

Savannah trees buffer herbaceous plant biomass against wild and domestic herbivores

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Abstract

Questions: Given the growing abundance and dominance of domestic herbivores in savannah ecosystems, can trees maintain plant herbaceous standing biomass under increasing herbivore pressure? Are there differences in the capacity of leguminous and non-leguminous trees in sustaining understory herbaceous biomass? And finally, to what extent does plant community composition underneath trees modulate the effects of herbivore assemblage and abundance on herbaceous biomass?

Location: Pasturelands¹ and protected areas along the borders of the Serengeti National Park, Tanzania, East Africa.

Method: Monthly herbaceous biomass was monitored non-destructively using a calibrated pasture disc. Measurements were taken within a network of paired exclosures and open plots, underneath large leguminous and non-leguminous tree canopies and outside canopies. Herbivore community assemblage compositions and abundances were characterised using monthly dung counts, and herbaceous plant community composition was surveyed annually every wet season over two years.

Results: Overall, we found that trees promote herbaceous standing biomass, particularly in the presence of moderate herbivory rather than under herbivore exclusion. Greater herbivore abundance and livestock dominance reduced herbaceous plant biomass, but trees, particularly leguminous trees, limited these negative effects. This capacity for trees to limit the effect of herbivores was related to herbaceous plant species composition. Understory plant communities that were compositionally typical of protected areas sustained the highest plant biomass when found in pasturelands with high herbivore pressure.

Conclusion: Our findings give greater credence to the importance of preserving large trees in savannah landscapes increasingly dominated by high abundances of livestock. Moreover, our results highlight that park managers and pastoralists need to maintain the specialist herbaceous understory community beneath trees in order to benefit from facilitative tree–understory interactions.

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KEYWORDS

facilitation, fire, livestock, mutualism, nitrogen symbiosis, plant–herbivore interactions, refugia, tree–grass ratio

1 | INTRODUCTION

Tropical savannahs are characterised by a continuous grass-dominated herbaceous layer interspersed by scattered trees or shrubs (Belsky, 1993; Scholes & Archer, 1997). Trees can act as small-scale biodiversity hotspots, provide structural complexity and spatial heterogeneity in savannah ecosystems (Belsky, Mwonga, Amundson, et al., 1993; Munzbergova & Ward, 2002). Most notably, trees play an important role in shaping spatial heterogeneity of herbaceous biomass. By competing for water, nutrients and light, trees can suppress understory plant biomass (Belsky, Mwonga, Amundson, et al., 1993; Ludwig, Dawson, Prins, Berendse, & Kroon, 2004; Smit, 2005; Riginos, Grace, Augustine, & Young, 2009). Yet, it is widely documented that savannah trees can also facilitate understory biomass by improving water relations, soil nutrient cycling and/or providing protection from herbivory (Belsky, Mwonga, Amundson, et al., 1993; Belsky, 1994; Riginos & Grace, 2008). The balance between competitive and facilitative effects of trees on the herbaceous understory has been found to be contingent on wider environmental factors such as annual rainfall (Belsky, Mwonga, Amundson, et al., 1993; Dohn et al., 2013), fire (Coetsee, Bond, & February, 2010), tree density (Riginos et al., 2009), individual tree size (Treydte, Grant, & Jeltsch, 2009; Moustakas, Kunin, Cameron, & Sankaran, 2013), functional type (i.e., leguminous with nitrogen-fixing symbionts *versus* non-leguminous trees), and species (Scholes & Archer, 1997; Blaser, Sitters, Hart, Edwards, & Venterink, 2013). Although insightful, the majority of these tree–herbaceous understory generalities are from studies in wildlife-dominated savannahs with low herbivore densities and several meta-analyses and reviews on savannah tree–herbaceous understory interactions exclude heavy grazing altogether (Blaser et al., 2013; Dohn et al., 2013; Treydte, Baumgartner, Heitkönig, Grant, & Getz, 2013). Yet, the savannah landscape is rapidly changing with a widespread loss of wild herbivores and their replacement with higher densities of livestock (Hempson, Archibald, & Bond, 2015, 2017). A pertinent question is whether trees exert competitive or facilitative effects on herbaceous understory productivity in savannah ecosystems which are increasingly grazed by livestock.

The competition–facilitation continuum predicts that with increasing stress, the net outcome of plant–plant interactions will be positive, supporting growth and reproductive success. Herbivores can add to stress, thus cancelling out facilitative interactions (Smit, Rietkerk, & Wassen, 2009), for example, by consuming the facilitated growth of understory plants. However, facilitative effects of savannah trees on understory plants can be greater in the presence of herbivores rather than when excluding them (Augustine & McNaughton, 2006; Treydte et al., 2009). Herbivores are attracted to nutrient-rich grasses found underneath trees, concentrating dung and urine deposits and enhancing growth and nutrient enrichment of understory

vegetation (Ritchie, Tilman, & Knops, 1998; Treydte, Heitkönig, Prins, & Ludwig, 2007; Treydte et al., 2013, 2009; Treydte, Riginos, & Jeltsch, 2010). At low densities of wild herbivores, such tree facilitative effects have been found to be stronger underneath leguminous trees with nitrogen-fixing symbionts or larger savannah trees due to already elevated soil and plant nutrient contents (Treydte et al., 2009; Blaser et al., 2013; Dohn et al., 2013; Moustakas et al., 2013). Yet, beneficial impacts of herbivores on tree understory vegetation may decline at high herbivore densities, irrespective of tree functional type or stature. In a single study in Kenya, beneficial soil fertility and herbaceous biomass effects under large leguminous and non-leguminous trees were lost under heavy livestock grazing due to soil compaction (Belsky, Mwonga, & Duxbury, 1993). Nevertheless, much more work is required to derive generalities of how herbivore pressure and livestock dominance in savannahs interact with the functional capacity of trees in tree–understory interactions.

At low herbivore density, in wildlife-dominated savannahs it is well known that plant communities found underneath trees can be compositionally distinct from those outside tree canopies, supporting understory specialists (Belsky, Mwonga, & Duxbury, 1993; Munzbergova & Ward, 2002; Smit, 2005; Riginos et al., 2009; Treydte et al., 2010; Stahlheber, Crispin, Anton, & D'Antonio, 2015). Less attention has been given to how understory plant species composition potentially mediates the impact of wild and domestic herbivores on savannah tree–herbaceous vegetation interactions. Compared to plant communities outside tree canopies (see Porensky, Wittman, Riginos, & Young, 2013; Young et al., 2013; Young et al., 2018), understory plant communities may be more resistant or resilient to changes in herbivore assemblage and intensity. To support growth in shaded conditions, understory plant species have a higher proportion of non-digestible fibres, tannins and other polyphenols that deter herbivores (Rohner & Ward, 1997; Treydte et al., 2007). Yet, greater access to soil nutrients may support resilient understory communities that are able to regrow and persist following herbivore damage (Ritchie et al., 1998; Hawkes & Sullivan, 2001; Riginos et al., 2009). Given the desirability of understory specialist plant species for herbivores (Smit, 2004, 2005), we would expect many understory specialist plant species to be reduced and eventually lost with increasing herbivore densities.

Across the savannah biome, the highest rates of tree clearance and land conversion from wildlife to livestock-dominated savannah are concentrated at the borders of protected areas, e.g., national parks (Beale et al., 2013; Fynn, Augustine, Peel, & Garine-Wichatitsky, 2016; Veldhuis et al., 2019). Thus, we directed our attention to an increasingly common juxtaposition of wildlife- *versus* livestock-dominated savannah across the border of the Serengeti National Park, Tanzania, and its impact on tree–herbaceous vegetation interactions. Utilising a network of small-scale exclosures underneath trees and

outside tree canopies, we studied the following: (a) whether savannah trees maintain herbaceous standing biomass with increasing livestock dominance and abundance; (b) whether there are differences in the maintenance of herbaceous biomass beneath leguminous and non-leguminous trees across different herbivore assemblages and abundances; and lastly (c) whether understory species composition modulates the effect of wild and livestock herbivory on savannah tree–herbaceous interactions. We hypothesised that savannah trees would facilitate herbaceous biomass from low to moderate herbivore pressure across herbivore assemblages, with greater plant biomass underneath leguminous trees due to nitrogen-fixing symbionts. However, we predicted that facilitative effects of both tree functional types would be lost at high herbivore pressure due to a loss of productive understory canopy specialists sensitive to intense herbivory.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was performed in grazed wooded savannahs south of the Serengeti National Park, Tanzania (latitude 2°00" to 2°30" S and longitude 34°00" to 34°30" E) with an elevation of 1,200–1,670 m a.s.l. Two rainfall regions were selected: a *wet region* (1,287 ± 191 mm annual rainfall, mean ± standard deviation between 2015 and 2017) in the west close to Lake Victoria and a *mesic region* (699 ± 105 mm annual rainfall) in the east within the rainfall shadow of the Ngorongoro crater (Huffman, 2017; Figure 1). Rainfall is seasonal, with a dry season from June to October and a bimodal wet season between November and May, including a short and long wet season, although this seasonality is stronger in the mesic rather than the wet region. Soils were less fertile in the wet region (means ± SD: carbon 6.0 ± 1.5 kg/m²; nitrogen 0.4 ± 0.1 kg/m² in the upper 0–15 cm) having sandy arenosols, compared to the mesic region (carbon 5.4 ± 1.0 kg/m²; nitrogen 0.6 ± 0.1 kg/m²) with gravelly leptosols and underlying calcareous tuff and granite/gneiss bedrock (ISRIC, 2018). Within rainfall regions, sites encompassing a wildlife–livestock herbivore gradient from inside to outside protected areas were selected on similar soil types. Tree overstory composition was similar across sites, with dominance of leguminous *Vachellia tortilis* (the genus *Vachellia* was formerly *Acacia*) and *Vachellia robusta* and non-leguminous *Commiphora africana* and *Commiphora schimperi* trees with the exception of pasturelands in the wet region where the overstory comprised leguminous *Vachellia drepanolobium* and non-legume *Balanites aegyptiaca* trees. Herbaceous plant species richness was higher in the mesic region, totalling 113 species in wildlife-protected areas and 101 in pastureland compared to 43 and 74 species, in the wet region wildlife-protected areas and pastureland. However, herbaceous species composition was not strongly influenced by rainfall region or herbivore regime but diverged primarily based on tree canopy type, fire history and tree height (see below).

Within wildlife-protected areas, apart from periodic episodes of migrating wildebeest (*Connochaetes taurinus*) and zebra (*Equus*

burchelli), wild herbivore densities are typically low and include elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), giraffes (*Giraffa camelopardalis tippelskirchii*), impala (*Aepyceros melampus*) and various species of antelope. In contrast, outside protected areas densities of livestock, namely cattle (*Bos indicus*), sheep (*Ovis aries*) and goat (*Capra aegagrus hircus*), are high. Estimated cattle densities average four cattle per km² (and up to 36 cattle per km²) bordering wildlife-protected areas (TAWIRI, 2016) and combined livestock biomass averages 380 kg metabolic biomass/km² during the dry season (Figure 1). The Serengeti National Park is not fenced, allowing free movement of wildlife outside of protected areas into adjacent pastureland. Likewise, herders regularly illegally graze livestock 5–8 km into the protected areas (Veldhuis et al., 2019).

2.2 | Study design

To capture a wide range of wildlife to livestock herbivore assemblages and intensities, we established sites inside protected areas, at the border of protected areas and outside protected areas on village pasturelands (Figure 1). In each rainfall region, we initially established four sites inside protected areas, at park boundaries and on pasturelands, with an extra four sites in an additional protected area in the mesic region (Figure 1). Vandalism and robbery at the boundaries of protected areas reduced our original experimental setup. Furthermore, a lack of livestock dung at remaining border sites suggested an absence of illegal grazing. As such, sites were classified as either *wildlife-protected areas* or *pasturelands*. The final design for the experiment consisted of eight sites in the wet region (4 × protected areas and 4 × pasture) and 14 sites in the mesic region (10 × protected areas and 4 × pasture; Figure 1). Within rainfall regions, all sites were within 10 km of one another.

Outside the park, intense livestock grazing usually results in reduced fire frequencies due to insufficient fuel loads in the dry season, in contrast to regular burning undertaken by park managers inside the protected areas (Veldhuis et al., 2019). By selecting sites at the periphery of protected areas we aimed to reduce variation in fire frequency given an increasing retraction of fire from the boundaries of the Serengeti ecosystem (Veldhuis et al., 2019). However, minimising variation in fire history was not possible and mesic protected areas ranged from 2 to 12 years since the last fire (average six fires over 16 year period from 2000), mesic pastures 6 years (six fires over 16 years), wet protected areas 2 years (seven fires over 16 years). Wet pastureland had no fires based on MODIS MCD 45A burn product over the years 2000–2016. Given our inability to adequately control for fire history this was included in our statistical analyses (outlined below). Nevertheless, no fires directly influenced our experimental plots over the duration of the study.

At each site, we selected four replicate *blocks* based on the same co-dominating canopy species at a given site as well as soil characteristics (type, texture, organic matter and nutrient contents). Each block comprised a 50 m × 50 m area and blocks were spaced ~500 m apart. At each block we established six permanent experimental

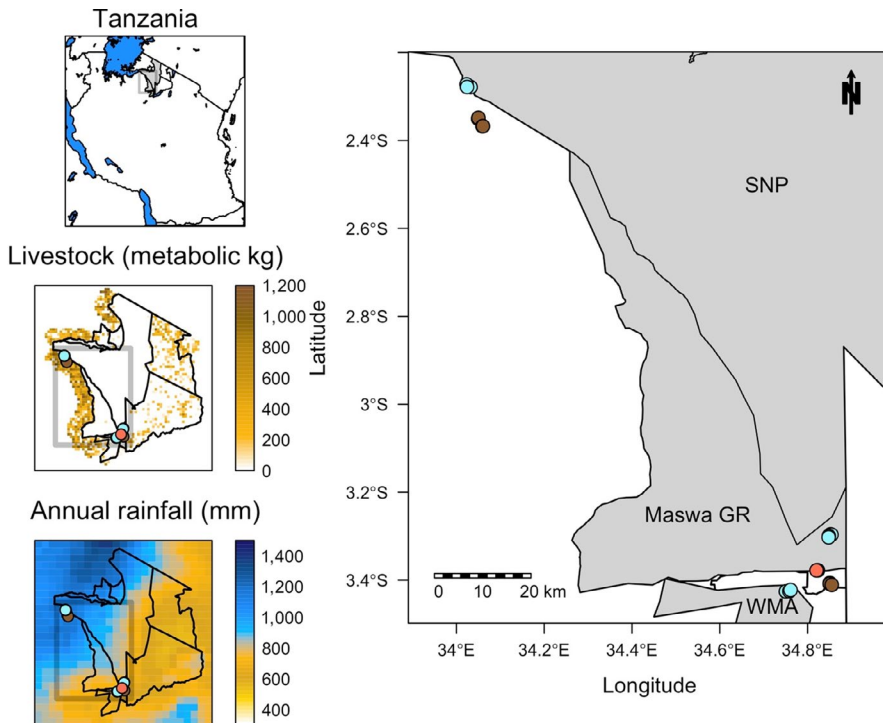


FIGURE 1 Enclosure experiment locations across a wild and domestic herbivore gradient surrounding the Serengeti National Park (SNP), Tanzania. Enclosure experiments were established in wildlife-protected areas (grey-filled areas and light blue symbols), at the borders of wildlife-protected areas where there is illegal livestock grazing (red symbols) and outside wildlife-protected areas on livestock-dominated village pastureland (brown symbols). Sites encompassing a wild–domestic herbivore gradient were established in two rainfall regions; wet (southwest) and mesic (southeast) savannahs. The distribution of livestock metabolic biomass kg/km² is from an aerial dry season census carried out in 2016 (TAWIRI, 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

plots, these included three open and three enclosed plots underneath leguminous trees, underneath non-leguminous trees and outside tree canopies. Due to the importance of tree size for herbaceous productivity, we aimed to minimize variation in selected tree heights (Treydte et al., 2007; Blaser et al., 2013). Across the system, mean tree heights (\pm SD and median in parentheses) for each species were as follows: the legumes were *Vachellia tortilis* 7.3 ± 1.2 m (6.8 m), *Vachellia robusta* 6.7 ± 1.1 m (7.0 m), *Vachellia drepanolobium* 4.4 ± 0.5 m (4.2 m) and the non-legumes were *Balanites aegyptiaca* 4.9 ± 1.1 m (4.8 m) and *Commiphora* species 4.9 ± 1.0 m (4.6 m). Across our study system, there remained a 2.5-fold variation in selected tree heights, so tree height was also included in our statistical analyses (outlined below). Tree height was measured annually using a clinometer (Nikon, Forestry Pro 550). Plots outside of tree canopies were selected following random cardinal directions from the centre of each block and situated a minimum distance of 1.5 times the canopy radius of the nearest tree (Treydte et al., 2007).

In each block, enclosures and open plots were paired underneath one leguminous and one non-leguminous tree. Enclosures underneath trees were triangular with the corner adjoining either the north- or the south-facing side of the tree with an approximate enclosed area of 2.3 m². Outside tree canopies we constructed square 1.6 m² enclosures paired with marked open plots within 10 m of these enclosures. Enclosures were either constructed out of steel metal mesh or wooden poles with barbed wire and sisal depending on the likelihood of fire and theft at specific sites, respectively. All enclosures were designed to exclude mammalian herbivores >5 kg body mass. Due to significant human and animal damage to trees and enclosures later in the experiment (after the initial robbery outlined above) a further four plots were excluded from the study, namely, paired enclosures and open plots under a leguminous tree that was burnt down in the mesic

pastureland, one enclosure under a leguminous tree and one outside tree canopy in different mesic protected area sites that were repeatedly damaged by wildlife. Across all sites, we had 128 vegetation plots.

2.3 | Measurements

Herbaceous biomass underneath trees and outside tree canopies was measured non-destructively using a pasture disc meter (Bransby & Tainton, 1977; Trollope & Potgieter, 1986; Moustakas et al., 2013), specifically calibrated to the Serengeti ecosystem. Herbaceous biomass was estimated from pasture disc meter readings (in cm) using the formula $y = 0.0563x^{0.68}$ where x is the disc reading in cm and y the grass biomass in kg/m². Pasture measurements were applied to herbaceous vegetation, namely graminoids and forbs, avoiding any large shrub or tree saplings. Ground cover in plots was primarily composed of herbaceous graminoids and forbs, averaging $57 \pm 24\%$ cover (mean \pm SD). Woody forbs and dwarf shrubs accounted for $0.5 \pm 2.5\%$ cover and did not influence pasture disc estimates (R-Integrated Nested Laplace Approximation [INLA] model, posterior mean $0.408 \pm -1.025/1.840$ with \pm lower and upper quartile estimates). The pasture meter disc had an area of 0.16 m² and was used four times inside each experimental plot. Herbaceous biomass measurements estimated using pasture disc meters were taken at monthly intervals between May 2016 to May 2018.

Spatial and temporal variation in herbivore abundance was characterised by counting fresh dung piles at each site. All fresh dung (i.e., less than a few days old) was counted along a 4 m \times 50 m transect every month. The herbivore assemblage was characterized by grouping dung into four herbivore guilds separating wild and domestic herbivores and loosely based on dietary niche and body size

(Riginos & Grace, 2008; Young et al., 2018). Our herbivore guilds included: large livestock grazers (referring to cattle), small livestock grazers and mixed feeders (referring to sheep and goats), wild grazers (for example wildebeest, zebra, impala and gazelles and including mixed feeders) and wild browsers (mainly large herbivores such as giraffe and elephant). Cattle dung comprised on average 64% of dung deposited in pastureland and 4% inside wildlife-protected areas. Our livestock gradient encompassed an estimated cattle metabolic biomass range of 0–1,522 kg per site on pastureland and 0–354 kg per site in wildlife-protected areas (means \pm SD: 408 \pm 418 kg for pastureland and 26 \pm 73 kg for wildlife-protected areas) over the duration of the study. Dung counts were used as part of a multivariate analysis (below) to generate a score for herbivore assemblages as well as using total dung count as a coarse measure of total herbivore abundance (Riginos & Grace, 2008; Young et al., 2013).

We estimated herbaceous species cover at peak above-ground biomass in all plots in May–June 2016, May 2017 and May 2018. Percent cover of each species was visually estimated within a 0.36 m² quadrat inside each plot. In total, 175 herbaceous plant species were recorded across all plots over the duration of the experiment.

2.4 | Rainfall data

As soil moisture can modulate the facilitative effect of trees on the herbaceous understory in savannah ecosystems (Ludwig, Dawson, et al., 2004; Ludwig, Kroon, Berendse, & Prins, 2004), we estimated soil moisture by proxy using daily precipitation. We obtained satellite-based daily rainfall from NASA's Goddard Earth Sciences Data and Information Services Center (Huffman, 2017) and half-hourly measurements of cloud cover were taken using multi-satellite microwave data at 10 km \times 10 km spatial resolution. Between May 2016 and May 2018 we further measured soil moisture in all plots at a 5 cm depth using a hand-held probe (Theta probe ML2, Delta-T, UK) every three months. Both satellite-based rainfall estimates and plot-scale soil moisture measurements were significantly positively related with a correlation of 0.78 (Pearson's correlation test: $t_{780} = 34.9$, $p < 0.001$). Using the daily satellite rainfall estimates, we calculated cumulative rainfall for the interval preceding each monthly biomass and herbivore dung measurement measured in mm.

2.5 | Statistical analysis

To generate a single measure of herbivore assemblage and plant species composition we used multivariate techniques. Firstly, to generate a herbivore assemblage score that could differentiate herbivore assemblages through time we applied principal response curves (PRC) to herbivore dung counts. PRC is based on redundancy analysis, but designed to help interpret multivariate response within a repeated-measure framework (Van den Brink & ter Braak, 1999). Dung counts were log + 1-transformed prior to analysis. Our herbivore guilds were strongly correlated with dominance of wild and

domestic herbivores; and as such the analyses were simplified to wild herbivore or livestock dominance. The analysis associated wild herbivore dominance with positive scores and livestock dominance with negative scores. Plant community composition over the two years (2016–2018) was analysed through non-metric multidimensional scaling (NMDS) using the annual survey of all experimental plots (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We restricted the NMDS to two axes; however, the first axis was strongly collinear with tree canopy type and was not included in our final model. To identify whether specific species cover was enhanced under different tree canopy types as well as different tree canopies across land uses (pastures and wildlife-protected areas), we used a method of differential analysis of count data. This analysis accounted for the low number of observations for the majority of species. *P*-values were generated contrasting estimated standard error of the log₂ change in species cover to zero (Love, Huber, & Anders, 2014).

In total, 2,916 plot pasture disc measurements were analysed over a 22 month period generating data from July 2016 to May 2018. Due to initial disturbances, the first two months of the biomass data collection were omitted from the analysis. To test the potential effect of trees on herbaceous understory standing biomass across a range of herbivore assemblages and intensities, we fitted a linear mixed model with an auto-correlated structure (accounting for repeated measures) using the Integrated Nested Laplace Approximation (INLA). INLA uses a Bayesian framework where the importance of factors can be determined via posterior parameter estimates (Rue, Martino, & Chopin, 2009). By using INLA, we were able to ensure positive estimates (i.e., above zero) of herbaceous biomass using a gamma distribution. Our primary global model included the following fixed factors: enclosure treatment (exclosed *versus* open to herbivory), tree canopy type (leguminous, non-leguminous and outside tree canopy), herbivore assemblage (PRC scores – outlined above), rainfall and herbaceous species composition (NMDS axis 2 scores) and their two-way interactions. In the global model, we had two three-way interactions between treatment, tree canopy and herbivore assemblage as well as treatment, tree canopy and herbaceous species composition. For the random component of the model, a nested structure was used reflecting the experiment's design with plot pair (i.e., paired open *versus* exclosed plots), nested within block and then site ($n = 5$, two in wet and three in mesic savannah). The potentially confounding variables tree height and fire history on herbaceous biomass (mentioned above) could not be included in our global model, because tree height covaried with tree canopy type, where leguminous trees were taller than non-leguminous trees and fire history covaried with NMDS axis 2. To consider the potential influence of tree height and fire history on our results we re-ran the model outlined above using tree height instead of tree canopy type and fire history instead of NMDS axis 2. Various assessment criteria for our global model suggested a good model fit, including a Watanabe–Akaike Information Criterion (a Bayesian equivalent of the well-known AIC) of –14,484, Deviance Information Criterion –14,100 and conditional predictive ordination –3763 (Ferkingstad, Held, & Rue, 2017). Using the Bayesian framework, we assessed the

support for the importance of each fixed factor in the model by examining the 95% credible intervals around the posterior mean.

All analyses were carried out in R version 3.5.3 (R Core Team, 2019) with 'prc', 'metaMDS', and modified 'bioenv' and 'mantel' functions for multivariate from the Vegan package (R Core Team); 'DESeq' function from the DESeq2 package (Love et al., 2014) and R-INLA models were tested using the 'inla' functions in the R-INLA package (Martins, Simpson, Lindgren, & Rue, 2013).

3 | RESULTS

3.1 | Herbaceous biomass under savannah trees with increasing livestock dominance and abundance

Herbaceous standing biomass was greater under savannah trees and when herbivores were excluded, independent of spatial and temporal rainfall patterns (Figures 2, 3). Over the duration of the study, mean herbaceous biomass was 0.19 ± 0.11 kg/m² (mean \pm standard deviation) under leguminous trees, 0.18 ± 0.11 kg/m² under non-leguminous trees and 0.14 ± 0.1 kg/m² outside tree canopies. On average, increasing livestock dominance reduced herbaceous biomass across canopy types (Figures 2, 3). Excluding herbivores had the greatest impact in pasturelands and livestock-dominated assemblages, leading to a 119% increase in herbaceous biomass in pasturelands compared to 54% increase in wildlife-protected areas across canopy types over the duration of the study (Figures 2, 3; herbivore assemblage \times enclosure treatment). The tree-induced (i.e., underneath tree compared to outside tree) increase in herbaceous understory biomass was stronger in the presence of herbivores compared to when they were excluded (Figures 2, 3; e.g., Tree canopy: Open versus leguminous tree). Overall standing herbaceous biomass was 60% and 48% higher underneath leguminous and non-leguminous trees, respectively, compared to outside tree canopies when accessible to herbivores; the magnitude of this tree-induced increase in herbaceous biomass reduced to 39% and 40%, respectively, when herbivores were excluded (Figure 2). The greatest positive effect of excluding herbivores was outside tree canopies with an increase of 159% in pasturelands and 78% in wildlife-protected areas when contrasting enclosed versus open plots.

Trees demonstrated a consistent facilitative effect in maintaining understory herbaceous biomass across temporally variable wild herbivore and livestock abundances (estimated by dung counts; Figures 2, 3). Higher herbivore abundance of both wildlife- and livestock-dominated assemblages was negatively related to herbaceous biomass, this effect being more pronounced outside of the tree canopy (Figure 4). Moreover, the model predicted differences between underneath trees and outside trees were stronger at high herbivore abundances than at low wild herbivore and livestock abundances (Figure 4). In part, this was due to higher variation in herbaceous biomass at low herbivore abundances. Despite a weak influence of herbivore assemblage on herbaceous biomass differences between canopies (Figure 3), the relationship was strongly driven by the high livestock abundances (Figures 2, 4).

Herbaceous biomass was positively related to rainfall with little influence of canopy type or enclosure treatment on this relationship (Figure 3). The increase in herbaceous biomass was greater in the mesic compared to the wet region during periods of high rainfall (Figure 3). The negative influence of herbivore abundance on herbaceous biomass was strongest during periods of low rainfall (Figure 2). This was due to a stronger negative influence of livestock-dominated assemblages during low rainfall periods compared to a positive influence of wild herbivore abundance during wetter periods (Figures 2, 3). In our system, we found that trees still exerted a positive effect on understory herbaceous biomass even during periods of high livestock dominance in the dry periods.

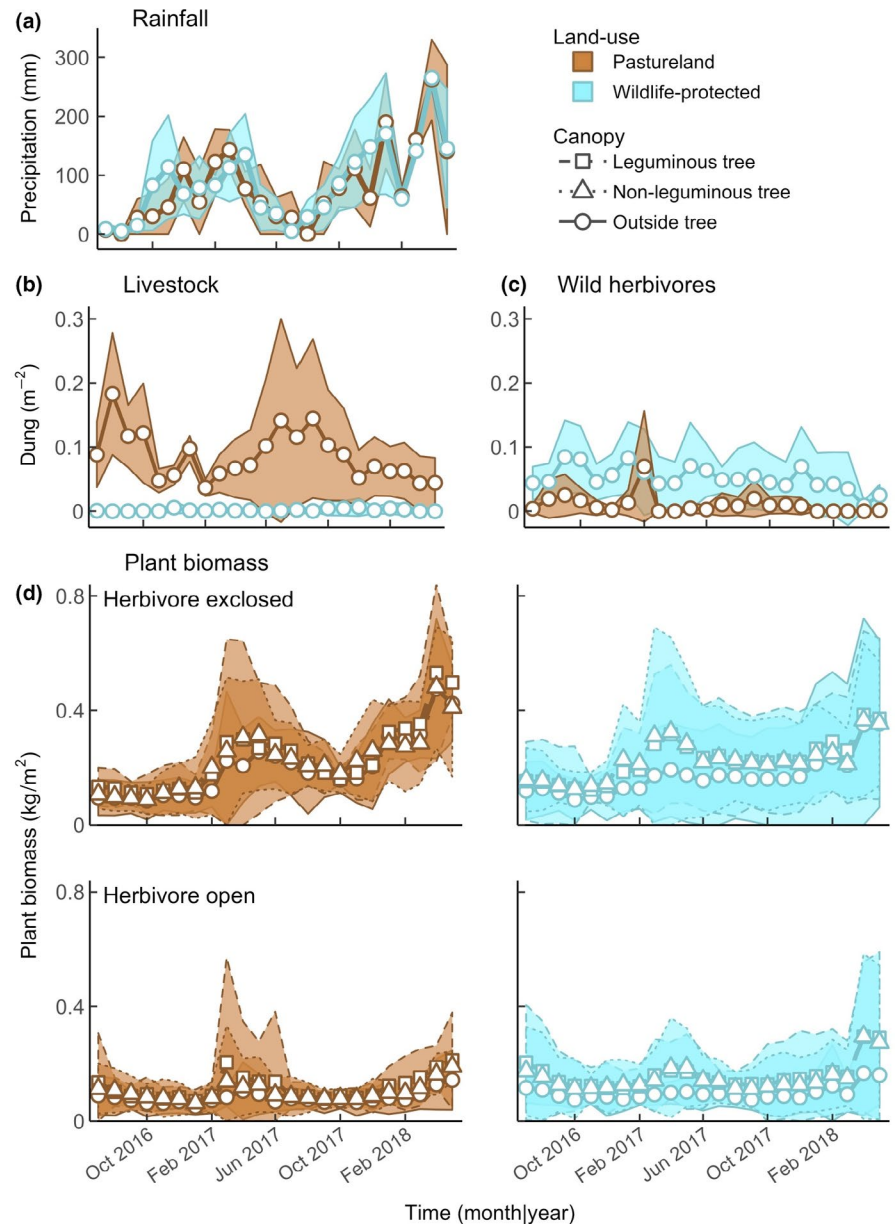
3.2 | Herbaceous biomass underneath leguminous versus non-leguminous trees

Overall there were no differences in the quantity of herbaceous biomass underneath leguminous versus non-leguminous trees whether enclosed or not and across spatially and temporally variable rainfall (Figures 2, 3). However, herbaceous biomass underneath leguminous and non-leguminous trees differed in their response to herbivore assemblage and abundance. Higher herbivore abundance reduced herbaceous biomass underneath non-leguminous trees and outside tree canopies accessible to herbivores (Figures 3, 4). In contrast, biomass underneath leguminous trees was not strongly influenced by herbivore abundance, suggesting the capacity of the herbaceous vegetation to limit herbivore effects (Figures 3, 4). Surprisingly, greater livestock dominance negatively influenced herbaceous biomass underneath non-leguminous trees whether enclosed or not, whereas the negative impact of livestock was only observed under leguminous trees and open plots accessible to herbivory (Figure 3). Likewise, herbivore abundance still exerted a negative influence on enclosed swards outside tree canopies (Figure 3). Both of these findings may allude to a legacy of previous livestock-dominated assemblages and higher herbivore abundance (mainly livestock) indirectly influencing herbaceous biomass via species composition. Indeed, the influence of herbivory on herbaceous biomass depended upon herbaceous community species composition (Figure 3).

3.3 | Modulating effects of understory species composition on the tree-herbaceous response to herbivory

Herbaceous species composition was primarily governed by whether the herbaceous plant community resided underneath a tree or outside of the tree canopy ($R^2 = 0.25$, $p < 0.001$) (Figure 5; Appendix S1). However, herbaceous species composition was also strongly influenced by year since last fire ($R^2 = 0.25$, $p < 0.001$) and height of tree studied ($R^2 = 0.21$, $p < 0.001$) (Appendix S1). Tree canopy functional type (legume and non-legume tree or outside canopy; $R^2 = 0.13$, $p < 0.001$) significantly influenced the herbaceous

FIGURE 2 Temporal patterns in (a) rainfall, (b) livestock, (c) wild herbivores and (d) standing above-ground herbaceous plant biomass inside wildlife-protected areas and on pastureland around the Serengeti National Park, Tanzania. Livestock (b) and wild herbivore (c) abundance has been estimated from dung counts and analysed as scores based on principal response curves. Pastoral land is shown in brown and wildlife-protected areas in light blue. Plant biomass (d) is shown inside herbivore exclosures in upper panels and in open plots accessible to herbivores in lower panels. Plant biomass under different canopies is differentiated using symbol shapes and lines: leguminous trees as squares and dashed lines, non-leguminous trees as triangles and dotted lines, and outside tree canopies as circles and solid lines. All shaded error margins are ± 1 standard deviation [Colour figure can be viewed at wileyonlinelibrary.com]



community but less so than underneath *versus* outside tree canopies (Appendix S1). Plant community composition underneath trees was more dissimilar to that outside tree canopies, particularly in wildlife-protected areas (Figure 5). The composition of plant communities underneath trees in pasturelands varied from being similar to that in wildlife-protected tree understories (i.e., positive NMDS1 and negative NMDS2) to communities typically found outside tree canopies across land-use types (i.e., negative NMDS1 and positive NMDS2). Tree canopies and plant community composition were strong determinants of herbaceous biomass; however, these patterns were clearly modulated by herbivore abundance (Figure 5). Taller study trees were associated with understory communities of greater herbaceous biomass in wildlife-protected areas (Appendix S1). However, tree height did not directly influence herbaceous standing biomass in this study (Appendix S3). Furthermore, longer periods without fire were negatively related to herbaceous standing

biomass in our system (Appendix S4), but fire history did not significantly interact with tree canopy type in determining the quantity of standing biomass at our study sites (Appendix S4).

Understory plant communities in wildlife-protected areas sustained greater herbaceous biomass across herbivore abundances (Figure 5). In pasturelands, the relationship between herbaceous species composition, herbaceous biomass and herbivore abundance was more complex. Herbaceous plant communities underneath trees in pasturelands that were compositionally similar to those of understories in wildlife-protected areas could sustain herbaceous biomass with increasing herbivore abundance (Figure 5). However, the positive effect of trees diminished at high herbivore abundances (Figure 5). *Panicum maximum* was the primary understory specialist in our study system, with a significant 11-fold cover increase underneath leguminous and non-leguminous trees compared to outside tree plots (Table 1; Appendix S2). *Panicum maximum* was followed by *Achyranthes aspera*

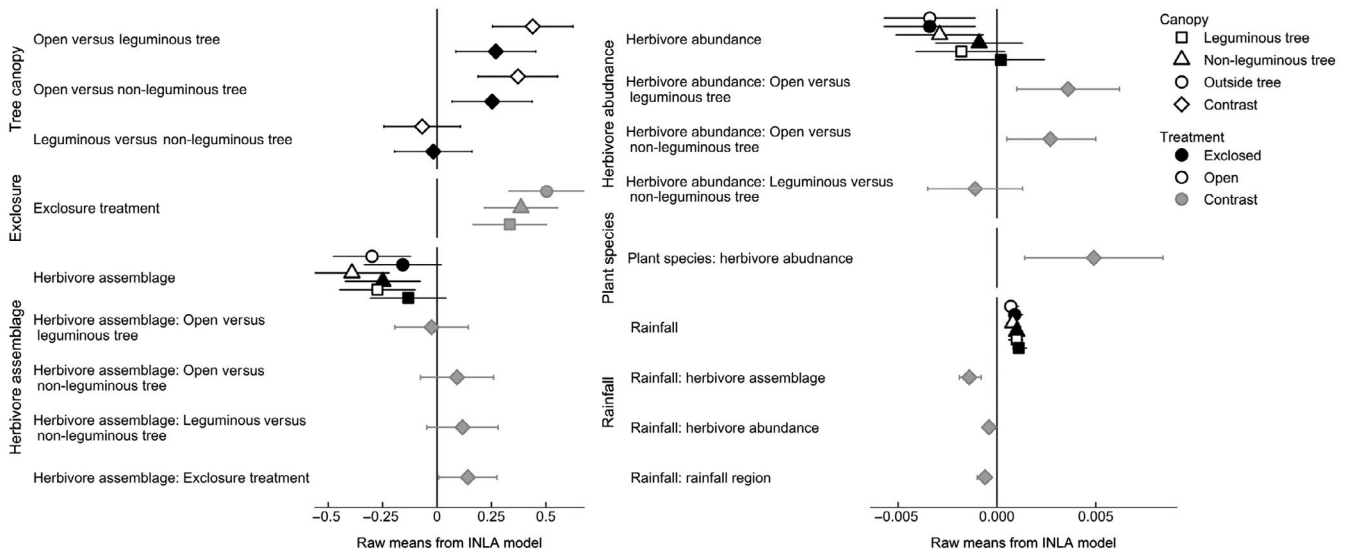


FIGURE 3 Raw mean effects of the Integrated Nested Laplace Approximation (INLA) analysis for the influence of tree canopy, exclusion treatment, herbivore assemblage and abundance, plant species composition, rainfall and their interactions on herbaceous biomass. Raw mean effects are shown for tree canopies, including leguminous trees (squares), non-leguminous trees (triangles), outside tree canopies (circles) and contrasts between canopies (diamonds) as well as exclusion treatments. Excluded areas are black-filled symbols, plots open to herbivory are white-filled symbols and contrasts between treatments, solid grey symbols. Raw mean effects from the INLA model are shown, with the distribution of the posterior means as the bar from the lower median (0.025) to the upper median (0.975) quantiles. If the lower or upper median quantiles of the posterior mean distribution do not overlap with zero (black line) the model term is important

with a fivefold cover increase underneath trees (Table 1; Appendix S2). *Themeda triandra* and *Panicum coloratum* were abundant outside trees in wildlife-protected areas, but instead were found mainly underneath trees in pasturelands (Table 1; Appendix S2). From the species identified as associating with tree understories, *Panicum maximum* was the only species strongly positively related to greater herbaceous biomass

inside exclusions (Pearson's correlation 0.47, $n = 57$, $p < 0.001$), but at the same time negatively related to increasing herbivore abundance outside exclusions (Pearson's correlation -0.35 , $n = 59$, $p = 0.006$). In total, 10 out of 175 species observed over three years were strong candidates as leguminous and/or non-leguminous tree understory specialists. Apart from the understory specialists mentioned above,

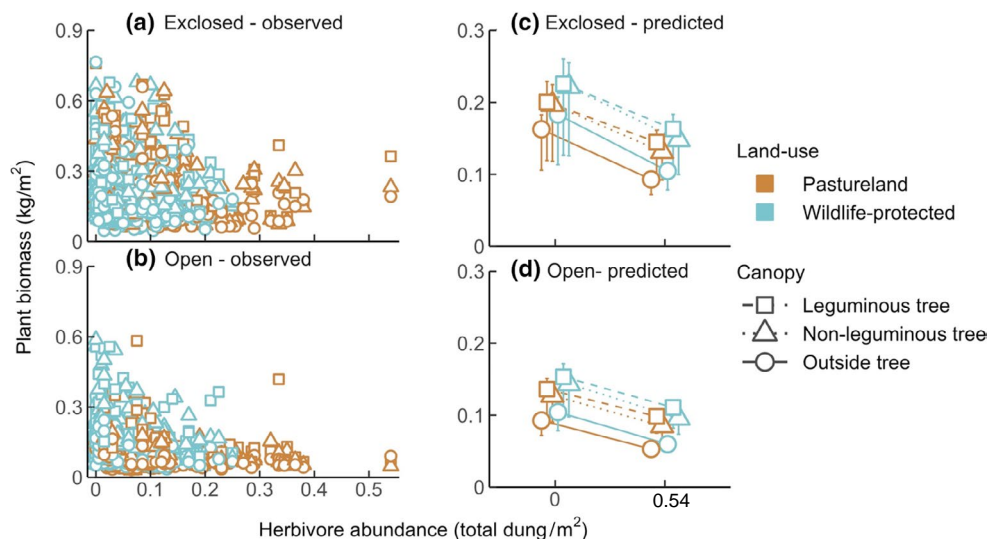


FIGURE 4 Standing herbaceous aboveground biomass in (a) excluded and (b) open plots in relation to observed herbivore abundance estimated from total dung (m^{-2}) as well as predicted (c) excluded and (d) open-plot plant herbaceous biomass from the Integrated Nested Laplace Approximation (INLA) model. Herbaceous plant biomass inside excluded plots is shown as filled symbols and herbaceous biomass in plots open to herbivores as unfilled symbols. Lines and symbols for pastoral land are shown in brown and wildlife-protected areas in light blue. Herbaceous biomass across canopies is shown as circles and solid lines outside tree canopies, underneath leguminous trees as squares and dashed lines and underneath non-leguminous trees as triangles with dotted lines. INLA model predictions in (c) and (d) are made in absence of herbivory and at highest abundance, i.e., maximal observed dung count. Error bars represent 95% credible intervals [Colour figure can be viewed at wileyonlinelibrary.com]

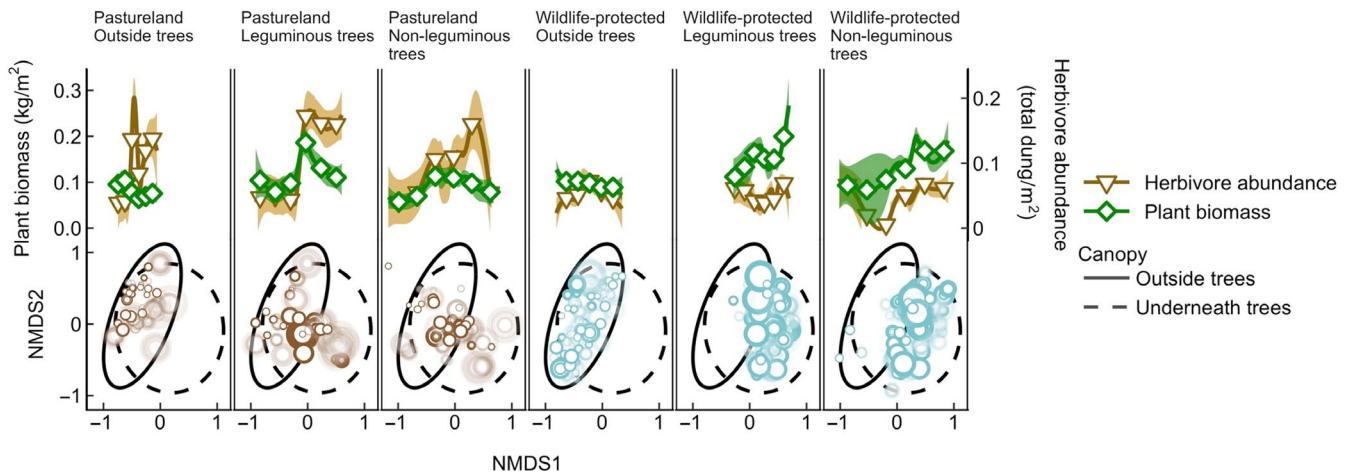


FIGURE 5 Species composition across land uses and tree canopy types in relation to average standing biomass and herbivore abundance (dung counts). In the upper part of the panels, open-plot herbaceous biomass (green with diamond symbols) and average total herbivore abundance (dung counts, dark yellow with inverted triangles) are shown as fitted Locally Estimated Scattered Smoothing (LOESS) lines with a smoothing span of 50%. The lower part of the panels presents non-metric dimensional scaling (NMDS) with plot-scale species communities (NMDS 'site' scores) with an ordination differentiating canopy types as outside tree canopies (solid line) and underneath trees (dashed). Symbol size for the lower panel is proportion to quantity of herbaceous biomass. Exclosed plot-scale scores are more transparent than those of open plots. Herbaceous biomass and herbivore dung lines have been LOESS-smoothed (mean \pm 1 standard deviation) [Colour figure can be viewed at wileyonlinelibrary.com]

most understory species occurred at low frequencies and percentage covers (Table 1; Appendices S2, S5).

4 | DISCUSSION

Our results show that trees can maintain herbaceous understory vegetation despite high herbivore pressure in both wildlife- and livestock-dominated savannahs. We observed these facilitative effects across spatially and temporally variable rainfall patterns. The facilitative effect of trees on the herbaceous layer was stronger in the presence of herbivores than without them. Although we found no difference in herbaceous biomass underneath leguminous and non-leguminous trees during our study, as is often the case in tropical savannahs (Belsky, Mwonga, Amundson, et al., 1993; Belsky, 1994; Blaser et al., 2013), plant biomass dynamics underneath leguminous trees was less strongly influenced by mammalian herbivory. Moreover, our study demonstrates that the three-way interaction between mature trees, understory plant biomass and herbivores is mediated by the herbaceous community composition. Plant communities found underneath trees in open wooded savannahs had a higher capacity to sustain herbaceous biomass with increasing herbivore abundance and livestock dominance. Therefore, to maintain herbaceous biomass in an increasingly livestock-dominated savannah ecosystem one must consider properties of the isolated trees (i.e., functional type and height) and their associated understory herbaceous species composition.

Utilisation of tree understories by herbivores in savannah ecosystems is well known and intensification of herbivory would be expected to negate positive effects of trees (Belsky, Mwonga, & Duxbury, 1993; Smit et al., 2009). Yet, we were able to detect

stronger differences (albeit lower biomass) underneath trees versus outside trees at higher wild herbivore and livestock abundances. We did not measure herbivore consumption rates beneath and away from trees that may have shaped observed plant biomass differences. Nevertheless, swards outside tree canopies, particularly in more livestock-dominated savannahs, showed higher standing plant biomass following release from herbivory (i.e., inside exclosures). This could be explained by either higher herbivore pressure away from trees (Augustine & McNaughton, 2006) or growth constraints of plants beneath trees following herbivore release, such as light limitation and/or self-thinning processes (Belsky, 1994; Hawkes & Sullivan, 2001). Nonetheless, observed herbivore dung counts are suggestive of higher foraging rates in savannahs dominated by understory specialist herbaceous species, for example *Panicum maximum*, compared to savannahs without these herbaceous species. Consistent with our hypotheses, our study shows that mature trees can buffer the impact of increasing herbivore presence, especially livestock dominance. As herbivore abundances increase, an ecological warning sign of the potential loss of this buffering capacity of trees in African savannahs is the loss of understory specialist species such as *Panicum maximum*.

Soil nutrients and water availability have been shown to be tightly coupled with growth and herbaceous biomass production of tree understories (Ludwig, Kroon, et al., 2004; Augustine & McNaughton, 2006). We expected greater biomass underneath leguminous compared to non-leguminous trees due to the presence of nitrogen-fixing symbionts enhancing nitrogen availability (Blaser et al., 2013). Although we found no difference in herbaceous standing biomass underneath tree functional types, under leguminous trees plant biomass was less influenced by wild and livestock herbivory than under non-leguminous trees. This could still suggest that leguminous trees enhance the resilience of understory communities due to higher soil

TABLE 1 Herbaceous species occurrence and cover increase under leguminous and non leguminous trees analysed using differential analysis of count data (Love et al., 2014). Mean cover \pm 1 standard deviation

Species	Family	Functional type	Occurrence (%)	Cover (%)	Understory increase (x-fold)	Wald statistic	P-value
<i>Achyranthes aspera</i> L.	Amaranthaceae	Forb	21.9	11.6 \pm 14.5	4.6	9.54	<.001
<i>Chloris gayana</i> Kunth	Poaceae	Grass	4.0	14.7 \pm 16.3	1.8	3.94	<.001
<i>Commelina benghalensis</i> L.	Commelinaceae	Forb	6.7	6.3 \pm 5.9	1.8	4.37	<.001
<i>Justicia betonica</i> L.	Acanthaceae	Forb	9.3	7.7 \pm 9.4	2.2	5.58	<.001
<i>Justicia matamensis</i> (Schweinf.) Oliv.	Acanthaceae	Forb	12.8	14.0 \pm 10.7	2.8	6.09	<.001
<i>Panicum coloratum</i> L. ^a	Poaceae	Grass	9.1	16.9 \pm 15.7	3.7	4.12	<.001
<i>Panicum maximum</i> Jacq.	Poaceae	Grass	32.0	32.5 \pm 23.7	10.7	13.24	<.001
<i>Sporobolus fimbriatus</i> (Trin.) Nees.	Poaceae	Grass	4.3	11.9 \pm 19.7	1.6	3.77	<.001
<i>Setaria verticillata</i> (L.) P.Beauv.	Poaceae	Grass	13.3	13.1 \pm 10.5	3.9	8.47	<.001
<i>Themeda triandra</i> Forssk. ^a	Poaceae	Grass	13.6	23.9 \pm 21.9	5.3	4.87	<.001

P-values have been generated by contrasting estimated standard error of \log_2 change in species cover to zero and have been back-calculated to fold change.

^a*Panicum coloratum* and *Themeda triandra* cover significantly increased underneath leguminous and non-leguminous trees between wildlife-protected areas and pasturelands. *Themeda triandra* cover also showed a significant 4.3-fold increase outside tree canopies, primarily in wildlife-protected areas and pastureland exclosures (Wald = 9.54, $p < 0.001$).

fertility allowing plants to compensate for tissue consumed by herbivores (Belsky, 1994; Belsky, Mwonga, Amundson, et al., 1993; Blaser et al., 2013; Riginos et al., 2009). Cover of the understory specialist *Panicum maximum*, strongly associated with greater biomass, was similarly negatively related to herbivore abundance. Thus, it is more likely that both leguminous and non-leguminous trees act as a refuge for herbaceous species sensitive to herbivory (Treydte et al., 2009), particularly in pasturelands. Supporting this, *Themeda triandra* and *Panicum coloratum* dominate herbaceous swards outside tree canopies in savannahs with low wild herbivore densities but were more often found underneath trees in livestock-dominated pastureland.

Optimising the spatial and temporal variability between mammalian wildlife and livestock foraging has increasingly been proposed as a way to facilitate herbivore coexistence in savannahs (Fynn et al., 2016; Tyrrell, Russell, & Western, 2017; Young et al., 2018). Here, we show that elevated herbaceous biomass underneath trees occurred during greater wildlife dominance in wetter periods but extended into drier periods and endured peaks in livestock dominance. Thus, pastoral grazing management plans should consider the temporal heterogeneity of herbaceous biomass provided by savannah trees (Smit, 2004, 2005). For instance, greater gains in herbaceous plant biomass could be achieved by land managers that cease livestock grazing during peak growing season on pasturelands with low densities of mature trees compared to land owners that remove large trees or continuously graze livestock

throughout the seasons. Additionally, our study suggests fire may also play a role in promoting heterogeneity of herbaceous biomass. Longer periods without fire contributed to homogenisation of plant species composition underneath trees and outside tree canopies. Although our analysis suggested that fire did not significantly interact with tree canopies to influence herbaceous biomass, our measure of fire was coarse and unlikely to detect localised reduced fire prevalence underneath tree canopies (Coetsee et al., 2010). Long-term fire suppression is becoming more widespread in savannah ecosystems as agropastoralists seek to remove rank grass through livestock grazing rather than fire (Hempson, Archibald, & Bond, 2015, 2017; Young et al., 2018). However, if the absolute number of wild herbivores and/or livestock becomes too high, this will result in the loss of distinct understory plant communities and a decline in herbaceous biomass. Although we did not account for the impact of individual herbivore species in our study, these observations align with herbivore manipulations that identify a stronger negative influence of total savannah herbivore numbers on productivity rather than the functional attributes of livestock per se (Veblen, Porensky, Riginos, & Young, 2016; Charles, Porensky, Riginos, Veblen, & Young, 2017; Young et al., 2018).

Pasturelands adjacent to wildlife-protected areas in tropical savannahs provide an important buffer area that can be occupied by wild herbivores for short durations of the year, as seen in our system (see also Veldhuis et al., 2019). To ensure these pasturelands sustain

herbaceous biomass as forage for both wildlife and livestock herbivores, it is necessary to preserve tall trees (Smit, 2004, 2005), i.e. >4 m, as in our study. Supporting a growing consensus of studies, we found taller trees maintain greater herbaceous biomass in the understory (Blaser et al., 2013; Moustakas et al., 2013; Treydte et al., 2009), and our results show that this maintenance of biomass also occurs as an indirect effect, mediated through herbaceous species composition. Moreover, in our nutrient-rich tropical savannahs, plant species turnover due to varying herbivory pressure is likely to be higher than in non-tropical savannahs where understory specialists can persist beside dead tree stumps for several decades (Stahlheber et al., 2015). The cover and distribution of understory species, such as those identified in this study, are therefore important indicators of the resilience of the African tropical savannahs under increasing herbivore pressure.

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AUTHOR CONTRIBUTIONS

SWS, JDMS, BJB, JB, RDL and SNH conceived and designed the study; SWS, JB, PJM, RDL, SNH and BJB collected the data; SWS analysed the data and wrote the first draft of the manuscript and all authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All primary data used in this study are presented in the manuscript and are available in the supporting information (Appendix S6). Primary data are also available on request on the AfricanBioServices data repository: <https://aficanbioservices.webhosting.rug.nl/HomePage>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Non-metric multidimensional scaling ordination of the dissimilarity in herbaceous species composition across all experimental plots

Appendix S2. Relative abundance (percentage cover) of herbaceous understory specialist species

Appendix S3. Raw mean effects (betas) of the Integrated Nested Laplace Approximation (INLA) model of herbaceous biomass replacing tree height for collinear tree canopy cover

Appendix S4. Raw mean effects (betas) of Integrated Nested Laplace Approximation (INLA) model of herbaceous biomass replacing fire history for species composition (NMDS 2 axis)

Appendix S5. List of all herbaceous species recorded over the duration of the experiment and family, functional group and habit

Appendix S6. Primary data used in the analysis

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