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Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores

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Wild herbivore populations are declining in many African savannas, which is related to replacement by livestock (mainly cattle) and the loss of megaherbivores. Although some livestock management practices may be compatible with the conservation of native savanna biodiversity, the sustainability of these integrated wild herbivore/livestock management practices is unknown. For instance, how will these herbivore mixes influence key processes for the long-term functioning of savanna ecosystems, such as soil carbon, nitrogen and phosphorus pools and cycling? The Kenya Long-term Exclosure Experiment studies the ecosystem consequences of manipulating the presence and absence of wild herbivores and cattle at moderate densities in a 'black cotton' savanna. Here we show that after 20 years, cattle presence decreased total soil carbon and nitrogen pools, while the presence of megaherbivores (mainly elephants) increased these pools and even reversed the negative effects of cattle. Our results suggest that a mix of cattle at moderate densities and wild herbivores can be sustainable, provided that the assemblage of wild herbivores includes the largest species.

African savannas harbour the highest density and diversity of mammalian herbivore species in the world, which play key roles in ecosystem structure and function[1,2]. These herbivore communities are, however, undergoing drastic declines, firstly through replacement, either completely or partially, by a different and less diverse assemblage of domestic herbivores, mainly composed of cattle[2–4], and secondly through the loss of the largest herbivore species, also called megaherbivores (>1,000 kg), such as elephant and rhinoceros[5,6]. The ecosystem consequences of the replacement of wildlife by cattle are considered to be mainly negative. Cattle compete with wildlife for forage resources, they are responsible for the replacement of palatable grasses by unpalatable ones and they increase woody species due to fire suppression through reduced fuel loads and decreased competition from grasses[1,7]. However, many studies focus on high cattle density (that is, overstocking), although there is a growing consensus that the presence of moderate numbers of cattle might be compatible with the conservation of native savanna biodiversity[2,8,9]. The loss of megaherbivores is likely to induce strong ecosystem consequences because these species not only maintain the physical structure of ecosystems[6,10], but also influence the feeding behaviour and competition/facilitation dynamics of other herbivore guilds[11,12]. Hence, studies suggest that 'wildlife-friendly' livestock management might be possible, but the sustainability of such wild herbivore/livestock mixes, as well as the role of megaherbivores in it, needs to be investigated. For instance, how various mixtures of cattle and different size classes of wild herbivores impact soil carbon (C) and nutrient sequestration and cycling remains unknown. These are key processes for the long-term functioning of savanna ecosystems.

Mammalian herbivores influence soil C and nutrients, such as nitrogen (N) and phosphorus (P), by either modifying their fluxes within the ecosystem, thereby changing their distribution within the different ecosystem pools (tree vs grass vs soil pools), or by altering the balance between C, N and P fluxes into and out of the ecosystem (for N, see Fig. 1). Herbivores function as important spatial transporters of C and nutrients within ecosystems, because they often consume these elements in the form of plant material in one location and transport them as dung and urine to another location[13–15]. Livestock herding practices throughout savannas in eastern and southern Africa often constrain livestock movement, especially overnight, in temporary enclosures such as 'bomas', 'corrals', 'paddocks' or 'kraals'[16–18]. Consequently, large quantities of nutrients are harvested as livestock feed across the savanna landscape during the day and are exported to, and concentrated in, these enclosures through dung and urine deposition overnight[16–19]. This type of livestock management creates hotspots of soil and forage nutrients within a nutrient-poor savanna matrix, which can persist for up to millennia after these enclosures are abandoned[20].

Megaherbivores have a disproportionately large role in nutrient movement and storage across the landscape because of their high food consumption rates and large diurnal movement ranges[21]. Moreover, elephants transfer C and nutrients from trees to soil by toppling and killing trees[22,23], and indirectly through the return of browse material in the form of dung and urine, which may increase soil C and nutrient pools. Conversely, the longer-term removal of adult trees might also reduce the build-up of organic matter and nutrients into the soil, because many savanna trees symbiotically fix N_2 from the atmosphere and accumulate C, N and P in the top soil[24,25]. The importance and extent of these two contrasting elephant-mediated effects on soil C and nutrient storage remains to be quantified. Domestic cattle and wild megaherbivores are likely to differentially affect soil C, N and P pools in the East African savanna, and thereby modify forage nutrient concentrations and quality. Experimental data is needed to verify these effects and predict the long-term consequences of cattle presence at moderate densities and the loss of megaherbivores on savanna soil pools and forage quality, as well as how these changes in the herbivore community may impact on each other.

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Twenty years ago, the Kenya Long-term Exclosure Experiment (KLEE) was established to examine the effects of different combinations of wildlife and cattle on plant communities and ecosystem processes in a Kenyan savanna[8,26,27]. This savanna is a working cattle ranch, where cattle co-occur with wild herbivores at moderate stocking densities (10–15 cattle km^{-2}). Using a series of 'semi-permeable' barriers, the KLEE excluded cattle and/or wild herbivore species, both mesoherbivores (15–1,000 kg, such as zebra and gazelle) and megaherbivores (mainly elephants), from experimental plots in 1995. The objective of our study was to examine the separate and interactive effects of the presence and absence of both wild meso- and megaherbivores, as well as cattle, on soil C, N and P pools in the KLEE plots 20 years after they were established. Additionally, we investigated whether and how differences in the soil C, N and P pools could feed back to forage nutrient concentrations and quality. Soil and grass samples were collected in these experimental plots and analysed for C, N and P concentrations.

Previous KLEE studies demonstrated that the effects of wild herbivores versus cattle on herbaceous plant communities were partly driven by differences in the overall density of herbivores[3,28]. Grass biomass decreased while productivity increased with higher herbivore density, particularly driven by the presence of cattle, because cattle have approximately three times the density of wild herbivores in the KLEE[3]. The composition of grass species changed over time; the palatable species *Brachiaria lachnantha* increased across all treatment plots and became dominant in plots without cattle, while cover of another preferred forage species, *Themeda triandra*, maintained its lower cover in plots with cattle[3,29]. However, grass biomass removal by cattle was reduced in the presence of megaherbivores, likely because the latter limited the availability of key forage resources[11,28,30]. The presence of megaherbivores also reduced the density of adult trees by toppling and killing them[31]. Wild mesoherbivores deposited less dung in plots they shared with only cattle than in plots they shared with cattle and megaherbivores[12]. Thus, megaherbivores were able to moderate the negative effects of cattle on wild mesoherbivores, likely because megaherbivores modified cattle foraging behaviour and diet[30]. Based on these previous observations, and on the differences in management practices among the wild and domestic herbivores, we hypothesized firstly that cattle cause a depletion of soil C, N and P pools, which feeds back to lower forage quality in the cattle plots, because cattle transport nutrients out of the savanna matrix (including the KLEE) and deposit dung and urine elsewhere (in bomas). And secondly, that megaherbivores are able to (partially or fully) compensate for cattle-induced loss of C, N and P in the soil by decreasing cattle forage consumption and hence the export of C, N and P in their dung, by increasing dung deposition of mesoherbivores and by augmenting the fluxes of C, N and P from woody vegetation into the soil (through the breaking, toppling and killing of trees).

Results

Herbivore treatment effects on soil C, N and P pools. After 20 years of controlled, replicated herbivore treatments, plots grazed by cattle (C) had on average 40% smaller soil C and N pools than plots where all herbivores were excluded (O; see Fig. 2 and Table 1). P pools were on average 26% smaller, but these differences were not significant after Holm–Bonferroni correction ($P > 0.002$). There were no significant differences in soil C, N and P pools between plots where wild mesoherbivores were allowed and plots where all herbivores were excluded (W vs O). Megaherbivores, however, increased soil C and N pools, and were able to even reverse the negative effects of cattle: the C and N pools were significantly larger in the plots where wild mega- and mesoherbivores as well as cattle co-occurred (MWC) compared with the plots where cattle were present in the absence of megaherbivores (C and WC). The plots with all herbivores (MWC) present also had larger C and N pools than the plots with no herbivores (O). The P pools displayed the same tendency between plots, and were only significantly different between plots with all herbivores (MWC) and plots with only cattle (C). Notably, we did not find any significant differences in soil bulk density between herbivore treatments, therefore modifications in the C, N and P pools were driven by changes in C, N and P concentrations (Table 1).

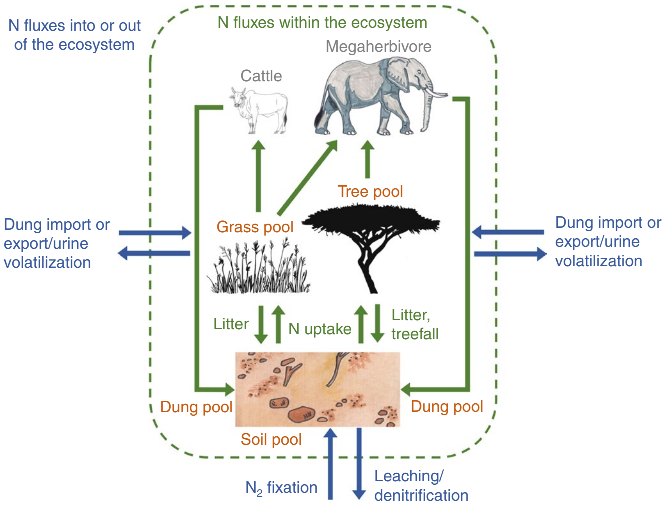

Fig. 1 | Herbivore effects on soil N. Conceptual framework showing how domestic cattle and wild megaherbivores (elephant) might influence the soil N pool by their impact on N fluxes within the ecosystem (for example, grass consumption and dung input) and into or out of the ecosystem (for example, changes in dung import/export or N_2 fixation).

After Holm–Bonferroni correction, the pools of soil C and N did not statistically differ under the canopies of monodominant *Acacia drepanolobium* trees compared with outside (Table 1). Because the canopy cover of trees varied across herbivore treatments (the presence of megaherbivores decreased tree density and thus canopy cover, Extended Data Fig. 1), the soil C, N and P pools calculated on the plot level showed less variation between herbivore treatments than the variation between sampled locations. Nevertheless, the distinctly different effects of the three herbivore types persisted for the soil C and N pools: cattle decreased these pools, megaherbivores increased them, and wild mesoherbivores had a negligible effect (Extended Data Fig. 2).

Herbivore treatment effects on forage quality. Plots with only cattle or with cattle and wild mesoherbivores had on average 17–26% lower grass N concentration and a 30–34% higher grass C/N ratio than plots without cattle or with only wild mesoherbivores (C and WC vs O and W; Fig. 3 and Table 1). Megaherbivores were again responsible for reversing the negative effect of cattle, as grass N concentrations and the C/N ratio were, respectively, highest and lowest when wild meso- and megaherbivores were allowed access to plots in addition to cattle (MWC). The herbivore treatments had no significant effect on grass P, C/P or N/P (Table 1 and Extended Data Fig. 3). Grass N concentrations increased considerably with increasing soil N pools, while the C/N ratio in grasses decreased (Fig. 4). No significant correlations between soil P pools and grass P concentrations or C/P ratios were observed (Extended Data Fig. 4).

Discussion

In this East African savanna, the impact of cattle on soil C and nutrient pools contrasted sharply with that of wild herbivores, especially megaherbivores. Both our hypotheses were supported by these experimental observations: cattle decreased total soil C and N pools

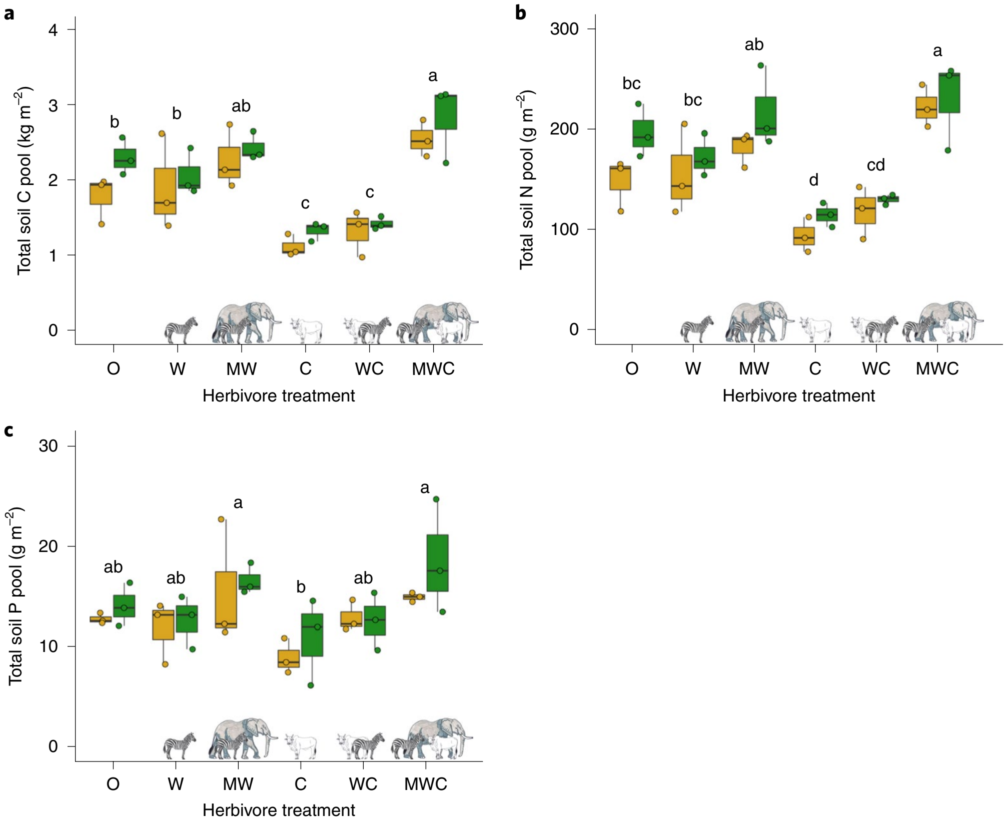

Fig. 2 | Herbivore treatment effects on soil C, N and P pools. a–c, Impact of herbivore treatments on soil C (**a**), N (**b**) and P (**c**) pools outside (golden boxplots and points) and under (green boxplots and points) the canopy of *A. drepanolobium* trees. Boxplots include the median and their whiskers the minimum and maximum values ($N=3$). Herbivore treatments include no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC) and wild mega- and mesoherbivores and cattle (MWC). Boxplots not sharing the same letter indicate significant differences between herbivore treatments combining sampled locations (outside and under the canopy), because there was no significant interaction between herbivore treatment and sampled location (results from analysis of variance (ANOVA), Table 1).

with or without the presence of wild mesoherbivores, but megaherbivores increased these pools and could even reverse the negative effects of cattle (Fig. 2). The large differences in N pools between the herbivore treatments were in turn reflected in forage quality (grass N concentration and C/N ratio; Figs. 3 and 4). Our results highlight the contrasting roles of domestic versus wild herbivores on soil and plant nutrients, and suggest a key role for wild megaherbivores, as only in their presence were soil C and nutrient pools not depleted due to cattle grazing.

Cattle export C and N outside the experimental plots. The considerable differences in soil C and N pools after 20 years of experimental herbivore treatments demonstrate that cattle and megaherbivores have strong and contrasting impacts on the input/output balances of C and N to and from the soil. These impacts occurred either through a change in the distribution of elements between the different ecosystem pools (tree vs grass vs soil pools) or by altering the balance between fluxes into and out of the experimental plots (Fig. 1). Even though we observed small changes in the distribution of C and N between the different ecosystem pools (cattle decreased grass pools, while megaherbivores decreased tree pools; Supplementary Fig. 1 in Supplementary Note 1), total ecosystem pools were significantly different between treatments (Supplementary Fig. 2). In plots where only cattle were present (C), or even in combination with wild mesoherbivores (WC), total ecosystem pools were significantly lower in C and N compared with plots with an intact wild herbivore assemblage (MW), demonstrating that cattle use led to a net export of C and N outside the plots. Indeed, grass consumption was highest in cattle plots (especially in C and WC plots) and dung deposition did not compensate for C and N lost through grazing (Supplementary Fig. 3 in Supplementary Note 2). For example, the differences between grass N output and dung N input in plots with cattle (C) were on average 0.14 g m^{-2} month^{-1}, adding up to an estimated net export of ~33 g m^{-2} across 20 years, which is in the same order of magnitude as our measured decline in soil N of 41 g m^{-2} (comparing C vs O; Fig. 2b). Moreover, the lowest C and N concentrations we found in the cattle plots C and WC were within the range of the baseline soil C and N concentrations of the study area around 20 years ago (1.4% C in 1995 vs 1.9% C in 2015 and 0.17% N in 1997 vs 0.17% N in 2015)[26]. This makes sense as cattle were present throughout the study area during pre-exclosure times, while the megaherbivore elephant was much less common than now[32] (and therefore the pre-exclosure C and N concentrations were not similar to our MWC plots). By excluding cattle for 20 years in the O, W and MW plots, soil C and N concentrations increased compared with the baseline data, likely because the net export of these elements by cattle (through higher offtake than return) was removed. Together, these data support our first hypothesis that cattle transport nutrients out of the savanna matrix by depositing dung and urine elsewhere. These results extend previous research in eastern and southern African savannas; sites where cattle are corralled overnight (for example, in bomas, paddocks and kraals) show high soil nutrient concentrations due to the accumulation of large quantities of dung and urine within these corrals[16–19]. Here, we demonstrate

Table 1 | Results of the linear mixed model analyses for the effects of herbivore treatments and sampled locations (outside or under the canopy of *A. drepanolobium* trees) on several soil and grass measurements

Terms	Herbivore treatment^a (H)		Outside/under canopy^b (C)		H x C^c	
	F value	*P* value	*F value*	*P* value	*F value*	*P* value
Soil measurements						
Soil C pool (kg m^{-2})	**16.9**	**<0.001 (0.001)**	4.7	0.041 (0.002)	0.30	0.91
Soil N pool (g m^{-2})	**16.0**	**<0.001 (0.001)**	6.5	0.018 (0.002)	0.46	0.80
Soil P pool (g m^{-2})	3.7	0.015 (0.002)	1.7	0.20	0.25	0.94
Soil C concentration (mg g^{-1})	**10.2**	**<0.001 (0.002)**	4.5	0.045 (0.003)	0.13	0.98
Soil N concentration (mg g^{-1})	**11.5**	**<0.001 (0.002)**	7.6	0.012 (0.002)	0.13	0.99
Soil P concentration (mg g^{-1})	2.2	0.094	2.6	0.12	0.28	0.92
Soil bulk density (g cm^{-3})	1.9	0.14	0.0	0.10	0.39	0.85
Grass measurements						
Grass N concentration (%)	**10.9**	**<0.001 (0.002)**	5.4	0.030 (0.002)	0.64	0.67
Grass P concentration (%)	1.9	0.14	7.0	0.015 (0.002)	2.6	0.054
Grass C/N ratio	**22.7**	**<0.001 (0.001)**	5.6	0.027 (0.002)	0.48	0.79
Grass C/P ratio	1.9	0.14	5.5	0.028 (0.002)	3.0	0.034 (0.002)
Grass N/P ratio	1.4	0.28	7.7	0.011 (0.002)	1.9	0.14

Models included block as a random effect. Bold values indicate a statistically significant difference after Holm–Bonferroni correction, with corrected *P* values given in parentheses. The grass C/P ratio was log-transformed to meet assumptions of normality and homogeneity of variance. ^{a}d.f. = 5, 22. ^{b}d.f. = 1, 22. ^{c}d.f. = 5, 22.

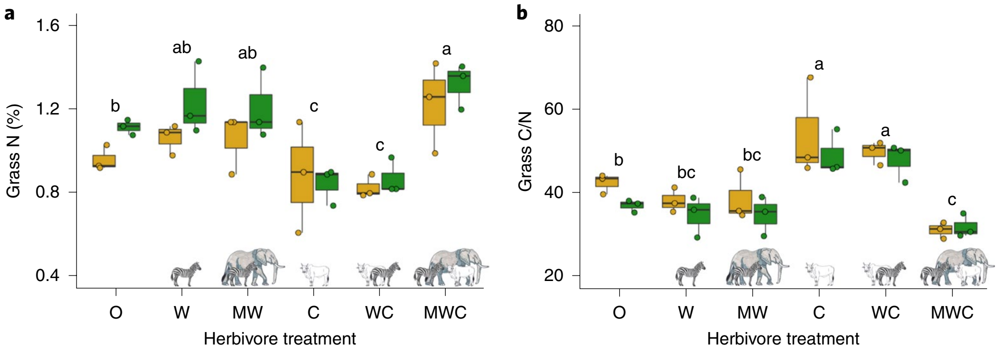

Fig. 3 | Herbivore treatment effects on grass N and C/N ratio. a,**b**, Impact of herbivore treatments on live grass N concentrations (**a**) and C/N ratio (**b**) outside (golden boxplots and points) and under (green boxplots and points) the canopy of *A. drepanolobium* trees. Boxplots include the median and their whiskers the minimum and maximum values ($N = 3$). Herbivore treatments include no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC) and wild mega- and mesoherbivores and cattle (MWC). Boxplots not sharing the same letter indicate significant differences between herbivore treatments combining sampled locations (outside and under canopy cover), because there was no significant interaction between herbivore treatment and sampled location (results from ANOVA, Table 1).

that cattle were responsible for depleted soil nutrient pools in the surrounding savanna landscape, but only in the absence of megaherbivores. We still lack a full explanation of this megaherbivore effect, but have identified several likely contributing factors.

Megaherbivores reversed the negative effect of cattle. In plots where wild megaherbivores co-occurred with cattle and wild mesoherbivores, the difference between the output flux of grass consumption and the input flux of dung input was around half that of the other cattle plots (MWC vs C and WC; 0.10 vs an average of 0.18 g m^{-2} month^{-1} for N), indicating that the net export of C, N and P out of these plots was lower (Supplementary Fig. 2). We suggest that this is because elephants reduce the availability of the preferred protein-rich forbs, which decreases the consumption of herbaceous vegetation, including grass by cattle[11,28], while at the same time increasing the dung deposition of wild mesoherbivores through facilitation[12]. As hypothesized, megaherbivores partially compensate for the loss of C and N in the soil through cattle; for example, the net export of N in MWC plots was on average 43% lower compared with C and WC plots. However, this alone would still result in a net export in MWC plots, which eventually would lead to a decline in soil C and N pools rather than the strong increase observed (Fig. 2). This suggests that megaherbivores were responsible for a large import of C and N to the soil.

We hypothesized that import could occur by way of an increase in the fluxes from woody vegetation to the soil induced by the toppling and killing of trees, and indirectly through the return of browse material in the form of dung. Indeed, the δ^{13}C signature of the soil suggests that a higher proportion of soil C originated from trees in the MWC plots compared with the cattle plots C and WC (Supplementary Fig. 4a in Supplementary Note 3), supporting our proposed mechanism. The presence of megaherbivores reduced tree pools (Supplementary Fig. 1) and we observed higher inputs of browser dung in plots with megaherbivores (as both elephant and

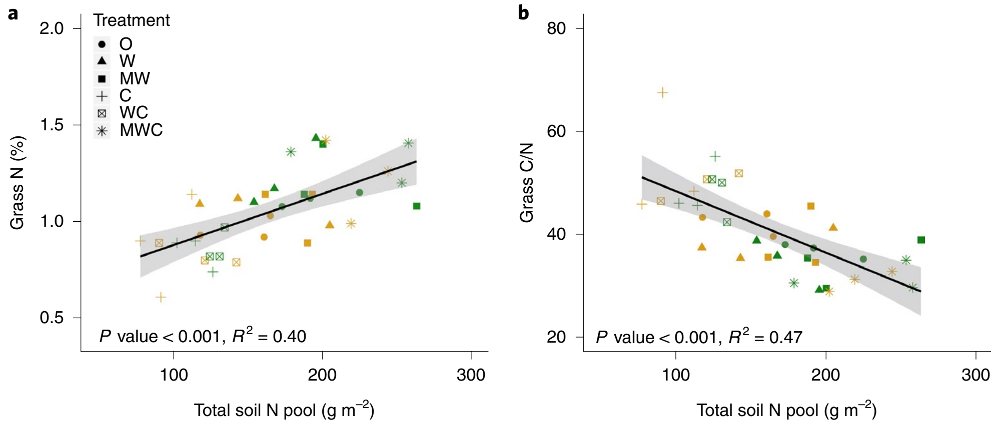

Fig. 4 | Relationship between soil and grass. a,**b**, Linear regressions showing relationships between total soil N pool and live grass N concentration (**a**) and C/N ratio (**b**). Data were pooled over herbivore treatments and sampled locations. Herbivore treatments include no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC) and wild mega- and mesoherbivores and cattle (MWC). Sampled locations are outside (golden symbols) and under (green symbols) the canopy of *A. drepanolobium* trees.

giraffe are browsers; Supplementary Fig. 4b). Total soil C increased with the proportion of soil C originating from trees (Supplementary Fig. 4c), which in turn decreased with canopy cover (Supplementary Fig. 4d), suggesting that the loss of trees induced by megaherbivores did not reduce the build-up of C and nutrients in the soil but instead contributed to it. However, the flux of elements into the soil is not large enough by itself (~19% of soil C across the 20 years, MWC vs C) to fully compensate for the export of elements through cattle dung.

Another mechanism by which herbivores might change soil N pools is by influencing atmospheric N_2-fixation rates[33,34]. In the KLEE plots, the *A. drepanolobium* trees are the main symbiotic N_2 fixers, so their decrease in density might decrease the input of N in plots to which megaherbivores had access[19,35]. Also, grass foliar δ^{15}N values were often negative (Supplementary Fig. 5b), suggesting that N_2 fixation by grass-associated endophytic microbes might be important[34,36], although mycorrhizal associations, which are common among savanna grasses[37], might also lower δ^{15}N values[38]. We observed a positive correlation between soil and grass δ^{15}N values (Supplementary Fig. 5c), indicating that the grasses obtained most of their N from the soil and not the atmosphere[38,39]. Regardless of the possible differences in N_2-fixation rates between herbivore treatments, the soil δ^{15}N signature did not differ (Supplementary Fig. 5b), indicating that N lost from the system (through, for example, ammonia volatilization, denitrification and leaching) and N input (through, for example, N_2fixation and deposition) were similar across treatments[38,39]. In conclusion, our data can only partly explain the mechanisms by which megaherbivores increase soil C and nutrient pools (that is, lower grass consumption in combination with higher dung deposition and increased flux from trees to soil) and additional studies are needed to gain more insight into potential alternative and/or additive mechanisms (for example, differences in N_2-fixation rates).

Herbivore effects on forage quality and nutrient cycling. The changes that herbivores induced in soil N fed back to the quality of their forage (Fig. 4). We only observed these relationships between soil N and grass N or C/N ratio, and not between soil P and grass P or C/P ratio (Extended Data Fig. 4), even though the soil N and P pools reacted similarly to the herbivore treatments (Fig. 2b,c). The weaker relationship between soil and plant P suggests that P is a less prominent limiting resource for plant growth than N, which is often the case in African savannas[40]. However, it may also indicate that plant P availability is less reflected by total soil P than plant N availability by total soil N due to biogeochemical differences. Additionally, the herbivore treatments were not strongly associated with significant variation in soil-extractable N or P fractions or mineralization rates (Supplementary Fig. 6 in Supplementary Note 4). Even though it is often assumed that African herbivores increase N cycling in savannas[41], it is not uncommon to find no effect on extractable N pools and/or mineralization rates[42–44]. The magnitude of the effect of herbivores on nutrient turnover is very dependent on grazing intensity, timing and the way herbivores impact the long-term nutrient balance[40,42]. Moreover, our flux measurements represent within-ecosystem cycling over a relatively short time period (several weeks), whereas total soil nutrient pools represent the long-term balance between ecosystem-level inputs and outputs, which in the end control the quantities of nutrients within an ecosystem and ultimately their availability to plants and their herbivores.

The potential role of fire. As fire has not been an active part of the study area since the 1960s[3], it did not affect the differences in soil nutrients observed between the experimental herbivore treatments. In general, however, fire does play a role in other African savannas, and potentially interacts with herbivory to impact tree/grass coexistence, plant productivity and quality, and soil C and nutrient sequestration[40,45,46]. Two years prior to our sampling, small-scale controlled burns were introduced into the KLEE to test these interactions[31]. However, the period was too short to expect any changes in soil, so these sub-plots were not included in this study. In future, however, they might provide information on how fire–herbivore interactions affect soil C and nutrient pools.

Sustainable management of East African savannas. Our results have major implications for the sustainable management of East African savannas. If cattle replace wildlife, soil C and nutrients will be more heterogeneously redistributed across the landscape, from areas where cattle graze to small patches where they are enclosed overnight[16,17,27]. In the long term, this displacement implies a reduction in forage quality in cattle-grazed areas that would negatively impact on both cattle and wild herbivores. However, a positive side-effect of this type of cattle management is that the nutrient-enriched patches are long-lived and can promote establishment of the nutrient-rich plant communities preferred by cattle and wild herbivores[13,16].

Our study was based in a relatively high productivity savanna where cattle are kept at moderate stocking densities. Livestock densities are currently much higher in many African savannas, especially in communal grazing lands[8,12]. Indeed, the widespread increase in livestock in Africa has resulted in a drastic loss of nutrient dispersal[7], an important ecosystem service provided by wild mammalian herbivores in Africa[21], and due to this and other negative cattle-induced effects, many high-density cattle ranches fail[47,48]. The major challenge African savannas face is how to encourage moderate stocking densities of cattle[8,27].

Our results suggest that a mix of cattle at moderate densities and wild herbivores can be sustainable. Our intriguing results in relation to megaherbivores suggest that the depletion of soil C and N pools and forage quality by cattle may be mitigated by the continent's largest mammals. In line with our results, a larger-scale study in the same area of Kenya has shown that study sites having both livestock and wildlife had higher forage quality than study sites with either wildlife or livestock[9]. The loss of elephants from savanna systems would be detrimental in terms of C and nutrient dynamics (not to mention in terms of other ecosystem functions[5]), and thus for the sustainable management of these ecosystems. However, populations of megaherbivores (for example, elephant and rhinoceros) are at risk of extinction due to both intense international trade pressure and intrinsic biological sensitivity[49]. Our results provide yet one more rationale for the conservation of the largest herbivores. Only with a diverse set of both wild meso- and megaherbivores will it be possible to simultaneously manage East African savannas for livestock production, ecosystem function and biodiversity conservation. To ensure this sustainable management we stress the need for more moderate livestock densities such as approximated in the KLEE.

Methods

Study area. The study was conducted in a semi-arid savanna at the Mpala Research Centre (36° 52′ E, 0° 17′ N; 1,800 m elevation) in Laikipia County, Kenya. Mean annual rainfall in the study area is ~550 mm with a distinct dry season from January to March. Our study site is located within a poorly drained 'black cotton' vertisol soil system, which is widespread in the tropics and East Africa[26,50]. The landscape is relatively homogeneous with a continuous grass layer dominated by the perennial grass species *Pennisetum stramineum*, *Pennisetum mezianum*, *T. triandra* and *B. lachnantha*, while the overstorey is dominated by *A. drepanolobium* (>97% of woody cover[26]). Mpala is managed for both cattle (*Bos indicus*) production at moderate densities (10–15 cattle km^{-2}) and wildlife conservation. Wild herbivores include the mesoherbivores Burchell's and Grevy's zebra (*Equus burchelli* and *Equus grevyi*), Grant's gazelle (*Gazella granti*), eland (*Taurotragus oryx*) hartebeest (*Alcelaphus buselaphus*), buffalo (*Syncerus caffer*) and oryx (*Oryx gazelle*), and the megaherbivores elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*). Density estimates of these herbivore species can be found in ref. [3]. Fire has not been an active part of the study area since the 1960s[3].

Kenya Long-term Exclosure Experiment. Since 1995, the KLEE has used semi-permeable barriers to manipulate the presence and absence of three types of mammalian herbivores[26]: livestock (cattle), wild mesoherbivores (15–1,000 kg) and wild megaherbivores (>1,000 kg). Three replicate blocks were established, each consisting of six 200 × 200 m plots with the following treatments: (1) no large herbivores, (2) wild mesoherbivores only, (3) wild mega- and mesoherbivores, (4) cattle only, (5) wild mesoherbivores and cattle, and (6) wild mega- and mesoherbivores and cattle (Extended Data Fig. 5). Long-term patterns of dung deposition in the KLEE plots confirm that the treatments are >90% effective at excluding targeted species and that the megaherbivore fences do not deter wild mesoherbivores from entering the plots accessible to them. Non-excluded mammalian herbivores (<15 kg) include steenbuck (*Raphicerus campestris*), hare (*Lepus* sp.) and several rodent species[51].

Cattle are herded (in groups of 100–120 individuals) into the C, WC and MWC plots for 2 h on each of two to three consecutive days, three to four times per year. The precise number of grazing days and timing of grazing is largely dependent on forage availability, but plots rarely experience more than 16 weeks without cattle grazing. This livestock grazing regime mimics the overall herding practice and grazing intensity at Mpala (10–15 cattle km^{-2})[12]. Herders allow the livestock to graze in one area for several days at a time until forage is depleted, after which they move the livestock to a different area until the forage recovers. The landscape is not fenced into paddocks, and herders actively manage livestock so that the entire range undergoes similar episodic grazing throughout the year. For more details of the experimental design, see ref. [26].

Soil measurements. We sampled the top 15 cm of soil in July 2015 using a corer with a diameter of 5.4 cm. In each plot we took three soil cores from under the canopy of randomly selected adult *A. drepanolobium* trees (<1.5 m from the stem) and three from positions outside the canopy (>3 m from the stem). We pooled the cores for each plot according to their sampled location (under or outside canopy cover). We weighed each of the pooled cores and dried them to constant weight to calculate soil bulk density. After that, the soil was mixed thoroughly, sieved (2 mm) and a sub-sample was ground for nutrient analyses. Total C and N concentrations were determined using an elemental analyser (Thermo ES Flash 1112). Total P concentrations were measured with a continuous segmented flow analyser (QuAAtro, SEAL Analytical) after combustion and hot HCl extraction.

We calculated the soil pools of C, N and P at the sampled locations in each plot by multiplying the values of soil bulk density by the C, N and P concentrations under and outside the canopy of *A. drepanolobium* trees. Additionally, we calculated the soil pools of C, N and P per plot by weighting the pools under and outside the canopy of *A. drepanolobium* trees according to the proportions of plot area located in one of these two sampled locations. We took hemispherical photographs at the four corners and centre of each plot at a height of 1 m to estimate these proportions (that is, the mean canopy cover per plot) using the program HEMISFER[52,53]. There was a strong correlation between *A. drepanolobium* tree density and mean canopy cover in each plot (Extended Data Fig. 1b).

Vegetation measurements. In July 2015 we clipped aboveground herbaceous biomass in two 25 × 25 cm sub-plots per plot with one under the canopy and one outside the canopy of a *A. drepanolobium* tree (next to where one of the soil cores was taken). Coverage of the clipped plots was strongly dominated (>85%) by the grass species *B. lachnantha* (Extended Data Fig. 6), which is a species that has increased across all treatment plots and is dominant in plots without cattle[3,29]. We divided the biomass material into three fractions, namely live grass, dead grass and herbs, which were dried separately. Samples of live grass were ground and analysed for total C, N and P concentrations using the methods described above.

Statistical analyses. To examine the impact of the herbivore treatments and the sampled location (outside or under canopy) on soil bulk density, soil C, N and P concentrations and pools, and grass N and P concentrations and ratios (C/N, C/P and N/P), we used linear mixed effect models with the six herbivore treatments and sampled location as fixed factors with interactions and block as the random effect. The obtained *P* values were corrected for multiple testing using the Holm–Bonferroni correction, and multiple comparisons were made using Tukey's tests. We used linear regressions to examine the relationships between soil N and P pools and the measured grass variables. The data met assumptions of normality and homogeneity of variance whereby we log-transformed the grass C/P and N/P ratios. All analyses were performed using the open source R software package[54]. We used the NLME package for mixed modelling[55] and made multiple comparisons using Tukey's test in the LSMEANS package[56].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets collected and analyzed in this study are available in figshare at https://doi.org/10.6084/m9.figshare.11636595.v1, https://doi.org/10.6084/m9.figshare.11636577.v2 and https://doi.org/10.6084/m9.figshare.11636502.v1. Source data for Figs. 2–4 and Extended Data Figs. 1–4 and 6 are provided as Source Data files.

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Author contributions

J.S., T.P.Y. and H.O.V. conceived the study. J.S., D.M.K. and T.P.Y. collected soil, plant and dung samples. D.M.K. and T.P.Y. provided additional data. J.S. and P.C. performed chemical analyses. J.S. and H.O.V. analysed the data and wrote the first draft of the manuscript. All authors contributed revisions.

Competing interests

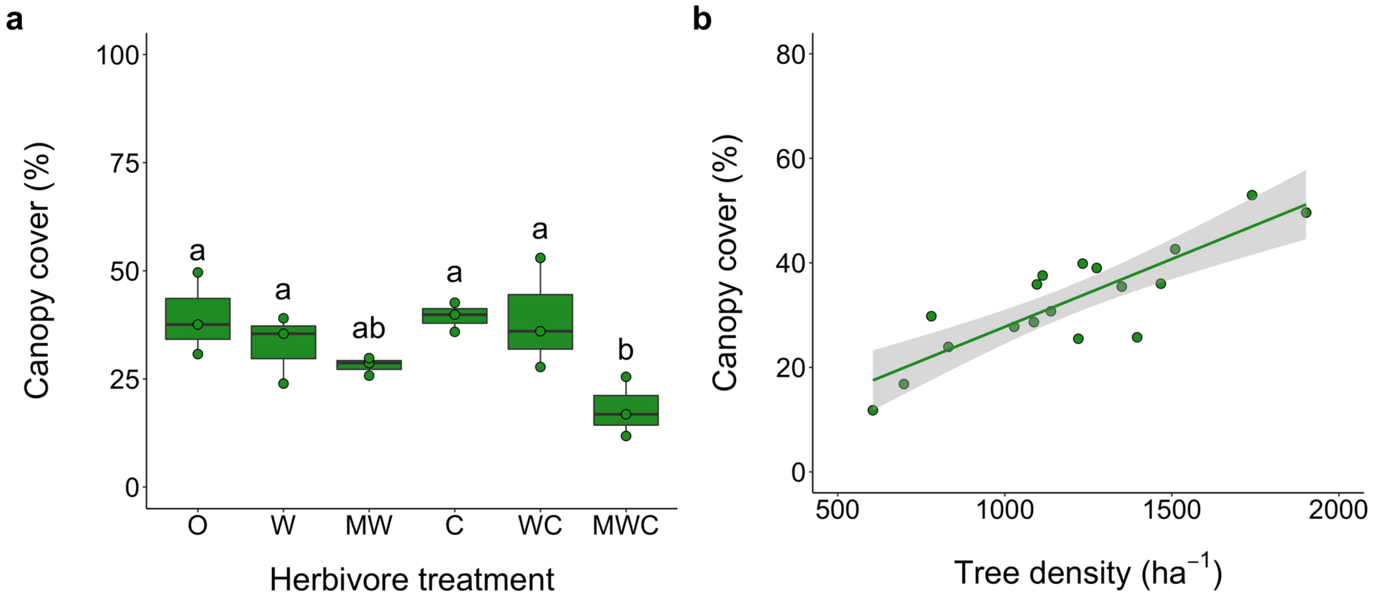
The authors declare no competing interests.

Additional information

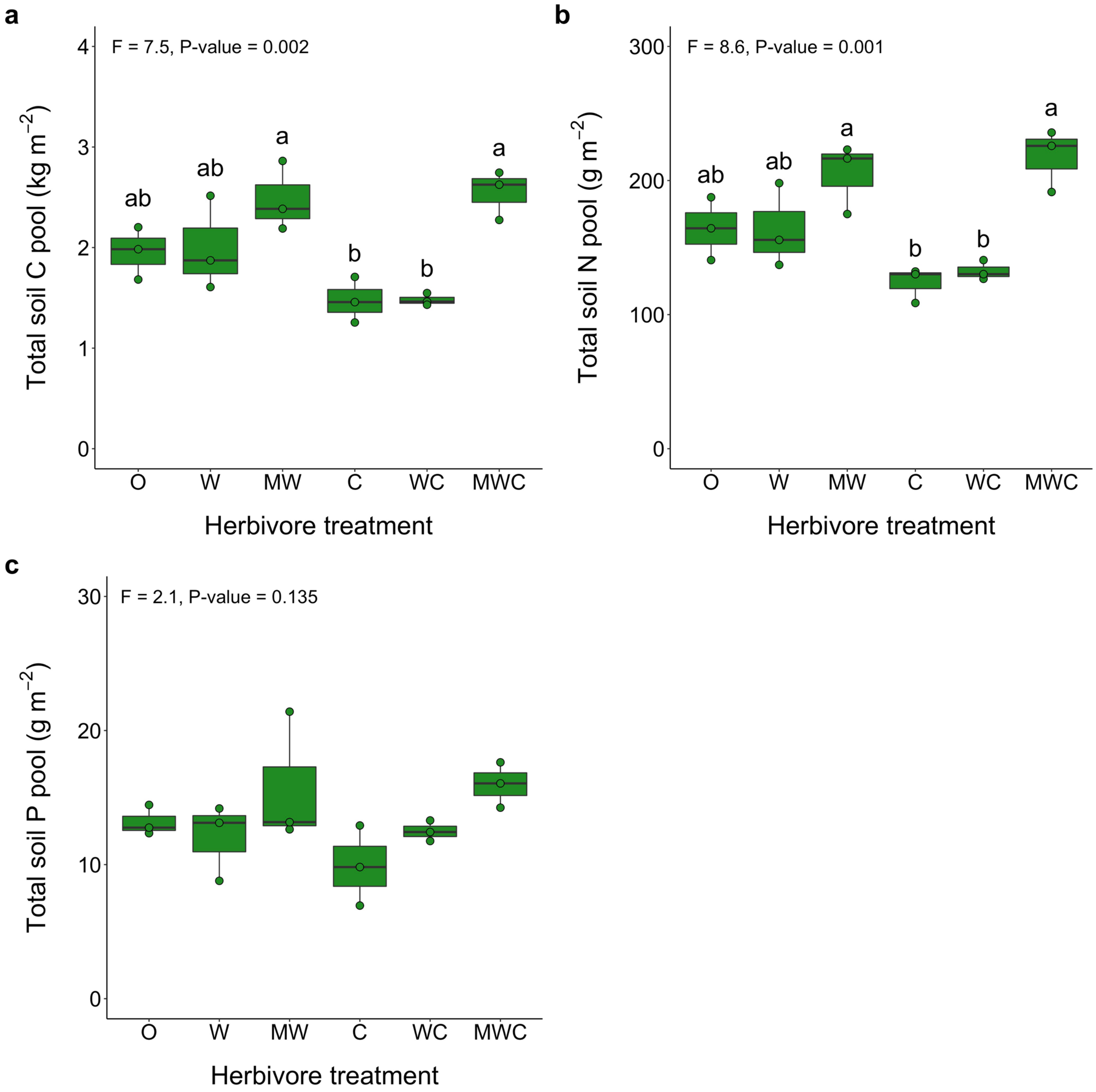
Extended data is available for this paper at https://doi.org/10.1038/s41893-020-0490-0.

Supplementary information is available for this paper at https://doi.org/10.1038/s41893-020-0490-0.

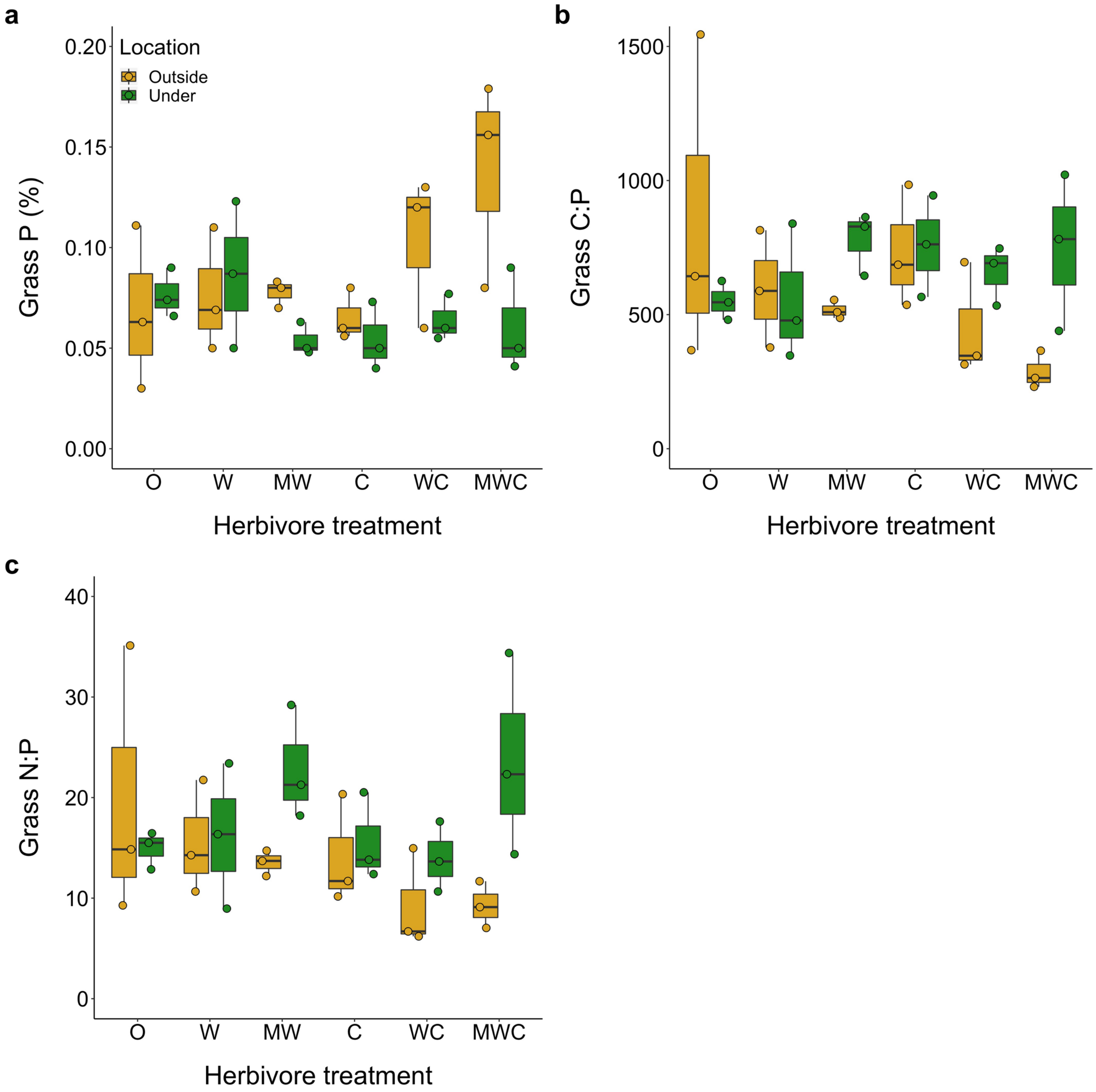
Correspondence and requests for materials should be addressed to J.S.



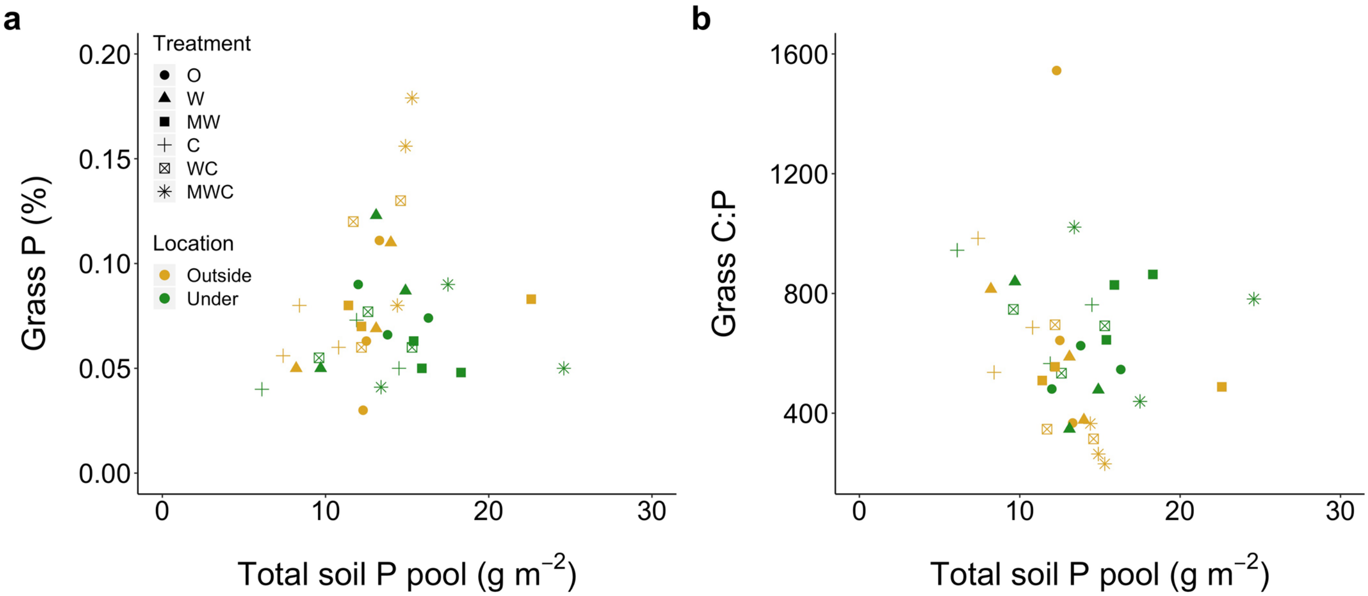
Extended Data Fig. 1 | Herbivore treatment effects on canopy cover. a, Impact of herbivore treatments on canopy cover estimated with hemispherical photographs. Herbivore treatments ($N = 3$) include: no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC), wild mega- and mesoherbivores and cattle (MWC). Boxplots not sharing the same letter indicate significant differences between herbivore treatments. **b**, Linear regression showing the relationship between tree density and canopy cover. See ref. [31] for details on tree surveys.



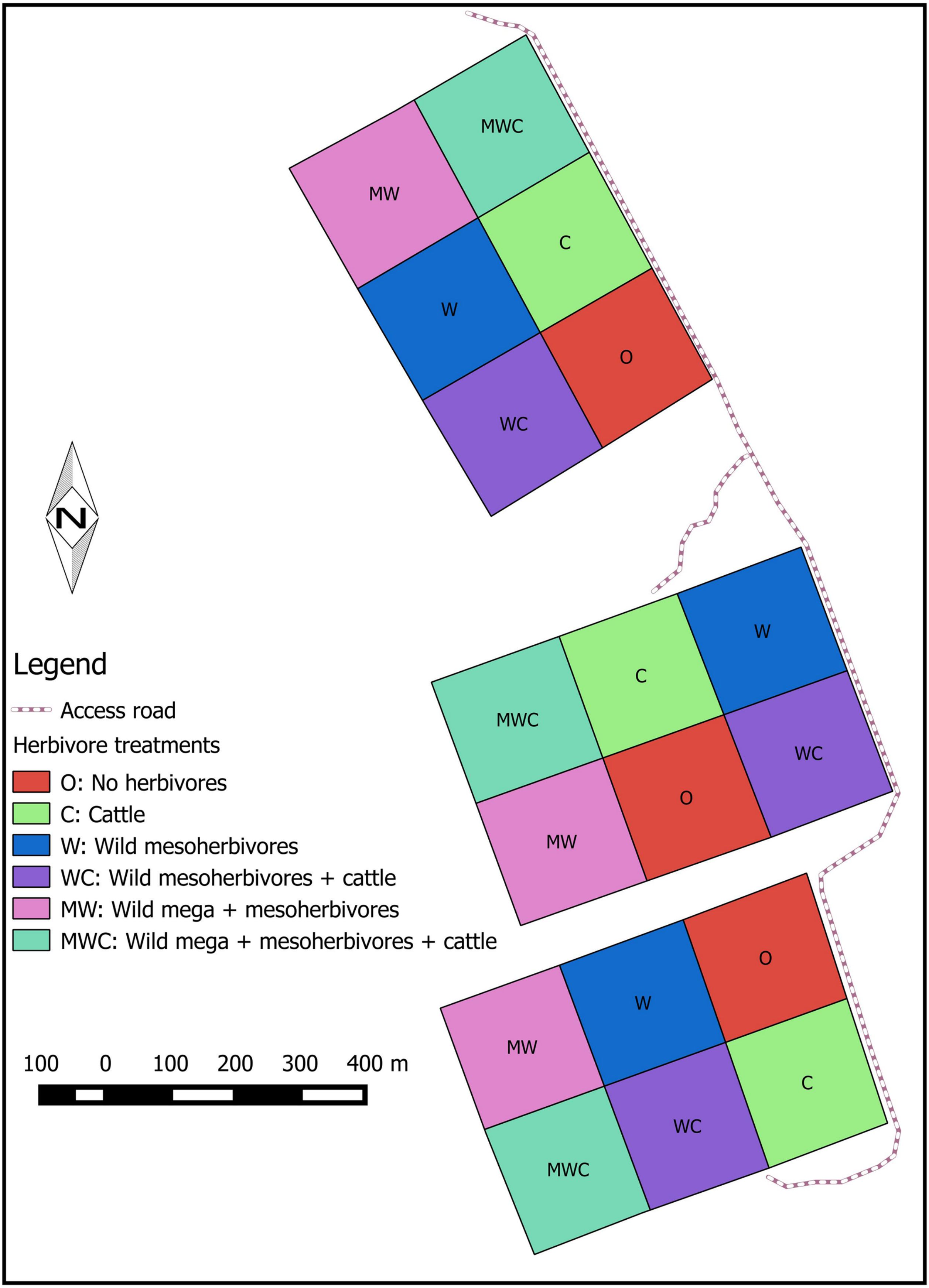
Extended Data Fig. 2 | Herbivore treatment effects on soil C, N and P pools. Impact of herbivore treatments on plot-level soil C **a**, N **b**, and P pools **c**, calculated using the proportions of plot area located under and outside the canopy of *A. drepanolobium* trees. Herbivore treatments ($N = 3$) include: no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC), wild mega- and mesoherbivores and cattle (MWC). Boxplots not sharing the same letter indicate significant differences between herbivore treatments.



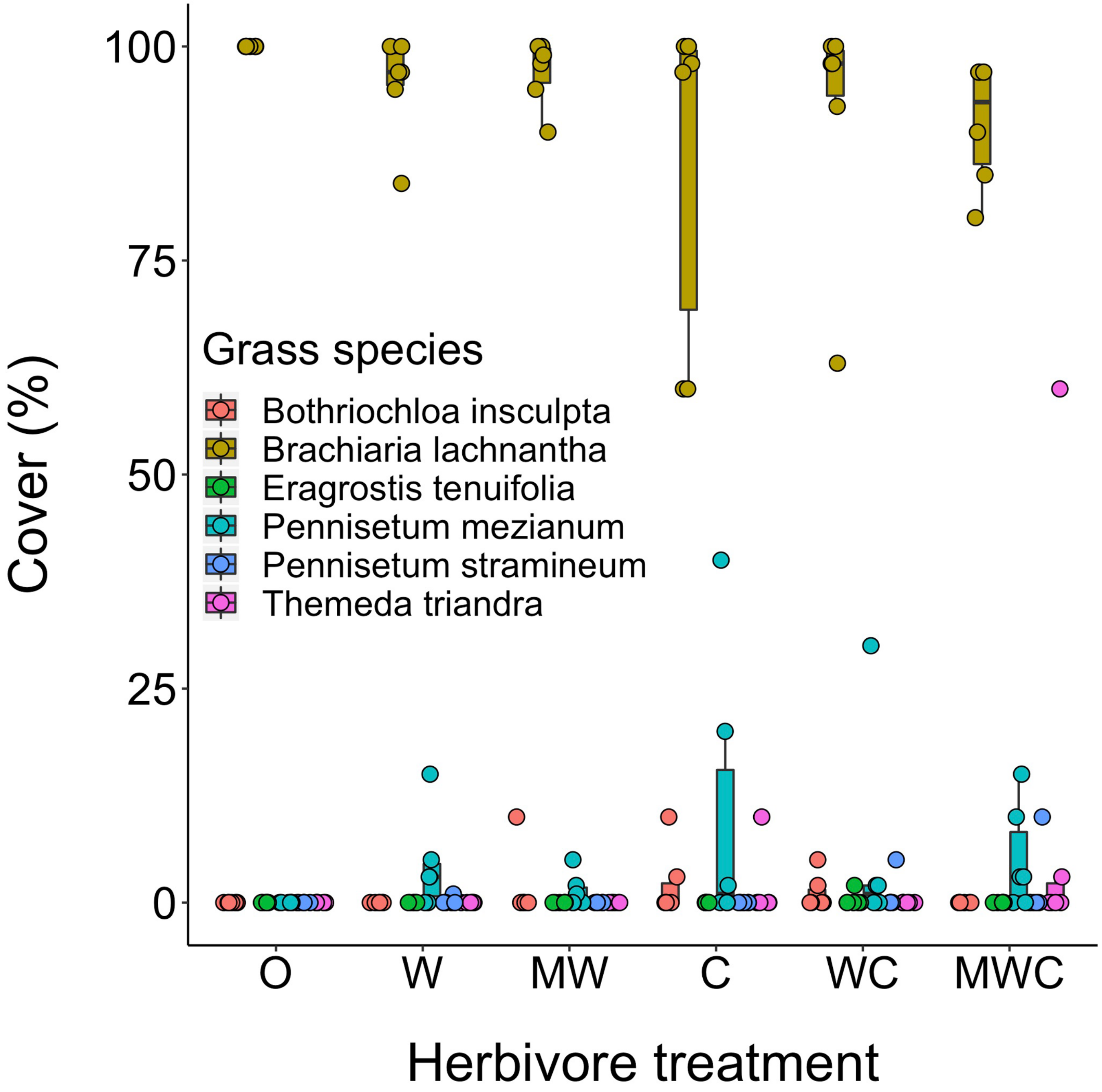
Extended Data Fig. 3 | Herbivore treatment effects on grass P, C:P and N:P ratios. Impact of herbivore treatments on live grass P concentrations **a**, C:P **b**, and N:P ratio **c**, outside (golden boxplots and points) and under (green boxplots and points) the canopy of *A. drepanolobium* trees. Herbivore treatments (*N* = 3) include: no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC), wild mega- and mesoherbivores and cattle (MWC).



Extended Data Fig. 4 | Relationship between soil and grass. Relationships between total soil P pool and live grass P concentrations **a**, and C:P ratio **b**, Herbivore treatments include: no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC), wild mega- and mesoherbivores and cattle (MWC). Sampled locations are outside (golden points) and under (green points) the canopy of *A. drepanolobium* trees.



Extended Data Fig. 5 | The Kenya Long-term Exclosure Experiment (KLEE). Schematic of the Kenya Long-term Exclosure Experiment (KLEE) plots. The letters inside each plot indicate the herbivore treatments.



Extended Data Fig. 6 | Coverage of clipped grass species in each KLEE plot. Coverage of different grass species in the two 25 x 25 cm subplots (one under the canopy and one outside the canopy of an *A. drepanolobium* tree) we clipped in each KLEE plot. Herbivore treatments include: no large herbivores (O), wild mesoherbivores (W), wild mega- and mesoherbivores (MW), only cattle (C), wild mesoherbivores and cattle (WC), wild mega- and mesoherbivores and cattle (MWC). *N* = 6 per treatment.

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☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	All analyses were performed with the open source R, version 3.4.3. We used the nlme package for mixed modeling and made multiple comparisons using Tukey's test in the lsmeans package.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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The datasets collected and analyzed for this study are available in figshare at https://doi.org/10.6084/m9.figshare.11636595.v1, https://doi.org/10.6084/m9.figshare.11636577.v2 and https://doi.org/10.6084/m9.figshare.11636502.v1.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The objective of our study was to examine the separate and interactive effects of the loss of wild mega- and mesoherbivores, and the presence of cattle, on soil C, N and P pools. Additionally, we investigated if and how differences in soil C, N and P pools could feed back on forage nutrient concentrations and quality. Thereto, we collected soil and plant samples in plots of the Kenya Long-term Exclosure Experiment (KLEE) and analysed these for C, N and P concentrations. Twenty years ago, KLEE was established to examine the effects of different combinations of wildlife and cattle on plant communities and ecosystem processes. In KLEE presence and absence of three types of large herbivores has been manipulated since 1995 by the use of semipermeable barriers: livestock (cattle, C), wild mesoherbivores (15-1000 kg, W) and wild megaherbivores (>1000 kg, M). Three replicate blocks were established, each consisting of six 200 x 200 m plots with the following treatments: 1) no large herbivores (O), 2) wild mesoherbivores only (W), 3) wild mega- and mesoherbivores (MW), 4) cattle only (C), 5) wild mesoherbivores and cattle (WC), and 6) wild mega- and mesoherbivores and cattle (MWC).
Research sample	Our research samples consisted of soil and aboveground herbaceous biomass per experimental KLEE plot.
Sampling strategy	We sampled soil at 0-15 cm depth. At each plot we took three soil cores from under the canopy of randomly selected adult Acacia drepanolobium trees (< 1.5 m from the stem) and three from positions outside the canopy (>3 m from the stem). We pooled the cores for each plot according to their sampled location (under or outside canopy). We clipped aboveground herbaceous biomass in two 25 x 25 cm subplots per plot, with one under the canopy and one outside the canopy of a A. drepanolobium tree (next to where one of the soil cores was taken). Our sample size was n = 3, which is the amount of replicates of each experimental treatment in KLEE.
Data collection	We collected soil and herbaceous biomass samples as described above in Sampling strategy. Judith Sitters took all samples together with a field assistant.
Timing and spatial scale	Collection of soil and herbaceous biomass samples was done in July 2015. The collection sites were randomly chosen within 200 x 200 m, the size of the experimental KLEE plots. Soil cores were sampled at a depth of 0-15 m (diameter of cores was 5.4 cm) and herbaceous sample material was clipped in two 25 x 25 cm subplots.
Data exclusions	No data were excluded from the analysis.
Reproducibility	This is not relevant to our study as KLEE is a non-reproduced large herbivore exclosure experiment. Data on soil C, N and P pools and herbaceous C, N and P concentrations were compared to other savanna types and we found values in a similar range.
Randomization	The experimental plots in KLEE are randomized per block (3 blocks), and collection of soil and herbaceous biomass samples was also done randomly by dividing the inner 100 x 100m subplot in each 200 x 200m experimental plot into four 25x25 m quadrats and randomly deciding in which two quadrats samples would be taken.
Blinding	The collected soil cores and herbaceous biomass used for C, N and P concentration analyses were numbered randomly and only later linked to the different treatments.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Fieldwork was done in July 2015 in a Kenya savanna; temperatures were around 35 degrees and no rain fell during this period.
Location	The study was conducted in a semi-arid savanna at the Mpala Research Centre (36°52'E, 0°17'N; 1800 m elevation) in Laikipia County, Kenya. Here, the Kenya Long-term Exclosure Experiment (KLEE) was established in 1995.
Access and import/export	The research was carried out under Government of Kenya research clearance permit No. NACOSTI/P/15/0830/4886. Soil and herbaceous biomass samples were exported to Belgium under a Phytosanitary Certificate from the Kenya Plant Health Inspectorate Service (No. KEPHIS/6707/2015).
Disturbance	Dirt roads lead up to the KLEE plots after which data collection was done on foot.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging