Interestingly, mineralization also varied significantly by the interaction between sampling year and treatment ($F_{6,782} = 3.39$, $p = 0.003$) and between sampling year and structural element ($F_{4,782} = 8.90$, $p < 0.001$) (Table 1; Figure S2), indicating that ambient weather likely moderated whether treatment *or* structural element drove interannual differences (Figure 2). Soils collected in 2016 (the first year of the drought) had the lowest rate of mineralization, 15% lower than in 2015 and 27% lower than 2018 (extremely wet year post-drought).

For example, in 2015, before the drought, herbivore treatment drove differences in rates of microbial carbon mineralization ($F_{3,100} = 2.93$, $p = 0.04$) (Table 2) (and not structural element; $F_{2,100} = 2.06$, $p = 0.13$). In pairwise comparisons, soils collected from plots with only wild herbivores (''Wild'') respired slowest, 26% slower than soils from plots where only cattle were present (''Cattle''), which respired fastest ($p = 0.03$). No other pairwise comparisons across treatment or feature were significant (Figure 2; Figure S2).

In 2016, during the drought, both herbivore treatment ($F_{3,338} = 3.01$, $p = 0.03$) *and* structural element ($F_{2,\ 339} = 26.16$, $p < 0.001$) drove differences in microbial carbon mineralization (Table 2) (though pairwise comparisons revealed no significant differences between individual pairs of treatments). Across all treatments, under-tree soils respired 12% faster than grassland matrix soils ($p < 0.001$) and 22% faster than termite mound soils ($p < 0.001$). Grassland matrix soils respired 11% faster than termite mound soils ($p = 0.003$) (Figure 2; Figure S2).

In 2018, after the drought, herbivore treatment ($F_{3,333} = 7.66$, $p < 0.001$), structural element ($F_{2,\ 333} = 63.21$, $p < 0.001$), and their interaction ($F_{6,\ 333} = 3.16$, $p = 0.005$) drove differences in carbon mineralization (Table 2). Pairwise comparisons revealed that soils from plots that had no large herbivores present (''None'') respired 14% faster than those from ''Wild'' plots ($p = 0.006$), 15% faster than those from ''Cattle'' plots ($p = 0.003$), and 18% faster than those from plots where wild large herbivores and cattle co-occur (''Wild and cattle'') ($p < 0.001$). However, across all herbivore treatments, soils under trees again had the highest rate of microbial carbon mineralization: 27% faster than termite mound soils ($p < 0.001$) and 35% faster than grassland matrix soils ($p < 0.001$). Interestingly, in 2018, the trend between grassland matrix and termite mound soils reversed from that in 2016. Post-drought, termite mound soils respired 11% faster than grassland matrix soils ($p = 0.015$) (Figure 2; Figure S2).

Table 3. Full Summary Results of Linear Mixed Effects Models Examining Fixed Effects of Herbivore Treatment, Structural Element on Concentration per Unit Area of Soil TEOC, TEN, MBC, and MBN

	TEOC kg/mg^2		TEN kg/mg^2		MBC kg/mg^2		MBN kg/mg^2	
Predictors	**Estimates**	***p***	**Estimates**	***p***	**Estimates**	***p***	**Estimates**	***p***
(Intercept)	− 6.16 (− 6.30–6.02)	< **0.001**	− 6.45 (− 6.64–6.26)	< **0.001**	− 4.08 (− 4.25–3.92)	< **0.001**	− 6.22 (− 6.48–− 5.97)	< **0.001**
Wildlife only	0.07 (− 0.07–0.21)	0.320	0.12 (− 0.06–0.31)	0.184	0.00 − 0.15–0.16)	0.950	− 0.01 (− 0.23–0.21)	0.946
Cattle only	0.10 (− 0.04–024)	0.153	0.21 (0.03–0.39)	**0.025**	0.11 (− 0.04–0.26)	0.143	0.09 (− 0.13–0.31)	0.431
No herbivores	0.19 (0.05–0.33)	**0.008**	0.31 (0.13–0.50)	**0.001**	0.02 (− 0.13–0.17)	0.798	0.02 (− 0.20–025)	0.841
Under canopy	0.14 (0.02–0.26)	**0.027**	0.68 (0.52–0.84)	< **0.001**	0.28 (0.15 0.41)	< 0.001	0.29 (0.10–0.48)	**0.003**
Termite mound	0.24 (0.12–0.36)	< **0.001**	0.27 (0.11–0.43)	**0.001**	− 0.50 (− 0.63–0.36)	< 0,001	− 0.35 (− 0.55–0.16)	< **0.001**
Random effects								
σ^2	0.22		0.38		0.26		0.54	
τ00	0.00$_{\text{repl}}$		0.01$_{\text{repl}}$		0.0$_{\text{repl}}$		0–02 $_{\text{repl}}$	
ICC	0.02		0.02		0.03		0.04	
N	3 $_{\text{repl}}$		3 $_{\text{repl}}$		3 $_{\text{repl}}$		3 repl	
Observations	353		353		349		338	
Marginal R^2/conditional R^2	0.058/0.074		0.191/0.299		0.277/0.299		0.109/0.144	

All models conducted on log-transformed data. Bolded p values are significant to the p = 0.05 level.

TEOC, TEN, and Microbial Biomass Concentration Per Unit Area

Structural element was the strongest driver of relative differences in concentration of soil TEOC ($F_{2,345} = 7.49$, $p < 0.001$), TEN ($F_{2,345} = 36.41$, $p < 0.001$), MBC ($F_{2,341} = 67.58$, $p < 0.001$), and MBN ($F_{2,331} = 17.63$, $p < 0.001$) per unit area (Table 3). (Bulk density did not differ by herbivore treatment; nor did it differ between the grassland matrix and under *A. drepanolobium* canopies. The only significant difference was lower bulk density in termite mound soils compared to the other two structural elements. As such, any effects of treatment on TEOC, TEN, and microbial biomass are likely not due to differences in compaction and are instead demonstrative of per unit area volumetric concentration.)

Pairwise comparisons demonstrated that termite mound sites had approximately 25% more TEOC per unit area than grassland matrix sites ($p < 0.001$) (Figure 3), indicating significant enrichment in soil organic carbon on mounds. While there was no significant systemic effect of treatment on TEOC concentration ($F_{3,345} = 2.47$, $p = 0.062$) (Table S2), pairwise comparisons revealed an approximately 20% higher TEOC concentration per unit area in ''None'' plots compared to ''Wild and cattle'' plots ($p = 0.046$). Under-tree sites had the greatest concentration of TEN: approximately 20% higher than termite mound ($p < 0.001$) and 50% higher than grassland matrix sites ($p = 0.002$), and with termite mound sites 28% higher than grassland matrix sites ($p < 0.001$) (Figure 3b). There was also a treatment effect ($F_{3,345} = 4.00$ $p = 0.008$) (Table S3), with 25% greater concentrations of TEN in ''None'' than in ''Wild and cattle'' plots ($p = 0.005$).

Soil microbial biomass carbon ($F_{2,341} = 67.58$, $p < 0.001$) and nitrogen ($F_{2,331} = 17.63$, $p < 0.001$) concentration per unit area were significantly influenced by structural element, but not

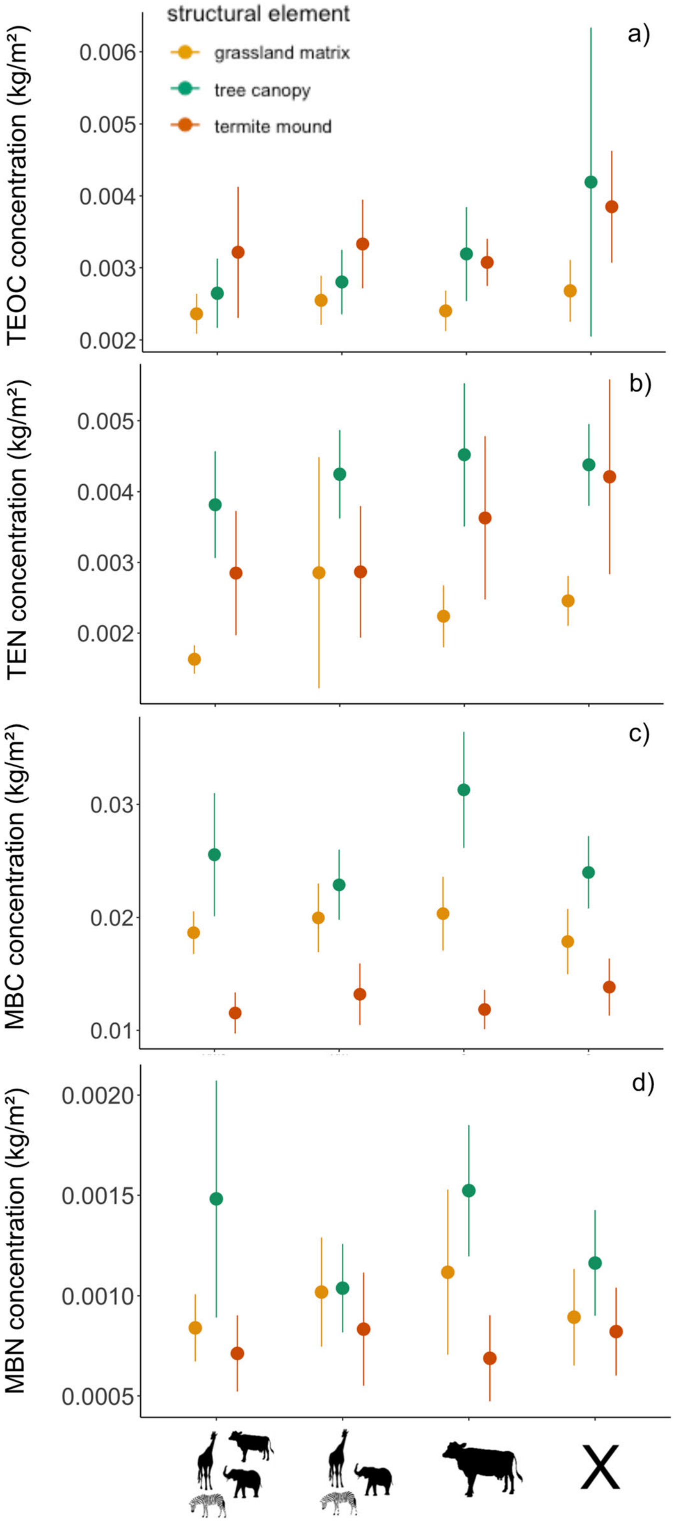


Figure 3. Mean concentration per unit area of: **a** total extractable organic carbon (TEOC), **b** total extractable nitrogen (TEN), **c** microbial biomass carbon (MBC), and **d** microbial biomass nitrogen (MBN) at each landscape feature, within each treatment in KLEE. Herbivore treatments (x-axis) organized as the herbivore types present decrease, from left (''wild + cattle'') to right (''none''). Whiskers indicate one standard error from the mean.

treatment (Table S2). MBC concentration was 26% greater at under-tree sites relative to grassland matrix sites ($p < 0.001$), and 53% relative to termite mound sites ($p < 0.001$); grassland matrix sites themselves had approximately 30% greater concentration of MBC relative to termite mounds ($p < 0.001$) (Figure 3c). Similarly, MBN concentration was 27% greater at under-tree sites relative to grassland matrix sites ($p = 0.017$) and 41% greater than at termite mounds ($p < 0.001$) (Figure 3d) (with grassland matrix again 30% greater than at termite soils ($p = 0.003$)).

Lastly, microbial biomass C:N (not converted to unit area) was significantly impacted by structural element ($F_{2,322} = 8.26$, $p < 0.001$), being lower at termite mounds than under trees ($p = 0.004$) or the grassland matrix ($p < 0.001$) (Figure S3).

Area-weighted TEOC, TEN, and Microbial Biomass Pools at Structural Elements

Once scaled to their proportional area within each herbivore treatment, the relative pool sizes of TEOC, TEN, MBC, and MBN were variably affected by treatment (Table 3). The grassland matrix TEOC pool ($F_{3,114} = 3.57$, $p = 0.016$) was smallest in ''Cattle'' plots: 26% smaller than in ''Wild and cattle'' plots ($p = 0.02$). The under-tree TEOC pool ($F_{3,114} = 4.05$, $p = 0.009$) increased with each experimental herbivore group 'loss': 71% larger TEOC in ''None'' compared to ''Wild and cattle'' plots ($p = 0.009$). There was no difference in the termite mound-associated TEOC pool size across treatments (Figure 4a).

Grassland matrix and termite mound TEN pool size did not differ across herbivore treatments (Table S3). However, the under-tree TEN pool size *increased* with each herbivore group 'loss' ($F_{3,114} = 12.60$, $p < 0.001$), with pairwise comparisons revealing the TEN pool size was 60% larger in ''None'' plots than in ''Wild and cattle'' plots ($p < 0.001$); 61% larger in ''Cattle'' plots than in ''Wild and cattle plots'' ($p < 0.001$); and 33% larger in ''Cattle'' plots than in ''Wild'' plots ($p = 0.02$) (Figure 4b).

The MBC pool in the grassland matrix decreased in size with each herbivore group 'loss' ($F_{3,114} = 3.77$, $p = 0.013$); the only significant pairwise difference was between the most extreme treatments, with a 29% larger pool in ''Wild and cattle'' than in ''None.'' The under-tree MBC pool also differed by treatment ($F_{3,113} = 26.18$, $p < 0.001$) and was by far the largest in ''Cattle'' plots (63% larger than in ''Wild and cattle'' plots, 48% larger than in ''Wild'' plots, and 24% than in ''None'' plots). Again, termite mound-associated MBC pool size did not differ across herbivore treatments (Figure 4c). The grassland matrix MBN pool followed similar patterns, generally decreasing with each herbivore group loss but with no significant differences across treatments. The under-tree MBN pool was (similar to the under-tree MBC pool) largest in the ''Cattle'' plots ($F_{3,111} = 13.27$, $p < 0.001$): 63% larger than in ''Wild and cattle'' plots, 51% larger than in ''Wild'' plots, and 27% larger than in ''None'' plots. The termite mound-associated MBN pool did not differ across treatments (Figure 4d).

Total Pool Size Comparison Across Treatments

Once summed for each treatment, there was no plot-level difference in pool size of TEOC ($F_{3,6} = 1.82$, $p = 0.24$), TEN ($F_{3,6} = 3.71$, $p = 0.081$), MBC ($F_{3,6} = 1.37$, $p = 0.34$), or MBN ($F_{3,6} = 0.92$, $p = 0.49$) across herbivore treatments (Figure 5; Table 4; Table S4). However, given the inherently low sample size of KLEE (n = 3), a power analysis suggests that six KLEE replicates would have revealed a significantly reduced TEN pool in ''Wild and cattle'' plots (supplemental information; Figure S6).

Discussion

Structural element, more than any other variable, influenced labile organic carbon and cycling in this savanna's surface soils. Ultimately, the effect of structural element was also contingent on herbivore treatment and weather. The effects of treatment on structural element-specific, area-scaled pools are unsurprising, given the engineering that different herbivore groups impose on the size and abundance of termite mounds and trees (Charles and others 2021; Pringle 2008) (Figure 1b). There has been little research, however, on how this engineering of the landscape's structural mosaic influences the spatial heterogeneity of its soil carbon (Ferraro and others 2022). Critically, we also demonstrated *interactions* between herbivore treatment and structural element, indicating that consumer group behaviors (selective consumption of nitrogen-rich forage in the grassland matrix; shade-seeking under trees; and so on) may complicate the story of animal influence beyond a mere rearranging of the savanna's mosaic.

Carbon Mineralization: Interacting Effects OF Structural Element and Herbivore Treatment by Year

Despite large interannual variation in rainfall, soils from under tree canopies showed consistently higher rates of carbon mineralization than from other structural elements. However, the positive effect of canopy cover was not significant in 2015; indeed, in 2015 the treatment effect of ''Wild'' was the only significant driver of difference, with lower mineralization rates than the other treatments (Figure 2). A potential explanation for 2015's lack of significant tree canopy effect and presence of significant herbivore treatment effect is that sampling took place shortly after a scheduled cattle grazing event in ''Cattle'' and ''Wild and cattle'' plots. (Sampling in 2016 and 2018 took place weeks after the most recent grazing event.) It is possible that 2015's sampling captured a large, short-term, and positive (though unreplicated) treatment effect driven by fresh inputs of cattle feces and urine (Augustine and McNaughton 2006), leaving ''Wild'' the only treatment without substantial inputs (of excreta or the abundant litter inputs in ''None''). In 2016, however, there was no effect of herbivore treatment on mineralization; highest rates of mineralization occurred in under-tree soils and the lowest in termite mound soils. Faster under-tree mineralization aligns with the expected conditions under leguminous trees in sub-Saharan savannas—high litterfall, high relative moisture and shade, and enhanced primary productivity and nitrogen fixation (Belsky and others 1993, 1989).

In 2018, structural element was again the primary driver of differences in mineralization. Soils from under trees had faster mineralization rates than those from the grassland matrix or termite mounds, across treatments, likely due to enrichment in organic carbon and nitrogen. Grassland matrix soils had slower mineralization rates than termite mounds (Figure 2), a switch from 2016 that could be drought related: mounds serve as relatively edaphically stable refugia for plants in dry conditions (Bonachela and others 2015). We hypothesize that mounds may *also* sustain microbial communities during droughts, allowing them to rebound quickly when conditions improve. Interestingly, herbivore treatment also influenced

Table 4. Full Summary Results of Linear Mixed Effects Models Examining Fixed Effect of Herbivore Treatment on Total Plot-scale Pool Size of Soil TEOC, TEN, MBC, and MBN

	Total TEOC kg/ha		Total TEN kg/ha		Total MBC kg/ha		Total MBN kg/ha	
Predictors	Estimates	*p*	Estimates	*p*	Estimates	*p*	Estimates	*P*
(Intercept)	24.31*** (15.60–33.03)	< **0.001**	20.48 *** (8.70–32.25)	**0.005**	197.61 *** (137.93–257.28)	< **0.001**	24.36 *** (13.60–35.12)	**0.001**
Wildlife only	2.06 (− 7.42–11.54)	0.614	11.97** (1.43–22.50)	**0.032**	8.90 (− 54.57–72.37)	0.743	2.90 (− 9.37–15.16)	0.584
Cattle only	2.99 (− 6.49–12.47)	0.469	11.23** (0.69–21.77)	**0.040**	47.01 (− 16.45–110.48)	0.120	7.95 (− 4.32–20.22)	0.164
No herbivores	8.63 * (− 0.S5–18.11)	0.067	11.94** (1.40–22.48)	**0.032**	4.99 (− 58.48–68.46)	0.854	1.84 (− 10.43–14.10)	0.727
Random effects								
σ^2	22.51		27.83		1009.13		37.69	
τ00	15.57_{repl}		41.62_{repl}		775.15_{repl}		2031_{repl}	
ICC	0.41		0.60		0.43		0.35	
N	3_{repl}		3_{repl}		3_{repl}		3_{repl}	
Observations	12		12		12		12	
Marginal R^2/conditional R^2	0.226 / 0.543	0.288/ 0.715	0.288/0.715		0.175 /0.533		0.140 / 0.441	

$^{*}p < 0.1$, $^{**}p < 0.05$, $^{***}p < 0.01$

All models conducted on log-transformed data. Bolded p values are significant to the $p = 0.1$ level, given the inherently low sample size of three replicates in KLEE.

mineralization in 2018, which was fastest in ''None'' plots. We propose that high post-drought primary productivity in ''None'' plots increased litter deposition; this, and increased soil moisture, would stimulate microbial biomass and activity relative to plots where increased biomass was removed by consumers (Munjonji and others 2020).

Soil Concentrations: Primary Effects of Structural Element

Concentrations of labile TEOC, TEN, and microbial biomass per unit area were primarily mediated by structural element, except for TEN which was *also* negatively affected by increased herbivore group presence (Figure 3, Figure S7). This interacting effect is perhaps due to herbivores' selective consumption of nitrogen-rich forage, resulting in higher C:N in the litter input pool (Ritchie and others 1998), or drought reducing the quantity of inputs in the year prior to sample collection (Augustine and McNaughton 2006; Piñeiro and others 2010).

Termite mounds had higher TEOC and TEN concentrations than the grassland matrix (Brody and others 2010), likely due to termites' importation of organic detritus (Kihara and others 2015), which is broken down and digested into stable aggregates (Jouquet and others 2016; Kihara and others 2015; Six and others 2002; Vesala and others 2017). TEN enrichment on mounds is likely also driven by nitrogen-fixation in termites' gut microbiomes (Sapountzis and others 2016), and the fungal combs that termites cultivate inside the mounds (Nobre and others 2011). TEN concentration was largest, however, beneath *A. drepanolobium* canopies, logical given the tree's mutualism with nitrogen fixing, root-associated bacteria (de Faria and others 1989; Fox-Dobbs and others 2010). Microbial biomass concentration was also elevated under tree canopies, likely by dynamic sources of nutrients from litterfall and fixation (Belsky and others 1989; Mlambo and others 2007).

The relatively slow mineralization we observed from termite mound soils in 2016 was explained by significantly lower concentration of microbial biomass. In Australian vertisols, microbial biomass is positively correlated with clay content (Holt 1996); termite mounds in KLEE have lower clay content than the surrounding soils (Brody and others 2010). A high density of termites may also locally limit litter availability for microbes (Holt 1996), and some fungus-farming termites express antimicrobial peptides in their saliva (Lamberty and others 2001). Termite mound samples also had lower microbial C:N, indicating a surface community higher in bacteria relative to non-mound soils, complementing Baker and others 2020 (which found that bacterial richness and diversity was higher on mounds than off, a divergence likely driven by their higher soil pH (Figure S4) (Baker and others 2020; Lauber and others 2008; Muvengwi and Witkowski 2020).

Area-Weighted Pools at Each Structural Element, Within Herbivore Treatments

Structural element-specific TEOC and TEN stocks were largely linked to the relative area of each structural element in each herbivore treatment (Figure 1c). As the largest relative area of grassland matrix is in the ''Wild and cattle'' plots, those plots have the largest grassland matrix-associated TEOC pool and the smallest tree canopy-associated TEOC pool (Figure 4a). Conversely, the tree canopy-associated TEN pool grew significantly with herbivore ''loss,'' corresponding with *A. drepanolobium*'s increasing proportional area. Interestingly, the size of the grassland matrix-associated TEN pool did not increase with increasing grassland matrix coverage (Figure 4b). This lack of effect is likely due to the countervailing effect of treatment on TEN *concentration*, which was significantly lower in the ''Wild and cattle'' plots compared to ''None'' (Figure 3). The behavior of consumers (for example, selecting higher-quality forage) may drive lower-quality litter input, such that an increase in grassland matrix area does not correlate to an increase in its TEN pool. The combined result showcases the interacting, even antagonistic effects of herbivore treatment and structural element.

Interestingly, the tree canopy-associated microbial biomass pool in ''Cattle'' plots was the largest of all treatments. It is possible that 3–4 × yearly cattle grazing increases microbial biomass under trees; greater tree cover reduces organic matter erosion from exposure, and periodically removing grass relieves intense competition for limited resources, enhancing tree growth and enhancing organic litter inputs to the soils beneath them (Riginos and others 2012; Rotich and others 2018). In South African savannas, similar rotational grazing stimulates microbial biomass and activity due to the cattle-derived nutrient subsidies (dung, urine) combined with a resting period post-grazing, which fuels vegetation recovery and organic inputs (Amelung and others 2017; Rotich and others 2018). Periodic cattle grazing, and prolonged periods between grazing events, could therefore contribute to enhanced microbial biomass (Figure 4c, d) and activity (Figure 2, middle panel) beneath *A. drepanolobium* in ''Cattle'' plots.

These data demonstrate that small-scale structural variability has a significant effect on both soil carbon mineralization and organic carbon (and associated) pools, with implications for more widespread rangeland carbon dynamics. Tree canopy coverage expansion in rangelands that have experienced large herbivore loss may result in larger stocks of labile organic carbon; but it is also possible for such gains to come with concomitant increases in carbon mineralization, loss of sequestered soil carbon, or less persistent carbon storage (Dass and others 2018; Kristensen and others 2022; Malhi and others 2022; Holdo and others 2009; Sandhage-Hofmann and others 2021). Indeed, 2016 mineralization rates scaled to the area of each herbivore treatment (as done for pools) indicate that increased tree cover in ''None'' compared to ''Wild and cattle'' (Figure 1c) results in a significant *net* increase in potential soil carbon mineralization (Figure S8). While these scaled data are not reflective of in situ emissions, the exercise demonstrates possibly compensatory increases in soil carbon mineralization as canopy cover increases.

Effects of Large-Bodied Consumer Community Composition on Net Carbon Cycling, Stocks

Contrary to studies analyzing *total* carbon and nitrogen in KLEE (Sitters and others 2020), *labile* carbon stocks in the surface soil appear to be unaffected by herbivore community composition. Rather, we observed that large herbivores' biggest effect on net labile carbon may be in engineering cover and abundance of distinct structural elements (Figure 1c), shifting the mosaic of labile carbon dynamics depending on herbivore community composition.

While our net results seem counter to those from Sitters and others (2020), they are instead complementary. Sitters and others (2020) observed the total carbon pool, which shrinks in plots where cattle graze and grows in those where elephants knock over trees. Our study indicates that the same structural engineering by elephants merely increases within-plot heterogeneity of labile carbon and nitrogen pools; this is likely because while

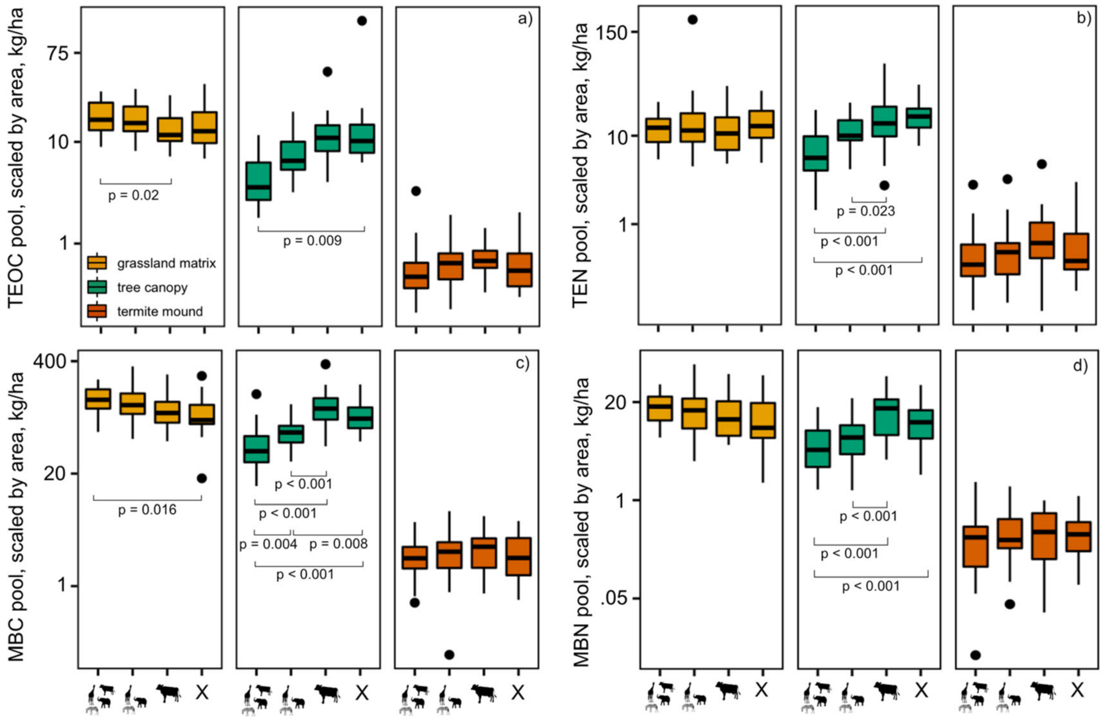


Figure 4. Boxplots of area-scaled pools for **a** non-microbial soil TEOC, **b** non-microbial soil TEN, **c** MBC, and **d** MBN associated with each structural element, within each herbivore treatment. Response variables are natural log-transformed for ease of visualizing comparisons between treatments (see supplement for raw data; Figure S5). Significant pairwise comparisons are indicated with brackets and the associated p value. Herbivore types present (all x-axes) decrease from left to right.

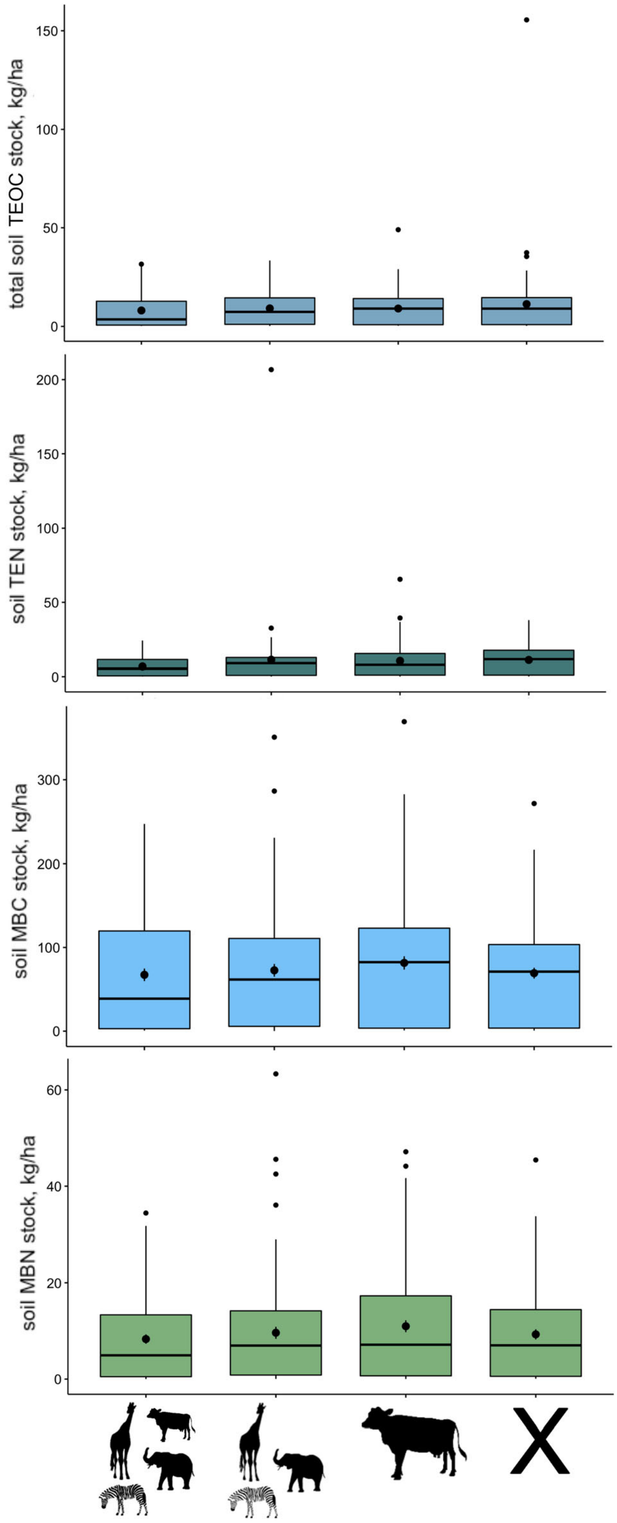


Figure 5. Boxplots of total pool sizes for (top to bottom) non-microbial soil TEOC, non-microbial soil TEN, MBC, and MBN in each of the four herbivore treatments. Means (including error bars showing one standard error from the mean) are indicated inside boxplots with large black dots. Herbivory types present, x-axis, decreases from left to right.

knocking over trees increases *total* carbon inputs to the soil, it locally reduces organic carbon and nitrogen inputs, which are enhanced by the trees when standing (Sitters and others 2020, 2013). Our combined results showcase the complexities of the carbon cycle's underpinnings. Measuring a fraction of a system's carbon cycle is not sufficient to fully characterize its response to changes in large herbivore community composition (Forbes and others 2019), particularly where these consumers engineer fine-scale structural heterogeneity.

CONCLUSIONS

Changes in Structure Increase Biogeochemical Heterogeneity

The most striking observations from this study are that *a) labile carbon dynamics differ significantly across the savanna's biogeochemically distinct structural elements, such that b) the effects of large herbivore community composition on aboveground structure indirectly mediate the system's soil biogeochemical heterogeneity.* Interestingly, labile carbon accrual and its mineralization by soil microbial activity appear to at least partially compensate for each other at the landscape scale, with increased microbial biomass and activity under trees muting effects of increased tree canopy coverage on the labile soil carbon pool as large herbivores are excluded. Ambient weather creates an additional scale of heterogeneity through time, underscoring that the effects of consumer community composition or structural element identity on labile carbon mineralization are not certain across climatic conditions (and even that, like for vegetation, small-scale heterogeneity may contribute to recovery in soil carbon dynamics after drought (Petipas and others 2017)).

It is critically important to acknowledge the multiple, multi-scale drivers of heterogeneity in soil carbon dynamics (Ettema and Wardle 2002). Small-scale heterogeneity is an understudied, critical aspect of functions like carbon cycling, which are traditionally characterized at the scale of landscapes or entire ecosystems (Ferraro and others 2022). Changes to small-scale heterogeneity can generate diffusion gradients and new lateral transfers of nutrients and energy (Turner and Chapin III 2005), shifting our conceptualization of a landscape's nutrient pools from a static image to a cacophony, teeming with flows. Our study shows that ecologists must consider the drivers of change in a landscape's structural heterogeneity (for example, drought, defaunation, land use change), given the subsequent effects on biogeochemical heterogeneity. With the ongoing and interacting threats of climate change, land use change, and biodiversity loss in this savanna, it is critical to include soil carbon heterogeneity in our assessments of its soil carbon dynamics.

FUNDING

U.S. Fish and Wildlife Service,98210-0-G563, National Geographic Society, 4691-91, 9106-12,9783-15, Division of Environmental Biology, 1720003, Directorate for Biological Sciences, 03-16402, 08-16453, 12-56004, 12-56034, 97-07477, National Science Foundation Graduate Research Fellowship Program, 165114.

OPEN ACCESS

DATA AVAILABILITY

Data from this study are available at the public-facing project GitHub repository (https://github.com/elizabethforbes/KLEEsoils_project), and at Zenodo. Data have been submitted to Dryad as an additional online repository and can be found at.

REFERENCES

Amelung W, Kotze E, Oomen RJ, Preez CC. 2017. Soil microbial communities in different rangeland management systems of a sandy savanna and clayey grassland ecosystem. South Africa. Nutr. Cycl. Agroecosyst. 107:227–245. https://doi.org/10.1007/s10705-017-9832-3.

Asner GP, Levick SR. 2012. Landscape-scale effects of herbivores on treefall in African savannas. Ecol. Lett. 15:1211–1217. https://doi.org/10.1111/j.1461-0248.2012.01842.x.

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. https://doi.org/10.1007/sl0021-005-0020-y.

Baker CCM, Vardaro JAC, Doak DF, Pansu J, Puissant J, Pringle RM, Tarnita CE. 2020. Spatial patterning of soil microbial communities created by fungus-farming termites. Mol Ecol 29:4487–4501. https://doi.org/10.1111/mec.15585.

Bekker MF, Malanson GP. 2008. Linear forest patterns in subalpine environments. Prog. Phys. Geogr. 32:635–653. https://doi.org/10.1177/0309133308101384.

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. J. Appl. Ecol. 26:1005–1024.

Belsky AJ, Mwonga SM, Duxbury JM. 1993. Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. Agrofor. Syst. 24:1–20. https://doi.org/10.1007/BF00705265.

Biederbeck VO, Janzen HH, Campbell CA, Zentner RP. 1994. Labile soil organic matter as influenced by cropping practices in an arid environment. Soil Biol. Biochem. 26:1647–1656. https://doi.org/10.1016/0038-0717(94)90317-4.

Blazewicz SJ, Schwartz E, Firestone MK. 2014. Growth and death of bacteria and fungi underlie rainfall-induced carbon dioxide pulses from seasonally dried soil. Ecology 95:1162–1172. https://doi.org/10.1890/13-1031.1.

Bonachela JA, Pringle Robert M, Sheffer E, Coverdale TC, Guyton JA, Caylor KK, Levin SA, Tarnita CE. 2015. Termite mounds can increase the robustness of dryland ecosystems to climate change. Science 347:651–655.

Brody AK, Palmer TM, Fox-Dobbs K, Doak DF. 2010. Termites, vertebrate herbivores, and the fruiting success of Acacia drepanolobium. Ecology 91:399–407.

Bünemann EK, Bongiorno G, Bai Z, Creamer RE, De Deyn G, De Goede R, Fleskens L, Geissen V, Kuyper TW, Mäder P, Pulleman M, Sukkel W, Van Groenigen JW, Brussaard L. 2018. Soil quality – A critical review. Soil Biol. Biochem. 120:105–125. https://doi.org/10.1016/j.soilbio.2018.01.030.

Charles GK, Riginos C, Veblen KE, Kimuyu DM, Young TP. 2021. Termite mound cover and abundance respond to herbivore–mediated biotic changes in a Kenyan savanna. Ecol. Evol. 11:7226–7238. https://doi.org/10.1002/ece3.7445.

Cleveland CC, Liptzin D. 2007. C:N: P stoichiometry in soil: Is there a ‘‘Redfield ratio’’ for the microbial biomass? Biogeochemistry 85:235–252. https://doi.org/10.1007/s10533-007-9132-0.

Crego RD, Ogutu JO, Wells HBM, Ojwang GO, Martins DJ, Leimgruber P, Stabach JA. 2020. Spatiotemporal dynamics of wild herbivore species richness and occupancy across a savannah rangeland: implications for conservation. Biol. Conserv. 242:108436. https://doi.org/10.1016/j.biocon.2020.108436.

Dass P, Houlton BZ, Wang Y, Warlind D. 2018. Grasslands may be more reliable carbon sinks than forests in California. Environ. Res. Lett. 13:074027. https://doi.org/10.1088/1748-9326/aacb39.

De Brito GS, Bautista S, López-Poma R, Pivello VR. 2019. Labile soil organic carbon loss in response to land conversion in the Brazilian woodland savanna (cerradão). Biogeochemistry 144:31–46. https://doi.org/10.1007/s10533-019-00570-9.

de Faria SM, Lewis GP, Sprent JI, Sutherland JM. 1989. Occurrence of nodulation in the Leguminosae. New Phytol. 111:607–619.

de Jager M, van de Koppel J, Weerman EJ, Weissing FJ. 2020. Patterning in mussel beds explained by the interplay of multilevel selection and spatial self-organization. Ecol Evol Front. https://doi.org/10.3389/fevo.2020.00007.

Deng L, Peng C, Kim D, Li J, Liu Y, Hai X, Liu Q, Huang C, Shangguan Z, Kuzyakov Y. 2021. Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. Earth-Sci. Rev. 214:103501. https://doi.org/10.1016/j.earscirev.2020.103501.

Ettema CH, Wardle DA. 2002. Spatial soil ecology. Trends Ecol. Evol. 17:177–183. https://doi.org/10.1016/S0169-5347(02)02496-5.

Ferraro KM, Schmitz OJ, McCary MA. 2022. Effects of ungulate density and sociality on landscape heterogeneity: a mechanistic modeling approach. Ecography 2022:1–16. https://doi.org/10.1111/ecog.06039.

Fierer N, Schimel JP. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Sci. Soc. Am. J. 67:798–805. https://doi.org/10.2136/sssaj2003.7980.

Fierer N, Schimel JP, Holden PA. 2003. Influence of Drying-Rewetting Frequency on Soil Bacterial Community Structure. Microb. Ecol. 45:63–71. https://doi.org/10.1007/s00248-002-1007-2.

Folorunso OA, Ohu JO, Adeniji FA. 1988. The role of soil spatial variability investigation in the management of the Chad Basin vertisols of N.E. Nigeria. Soil Technol. 1:149–156.

Forbes ES, Cushman JH, Burkepile DE, Young TP, Klope M, Young HS. 2019. Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. Funct. Ecol. 33:1597–1610. https://doi.org/10.1111/1365-2435.13376.

Fox-Dobbs K, Doak DF, Brody AK, Palmer TM. 2010. Termites create spatial structure and govern ecosystem function by affecting N2 fixation in an East African savanna. Ecology 91:1296–1307.

Gichangi EM, Njarui DMG, Gatheru M, Magiroi KWN, Ghimire SR. 2016. Effects of Brachiaria grasses on soil microbial biomass carbon, nitrogen and phosphorus in soils of the semi arid tropics of Kenya. Trop. Subtrop. Agroecosyst. 19:193–203.

Haney RL, Franzluebbers AJ, Hons FM, Hossner LR, Zuberer DA. 2001. Molar concentration of K2SO4 and soil pH affect estimation of extractable C with chloroform fumigation–extraction. Soil Biol. Biochem. 33:1501–1507. https://doi.org/10.1016/S0038-0717(01)00065-7.

Hartig, F., 2022. DHARMa: Residual diagnostics for hierarchical (Multi-Level / Mixed) Regression Models.

Hessburg PF, Miller CL, Parks SA, Povak NA, Taylor AH, Higuera PE, Prichard SJ, NorthCollins MPBM, HurteauLarson MDAJ, Allen CD, Stephens SL, Rivera-Huerta H, Stevens-Rumann CS, Daniels LD, Gedalof Z, Gray RW, Kane VR, Churchill DJ, Hagmann RK, Spies TA, Cansler CA, Belote RT, Veblen TT, Battaglia MA, Hoffman C, Skinner CN, Safford HD, Salter RB. 2019. Climate, environment, and disturbance history govern resilience of Western North American forests. Ecol Evol Front. https://doi.org/10.3389/fevo.2019.00239.

Holdo RM, Mack MC. 2014. Functional attributes of savanna soils: contrasting effects of tree canopies and herbivores on bulk density, nutrients and moisture dynamics. J. Ecol. 102:1171–1182. https://doi.org/10.1111/1365-2745.12290.

Holdo RM, Sinclair ARE, Dobson AP, Metzger KL, Bolker BM, Ritchie ME, Holt RD. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem carbon. PLoS Biol. 7:e1000210. https://doi.org/10.1371/journal.pbio.1000210.

Holt JA. 1996. Mound-building termites and soil microbial biomass: an interaction influencing termite abundance. Insect Socieaux 434:427–434.

Jones AR, Gupta VVSR, Buckley S, Brackin R, Schmidt S, Dalal RC. 2019. Drying and rewetting effects on organic matter mineralisation of contrasting soils after 36 years of storage. Geoderma 342:12–19. https://doi.org/10.1016/j.geoderma.2019.01.053.

Jouquet P, Bottinelli N, Shanbhag RR, Bourguignon T. 2016. Termites: The neglected soil engineers of tropical soils. Soil Sci. 181:157–165. https://doi.org/10.1097/SS.0000000000000119.

Kaiser M, Kleber M, Berhe AA. 2015. How air-drying and rewetting modify soil organic matter characteristics: An assessment to improve data interpretation and inference. Soil Biol. Biochem. 80:324–340. https://doi.org/10.1016/j.soilbio.2014.10.018.

Kihara J, Martius C, Bationo A. 2015. Crop residue disappearance and macrofauna activity in sub-humid western Kenya. Nutr. Cycl. Agroecosyst. 102:101–111. https://doi.org/10.1007/s10705-014-9649-2.

Kimuyu DM, Veblen KE, Riginos C, Chira RM, Githaiga JM, Young TP. 2017. Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores. Ecol. Appl. 27:786–798. https://doi.org/10.1002/eap.1482.

Kristensen JA, Svenning JC, Georgiou K, Malhi Y. 2022. Can large herbivores enhance ecosystem carbon persistence? Trends Ecol. Evol. 37:117–128. https://doi.org/10.1016/j.tree.2021.09.006.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest package: Tests in linear mixed effects models. J. Stat. Softw. 82:1–26. https://doi.org/10.18637/jss.v082.i13.

Lamberty M, Zachary D, Lanot R, Bordereau C, Robert A, Hoffmann JA, Bulet P. 2001. Insect immunity. J. Biol. Chem. 276:4085–4092.

Lamont BB. 1995. Testing the effect of ecosystem composition/structure on its functioning. Oikos 74:283. https://doi.org/10.2307/3545658.

Lauber CL, Strickland MS, Bradford MA, Fierer N. 2008. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil Biol. Biochem. 40:2407–2415. https://doi.org/10.1016/j.soilbio.2008.05.021.

Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Liu Q, Herman PMJ, Mooij WM, Huisman J, Scheffer M, Olff H, van de Koppel J. 2014. Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. Nat Commun. https://doi.org/10.1038/ncomms6234.

Lowery B, Hickey, WJ, Arshad MAC, Lal R. 1996. Soil water parameters and soil quality, in: JW Doran, AJ Jones (Eds), Methods for Assessing Soil Quality. Soil Science Society of America, Madison, WI, pp. 143–155https://doi.org/10.2136/sssaspecpub49.c8

Luo Y, Keenan TF, Smith M. 2015. Predictability of the terrestrial carbon cycle. Glob. Change Biol. 21:1737–1751. https://doi.org/10.1111/gcb.12766.

Maestre FT, Eldridge DJ, Soliveres S, Kéfi S, Delgado-Baquerizo M, Bowker MA, García-Palacios P, Gaitán J, Gallardo A, Lázaro R, Berdugo M. 2016. Structure and functioning of dryland ecosystems in a changing world. Annu. Rev. Ecol. Evol. Syst. 47:215–237. https://doi.org/10.1146/annurev-ecolsys-121415-032311.

Malhi Y, Lander T, le Roux E, Stevens N, Macias-Fauria M, Wedding L, Girardin C, Kristensen JÅ, Sandom CJ, Evans TD, Svenning JC, Canney S. 2022. The role of large wild animals in climate change mitigation and adaptation. Curr. Biol. 32:R181–R196. https://doi.org/10.1016/j.cub.2022.01.041.

Migliavacca M, Musavi T, Mahecha MD, Nelson JA, Knauer J, Baldocchi DD, Perez-Priego O, Christiansen R, Peters J, Anderson K, Bahn M, Black TA, Blanken PD, Bonal D, Buchmann N, Caldararu S, Carrara A, Carvalhais N, Cescatti A, Chen J, Cleverly J, Cremonese E, Desai AR, El-Madany TS, Farella MM, Fernández-Martínez M, Filippa G, Forkel M, Galvagno M, Gomarasca U, Gough CM, Göckede M, Ibrom A, Ikawa H, Janssens IA, Jung M, Kattge J, Keenan TF, Knohl A, Kobayashi H, Kraemer G, Law BE, Liddell MJ, Ma X, Mammarella I, Martini D, Macfarlane C, Matteucci G, Montagnani L, Pabon-Moreno DE, Panigada C, Papale D, Pendall E, Penuelas J, Phillips RP, Reich PB, Rossini M, Rotenberg E, Scott RL, Stahl C, Weber U, Wohlfahrt G, Wolf S, Wright IJ, Yakir D, Zaehle S, Reichstein M. 2021. The three major axes of terrestrial ecosystem function. Nature 598:468–472. https://doi.org/10.1038/s41586-021-03939-9.

Munjonji L, Ayisi KK, Mudongo EI, Mafeo TP, Behn K, Mokoka MV, Linstädter A. 2020. Disentangling drought and grazing effects on soil carbon stocks and CO2 fluxes in a semi-arid African savanna. Front Environ Sci. https://doi.org/10.3389/fenvs.2020.590665.

Muvengwi J, Witkowski ETF. 2020. Cascading effects of termite mounds in African savannas. N. Z. J. Bot. 58:167–193. https://doi.org/10.1080/0028825X.2020.1767162.

Nobre T, Rouland-Lefèvre C, Aanen DK. 2011. comparative biology of fungus cultivation in termites and ants,In: D Bignell,Y Roisin, N Lo (Eds), Biology of Termites: A Modern Synthesis. Springer Netherlands, pp 193–210. https://doi.org/10.1007/978-90-481-3977-4

Odadi WO, Young TP, Okeyo-Owuor JB. 2007. Effects of wildlife on cattle diets in Laikipia rangeland. Kenya. Rangel. Ecol. Manag. 60:179–185. https://doi.org/10.2111/05-044R3.1.

Ogutu JO, Piepho H-P, Said MY, Ojwang GO, Njino LW, Kifugo SC, Wargute PW. 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? PLOS ONE 11:e0163249. https://doi.org/10.1371/journal.pone.0163249.

Petipas RH, Brody AK. 2014. Termites and ungulates affect arbuscular mycorrhizal richness and infectivity in a semiarid savanna. Botany 92:233–240. https://doi.org/10.1139/cjb-2013-0223.

Petipas RH, González JB, Palmer TM, Brody AK. 2017. Habitat-specific AMF symbioses enhance drought tolerance of a native Kenyan grass. Acta Oecologica 78:71–78. https://doi.org/10.1016/j.actao.2016.12.005.

Piñeiro G, Paruelo JM, Oesterheld M, Jobbágy FOREXAMPLE. 2010. Pathways of grazing effects on soil organic carbon and nitrogen. Rangel. Ecol. Manag. 63:109–119.

Porensky LM, Wittman SE, Riginos C, Young TP. 2013. Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. Oecologia 173:591–602. https://doi.org/10.1007/s00442-013-2637-4.

Pringle RM. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. Ecology 89:26–33. https://doi.org/10.1890/07-0776.1.

Pringle RM, Tarnita CE. 2017. Spatial self-organization of ecosystems: Integrating multiple mechanisms of regular-pattern formation. Annu. Rev. Entomol. 62:359–377. https://doi.org/10.1146/annurev-ento-031616-035413.

Ratajczak Z, Collins SL, Blair JM, Koerner SE, Louthan AM, Smith MD, Taylor JH, Nippert JB. 2022. Reintroducing bison results in long-running and resilient increases in grassland diversity. Proc. Natl. Acad. Sci. 119:e2210433119. https://doi.org/10.1073/pnas.2210433119.

Riginos C, Porensky LM, Veblen KE, Odadi WO, Sensenig RL, Kimuyu D, Keesing F, Wilkerson ML, Young TP. 2012. Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). Pastor. Res. Policy Pract. 2:10. https://doi.org/10.1186/2041-7136-2-10.

Ritchie ME, Tilman D, Knops JMH. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79:165–177. https://doi.org/10.1890/0012-9658(1998)079[0165:HEOPAN]2.0.CO;2.

Rotich HK, Onwonga R, Mbau JS, Koech OK. 2018. Soil organic carbon content and stocks in relation to grazing management in semi-arid grasslands of Kenya. J. Rangel. Sci. 8:143–155.

Sandhage-Hofmann A, Linstädter A, Kindermann L, Angombe S, Amelung W. 2021. Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass. Glob. Change Biol. 27:4601–4614. https://doi.org/10.1111/gcb.15779.

Sapountzis P, de Verges J, Rousk K, Cilliers M, Vorster BJ, Poulsen M. 2016. Potential for nitrogen fixation in the fungus-growing termite symbiosis. Front. Microbiol. 7:1–5. https://doi.org/10.3389/fmicb.2016.01993.

Schmitz OJ, Wilmers CC, Leroux SJ, Doughty CE, Atwood TB, Galetti M, Davies AB, Goetz SJ. 2018. Animals and the zoogeochemistry of the carbon cycle. Science. https://doi.org/10.1126/science.aar3213.

Sitters J, Edwards PJ, Olde Venterink H. 2013. Increases of soil C, N, and P pools along an acacia tree density gradient and their effects on trees and grasses. Ecosystems 16:347–357. https://doi.org/10.1007/s10021-012-9621-4.

Sitters J, Kimuyu DM, Young TP, Claeys P, Olde Venterink H. 2020. Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. Nat. Sustain. 3:360–366. https://doi.org/10.1038/s41893-020-0490-0.

Six J, Conant RT, Paul EA, Paustian K. 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241:155–176.

Slessarev EW, Lin Y, Jiménez BY, Homyak PM, Chadwick OA, D'Antonio CM, Schimel JP. 2020. Cellular and extracellular C contributions to respiration after wetting dry soil. Biogeochemistry 147:307–324. https://doi.org/10.1007/s10533-020-00645-y.

Somasundaram J, Lal R, Sinha NK, Dalal R, Chitralekha A, Chaudhary RS, Patra AK. 2018. Cracks and potholes in Vertisols: characteristics, occurrence, and management. Adv. Agron. 149:93–159. https://doi.org/10.1016/bs.agron.2018.01.001.

Soussana J-F, Lemaire G. 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. Agric. Ecosyst. Environ. 190:9–17. https://doi.org/10.1016/j.agee.2013.10.012.

Staver AC, Asner GP, Rodriguez-Iturbe I, Levin SA, Smit IPJ. 2019. Spatial patterning among savanna trees in high-resolution, spatially extensive data. Proc. Natl. Acad. Sci. 116:10681–10685. https://doi.org/10.1073/pnas.1819391116.

Tobiašová E, Barančíková G, Gömöryová E, Makovníková J, Skalský R, Halas J, Koco Š, Tarasovičová Z, Takáč J, Špaňo M. 2016. Labile forms of carbon and soil aggregates. Soil Water Res. 11:259–266. https://doi.org/10.17221/182/2015-SWR.

Turner MG, Chapin III FS. 2005. Causes and consequences of spatial heterogeneity in ecosystem function,In: G ovett (Ed), Ecosystem Function in Heterogeneous Landscapes. Presented at the Cary Conference, Springer, New York, , pp 9–30.

Unger S, Máguas C, Pereira JS, David TS, Werner C. 2010. The influence of precipitation pulses on soil respiration – assessing the ''Birch effect'' by stable carbon isotopes. Soil Biol. Biochem. 42:1800–1810. https://doi.org/10.1016/j.soilbio.2010.06.019.

Vance ED, Brookes PC, Jenkinson DS. 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19:703–707. https://doi.org/10.1016/0038-0717(87)90052-6.

Veblen KE, Porensky LM, Riginos C, Young TP. 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecol. Appl. 26:1610–1623. https://doi.org/10.1890/15-1367.1.

Wang X, Zhang W, Shao Y, Zhao J, Zhou L, Zou X, Fu S. 2019. Fungi to bacteria ratio: historical misinterpretations and potential implications. Acta Oecologica 95:1–11. https://doi.org/10.1016/j.actao.2018.10.003.

Wells HBM, Crego RD, Ekadeli J, Namoni M, Kimuyu DM, Odadi WO, Porensky LM, Dougill AJ, Stringer LC, Young TP. 2022a. Less is more: lowering cattle stocking rates enhances wild herbivore habitat use and cattle foraging efficiency. Front. Ecol. Evol. 10:825689. https://doi.org/10.3389/fevo.2022.825689.

Wells HBM, Porensky LM, Veblen KE, Riginos C, Stringer LC, Dougill AJ, Namoni M, Ekadeli J, Young TP. 2022b. At high stocking rates, cattle do not functionally replace wild herbivores in shaping understory community composition. Ecol Appl. https://doi.org/10.1002/eap.2520.

Young TP, Okello B, Kinyua D, Palmer TM. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia. Kenya. Afr. J. Range Forage Sci. 14:92–104.

Young TP, Palmer TM, Gadd ME. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia. Kenya. Biol. Conserv. 122:351–359. https://doi.org/10.1016/j.biocon.2004.08.007.

Young TP, Porensky LM, Riginos C, Veblen KE, Odadi WO, Kimuyu DM, Charles GK, Young HS. 2018. relationships between cattle and biodiversity in multiuse landscape revealed by Kenya long-term exclosure experiment. Rangel. Ecol. Manag. 71:281–291. https://doi.org/10.1016/j.rama.2018.01.005.

Zaehle S. 2013. Terrestrial nitrogen-carbon cycle interactions at the global scale. Philos. Trans. r. Soc. B Biol. Sci. 368:20130125. https://doi.org/10.1098/rstb.2013.0125.

Zornoza R, Guerrero C, Mataix-Solera J, Arcenegui V, García-Orenes F, Mataix-Beneyto J. 2007. Assessing the effects of air-drying and rewetting pre-treatment on soil microbial biomass, basal respiration, metabolic quotient and soluble carbon under Mediterranean conditions. Eur. J. Soil Biol. 43:120–129. https://doi.org/10.1016/j.ejsobi.2006.11.004.

Zornoza R, Mataix-Solera J, Guerrero C, Arcenegui V, Mataix-Beneyto J. 2009. Storage effects on biochemical properties of air-dried soil samples from Southeastern Spain. Arid Land Res. Manag. 23:213–222. https://doi.org/10.1080/15324980903038727.