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ORIGINAL ARTICLE

Proximity to high densities of pastoral settlements reduces grassland regrowth in a protected tropical savanna

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Abstract

Sedentarization of pastoralist communities is reshaping the structure and functioning of tropical savannas. Of particular concern is how permanent pastoral settlements change grassland vegetation inside "protected" areas. In this study, we investigate the spatial impact of pastoral settlements on grassland regrowth in Nech Sar National Park, Ethiopia. Within the National Park, we established herbivore exclosures across the central grassland plains at varying distances from a high concentration of pastoral settlements. Plant species composition, biomass, and regrowth after clipping were measured every 6 months, inside and outside exclosures in close proximity and further away from pastoral settlements. After 18 months, close proximity to high densities of pastoral settlements negatively influenced grassland regrowth compared to further away from pastoral settlements. Excluding herbivores resulted in lower regrowth compared to grazed swards independent of distance from high densities of pastoral settlements. Cover of the dominant grass species *Bothriochloa insculpta* was lower when grazed and following clipping, whereas *Chrysopogon plumulosus* cover was higher closer to settlements. These grasses were dominant across the plain; yet further away from settlements there was a higher number of co-dominant grassland species. These findings suggest that subtle changes in grassland community composition, likely following livestock grazing, contribute to spatial differences in savanna grassland regrowth near to and far from pastoral settlements. Furthermore, specific grassland species may be used as indicators of the wider spatial impact of pastoral settlement sedentarization on savanna regrowth.

KEYWORDS
boma, enclosure, evenness, forb, grazing, homestead, plant functional group, tukul, woody encroachment

Wana and Smith contributed equally to the development of the manuscript.

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1 | INTRODUCTION

Pastoral settlements have shaped the structure and functioning of tropical grasslands and savannas for millennia. Recent environmental, political, and cultural changes contribute to shifts in pastoralism from predominantly mobile to sedentary communities (Boles et al., 2019; Reid et al., 2005; Western et al., 2009). How the functioning of savannas responds to this sedentarization of pastoralist communities is of particular concern both within and along the borders of protected areas (Reid et al., 2005; Veldhuis et al., 2019). In tropical savannas, pastoral settlements are synonymous with the presence of cattle and other livestock. Inside settlements, herding livestock into enclosures concentrates seeds and excrement—and thus nutrients—from grazing the surrounding savanna. Once abandoned, former enclosures become highly productive and long-term grassy glades (Muchiru et al., 2008, 2009; Porensky & Veblen, 2015). In contrast, for up to several kilometers from settlements, savanna grass biomass may be depressed by livestock grazing (Groom & Western, 2013; Western et al., 2009). High densities of livestock grazing maintained over a prolonged time typically displace wildlife (Valls-Fox et al., 2018; Veldhuis et al., 2019), reduce fuel loads for fires (Probert et al., 2019; Veldhuis et al., 2019), and deplete savanna plant and soil nutrients (Sitters et al., 2020). Hence, spatial context is critical when evaluating the impact of pastoral settlements on the functioning of savannas within or at the borders of wildlife protected areas.

Regrowth of plant biomass following disturbance is fundamental to the resilience of tropical grasslands and savannas. Savanna grasslands demonstrate a remarkable capacity to regrow following endogenous disturbances by wild herbivores and fire, often regrowing ground-layer cover within months (Leriche et al., 2003; Van de Vijver et al., 1999; Van Langevelde et al., 2003). However, savanna grasslands are slower to recover from exogenous human-induced disturbances including damage to the soil following cultivation and excessive removal of aboveground biomass due to chronic high-intensity livestock grazing (Belsky, 1986b, 1992; Buisson et al., 2019). Livestock grazing pressure is typically highest closer to settlements because herded cattle and other livestock start and end each day in enclosures (Coppolillo, 2000, 2001). Thus, the regrowth capacity of savanna grasslands would be expected to be lower closer to pastoral settlements and higher further away from them. Further, several wild herbivore species avoid grazing near to pastoralists and livestock altogether, leading to high wild herbivore pressure further away from settlements, generating a livestock–wildlife gradient (Groom & Western, 2013; Valls-Fox et al., 2018). High concentrations of pastoral settlements at the borders of protected areas can displace wild herbivores which increases herbivore consumption and reduces net plant productivity in the core of protected areas (Veldhuis et al., 2019). Therefore, permanent pastoral settlements could potentially reduce savanna regrowth both near to and far away from settlements.

The regrowth capacity of savanna grassland depends strongly upon plant functional groups and species composition. Grass-dominated communities are expected to have higher regrowth capacity than communities dominated by woody or forb species, because basal growing tissue of grasses enables them to quickly compensate tissue loss from herbivory and fire (Belsky, 1986a; Hawkes & Sullivan, 2001; McNaughton, 1983). Pastoralists may increase grass dominance closer to settlements because they harvest woody species for construction materials, fuelwood, and collect woody and forb species for food and medicine (Abate et al., 2010; Veblen, 2013; Young et al., 1995). Yet, even within plant functional groups, there is substantial variation in regrowth following disturbance. For instance, Belsky (1986a) found a sevenfold variation in regrowth in a clipping experiment on 14 common savanna grasses. High-intensity, year-round livestock grazing can act as strong selection pressure on savanna grassland species composition in wildlife grazed savannas, selecting for grassland species tolerant of higher biomass removal and generating distinct communities (Smith et al., 2020; Tegegn et al., 2011; Young et al., 2013). The consequence of changes in grass species composition caused by livestock grazing for plant productivity is less predictable. Livestock-induced changes in savanna grassland composition variously increase, decrease, or have no effect on savanna plant productivity (Charles et al., 2017; Smith et al., 2020; Veblen et al., 2016). Although pastoral settlements may lead to greater grass dominance closer to settlements, changes in regrowth capacity will likely depend on species-specific responses to disturbance.

In Ethiopia, wildlife protected areas cover 16.4% of the land area. These areas are becoming contested spaces, because pastoral communities need access to productive grazing areas for livestock (Jacobs & Schloeder, 2001; Kelboro & Stellmacher, 2015). As a demonstration of land ownership and to ensure access to grazing land sedentarization of pastoral communities is increasing, including within the borders of wildlife "protected" areas. In this study, we investigate the spatial impact of high densities of pastoral settlements on savanna grassland regrowth inside Nech Sar National Park, southern Ethiopia using a clipping experiment with and without exclusion of grazing. Nech Sar was established as a National Park to conserve the Swayne's hartebeest (*Alecelaphus buselaphus swaynei*), and the Park contains other wild herbivores, including plains zebra (*Equus quagga*), Grant's gazelle (*Nanger granti*), and greater kudu (*Tragelaphus strepsiceros*). Local Guji and Kore pastoralists mainly graze cattle (*Bos indicus*). We hypothesize that: (i) grasslands near pastoral settlements have a lower regrowth capacity than those further away from settlements; (ii) excluding herbivores has a stronger positive impact on grassland regrowth closer to settlements compared to further away from them; and (iii) changes to plant functional group and reduction in key grass species underlie changes in grassland regrowth capacity closer to pastoral settlements.

2 | METHODS

2.1 | Study area

Our study was conducted on the central grassland plains of Nech Sar National Park (5°55′42″N; 37°39′52″E), southern Ethiopia (Figure 1). The elevation of the central grassland plains varies between 1250

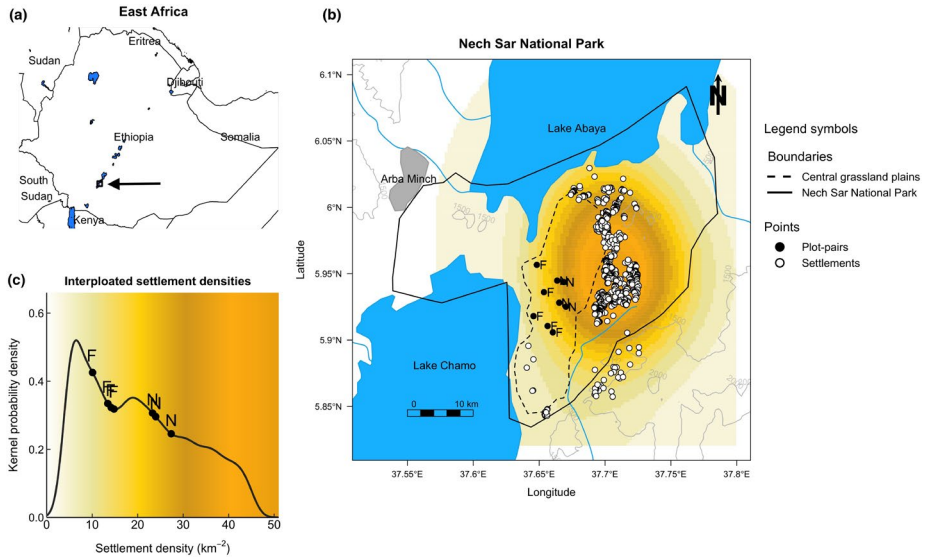


FIGURE 1 The location of (a) Nech Sar National Park, Ethiopia, (b) experimental paired plots and pastoral settlements within Nech Sar National Park, and (c) the distribution of experimental paired plots in relation to interpolated settlement densities within the central grassland plains as of 2014. Paired plots have been classified as *near to* (labeled "N") with density >23 settlements km^{-2} *far from* from (labeled "F") with density <13 settlements km^{-2}

and 1360 m.a.s.l. The grassland plains have an arid to semi-arid climate with an annual precipitation of ~300 mm [1983–2013 TAMSAT estimates (Maidment et al., 2014; Tarnavsky et al., 2014)]. Rainfall is bimodally distributed with two wet seasons, the long wet season from March to May and the short wet season from September to October. Monthly mean air temperature ranges between 24°C and 28°C (Shetie, 2017). The soil of the area predominantly consists of vertisols, fertile soil with a high clay, and organic matter content, with pockets of andosols and vertic cambisols (Shetie et al., 2017; Yusuf et al., 2011). The central grassland plains are dominated by the grass *Chrysopogon plumulousus* "white grass" in the Amharic language from which the name Nech Sar is derived (Fetene et al., 2016). The area of grassland plains has reduced by as much as 75% since 1985, being replaced by woody shrub species such as *Dichrostacyhs cinerea*, *Vachellia* (formerly *Acacia*) sp., and invasive herbs such as *Abutilon* sp. (Fetene et al., 2016, 2019; Yusuf et al., 2011). At the time of the study, the central grassland plains were approximately 80 km^2 within the larger national park area of 514 km^2.

Nech Sar was established as a National Park in 1974. In 1984, the local pastoral communities of the Guji and Kore were evicted from the National Park. Subsequent poor governance, at national and district levels, and disputes over relocations of park boundaries alienated pastoralists, who no longer acknowledge the park boundaries [for details see (Kelboro & Stellmacher, 2015)]. Since the 1990s permanent settlements have increased around the Sermelle stream northeast of the grasslands plains due to the stream's year-round supply of water (pers. comm. Park Ecologist, Bayissa Bussa). Sedentarization of pastoralist communities is evident with a shift from traditional tukuls (buildings with rounded grass roofs to construction of tin-roof buildings (Fetene et al., 2019)). At the same time, wild herbivore populations have declined, exacerbated by revenge killings of wildlife by pastoralists (Fetene et al., 2019; Shibru et al., 2020). During this study, observed wild herbivore densities on the grassland were 8.1 plains zebra km^{-2}; 1.0 Grant's gazelle km^{-2}; 0.3 greater kudu km^{-2}, and 0.06 Swayne's hartebeest km^{-2} (Figure S1). Domestic herbivores comprised 1.4 cattle km^{-2} with no sheep or goats observed (Figure S1). The central grassland plains have been largely fire-free for over 40 years (National Park rangers Admasu Akamo and Asnake Zegeye pers. comm. and Yusuf et al., 2011) with only seven fires (500 m × 500 m) detected using remote sensing (MODIS MCD64A1 burn product) between 2000 and 2012 (Roy et al., 2008).

2.2 | Pastoral settlements

The spatial impact of pastoralists and accompanying livestock pressure on the grassland plains was approximated using the location and distribution of pastoral settlements. Prior to establishing study sites in April 2012, the location of pastoral settlements was identified using Google Earth Pro color satellite images. High-resolution satellite images for the grassland plains represent a mixture of two years (2003 or 2012). Using ArcGIS Pro, we constructed a 1 × 1 km grid of polygons covering the central grassland plains and extending approximately 5 km from the grassland plains. Grid cells were visually scanned for locations of settlements. Point locations were assigned to any settlement structure, including pastoral settlements, circular grass-roofed tukuls or tin-roofed buildings, and livestock enclosures (typically circular structures made of dead woody shrubs or wooden fenced palisades). If pastoralist settlements and livestock enclosures were adjoining or nested within a fenced compound, then adjoining structures or compounds were treated as a single settlement location. Active livestock enclosures were difficult to distinguish (using 2012 imagery) from abandoned enclosure scars that consist of a

grassy glade surrounded by a ring of shrubs (Veblen, 2013; Young et al., 1995). To address this problem, we reassessed settlement locations after our experiments using Google Earth 2014 satellite imagery, which provided complete coverage of the central grassland plains and surrounding areas with higher image resolution.

The majority of pastoral settlements surrounding the central grassland plains were found in a dense cluster northeast of the plains, in the lee side of a hillside spreading from the Sermelle stream to the southeastern shores of Lake Chamo (Figure 1). The highest density of settlements recorded was around 50 settlements per km^2. Given the spatial configuration of pastoral settlements, we adopted an approach of spatially interpolating settlement densities and used this variable as a measure of pastoral settlement impact. Point settlement locations were interpolated assuming kernel density with a Gaussian distribution. Settlement density estimates for the central grassland plains were significantly positively related between our different satellite imagery years 2003 and 2012 versus 2014 (Spearman's rank correlation: r_s =0 .98, p < 0.001). Settlement distribution maps were presented to the Park Warden, Shimelis Zenebe, who confirmed our spatial representation of pastoral settlements around the grassland plains.

2.3 | Site selection and study design

To determine the combined impacts of proximity to pastoral settlements and herbivory on grassland biomass and regrowth, we established exclosures at varying distances from settlements. In April and May 2012, we established nine plot pairs in a grid matrix of 5 km × 3 km from east to west on the grassland plains (Figure 1). Each plot within a pair either excluded or was open to herbivore grazing (as detailed below). Plot pairs were between 500 m and 2500 m apart and ranged between 2300 m and 5600 m in distance from the nearest pastoral settlement. Based on the distribution of pastoral settlements, we assumed livestock herding pressure would be highest in the east, closest to the highest concentration of pastoral settlements, and decline westward toward the center of the grassland plains (Figure 1). Using the spatial interpolation of settlement locations and densities, paired plots were classed as *near to* high-density settlements (four pairs with interpolated settlement densities of >23 settlements km^{-2}) or *far from* high density of settlements (five pairs with interpolated densities of <13 settlements km^{-2}; Figure 1). Interpolated settlement density estimates of plot pairs were negatively correlated with distance to the densest cluster of pastoral settlements northeast of the Sermelle stream (Pearson's correlation: r_p = −0.86, p<0.001) and weakly negatively correlated with distance to the nearest settlement (Pearson's correlation: r_p = −0.13, p = 0.002).

The plots within pairs were randomly assigned as treatments either excluding herbivores or open to grazing, hereafter *exclosed* and *grazed* plots, and were 20 m × 20 m in size. Exclosed plots had a 2-m-high fence around them, constructed using wooden poles wrapped with wire mesh (aperture size: 7.6 cm × 7.6 cm) designed to keep out all large herbivores (>5 kg in size). Within the plot pairs, exclosed and grazed plots were at least 20 m apart to avoid edge effects, with a maximum distance of 60 m to minimize spatial variation in the landscape. Inside each exclosed and grazed plot, five permanent quadrats of 1 m^2 were selected following four random cardinal directions and one quadrat in the center of the plot. Quadrats were located a minimum of 1 m from fenced boundaries. Each quadrat was surveyed for plant species cover and clipped (as detailed below) to determine grassland biomass and regrowth.

To assess grassland regrowth following disturbance, we undertook a clipping experiment with plant material clipped to 5 cm to allow vegetation regrowth (Van de Vijver et al., 1999). Each permanent quadrat was subdivided into four quarters each 0.5 m × 0.5 m in size. The northeast quarters of all quadrats were clipped on three occasions: (1) in November 2012, six months after the initial experimental setup and after the short rainy season, (2) in June 2013 after the long rainy season, and finally (3) in November 2013 after the short rainy season. The northwest quarters were clipped twice in (1) June 2013 and (2) November 2013 and southwest quarter clipped only once in November 2013. The southeast quarter was left unclipped. This sequential clipping allowed us to assess regrowth: The first clipping measured previously unclipped biomass, hereafter *original biomass*, the second clipping measured *first regrowth* one growing season after the first clipping, and a third clipping measured *second regrowth* one growing season after the second clipping. In addition, regrowth can be contrasted to original biomass clipped at the same point in time (e.g., regrowth in the northeast quarter in June 2013 can be compared with original biomass in the northwest quarter). Within each of these clipping treatments, we had 270 measurements of original biomass (i.e., three clipped quarters over three seasons), 180 measures of first regrowth (i.e., northeast quarter and northwest quarters), and 90 measures of second regrowth (i.e., northeast quarter only).

Immediately prior to clipping, grassland canopy composition was identified to species, and relative cover was visually estimated for all vascular plant species in the entire quadrat. After clipping, biomass was immediately sorted into three functional groups: grasses and sedges (hereafter "graminoids"); herbaceous dicotyledons (hereafter "forbs"); and dwarf shrubs (Hawkes & Sullivan, 2001). Clipped plant material was transported on the same day to the botanical laboratory at Arba Minch University (Figure 1) and oven dried at 40°C for 72 h, and dry biomass was weighed (±0.05 g). All biomass measures refer to dry biomass. Original biomass was expressed as g m^{-2} and regrowth after clipping as g m^{-2} $season^{-1}$.

2.4 | Statistical analysis

Grassland regrowth was assessed by contrasting quantities of original biomass versus regrowth and as the capacity of regrowth to attain similar biomass as original biomass. The latter was calculated by subtracting original biomass from the first and second regrowth

using original biomass measures from the same season. The quantity of biomass was analyzed using generalized linear mixed models fitted assuming a Gamma distribution to ensure positive estimates of grassland biomass. Grassland biomass was assessed in relation to proximity to high densities of settlements (near vs. far), herbivore exclusion (excluded vs. grazed), and clipping treatments (original biomass, first and second regrowth) and all two- and three-way interactions as fixed factors, and plot pair as a random factor. The difference between regrowth and original biomass was analyzed using a linear mixed model fitted with a Gaussian distribution (allowing negative values) and with the same model structure with the exception that clipping treatments only contrasted first and second regrowth. These models were applied to total grassland biomass and individual plant functional group biomass, namely graminoids, forbs, and dwarf shrubs. Additionally, we repeated two sets of models testing absolute distance of paired plots to the nearest pastoral settlement and distance to the densest cluster of pastoral settlements instead of our categorical measure of near to vs. far from high densities of pastoral settlements (Tables S1 and S2). The statistical significance of each term in the models was determined by contrasting models using maximum likelihood (ML) with and without fixed factors to generate *P*-values (Bolker et al., 2009; Zuur et al., 2009).

Plant community composition was visualized using nonmetric multidimension scaling (NMDS). Prior to ordination, plant species cover was transformed using Hellinger distance. The optimal number of NMDS axes (k = 3) was chosen based on stress plots. We applied permutational multivariate analysis of variance to test for differences in species composition in relation to proximity to pastoral settlements and herbivore exclusion (Oksanen et al., 2019). The contribution of individual species to plant grassland community differences near to and far from high densities of pastoral settlements was determined using similarity percentage analysis (SIMPER) based on the contribution of individual species to overall Bray–Curtis dissimilarity (Clarke, 1993). Changes in species cover of the most abundant species were analyzed using a generalized linear mixed model with proximity to high densities of settlements, herbivore exclusion, and season as fixed factor and plot pair as the random factor. Species cover was analyzed by fitting a beta distribution to ensure all estimated values were confined within 0 and 1 and later converted to percentages between 0 and 100%. Additionally, we identified plant species associated with proximity to pastoral settlements using indicator species analysis. This analysis identifies species regularly found in a defined category (e.g., habitat), or in our study near to vs. far from high densities of settlements, based upon the occurrence and abundance of species found in each category (De Cáceres et al., 2010).

All analyses were carried out in R version 3.5.3 (R Core Team, 2019) with "glmmadmb," "glmmTMB," and "lmer" from the glmmADMB, glmmTMB, and lme4 package (Bates et al., 2015; Brooks et al., 2017); "metaMD," "adonis," and "simper" from the Vegan package (Oksanen et al., 2019); and "multipatt" in the indicspecies package (De Cáceres et al., 2010).

3 | RESULTS

3.1 | Total grassland biomass and regrowth after clipping

Total original biomass for previously unclipped swards was similar near to and far from high densities of pastoral settlements for grazed and exclosed swards. The original biomass averaged 97.6 ± 55.5 g m^{-2} (mean ± SD) near to and 116.4 ± 79.6 g m^{-2} far from pastoral settlements averaged across grazed and exclosed swards (Figure 2a; Table 1). First and second regrowth after clipping was 2.4 times lower than the original biomass (Figure 2a; Table 1). On average, regrowth only partially attained the same quantities as the original biomass both near to and far from high densities of pastoral settlements. Yet, regrowth after clipping was significantly (p = 0.02) higher far from pastoral settlements compared to near to pastoral settlements, averaging 47% and 69% higher for first and second regrowth, respectively (Figure 2a).

Second regrowth showed a small but significant increase of 9%, from 52.8 g m^{-2} to 57.6 g m^{-2}, compared to the first regrowth far from pastoral settlements across grazed and exclosed swards (settlement × clipping; Table 1). In contrast, regrowth near high densities of pastoral settlements was consistent across clipping frequencies averaging 35.8 g m^{-2} for first regrowth and 34.0 g m^{-2} for second regrowth. In our separate analyses, regrowth was higher further from the densest cluster of pastoral settlements for the second regrowth, but not for the first regrowth (distance × clipping; Table S1). Original biomass and regrowth inside grazed plots increased with distance from the densest settlement cluster and the nearest identified settlement, but there was no effect of these distance measures on biomass and regrowth inside exclosures (distance × exclosure; Tables S1 and S2).

Excluding herbivores significantly increased the original biomass and first and second regrowth compared to grazed swards (Figure 2a; Table 1). Mean original biomass was 48% higher, and first regrowth was 44% higher and second regrowth 52% higher when excluding herbivores compared to grazed swards. Herbivore exclusion was the only factor to significantly influence regrowth from attaining a similar quantity as the original biomass (Figure 2e; Table 1). Excluding herbivores reduced the capacity of the first and second regrowth to attain a similar quantity as the original biomass (Figure 2e). It is noteworthy that this negative effect of herbivore exclusion on regrowth was stronger near to rather than far from high densities of pastoral settlements, although there was no significant settlement ×herbivore exclusion interaction (p = 0.13; Table 1). Distance from the densest cluster of pastoral settlements and to the nearest pastoral settlements had no significant impact on whether regrowth after clipping attained similar biomass quantities to the original biomass (Table S1 and S2).

3.2 | Plant functional groups and grassland species

Grassland biomass comprised 83 ± 23% (mean ± SD) graminoids, 9 ± 17% forbs, and 8 ± 16% dwarf shrubs. Patterns for graminoid

biomass and regrowth followed similar patterns to those of the total grassland community (Figure 2b,f; Table 1). The only exception was that there was no significant increase in second regrowth far from high densities of pastoral settlements compared to near to settlements (Table 1). Dwarf shrub biomass was negatively influenced by clipping, while otherwise demonstrating limited response to proximity to high densities of pastoral settlements or herbivore exclusion (Figure 2d,h; Table 1). Dwarf shrub biomass and regrowth demonstrated the largest temporal and spatial variation across all studied plant functional groups.

Forb biomass was not significantly influenced by clipping, and there was no significant difference in regrowth compared to the original biomass (Figure 2c,g: Table 1). Forb biomass and regrowth were significantly influenced by an interaction between proximity to high-density pastoral settlements and herbivore exclusion. Near to high densities of pastoral settlements, herbivore exclusion significantly increased the biomass and regrowth of forbs, whereas the opposite occurred far from high densities of pastoral settlements (settlement × exclosure; Table 1; Figure 2c,g).

Grassland species composition was significantly ($p < 0.001$), but weakly, shaped by proximity to high density of pastoral settlements ($F_{1,269} = 18.2$, $R^2 = 0.06$) and herbivore exclusion ($F_{1,269} = 1.38$, $R^2 = 0.02$). Grasslands near high densities of pastoral settlements, and swards excluding herbivores, contained a nested subset of the larger species pool found far from settlements and grazed swards, respectively (Figure S2). For example, a total of 40 species were found near to high densities of pastoral settlements, including only seven unique species that were not found in the larger species pool of 50 species located further from high densities of pastoral settlements.

The grasses *Chrysopogon plumulosus* and *Bothriochloa insculpta* dominated grassland communities near to and far from high densities of pastoral settlements (Figure 3). The cover of *B. insculpta* was significantly lower when grazed ($p = 0.02$) and significantly ($p = 0.02$) declined during the experiment over the seasons, likely negatively influenced by clipping (Figure 4a,b). In contrast, *C. plumulosus* was significantly ($p = 0.01$) higher in grassland swards closer to high densities of pastoral settlements (Table S3; Figure 4c,d). In grassland communities far from high densities of pastoral settlements, other grassland species co-dominated communities in addition to *C. plumulosus* and *B. insculpta*. Notable in this case is the co-dominance of stoloniferous grass *Cynodon nlemfuensis* when excluding herbivores and tussock grass *Heteropogon contortus* when grazed (Figure 3). These species were significantly ($p < 0.001$) associated with grassland communities far from high densities of pastoral settlements (Table S4). From our indicator analysis, a greater number of grass species, including *C. nlemfuensis*, were indicative of grassland communities far from high densities of pastoral settlements, further supporting the importance of co-dominance of grass species for grassland regrowth (Table S4). Further, forb species including *Plectranthus punctatus*

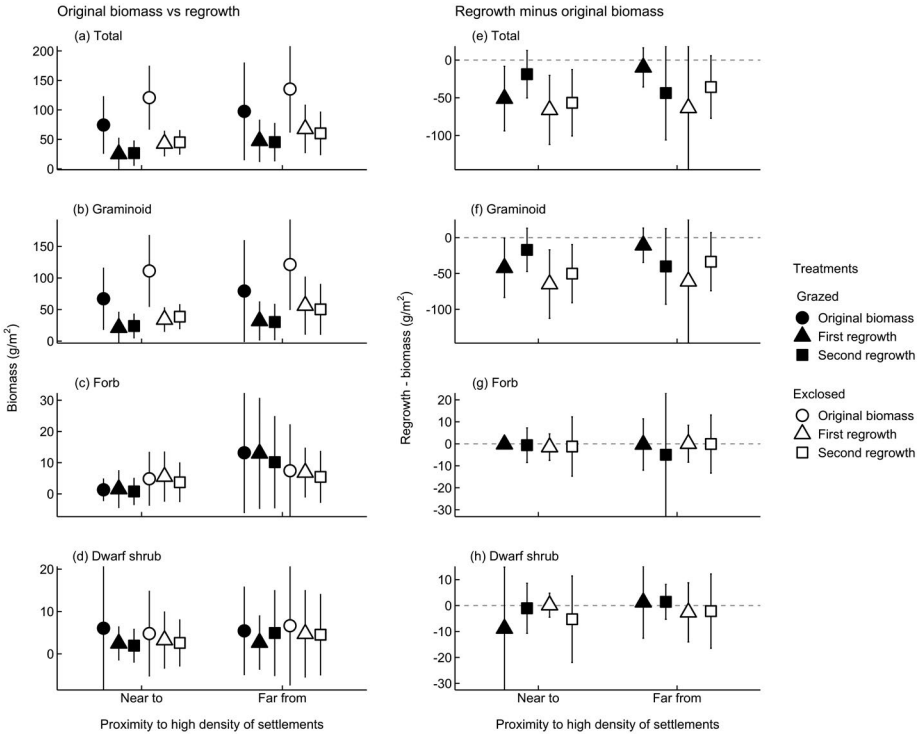


FIGURE 2 Original biomass compared to first and second regrowth after clipping treatments (left panels) and regrowth minus original biomass (right panels) in relation to proximity to high densities of settlements and herbivore exclusion. Total (a, e), graminoid (b, f), forb (c, g), and dwarf shrub (d, h) biomass and regrowth are shown separately. Regrowth is a measure of biomass per season (g m^{-2} $season^{-1}$). In the (e–h) panels, the gray dashed line represents no difference between regrowth after clipping and original biomass. Error bars represent ±1 standard deviation

and legumes such as *Alysicarpus glumaceus* and *Tephrosia* sp. were indicative of grassland communities far from high densities of pastoral settlements and were either rarely found or absent in grassland communities near pastoral settlements (Table S4).

4 | DISCUSSION

In this study, proximity to high densities of pastoral settlements reduced the regrowth of savanna grasslands and the exclusion of wild and domestic herbivores did not ameliorate the effect. Instead, excluding herbivores resulted in lower grassland regrowth in swards both near to and far from pastoral settlements. In part, the positive effect of grazing on regrowth may be due to the smaller quantity of regrowth required to attain grazed biomass, because of the lower quantity of grazed biomass compared to inside exclosures. Grasses comprised the bulk of grassland biomass and regrowth. For the dominant grasses across the Nech Sar grassland plains, *Chrysopogon plumulosus* cover was higher closer to high densities of pastoral settlements whereas *Bothriochloa insculpta* cover was lower outside exclosures and declined during the experiment, likely due to repeated clipping. Grassland communities further from pastoral settlements had greater cover of co-dominant grasses, notably *Cynodon nlemfuensis* and *Heteropogon contortus* that sustained grass cover following grazing and clipping. Collectively, these results suggest that

TABLE 1 Statistical outputs from modeling the impact of proximity to high densities of pastoral settlements, herbivore exclusion and clipping frequency on grassland biomass and regrowth for (a) total biomass, (b) graminoids, (c) forbs and (d) dwarf shrubs

	Biomass vs. regrowth			Regrowth minus biomass		
Models and variables	***F***	**df**	***p***	***F***	**df**	***p***
(a) Total biomass						
Pastoral settlements	1.6	1	0.21	0.2	1	0.67
Herbivore exclosure	68.4	1	<0.001	12.3	1	<0.001
Clipping frequency	206.4	2	<0.001	0.4	1	0.33
Settlement × exclosure	1.1	1	0.29	2.3	1	0.13
Settlement × clipping	7.9	2	0.02	1.0	1	0.33
Exclosure × clipping	0.5	2	0.78	1.0	1	0.98
Settlement × exclosure × clipping	0.4	2	0.81	3.0	1	0.08
(b) Graminoids						
Pastoral settlements	0.4	1	0.54	0.1	1	0.75
Herbivore exclosure	87.2	1	<0.001	12.6	1	<0.001
Clipping frequency	219.3	2	<0.001	0.5	1	0.49
Settlement × exclosure	0.2	1	0.64	2.4	1	0.12
Settlement × clipping	3.6	2	0.17	0.8	1	0.38
Exclosure × clipping	1.0	2	0.61	1.3	1	0.75
Settlement × exclosure × clipping	0.2	2	0.89	2.0	1	0.15
(c) Forbs						
Pastoral settlements	6.1	1	0.01	0.1	1	0.71
Herbivore exclosure	5.4	1	0.02	0.7	1	0.41
Clipping frequency	4.3	2	0.12	0.1	1	0.73
Settlement × exclosure	30.9	1	<0.001	1.3	1	0.26
Settlement × clipping	3.1	2	0.21	0.1	1	0.77
Exclosure × clipping	1.8	2	0.41	0.1	1	0.72
Settlement × exclosure × clipping	2.0	2	0.37	0.1	1	0.81
(d) Dwarf shrubs						
Pastoral settlements	0.9	1	0.32	3.4	1	0.06
Herbivore exclosure	0.4	1	0.51	1.5	1	0.22
Clipping frequency	7.8	2	0.02	0.1	1	0.83
Settlement × exclosure	0.1	1	0.74	1.4	1	0.23
Settlement × clipping	3.0	2	0.26	0.1	1	1
Exclosure × clipping	0.8	2	0.66	0.7	1	0.4
Settlement × exclosure × clipping	0.9	2	0.65	1.0	1	0.32

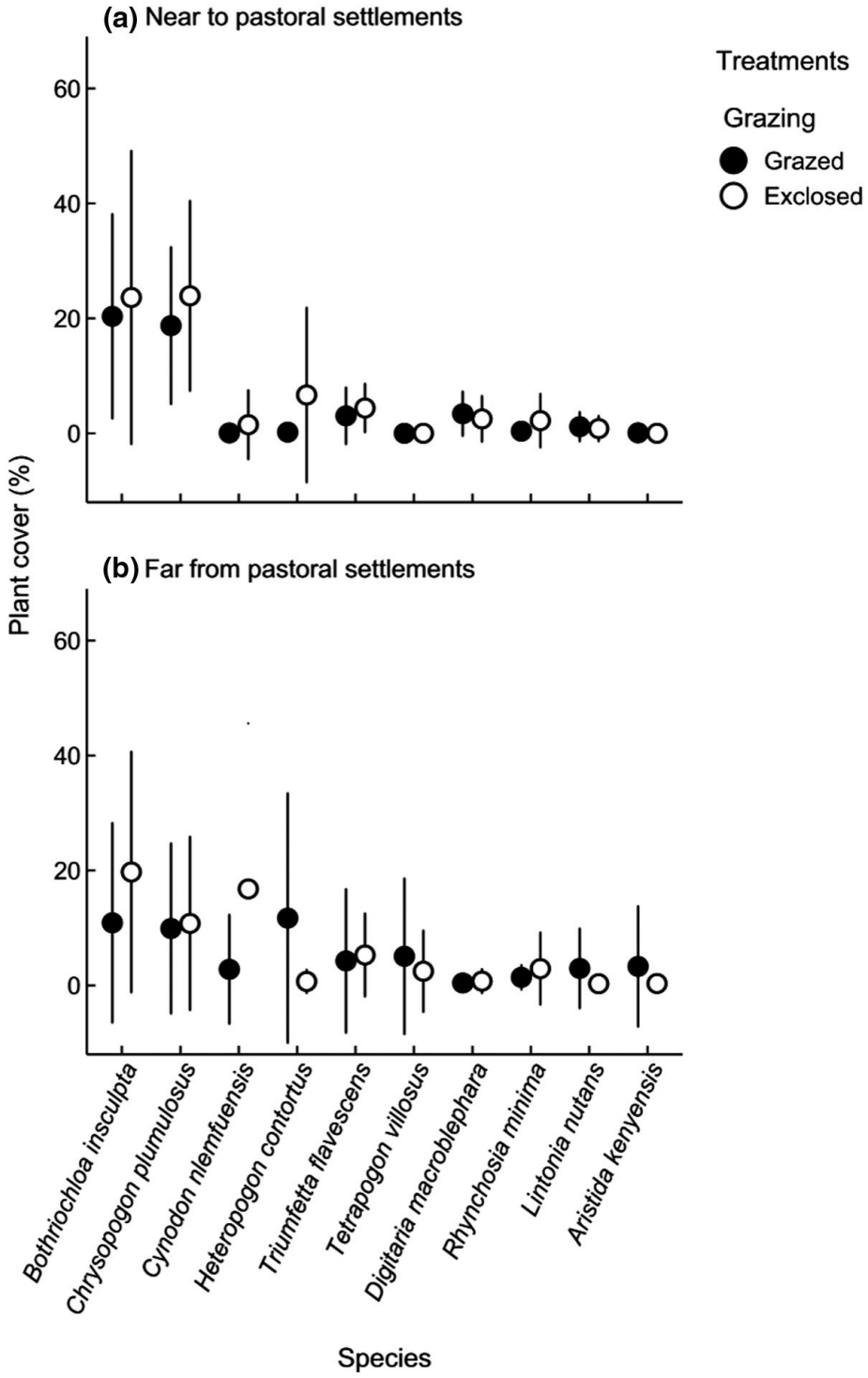


FIGURE 3 Average plant cover of dominant grassland species (a) near to and (b) far from a high density of pastoral settlements and for grazed swards and inside herbivore exclosures. Average species cover is a combination of original biomass and clipping treatments. Error bars represent ±1 standard deviation

pastoral settlements can alter savanna regrowth and this is mediated through subtle changes in community composition.

As savannas are increasingly being disturbed and modified by humans, a key concern is the alteration, or even loss, of ecosystem functions. In Nech Sar National Park, after six months biomass regrowth was 2.4 times lower than previously unclipped swards. This rate of recovery was slower than clipping experiments in other African savanna grasslands spanning from wet to arid climatic conditions (Leriche et al., 2003; Van de Vijver et al., 1999; Van Langevelde et al., 2003). This may be due to the pervasive impact of pastoralists settlements across the entire central grassland plains in Nech Sar National Park. Pastoralists and

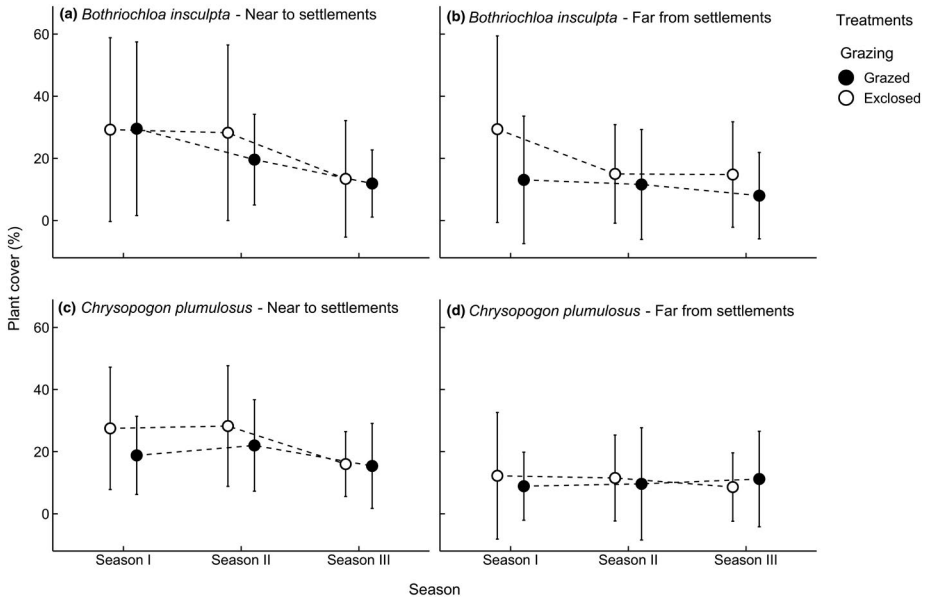


FIGURE 4 Dominant grass species *Bothriochloa insculpta* cover (a) near to and (b) far from a high density of pastoral settlements, and *Chrysopogon plumulosus* cover (c) near to and (d) far from settlements and across seasons and for grazed swards and inside herbivore exclosures. Average species cover is a combination of original biomass and clipping treatments. Error bars represent ±1 standard deviation

livestock have been reported throughout the grassland plains (Fetene et al., 2016, 2019), though pressure is likely higher closer to settlements. However, our results suggest that the slow rate of recovery of Nech Sar grasslands may relate to the sensitivity of dominant grasses to proximity to pastoral settlements, grazing, and likely to clipping. Dominant grasses *C. plumulosus* and *B. insculpta* are preferred by livestock, and the abundance of these grasses declines with increasing abundance of livestock (Cornelius & Schultka, 1997; Kassahun et al., 2008). The slower rate of regrowth of Nech Sar compared to other African grasslands thus seems driven by the response of two dominant grass species. Although recent pressure from livestock has not removed these dominant grasses from Nech Sar grassland plains, intensification of livestock grazing (e.g., stimulated by our clipping experiment) will lead to a decline in species cover.

Excluding herbivores is an established approach to restore heavily livestock-grazed ecosystems in Ethiopia and tropical savannas (Buisson et al., 2019), restoring plant cover and soil nutrients (Mekuria & Veldkamp, 2012) and woody cover and diversity (Yami et al., 2006; Yayneshet et al., 2009). Restoring palatable species is more challenging using only exclosures, even after several decades (Seymour et al., 2010). Indeed, a growing body of evidence suggests that large mammalian wild herbivores, and to a lesser extent livestock, stabilize savanna grassland productivity by maintaining community evenness (Charles et al., 2017; Mortensen et al., 2018; Riginos et al., 2018). Our findings support this and highlight the role of wild and domestic herbivores in sustaining grassland regrowth. To sustain ecosystem functioning in Nech Sar grasslands, emphasis should be placed on conserving wild herbivore assemblages (Fetene et al., 2019; Shibru et al., 2020) rather than excluding herbivores altogether.

Woody encroachment in savannas is commonly associated with pastoral settlements and intensification of livestock grazing, as reported in other studies in Nech Sar National Park (Fetene et al., 2016, 2019; Utaile et al., 2020; Yusuf et al., 2011). However, at our sites, dwarf shrub species occurred at low abundances and were unaffected by proximity to pastoralist settlements or (short term) herbivore exclusion. Instead, forb biomass was most responsive to proximity to pastoral settlements and herbivore exclusion; forb biomass increased following herbivore exclusion near to high densities of pastoral settlements, with the opposite pattern observed far from settlements. Additionally, in our study, a number of forb species were indicators for plant communities far from high densities of pastoral settlements, because these forbs were rare or absent near settlements. Species included palatable leguminous forbs, such as *Alysicarpus glumaceus*, which is likely grazed out by livestock (Boonman, 1993), and forbs typically consumed by pastoralists for food or collected for medicinal purposes, such as *Corchorus trilocularis* (Belayneh et al., 2012). Forbs are often ignored in savanna vegetation ecology compared to grasses and woody species (Siebert & Dreber, 2019). Changes in forb biomass and absence of certain species may serve as key indicators of pastoral transformation of the savanna landscape.

Sedentarization of pastoralists communities has been shown to alter plant productivity (Groom & Western, 2013; Western et al., 2009), woody cover (Porensky & Veblen, 2015; Veblen, 2013), and fire frequencies (Probert et al., 2019; Veldhuis et al., 2019). Our study demonstrates that sedentarization of pastoralists alters savanna grassland regrowth. We found that changes in grassland regrowth are dependent on dominant species within savanna grasslands. Grassland communities with several co-dominant species have higher regrowth capacity. Monitoring of the impact of pastoral settlements

is increasingly being conducted using remote sensing technologies. However, our results suggest that changes in grassland regrowth may be subtle in the form of minority presence of grass, forb, and legume species and hard to detect using remote sensing tools.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHORS' CONTRIBUTION

DW and JDMS conceived and designed the study. DW collected vegetation data. KERC collected remote sensed data. SWS undertook the statistical analysis. SWS led writing of the manuscript, and all authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/badge/DOI/10.5281/zenodo.4587689.svg.

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SUPPORTING INFORMATION

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