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# The past, present, and future of herbivore impacts on savanna vegetation

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## Abstract

1. Herbivory is a key process structuring vegetation in savannas, especially in Africa where large mammal herbivore communities remain intact. Exclusion experiments consistently show that herbivores impact savanna vegetation, but effect size variation has resisted explanation, limiting our understanding of the past, present and future roles of herbivory in savanna ecosystems.
2. Synthesis of vegetation responses to herbivore exclusion shows that herbivory decreased grass abundance by 57.0% and tree abundance by 30.6% across African savannas.
3. The magnitude of herbivore exclusion effects scaled with herbivore abundance: more grazing herbivores resulted in larger grass responses and more browsing herbivores in larger tree responses. However, existing experiments are concentrated in semi-arid savannas (400–800-mm rainfall) and soils data are mostly lacking, which makes disentangling environmental constraints a challenge and priority for future research.
4. Observed herbivore impacts were ~2.1× larger than existing estimates modelled based on consumption. Wildlife metabolic rates may be higher than are usually used for estimating consumption, which offers one clear avenue for reconciling estimated herbivore consumption with observed herbivore impacts. Plant-soil feedbacks, plant community composition, and the phenological or demographic timing of herbivory may also influence vegetation productivity, thereby magnifying herbivore impacts.
5. Because herbivore abundance so closely predicts vegetation impact, changes in herbivore abundance through time are likely predictive of the past and future of their impacts. Grazer diversity in Africa has declined from its peak 1 million years ago and wild grazer abundance has declined historically, suggesting that grazing likely had larger impacts in the past than it does today.
6. Current wildlife impacts are dominated by small-bodied mixed feeders, which will likely continue into the future, but the magnitude of top-down control may also depend on changing climate, fire and atmospheric $CO_2$.
7. *Synthesis*. Herbivore biomass determines the magnitude of their impacts on savanna vegetation, with effect sizes based on direct observation that outstrip

existing modelled estimates across African savannas. Findings suggest substantial ecosystem impacts of herbivory and allow us to generate evidence-based hypotheses of the past and future impacts of herbivores on savanna vegetation.

**KEYWORDS**
browser, exclusion experiment, grazer, mixed feeder, plant–herbivore interactions, savanna, top-down

## 1 | INTRODUCTION

Herbivores impact vegetation productivity and structure consistently across diverse ecosystems, but the magnitude of their effects vary substantially in ways that are not easily predicted (Jia et al., 2018). Herbivore effects are of particular interest in savanna ecosystems in Africa (Charles-Dominique et al., 2016; Owen-Smith, 2013), where an especially diverse mammal herbivore community potentially stabilizes tree-grass coexistence and can have impacts on vegetation structure that locally rival the effects of fire and resource limitation in magnitude (Bond, 2005). This observation has motivated the establishment of a patchwork of herbivore exclusion experiments throughout well-studied African savanna sites. Despite intensive study, however, results seemingly mirror those from global meta-analysis: herbivores consistently decrease net vegetation growth and biomass (e.g. Yayneshet et al., 2009; Sankaran et al., 2013; Staver & Bond, 2014; Charles et al., 2017), but we do not understand how or why effect sizes vary. Herbivore effects have proved more difficult to generalize than equivalent top-down impacts of fire (e.g. Hoffmann et al., 2003; Bond & Keeley, 2005; Staver, Archibald, et al., 2011; Lasslop et al., 2016), and we still lack a quantitative understanding of what determines the severity of herbivore impacts across savanna ecosystems. As a result, we remain unable to predict, at anything more precise than a conceptual level (Dantas & Pausas, 2020; Doughty et al., 2015; Hempson et al., 2017), the paleoecological, historical, and future roles of herbivory in shaping savanna dynamics and distributions.

The simplest hypothesis for what makes herbivore impacts vary is that herbivore impacts scale with herbivore abundance. This intuitive possibility is supported by findings within individual experiments showing that vegetation responds more strongly to more complete herbivore exclusion than to partial exclosure (in what are sometimes referred to as ‘Russian doll’ experiments; see, e.g. Charles et al., 2017; McCaughley et al., 2018; Staver & Bond, 2014). This hypothesis is also fundamental to much of the landscape-scale observational work that examines herbivore effects in savannas, for example, in grazing lawns. Grazing lawns are short-grass savanna patches that result from intensive grazing (Hempson et al., 2015; McNaughton, 1984), which can feed back to enhance nutrient cycling, increase grass productivity and nutrition, and improve visibility for predator avoidance. These changes in turn attract more herbivores, establishing a positive feedback that relies on the assumption that varying herbivore densities determine herbivore impacts in savanna landscapes. Tree-layer examples are less iconic but equally clear: intense browsing may create tree-layer analogues to grazing lawns (Cromsigt & Kuijper, 2011; Fornara & du Toit, 2007; Voysey et al., 2020), gradients in herbivore abundance impact tree species distributions (Staver et al., 2012), and episodic reductions in browsing pressure (from disease or hunting) have been linked to pulses in tree establishment (Daskin et al., 2015; Prins & van der Jeugd, 1993). However, the hypothesis that herbivore impact scales with herbivore abundance has not yet been evaluated directly for insight into variation in vegetation responses to herbivore exclusion across landscapes, nor has it been evaluated at large scales to determine potential biome-wide impacts of herbivory on savanna structure and distribution. As a result, however intuitive, the idea that more herbivores have larger impacts cannot yet be quantitatively incorporated into predictive models of savanna vegetation structure and dynamics.

A complementary possibility is that environmental context shapes the severity of herbivore impacts on vegetation, both directly via effects on plant productivity and indirectly via changes in herbivore abundance, community composition and therefore use intensity. In savannas, the intensity of herbivory has been hypothesized to increase to a peak at mean annual rainfall of ~650 mm and then to decline as higher productivity decreases forage quality (higher C:N) and fire replaces herbivory as the dominant disturbance (Archibald & Hempson, 2016). Soil properties may have analogous effects on both plant productivity (Staver et al., 2017) and forage quality, suggesting that herbivore effects should be more intense in nutrient-rich settings (Archibald & Hempson, 2016; Bell, 1982; Olff et al., 2002 but see Borer et al., 2020). Because smaller-bodied herbivores are thought to require more nutritious food than larger bulk feeders, overall herbivore abundance and diversity is fairly low in high-rainfall savannas (Hempson et al., 2015) and in low-nutrient systems (Olff et al., 2002). The clear prediction, linked to the hypothesis that more herbivores result in more severe impacts, is that herbivore impacts on savanna vegetation should peak at intermediate rainfall and should be more intense on more nutrient rich than on nutrient poor soils.

There are plausible alternatives to this abundance framework, all centred around the idea that herbivore effects on vegetation may have resisted generalization because they are intrinsically complex (Green et al., 2005). One alternative is that rare herbivores or selective feeding may have disproportionately large ecosystem impacts, if herbivory decreases productivity via impacts on hydrology (Veldhuis et al., 2014) or at specific plant life stages that imposes a demographic bottleneck with cascading ecosystem effects. Demographic bottlenecks probably do shape the dynamics of browsing impacts on savannas (Augustine & McNaughton, 2004; Moncrieff et al., 2011; Prins & van der Jeugd, 1993; Staver & Bond, 2014), and there is a storied tradition in the savanna rangeland literature arguing that strategic adaptive management of contingencies offers opportunities for small changes in management to have large effects (Briske et al., 2005; Westoby et al., 1989). There are documented examples of this phenomenon. For instance, both porcupines and elephants can selectively eat the bark of relatively large trees, which makes them more susceptible to fires; thus, trivial rates of energy consumption potentially have large effects on savanna vegetation structure (Moe et al., 2009; Moncrieff et al., 2008). Similarly, seed and seedling predation by insects and rodents potentially impacts tree establishment even though direct energetic impacts are mild (Maclean et al., 2011; Vaz Ferreira et al., 2010). In the grass layer, rhinos impact landscape-level fire behaviour, and even highly selective rhino removals for population management can have outsized impacts on landscape fire dynamics (Waldram et al., 2008). Overall, the relative impact of negative herbivore effects on productivity is not known, but, if substantial, then selective feeding may have trophic impacts that swamp the more obvious potential impacts of total herbivore abundance and environment.

A second alternative is that abundant herbivores may instead have disproportionately small ecosystem impacts, if herbivory stimulates compensatory productivity (Hilbert et al., 1981; McNaughton, 1979; Oesterheld & McNaughton, 1991; Richie & Penner, 2020). Increases in grass productivity (not standing biomass) as a result of intensive herbivory have been widely observed in savanna ecosystems (Milchunas & Lauenroth, 1993), via diverse mechanisms ranging from enhanced decomposition (Leriche et al., 2003), positive feedbacks in nutrient cycling via deposition of dung and urine (Augustine et al., 2003), and prevention of self-shading (Zimmerman et al., 2010). In grasses, hypotheses diverge for where compensatory feedbacks are expected: the grazing optimization hypothesis suggests intermediate levels of herbivory should stimulate productivity the most (Hilbert et al., 1981; McNaughton, 1984), whereas alternative models suggest that intense but episodic grazing should instead have the largest stimulating effect (Oesterheld & McNaughton, 1991; Richie & Penner, 2020). Examples of these compensatory mechanisms are rarer in trees but have been shown to occur (Goheen et al., 2007), and nutrient recycling on grazing lawns may increase tree productivity on lawns just as it does to grasses (Fornara & du Toit, 2007; Voysey et al., 2020). Overall, variation in the intensity of these compensatory mechanisms across different herbivore use intensities is unknown, but they could potentially cause herbivory to have a smaller-than-expected impact on vegetation structure.

In this review, we ask whether there is clear evidence, across a number of herbivore experiments established in African savannas, of whether herbivore abundance and abiotic environment are primary determinants of the severity of herbivore impacts on vegetation. We ask whether abundances of different herbivore functional types (grazer, mixed feeder, browser) are predictive of the separate responses of grasses and trees to herbivore exclusion (Section 2) and evaluate the magnitude of these responses compared to existing estimates of productivity and consumption fluxes in savannas (Section 3). We then use the results of this synthesis, combined with an evaluation of how herbivore abundances have changed in savannas (Section 4), to predict how herbivores potentially impacted savannas in the past and how their role is changing into the future (Section 5). We conclude by offering suggestions for how targeted research can deepen our understanding of herbivore impacts on savannas and resolve outstanding uncertainties (Section 6).

## 2 | DETERMINANTS OF VEGETATION RESPONSES TO HERBIVORE EXCLUSION

We begin by summarizing the results of experimental herbivore exclusions from African savannas. Major experiments are widely known and well-studied, and we relied on our own expert knowledge of existing herbivore experiments, supplemented by a literature search which yielded only a few extra publications (see Table 1; Appendix S1). All results presented in this synthesis were digitized from graphics in published papers or were captured from published data tables. We included only experiments that compared a 'control', with all free-ranging herbivores present, to a full herbivore exclusion treatment, usually excluding herbivores with body mass ≥ a hare/large rodent. Some although not all of these experiments included free-ranging livestock in 'control' treatments (see Table 1). From each study, we extracted one measure of grass abundance (e.g. standing grass biomass, grass canopy cover, grass basal area) and one measure of tree abundance or growth (e.g. tree canopy height, tree biomass, tree height increment, tree survival; see Appendix S1). We then calculated a response ratio, defined as the vegetation metric measured inside the exclosure (without herbivores) divided by the measurement outside the exclosure (with herbivores). Log response-ratio is a widely used estimate of effect size when multiple different metrics need to be compared across studies (e.g. Elser et al., 2007); response ratios are reported here as raw values, but plotted on a log scale, such that values >1 correspond to vegetation increases with herbivore exclusion and <1 to decreases with herbivore exclusion.

We used one estimate per dataset and so included only the latest available sample date when multiple works had been published using the same data. However, when independent datasets had been collected for the same experiment, we extracted multiple estimates and averaged them. Because experiments are distributed so heterogeneously across systems, we also averaged estimates from independent studies within the same roughly similar landscape feature, aiming to include only estimates that were spaced apart by at least 50 km (see Figure 1a). However, we made an exception in systems with clear differences among soil types that could be consistently characterized (i.e. four separate experiments at Mpala Research Center in Laikipia, Kenya, on two soil types), where we averaged experiments within a soil type. Where

**TABLE 1** Herbivore exclosure response ratios and herbivore abundances across sites. See Appendix S1 for study-specific estimates with detailed reference information. The unit mkg refers to metabolic kilograms

| ID | Site | Rain (mm) and soils | Grass response | Tree response | Grazers (mkg/$km^2$) | Browsers (mkg/$km^2$) | Mixed feeders (mkg/$km^2$) | Megas (mkg/$km^2$) | Mesos (mkg/$km^2$) | Livestock present? | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Amboseli, Kenya | 275 | | 5.59 | 394 | 51 | 130 | 141 | 434 | No | Western and Maitumo (2004) |
| 2 | Hluhluwe, R.S.A. | 714 | 1.66 | 1.32 | 1,795 | 279 | 610 | 1,087 | 1,597 | No | Staver and Bond (2014) |
| 3 | iMfolozi, R.S.A. | 652 | 3.24 | 1.37 | 1,260 | 240 | 891 | 856 | 1,535 | No | Staver and Bond (2014) |
| 4 | Hlangwine, Kruger, R.S.A. | 667 ⋄ | | 1.70 | 512 | 114 | 360 | 546 | 441 | No | Asner et al. (2009) and Wigley et al. (2014) |
| 5 | Makhohlola, Kruger, R.S.A. | 600 ⊕ | | 1.96 | 627 | 167 | 723 | 679 | 837 | No | Wigley et al. (2014) |
| 6 | Nkuhlu, Kruger, R.S.A. | 528 ⋄ | 2.33 | 1.26 | 502 | 153 | 514 | 524 | 644 | No | Jacobs and Naiman (2008), Asner et al. (2009), Scogings et al. (2011) and Van Coller et al. (2013) |
| 7 | Nwaswitshumbe, Kruger, R.S.A. | 417 ⊕ | | 2.11 | 189 | 41 | 254 | 263 | 220 | No | Asner et al. (2009) and Wigley et al. (2014) |
| 8 | Letaba, Kruger, R.S.A. | 475 ⋄ | | 1.18 | 278 | 49 | 422 | 441 | 307 | No | Asner et al. (2009) |
| 9 | red granites, Mpala, Kenya | 612.8 ⋄ | 2.21 | 3.58 | 502 | 467 | 1,291 | 935 | 1,324 | Yes | Goheen et al. (2013), McCauley et al. (2018) and Wigley et al. (2020) |
| 10 | KLEE, Mpala, Kenya | 615 ⊕ | 1.07 | 0.81 | 837 | 29 | 142 | 116 | 891 | Yes | Riginos and Young (2007) and Charles et al. (2017) |
| 11 | Serengeti, Tanzania | 661 | | 1.08 | 3,523 | 100 | 177 | 122 | 3,678 | No | Morrison et al. (2018) |
| 12 | Seronera, Serengeti, Tanzania | 775 | 10.36 | | 4,524 | 304 | 388 | 341 | 4,874 | No | Ritchie (2014) |
| 13 | Northern Serengeti, Tanzania | 772.5 | 2.16 | | 3,981 | 91 | 178 | 107 | 4,144 | No | Veldhuis et al. (2020) |
| 14 | Eastern Serengeti, Tanzania | 693.5 | 3.83 | | 3,974 | 91 | 289 | 218 | 4,137 | No | Veldhuis et al. (2020) |
| 15 | Southeast Serengeti, Tanzania | 518 | 3.33 | | 3,349 | 0 | 83 | 0 | 3,432 | No | Veldhuis et al. (2020) |
| 16 | Tigray, Ethiopia | 542.5 | 2.20 | 2.05 | 1,974 | 0 | 660 | 0 | 2,635 | Yes | Yayneshet et al. (2009) |

⋄ Site on known sandy soils; ⊕ Site on known clay soils.

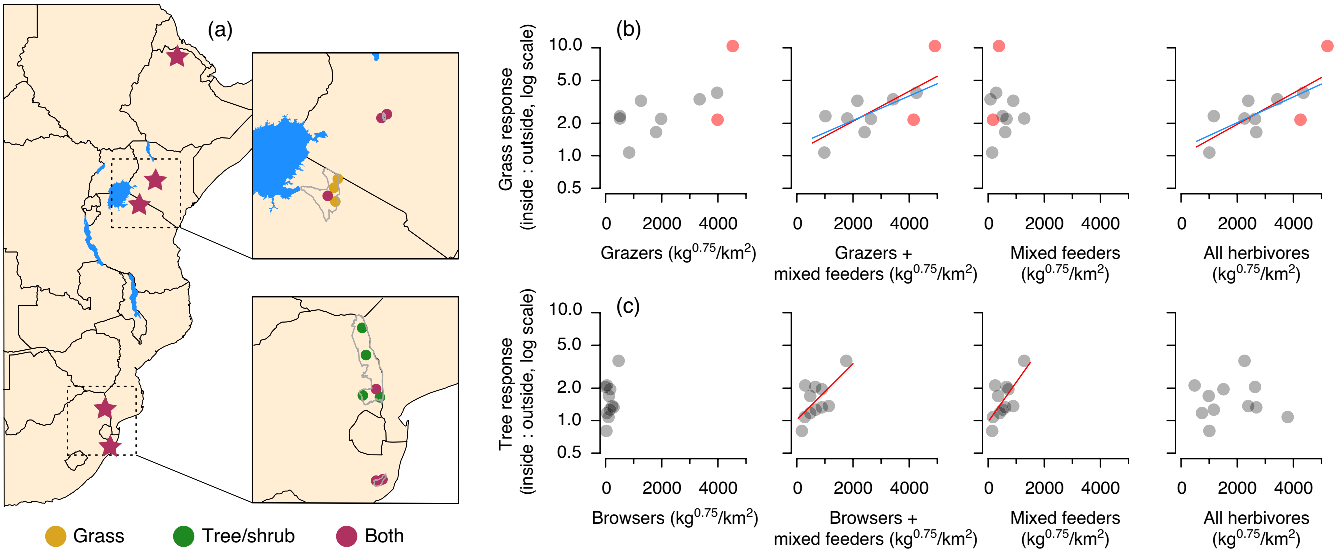

**FIGURE 1** Herbivore abundance effects on vegetation response to savanna herbivore exclusion in Africa. Map of experiment sites (a), herbivore metabolic biomass effects on the response ratio of grasses (b) and of trees (c) to full herbivore exclusion. In b and c, the response ratio is calculated by dividing the measured metric inside the exclosure by the value outside; note that values are plotted on a log scale. Only model fits identified as preferred via AIC minimization are shown. In b, we show in red the best models fitted to all points and in blue the best model fitted to all points excluding the two shown in red. Both 'outliers' are from the Serengeti. We are skeptical of the highest estimate, since the response ratio is >2× higher than the rest; the other red point corresponds to a site from the northern Serengeti ecosystem, with herbivore population estimates that include migratory wildebeest and zebra, but which is sampled for biomass in May–July well before the migration arrives in that part of the Serengeti in November (Holdo, Holt, et al., 2009). Note that two other Serengeti sites (in the central and eastern Serengeti) where the migration always or usually arrives before grass was sampled have been included in all analyses. Metabolic biomass presented here is classic metabolic biomass calculated by the 0.75 scaling exponent for basal metabolic rate; equivalent results for metabolic biomass calculated via Lovegrove's 0.899 exponent (Lovegrove, 2000) for wildlife and 0.75 for livestock are presented in Figure S3

available, we also digitized estimates of mean annual rainfall and soil type, and recorded dates for establishment of the experiment and latest data available.

We used multiple data sources to estimate herbivore population abundances at the site of each experiment, relying on (a) the publications from which we extracted vegetation response ratios, where they provided herbivore population densities, (b) other publications from the same site, where they did not, and (c) a published meta-analysis of herbivore population sizes across African protected areas, where no site-specific estimates were available (Hempson et al., 2015). For obvious reasons, we could include only those herbivore population estimates that were actually provided, which typically included most ungulates but no smaller herbivores. For analysis, herbivore numbers were converted into metabolic biomass (= number of individuals × individual body mass$^{0.75}$) and summed across herbivore dietary strategy (browsers vs. mixed feeders vs. grazers) and across body size (mega vs. mesoherbivores, where megaherbivores have body mass ≥ 1,000 kg and mesoherbivores have 4 kg ≤ body mass < 1,000 kg). All data extracted from papers or otherwise compiled for each herbivore exclusion experiment are provided in Appendix S1, including details of the publication and figure/table from which vegetation response ratios were extracted and of how estimates were grouped across studies. All calculations and site means are provided in Table 1 to aid interpretation of statistical results.

Results were clear: vegetation response to herbivore exclusion increased with herbivore biomass (see Table 2). Grass responses to herbivore exclusion increased most predictably with respect either to grazer and mixed feeder metabolic biomass or to all herbivore metabolic biomass (see Figure 1b; Table S2); grazer importance was driven by high grazer population densities in the Serengeti, the only migratory grazing system with herbivore exclusion experiments, whereas mixed feeding resolved differences among responses mostly in non-migratory systems. Meanwhile, tree responses increased most predictably with respect either to mixed feeders alone or to the combination of mixed feeders and browsers (see Figure 1c; Table S3); in this case, mixed feeders seemingly always achieved much higher population densities than browsers (see also Staver & Hempson, 2020) and therefore had an outsized impact on vegetation. Megaherbivore biomass had no special vegetation impact, except inasmuch as it contributed to overall herbivore biomass. In sum, grazing mammals ate more grass when there were more of them, and browsing mammals ate more trees when there were more of them.

Effects of rainfall were not obvious in statistical analysis. Nearly all exclosures were established at sites with mean annual rainfall between 400- and 800-mm mean annual rainfall. The only exception – a browsing exclosure at Amboseli National Park with 275-mm mean annual rainfall (Western & Maitumo, 2004) – had a particularly high tree response ratio, which induced an apparent decrease in herbivore exclusion effect with increasing rainfall and/or increased the importance

**TABLE 2** Statistical best linear model results for log tree and grass response ratios. Here, ‘grazers’, ‘mixed feeders’ and ‘browsers’ refer to metabolic biomass of each type of herbivore and ‘total’ to total metabolic biomass, calculated as the sum across all species of the body mass of an individual raised to the power 0.75 × its population density per km$^2$. Parentheses indicate that biomass was summed before the statistical models were applied [i.e. ‘(browsers + mixed feeders)’ is a single independent variable]. Equivalent results using a modified scaling exponent are provided in Table S4

| Response | Term | Estimate ± *SE* | *t* | *p* | *F* | $R^2$ | *p* |
|---|---|---|---|---|---|---|---|
| log (grass RR) | Intercept | 0.095 ± 0.32 | 0.3 | 0.77 | 9.22 | 0.535 | 0.016 |
| | (grazers + mixed feeders) | 0.00032 ± 0.00011 | 3.0 | 0.016 | | | |
| | Intercept | 0.0055 ± 0.32 | 0.02 | 0.99 | 10.90 | 0.577 | 0.011 |
| | Total | 0.00033 ± 0.00010 | 3.3 | 0.011 | | | |
| log (grass RR)[a] | Intercept | 0.23 ± 0.27 | 0.9 | 0.42 | 6.10 | 0.504 | 0.049 |
| | (grazers + mixed feeders) | 0.00026 ± 0.00011 | 2.5 | 0.049 | | | |
| | Intercept | 0.16 ± 0.29 | 0.5 | 0.61 | 6.72 | 0.528 | 0.041 |
| | Total | 0.00027 ± 0.00011 | 2.6 | 0.041 | | | |
| log (tree RR) | Intercept | −0.026 ± 0.18 | 0.5 | 0.61 | 8.85 | 0.496 | 0.016 |
| | Mixed feeders | 0.00084 ± 0.00028 | 2.6 | 0.41 | | | |
| | Intercept | 0.019 ± 0.18 | 0.9 | 0.42 | 7.47 | 0.454 | 0.023 |
| | (browsers + mixed feeders) | 0.00060 ± 0.00022 | 2.5 | 0.49 | | | |

[a] Grass RRs modeled without two Serengeti datapoints (shown in red on Figure 1, in which we also fully describe the rationale for fitting two models).

of megaherbivore density (see Figure S1; Table S3); however, given that the response variable was seedling growth over a period of only 4 years, a metric likely highly sensitive to browsing compared to more widely measured sapling and adult tree variables, we were not confident in this result. Overall, we note mostly that exclosures have been established mainly in systems where herbivores are fairly abundant and where herbivore effects are expected, representing a potential bias towards positive results. These existing exclosures are insufficient to evaluate whether rainfall determines herbivore impacts only by influencing potential herbivore population sizes (Archibald & Hempson, 2016; Hempson et al., 2015) or instead whether per-capita herbivore impacts also vary with respect to rainfall (or more precisely, vegetation productivity). We also recommend incorporating not just mean annual rainfall, which most studies report, but also rainfall seasonality and measured annual rainfall totals as they vary through time, which most studies do not report. Finer temporal resolution on data reporting may help disentangle the direct versus indirect effects of rainfall on herbivore impact, since both rainfall and grass consumption by herbivores are known to vary interannually in savannas, with relatively short-term responses by the grass layer (Staver et al., 2018; Wigley-Coetsee & Staver, 2020), such that interannual means may also be insufficient to disentangle rainfall effects (Sala et al., 2012).

Finally, we can offer no conclusive evaluation of how vegetation responses to herbivore exclusion depend on soil nutrients. Soils information is rarely reported in a form that allows comparison across sites, although some geologic parent material or soil type information is often included. We suggest that all herbivore exclusion experiments in savannas should publish basic soils information to facilitate cross-comparison among sites: soil texture (% sand and clay) and soil nutrient concentrations (total % C, total % N and total % P), at least at control sites. Soil depth can also change vegetation productivity, and estimates of soil depth to bedrock or water table should also be provided, where available. Here, we have undertaken a basic pilot comparison among sites in Kruger National Park, South Africa, and Mpala Research Center, Kenya, because those two sites both feature a strong and parallel soil contrast between a nutrient- and clayey versus a nutrient-poor and sandy soil type (only three grass responses but seven tree responses recorded; see Table S4; Figure S1). Soils offered no clear additional explanatory power in either case. However, because existing work so clearly shows that soils impact grass productivity, alone and in interaction with rainfall variability (Dye & Spear, 1982; Staver et al., 2018), additional data and further analyses are clearly needed.

In sum, we find strong support for the hypothesis that the intensity of herbivore impacts scale with herbivore abundance (see Figure 1). Impacts on the grass layer were proportional to the metabolic biomass of grazing herbivores (including grazers and mixed feeders), while impacts on the woody layer were instead proportional to the metabolic biomass of browsing herbivores (again including browsers and mixed feeders).

## 3 | THE MAGNITUDE OF VEGETATION RESPONSES TO HERBIVORE EXCLUSION

The most surprising aspect of this experimental synthesis is the consistently large magnitude of reductions in vegetation abundance due to herbivory. On average, the response ratios of grasses and trees to herbivore exclusion were 3.24 and 1.68, respectively, from an experiment set focused in environments where herbivore impacts peak in savanna ecosystems. These response ratios can be easily translated into estimates of the ecosystem impact of herbivores, suggesting that herbivores reduce grass abundance by 57.0% and reduce tree growth and/or abundance by 30.6%.

These estimates are 3–5× larger in magnitude than existing modelled estimates based on the metabolic demand of herbivores, which peak at an average of ~10% of aboveground biomass (Archibald & Hempson, 2016); these estimates take herbivore population sizes and use well-established relationships from the agricultural literature (Dong et al., 2006; National Research Council, 1996) to estimate consumption. Unfortunately, providing further resolution on these calculations to evaluate the magnitude of tree responses to browsing is impossible, since difficulties in generalizing tree productivity in savannas (Staver, 2017; SEOSAW, 2021) obscure direct comparison of herbivore impact versus consumption. However, because determinants of grass productivity are comparatively well understood (see especially Sala et al., 2012), we can directly examine how estimated grazing and grass productivity fluxes at individual sites compare with herbivore impacts on grass biomass accumulation (i.e. pools) to evaluate the source of the large magnitude of grazing impacts observed here.

To do this, we liken standing vegetation biomass to a biogeochemical pool, which changes over time as a result of the difference between vegetation productivity (i.e. net primary productivity, NPP) as the influx and, at least at the scale of a season, consumption by herbivores as the main outflux, such that

$$\Delta\text{standing biomass} = \text{NPP} - \text{consumption},$$

where we can directly estimate herbivore impacts on vegetation abundance of both trees and grasses via experiments and use published tools to estimate productivity and consumption fluxes. Broadly speaking, there are three complementary possibilities to explain the discrepancy between observed herbivore impacts and published estimates of herbivore consumption, which we will disentangle in some detail. Firstly, estimates of grass consumption may simply be too low. Secondly, in addition to removing biomass via consumption, herbivores may also impact grass productivity, such that exclusion treatments and large-scale syntheses of grass productivity alike offer an inaccurate estimate of productivity under intense herbivory. Finally, vegetation biomass pools may accumulate over time and in a variable environment, decoupling pools (i.e. standing biomass) from fluxes (i.e. annual change in biomass, consumption and productivity). We note that, because variation in tree and shrub productivity is poorly understood in savannas, we have not been able to compare the estimated browsing consumption flux to observed outcomes for tree and shrub vegetation. However, tree growth and abundance responses to herbivore exclusion were also large compared to previous estimates based on consumption, and so we also discuss possible applications to trees and shrubs where possible, since reconciling tree and shrub productivity, consumption, and standing biomass should be a subject for future work.

### 3.1 | The consumption flux

First, we consider the possibility that existing estimates of consumption are too low. The most obvious source of low consumption estimates is that continental averages underestimate herbivore densities at the sites of herbivore experiments themselves. We begin by updating existing estimates using herbivore density estimates from the reserves or regions in which exclosures are located. Combining landscape estimates of herbivore consumption via metabolic demand[1] with estimates of annual grass productivity depending on rainfall (Sala et al., 2012), we estimate that, by standard measures, grazers and mixed feeders have a combined annual metabolic demand of ~25% of aboveground grass productivity – such that herbivore impact on grass biomass is on average 2.1× greater than estimated metabolic demand. Moreover, we estimate that herbivore impacts on grass biomass increase at almost double the rate that estimated consumption does [i.e. that reduction in grass biomass = 1.88 (±0.18) × grazing consumption$_{0.75}$ + 0; $R^2 = 0.921$, $N = 10$, $p < 0.001$; see Figure 2a]. Thus, direct observations of grazing impacts still yield much higher estimates of impact than consumption calculated via standard estimates of metabolic demand.

In the same vein, it is also possible that herbivore exclosures tend to be placed with bias into patches where herbivore pressure is more intense than it is within the larger landscape. Comprehensive evaluation of this possibility is not feasible, because few experiments directly estimate herbivore densities within control or partial exclosure plots. As preliminary evidence, based on 10 exclosures from one park (Hluhluwe iMfolozi Park in South Africa, #2 and 3 in Table 1), we have compared dung counts at exclosure sites ('control' treatment; Staver & Bond, 2014) with dung counts conducted using the same methodology at 202 sites throughout the park (Staver et al., 2012). If anything, the sites of herbivore exclosures experienced slightly lower herbivore pressure than the park as a whole (see Figure S2). However, herbivore pressure clearly varied substantially in space even over small distances, and so it is clear that, where possible, the density of herbivores at the site itself should be published alongside herbivore experimental responses to facilitate comparison of fluxes. For now, we discard local-scale variation as a dominant explanation for the discrepancy between observed herbivore impact and the scale of the consumption flux estimated from reserve-level herbivore density.

There is another possibility, with more profound implications. Empirical observations of wild herbivore metabolic demand suggest that conventional estimates of wildlife metabolic rates are too low. Standard calculations assume that individual herbivore base metabolic rate scales as the 0.75 power of herbivore biomass (i.e. that basal metabolic rate = biomass$^{0.75}$), both in longstanding biological work (Kleiber, 1932) and in more agricultural and applied contexts [e.g. in IPCC emissions estimates (Dong et al., 2006) or by the beef production industry to estimate forage demand (National Research Council, 1996)]. However, modern re-evaluations of this classic estimate have argued that Kleiber's 0.75 may not be the appropriate metabolic exponent for all Afrotropical wildlife and instead suggest that 0.899 is the more accurate metabolic exponent for meso- and megaherbivores, implying much higher energetic demand (Lovegrove, 2000;

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[1] Dry matter intake = body mass$^{0.75}$ × (0.0119 NE$_{ma}^2$ + 0.1938)/NE$_{ma}$, where NE$_{ma}$ is the net energy concentration of the herbivore's diet, taken at the default value of 6. DMI is measured in kg individual$^{-1}$ day$^{-1}$.

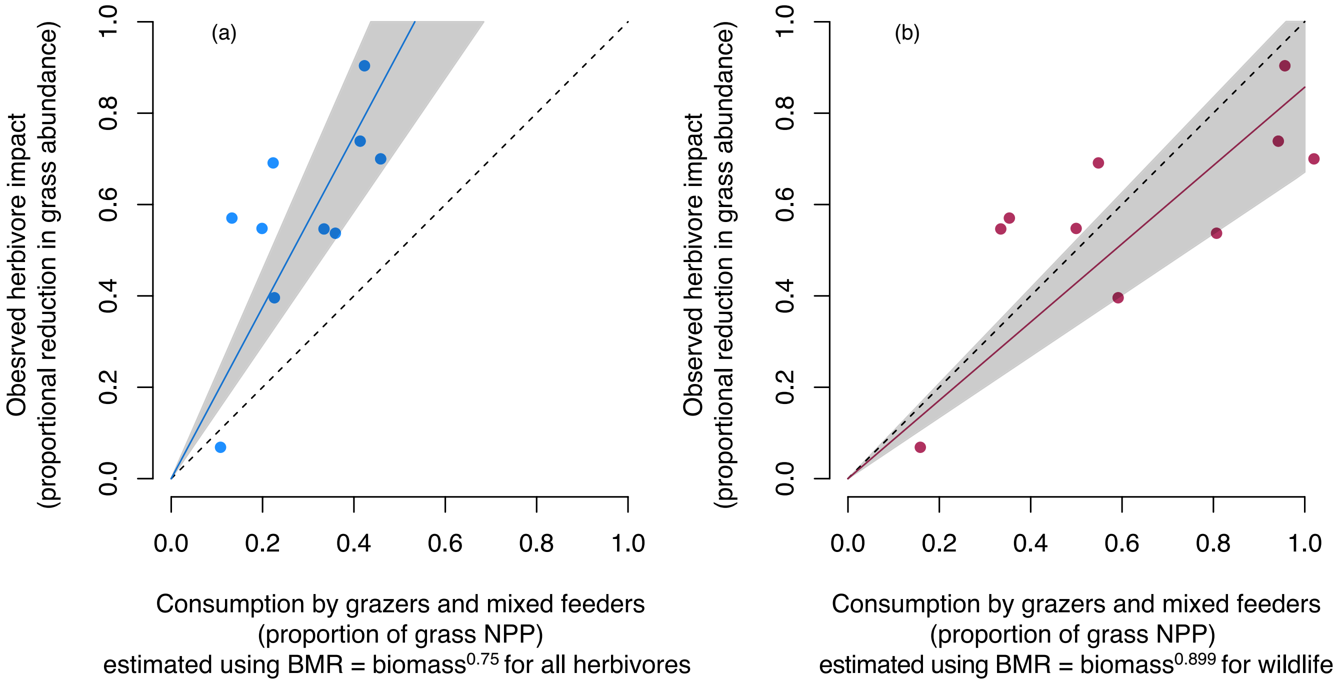

**FIGURE 2** Response of observed herbivore impact to herbivore consumption estimated via Kleiber's (1932) classic scaling exponent for basal metabolic rate (BMR = individual biomass$^{0.75}$) (a) versus a modified exponent applying Lovegrove's (2000) exponent to wildlife only (BMR = individual biomass$^{0.899}$ for wildlife and = individual biomass$^{0.75}$ for livestock) (b). Kleiber's exponent results in rates of herbivore impact that outstrip estimated consumption by 2.1× on average [i.e. reduction in grass biomass = 1.88 (±0.18) × grazing consumption$_{0.75}$ + 0; $R^2 = 0.921$, $N = 10$, $p < 0.001$], whereas the modified exponent results in rates of impact that are in line with estimated consumption [0.98× on average; reduction in grass biomass = 0.86 (±0.08) × grazing consumption$_{\mathrm{mod}}$ + 0; $R^2 = 0.923$, $N = 10$, $p < 0.001$]

see also Glazier, 2005; Kolokotrones, 2010). Applying Lovegrove's 0.899 to calculate metabolic biomass of wild herbivores but maintaining the widely used 0.75 exponent for domestic livestock, we find that grazers and mixed feeders have a combined metabolic demand of ~55% (not ~25%) of aboveground grass productivity. In this scenario, herbivore impacts on grass abundance are approximately equal to estimated metabolic demand on average (0.98 instead of 2.1× greater than estimated metabolic demand). Moreover, we estimate that herbivore impacts on grass biomass increase in close step with estimated increases in grass consumption [i.e. reduction in grass biomass = 0.86 (±0.08) × grazing consumption$_{\mathrm{mod}}$ + 0; $R^2 = 0.923$, $N = 10$, $p < 0.001$; see Figure 2b].[2]

This metabolic hypothesis could entirely reconcile estimates of herbivore consumption with our estimates of herbivore impact (see Figure 2) and may even result in estimates of consumption that exceed estimates of impact (especially at high herbivore densities; see Figure 2b). If true, it offers a compelling argument that we should be using direct, local estimates of metabolic rate to estimate potential ecosystem-level herbivore impacts. Note, however, that we have preserved all terms from established livestock metabolic demand estimates except the base metabolic rate scaling exponent.[1] These additional terms correct for energy expenditure above basal metabolic rate (Dong et al., 2006), which suggests they should be examined directly for their applicability to wildlife. Additionally, while we have preserved the 0.75 exponent for livestock because of its wide use, the large impact of the choice of exponent on ecosystem fluxes estimates suggests that it may also be worthwhile revisiting variations in metabolic rate among species and breeds of domesticates across free-ranging, fenced, and indoor settings (see, e.g., Archer et al., 1999, Griffith et al., 2008). That said, while experiments directly comparing cattle with wildlife are rare, one example (KLEE at Mpala, Kenya; #10 in Table 1) suggests that grass accumulation decreased less when grazed by cattle compared to wildlife, even after controlling for stocking densities (Charles et al., 2017), suggesting that cattle may indeed consume less grass per unit raw biomass than their wildlife equivalents, although there may be alternative explanations for this result.

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[2] See also Tables S1–S3 for results of a full suite of statistical analyses using modified metabolic biomass estimates and Figures S3–S4 for modified figures. Note that we also tried estimating consumption using 50% instead of 100% of mixed feeder biomass for both exponents, and found that including 100% of mixed feeder metabolic biomass improved model fit over including only half of mixed feeder metabolic biomass (AIC$_{0.75}$ = −4.08; AIC$_{\mathrm{mod}}$ = −4.63), but that qualitative relationships remained the same in the case of both Kleiber [impact = 2.5 × consumption on average; reduction in grass biomass = 1.97 [0.24] × grazing consumption$_{0.75}$ + 0; $R^2 = 0.882$, $N = 10$, $p < 0.001$) and the modified exponent [impact = 1.2 × consumption on average; reduction in grass biomass = 0.90 (0.11) × grazing consumption$_{0.75}$ + 0; $R^2 = 0.878$, $N = 10$, $p < 0.001$]. Updated estimates of herbivore metabolic biomass have no qualitative impact on the results reported in Section 2: Determinants of Vegetation Responses to Herbivore Exclusion, except that rainfall appears to have a weak negative effect on grass response to herbivore exclusion. This result is sensitive to the inclusion or exclusion of extreme sites in the Serengeti, and the effect of rainfall within the preferred model is not statistically significant ($t = -1.29$, $p = 0.23$; see also Table S4), emphasizing the conclusion that further comprehensive work is needed to evaluate direct rainfall effects on the herbivore vegetation impacts.

### 3.2 | The productivity flux

We next consider the effect on ecosystem fluxes of direct herbivore impacts on vegetation productivity. On the one hand, if estimates of herbivore impact are indeed larger than herbivore metabolic demand, reductions in grass productivity by herbivores (Charles et al., 2017; Veldhuis et al., 2014) offer a complementary explanation for the large magnitude of observed herbivore impacts on vegetation. On the other hand, if consumption (via modified estimates of metabolic demand) instead outstrips estimates of impact, increases in grass productivity, stimulated by grazing (Augustine et al., 2003; Charles et al., 2017; Hempson et al., 2015; Leriche et al., 2003; Milchunas & Lauenroth, 1993), may help reconcile biomass fluxes and pools in the opposite direction. Expectations for tree and shrub productivity are less resolved (but see Goheen et al., 2013), although browsers clearly impact tree species composition in African savannas (Greve et al., 2012; Staver et al., 2012).

Overall, we posit that herbivore interactions with productivity probably cannot explain the large magnitude of herbivore impacts on vegetation observed here and that productivity feedbacks thus have smaller impacts on vegetation structure than consumption does. First of all, herbivore impacts on productivity can vary in sign, whereas we found that grazing and browsing almost always decreased both grass and tree/shrub abundance. To explain the large magnitude of negative herbivore impacts on standing biomass, herbivore impacts on productivity would need to be large and consistently negative, which contradicts most published work (Augustine et al., 2003; Charles et al., 2017; Milchunas & Lauenroth, 1993). Feedbacks with productivity could certainly resolve some of the unexplained variation in herbivore impact, however, especially among sites experiencing relatively similar herbivore pressure. Secondly, we found that large herbivore exclusion effects emerged quickly, on the time-scale of years, whereas both negative and positive feedbacks can be slow to develop (Augustine et al., 2003; Treydte et al., 2006; Veblen, 2012; Veldhuis et al., 2014). And finally, if non-consumptive effects of herbivores dominated, then we might expect that browsers (and not just grazers) would increase grass responses to herbivore exclusion and that grazers would increase tree responses (i.e. that total herbivore abundance would be more predictive of impact than diet-specific herbivore abundance). Our results directly contradict this prediction: herbivore impacts were tied, not to the total abundance of herbivores in the system, but rather to the abundance of browsing herbivores eating trees and grazing herbivores eating grass (see Figure 1).

However, we do see (at least in grasses) a systematic role for herbivory to stimulate productivity. We observed that intermediate grazing intensity tended to have a disproportionately large impact on grass abundance, whereas intense grazing tended instead to achieve high consumption at relatively modest per-capita impact (see Figure 2b). Among systems with substantial herbivory, four out of five sites falling below the 1:1 impact versus consumption line are from the Serengeti. These Serengeti sites are intensively grazed, but grazing is concentrated during a short period, punctuating a longer, ungrazed recovery period. This finding mirrors well-replicated observations from rotational grazing systems, showing that short-term, intensive grazing has less persistent ecosystem-level impacts than resident grazing at similar average intensities (Briske et al., 2008). This suggests that grazing may stimulate productivity especially in systems where grazing is intense but episodic (Oesterheld & McNaughton, 1991; Richie & Penner, 2020), decreasing the per-capita impact of migratory grazers on ecosystem structure compared to resident herbivores.

### 3.3 | The time scale of vegetation accumulation

A final possibility is that, because vegetation accumulates over time and in a variable environment, the observed effects of herbivore exclusion on grass or tree and shrub abundances may not directly reflect annualized estimates of productivity and consumption. If plant growth is non-linear, following a characteristic logistic-type function, relatively small consumption, early in but persistent throughout the growing season or lifespan of a plant, might result in multiplicative effects of consumption on productivity and thus on biomass accumulation. Among grasses, if grazers eat the first leaves to emerge, consumption could decrease photosynthetic potential, thereby decreasing seasonal NPP (Buttolph & Coppock, 2004; Teague et al., 2013). This potential mechanism is not widely discussed as a determinant of grass productivity, although the timing of consumption might especially shape how mixed feeders impact savanna ecosystems, since they change their diets seasonally in response to changing tree versus grass forage availability (Codron et al., 2007). In support of this, we found that counting 100% instead of 50% of mixed feeder metabolic biomass somewhat counterintuitively improved predictions of impact on grasses (see Table S1) and produced better correspondence between grazer impacts on grass and estimated grazer consumption (see Figure 2).

The real influence of demographic constraints on productivity are nonetheless likely more prominent in the tree and shrub layer. Whereas grass biomass typically accumulates on the time-scale of one or a few years, which makes grass dynamics relatively predictable (Sala et al., 2012; Staver et al., 2018), tree and shrub establishment is much more variable in time (Prins & van der Jeugd et al., 1993; Staver, Bond, et al., 2011) and less coupled to observed environmental gradients (Staver, 2017). This variability is in large part the product of demographic bottlenecks, with strong herbivore effects concentrated at the sapling stage which have large and persistent ecosystem consequences (Moncrieff et al., 2011; Prins & van der Jeugd, 1993; Staver & Bond, 2014). Unfortunately, we have been unable, here, to compare observed experimental herbivore impacts on trees and shrubs with productivity and consumption fluxes from the published literature, for the simple reason that no such synthesis of tree and shrub productivity has been published. However, observed impacts on trees are nonetheless quite large (~30.6% on average) and may even exceed the accumulated effects of per-capita grazing on grass (the slope of tree impact vs. browser and mixed feeder biomass is almost 2× as high as the slope of grass impact vs. grazer and mixed feeder biomass; see Table 2, Table S4). Comparing tree and shrub productivity, consumption and accumulated impacts will undoubtedly be informative in future, and differences in tree and grass productivity may play a role in increasing the impact of browsing on trees. However, we hypothesize that browsing impacts trees via demographic effects that accumulate over time, such that considering the timescales of tree growth will be central to reconciling productivity and consumption fluxes with standing pools.

Overall, we find that the magnitudes of herbivore impacts on vegetation scale directly with herbivore abundances and that herbivore impacts are large compared to previous estimates. One compelling possibility is that herbivore metabolic demand is higher among African wildlife than widely assumed (Lovegrove, 2000), resulting in rates of consumption by herbivores that are larger than existing estimates. Another possibility is that herbivores impact vegetation not just via consumption but also via changes in productivity; mechanisms could include hydrological feedbacks, accelerated nutrient cycling, and changes in grass community composition as a result of herbivory. Herbivory-induced bottlenecks on vegetation productivity – on the time-scale of years in grasses and much longer in trees and shrubs – may also play a role. Regardless of the mechanism, herbivore impacts are consistent and of a magnitude that could impact ecosystem dynamics.

## 4 | DETERMINANTS OF HERBIVORE ABUNDANCE IN AFRICAN SAVANNAS AND TRENDS THROUGH TIME

Since herbivore diet and abundance directly determine the magnitude of herbivore vegetation impacts in savannas, understanding how herbivore communities have varied through time is paramount for contextualizing changing herbivore effects. Over the past 7 million years, evolution, diversification, and extinction have systematically changed the functional composition of savanna herbivore communities. Broadly speaking, this period in the Mio-Pliocene was characterized by a novel expansion of $C_4$ grassland ecosystems, leading to significant turnover as herbivore lineages evolved traits to utilize grass resources (Janis et al., 2004). Relative to the Miocene, the proportion and diversity of browsing-adapted taxa generally decreased as open systems expanded (Faith et al., 2019; Janis et al., 2004; Morales-García et al., 2020), with grazers increasing and reaching peak diversity in Africa approximately 1 million years ago (see Figure 3a).

Since then, African ecosystems have been subject to a range of environmental and land use changes, resulting in ongoing changes to herbivore communities that have likely shaped how herbivores impact savanna vegetation dynamics. Modern ecological theory offers insights into likely changes in the factors that regulate herbivore communities, and fossil and historical records offer direct evidence of those changes. In this section, we review both lines of evidence

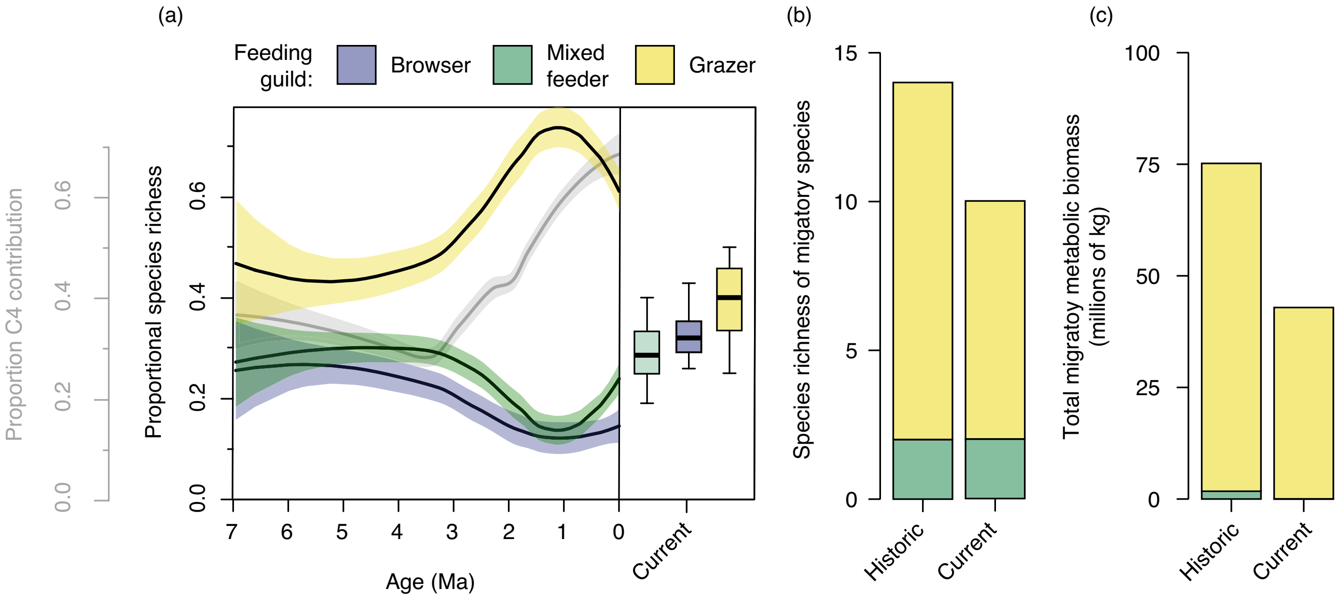

**FIGURE 3** Past changes in richness and abundance of grazers compared to mixed feeders and browsers in Africa. We evaluate African herbivore species richness by feeding guild in the eastern African fossil record compared to modern richness at the same sites (a; from Faith et al., 2019; Hempson et al., 2015), and, for perspective on possible grazer abundances, we also evaluate richness and total biomass of all mass migrations in the African historical record versus today (b, c; from Harris et al., 2009). We also provide estimated $C_4$ contributions to soil carbonates from East Africa, for a sense of the timing of grassy ecosystem expansion on the continent (in grey on a; from Levin, 2015). Grazer diversity increased from ~4 Ma to 1 Ma, but extinctions then decreased grazer diversity relative to mixed feeders and browsers. The loss of grazers continued into the historical era; migration extirpation has restricted mass migration to fewer species and has substantially decreased total migratory grazer populations in Africa. In a, errors on temporal trends give 97% confidence intervals, and box-and-whisker plots give median, quartiles and ranges excluding outliers. Blue corresponds to browsers, green to mixed feeders, yellow to grazers, and grey to $C_4$ grass across the entire figure

and what they tell us about the history of herbivore abundance and potential herbivore impacts in African savannas.

Herbivore population sizes are determined by a combination of bottom-up and top-down factors (resource scarcity and predation, respectively). Today (Knapp et al., 2008) and since the late Pliocene (~3 Ma; deMenocal, 1995, 2004), African savannas have usually been characterized by a marked rainfall seasonality and interannual rainfall variability, such that bottom-up limits to herbivore population sizes predominantly depend on the adequacy of diet quality and quantity during the dry season and/or occasional droughts. These forage bottlenecks place a strong constraint on herbivore population dynamics, and many herbivore populations rely on 'key resources' (Illius & O'Connor, 1999) that determine herbivore population density. Herbivore populations that have large, stable key resources tend to have larger population sizes with less variation than herbivore populations with small, variable key resources (Abraham et al., 2019; Illius & O'Connor, 2000; Staver & Hempson, 2020; Wang et al., 2006). Because forage variability is spatially heterogeneous and can differ substantially between trees and grasses both seasonally (Ryan et al., 2016) and interannually (Case et al., 2019; Sala et al., 2012), herbivore species display a range of strategies that maximize the size and stability of their key resources.

The first strategy is migration, prevalent especially among grazers to alleviate strong seasonality in grass availability and quality. Migratory grazers track the areas in a landscape that provide them with the most abundant quality forage (Anderson et al., 2010; Holdo, Holt, et al., 2009), and even populations that are not habitually migratory can move in response to episodic drought-related scarcity (Staver et al., 2018). These key resources (in the form of dry-season or drought forage refugia) allow them to avoid major crashes in population size in response to scarcity (Abraham et al., 2019), maintaining much larger population sizes than non-migratory populations of the same species (Staver & Hempson, 2020).

On historical time-scales, grazing migrations were once abundant, but have since collapsed in many places where they formerly occurred (see Figure 3b,c; Harris et al., 2009) as hunting, land use and fragmentation, and fencing of protected areas have decimated grazer populations (Dobson et al., 2010; Ripple et al., 2015). Patterns on longer time-scales are less clear. In Africa, specialist grazers represented the majority of herbivore extinctions over the last 1 million years (see Figure 3a), with the most recent phase of extinctions concentrated between 13 and 6 ka (Faith, 2014). This long-term decline in grazer diversity is associated with the onset of high-amplitude glacial–interglacial cycles coupled with more frequent and severe pulses of aridity that would have limited access to grass forage (deMenocal, 2004; Faith, 2014; Faith et al., 2019). Unfortunately, diversity does not necessarily correspond to abundance, and much less is known about how migratory grazer abundances have changed through pre-history. High-resolution serial isotopic measurements of tooth enamel can indicate whether individual animals feed in geologically distinct regions (Sr), on hydrologically distinct sources (O), or from distinct vegetation types (C) (Hobson, 1999) and have been used to identify migratory behaviour in the extinct Australian mega-browser *Diprotodon optatum* (Price et al., 2017) to examine migration patterns in non-analogue Pleistocene herbivore populations in the Cape Floral Region (Copeland et al., 2016; Hodgkins et al., 2020), and to show, for example, that mastodons but not mammoths displayed migratory behaviour (Hoppe et al., 1999). However, there is as yet no comprehensive analysis of how pre-historic migratory grazing communities have changed in Africa or elsewhere. It is nonetheless clear that, while great migrations still exist – most famously in the Serengeti ecosystem – all evidence suggests that past herbivore communities were likely more dominated by grazers in general (see Figure 3a; Faith et al., 2019) and migratory grazers specifically (see Figure 3b,c; Harris et al., 2009), likely translating into larger grazing impacts on the grass layer (see Figure 5a).

The second major trait that allows herbivores access to a forage reservoir is mixed feeding. Mixed feeders switch their diets seasonally, particularly beneficial in landscapes where tree and grass phenologies differ, usually in such a way that browse is available in dry season when graze is not. If the costs of switching between forage sources are relatively low (e.g. if mixed feeders are efficient at foraging and digesting both trees and grass; Illius & Gordon, 1992; Pérez-Barbería & Gordon, 1999; Perez-Barberia & Gordon, 2001), then seasonal dietary switches offer up a key resource that effectively increases the size (Staver & Hempson, 2020) and stability (Abraham et al., 2019; Young, 1994) of herbivore populations.

Historical changes in the dominance of mixed feeders have received less direct attention than those of migratory grazers. This is probably in part because they remain so abundant in modern savannas (Staver & Hempson, 2020), since mixed feeding offers a strategy for alleviating seasonal forage scarcity that does not rely on spatial heterogeneity in forage availability and which is robust to landscape fragmentation and fencing. These combine to make mixed feeding fairly robust to ongoing land-use change (Abraham et al., 2019). Over the past million years, the diversity of mixed feeders increased in savanna herbivore communities at the expense of grazers (Faith et al., 2019). However, given that mixed feeding is so beneficial in an environment where two food sources are abundant (Staver & Hempson, 2020), the overall lack of diversity of mixed feeders in savanna ecosystems (Figure 3a) is something of a paradox. One possibility is that the benefits of mixed feeding, while obvious at a population level, are less clear in diverse communities of specialists (following from Abrams, 2006). Alternatively, it may be that the mixed feeding strategy is associated with fewer opportunities for diversification over evolutionary timescales. For example, mixed feeders may have reduced potential for allopatric speciation and diversification (e.g. Vrba, 1985, 1992) if their dietary flexibility and/or association with ecotones (e.g. between forest and grassland) means fewer vicariance events stemming from the shifting distribution and fragmentation of habitats through time (e.g. Lorenzen et al., 2012; Faith & Behrensmeyer, 2013). In support of this, we note that impalas (*Aepyceros*) have persisted with little morphological change since the late Miocene (Leakey & Harris, 2003), with their long-term evolutionary stasis (compared to other Bovidae) attributed to ecological flexibility (Vrba, 1980, 1984).

Finally, while population potentials increase with resource availability, actual population size is also determined by top-down factors including most notably predation and pathogens. Specific adaptations that mitigate the effect of pathogens have undoubtedly evolved (e.g. resilience to sleeping sickness), but the diversity and rapid rates of evolution among pathogens limit generalizations about these adaptations. Predation rates, however, are strongly linked to body size, with very large species experiencing considerably lower predation mortality than small- to medium-sized species (Hopcraft et al., 2010, 2011; Sinclair et al., 2003). Adult megaherbivores have individual body masses (≥1,000 kg) that allow them to escape the top-down effects of predation to achieve abundant populations. Interestingly, large body sizes also allow herbivores to migrate more easily and to trade forage quantity for quality (Olff et al., 2002), which in sum mean that megaherbivores are likelier to incorporate graze into their diets than mesoherbivores are (Damuth, 1987).

Changes in the body-size distributions of herbivore communities through time are well known. Megaherbivore richness in Africa has declined over the last 4 million years (see Figure 4), resulting from the extinction of claw-footed chalicotheres, short-necked giraffes and an array of proboscideans, hippos and rhinos, among others (Faith et al., 2018). Globally, around two-thirds of all large-bodied mammal genera (>44 kg) disappeared at the end-Pleistocene, as human populations dispersed out of Africa (Rowan & Faith, 2019; Smith et al., 2018). Mechanisms are disputed, but the result has been a herbivore community that is relatively enriched in small- and medium-bodied mammals, likely more dependent on browsing than on grazing (Damuth, 1987). These changes in body size have likely been exacerbated by parallel predator extinctions. Whereas most continents suffered significant losses of large (>22 kg) carnivore taxa since the late Pleistocene (Malhi et al., 2016), Africa instead gradually lost large carnivore richness and functional diversity throughout the last 3–4 million years (Faith et al., 2020; Werdelin & Lewis, 2005, 2013). However, while there is no evidence for African carnivore extinctions at the end of the Pleistocene, African predator populations have recently come under increasing threat from land-use change, ritual and trophy hunting, and agricultural replacement of prey (Estes et al., 2011; Ripple et al., 2014). Modern evidence suggests that these predator extinctions likely allowed mesoherbivore populations to expand as megaherbivore populations collapsed, together resulting in a wholesale decrease in body size among African herbivore communities. This has been hypothesized to have major effects on vegetation (Bakker et al., 2016; Malhi et al., 2016). We note, however, that the results of our exclosure synthesis suggest no special role for megaherbivores (see Table S1), except in how they impact overall herbivore abundances and perhaps also their diet composition.

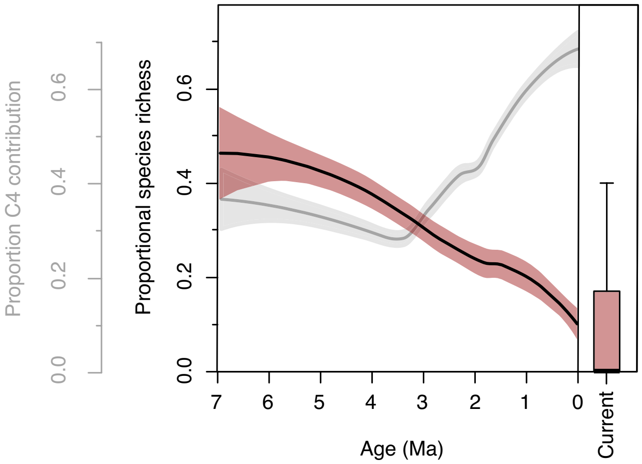

**FIGURE 4** Past changes in proportional richness of megaherbivores (body mass ≥ 1,000 kg) compared to their modern richness at the same sites (from Faith et al., 2019; Hempson et al., 2015). Estimated $C_4$ contributions to soil carbonates from East Africa are repeated from Figure 3 for context (in grey; from Levin, 2015). Errors on temporal trends give 97% confidence intervals, and box-and-whisker plots give median, quartiles and ranges excluding outliers. Red corresponds to megaherbivores and grey to $C_4$ grass

In sum, there are thus three main herbivore traits (the 3Ms) that promote large herbivore population densities: Migration and Mixed feeding serve to maximize the size and stability of the key resource, while large body size—with the largest species referred to as Megaherbivores—serves to minimize predation and expand potential dietary breadth. Overall, it is clear that grazers represent a much more restricted component of savanna ecosystems than they did in the past, both 100 years and 1 million years ago, replaced by a herbivore community increasingly dominated by mixed feeders. Megaherbivores have also decreased in richness and perhaps also abundance. Trends are likely only to continue, as fragmentation, fencing, and hunting continue to isolate African savanna-protected areas and to exacerbate ongoing loss of migratory populations (Harris et al., 2009; Shaw, 2016). Increasing drought intensity and severity may also contribute, since grazers that rely on movement to drought refugia to escape drought effects (Abraham et al., 2019; Staver et al., 2018) may no longer be able to avoid starvation. Grazing megaherbivores – most famously white rhinos (Waldram et al., 2008) – are also on the brink of local extirpation or even extinction from poaching (Owen-Smith, 1989; Ripple et al., 2015). From the standpoint of grass consumption, the rise of mixed feeders has potentially compensated for some of this loss, at least within protected areas (Staver & Hempson, 2020), but even mixed feeders rarely achieve the true mass effects of a large grazing migration. Trends in herbivore communities have in turn likely reshaped the dominant impacts of herbivores on vegetation, with a shift from grazing-dominated impacts to impacts split between grazing and browsing, reflecting the relatively high density of mixed feeders in savanna protected areas today.

## 5 | THE PAST AND FUTURE OF HERBIVORE IMPACTS ON SAVANNA VEGETATION

We find that, today, herbivore impacts on savanna ecosystems are large and scale with herbivore abundance: impacts on the savanna

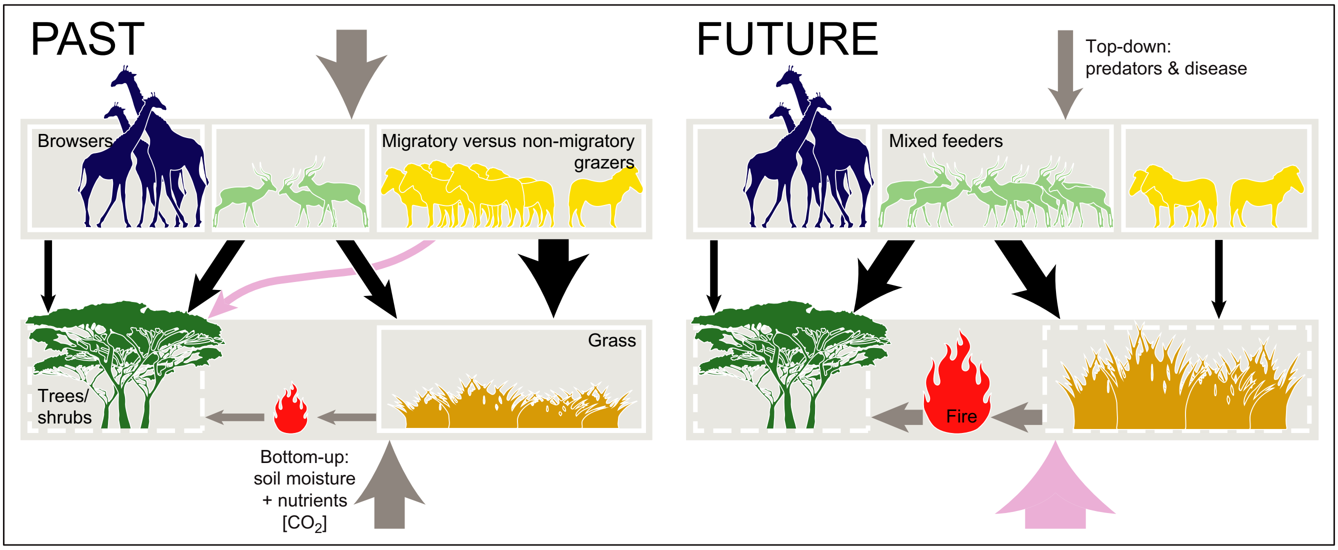

**FIGURE 5** Hypothesized past and future of herbivore impacts on vegetation structure in African savannas. We have targeted our 'past' conceptual hypothesis at the interval of peak grazer diversity ~1 million years ago; the 'future' should correspond to the present with trends that intensify into the end of the 21st century and beyond. In the past, wild grazers were more abundant in African savannas, with intense effects on grass but uncertain effects on trees. In the present and future, we hypothesize that mixed feeder effects will dominate, with intensive effects on both grasses and trees, because grazer migrations have been or may yet be extirpated in many savannas; bottom-up constraints have changed to favour grass growth and woody encroachment, but their magnitude relative to those of herbivore and fire are unknown. Arrow width roughly scales with the magnitude of the interaction. Arrows in black are the subject of this review; those in pink are what we identify as dominant sources of uncertainty, with uncertain outcomes for vegetation denoted with dashed white boxes

grass layer increase with the abundance of grazing herbivores and impacts on the tree layer increase with the abundance of browsing herbivores (see Figure 1). As such, the past, present, and future impacts of herbivores on savanna ecosystems are likely the direct result of variation in herbivore abundance. To an extent, changes in herbivore communities through time can be constrained, both via our theoretical understanding of the controls on herbivore populations (the 3Ms: mixed feeding, migration, and megaherbivory) and via direct observations from the historical and fossil records. Overall, the net result has been that the diversity and abundance of wild grazers have decreased over time, replaced in some agricultural contexts by grazing livestock and in protected areas and savannas with intact wildlife communities by smaller-bodied mixed feeders (see Figure 3). Thus, even in Africa, where herbivores continue to substantially impact vegetation, the dynamics of top-down herbivore control of savanna vegetation may have changed substantially. In this section, we highlight likely changes in the impacts of herbivores on vegetation in African savannas, identify key uncertainties for further study, and evaluate what this means for herbivore impacts in savannas more broadly.

Past herbivore communities were likely more dominated by wild grazers and megaherbivores on both historical (see Figure 3b,c; Harris et al., 2009) and paleoecological time-scales (see Figures 3a and 4; Faith, 2014; Faith et al., 2019). Migratory grazers especially were likely a more significant component of savanna herbivore communities (Harris et al., 2009), translating into larger grazing impacts on the grass layer. Herbivore exclusions in the Serengeti provide support for the hypothesis that migratory grazer impacts on the grass layer can be substantial (Anderson et al., 2007; Ritchie, 2014; Veldhuis et al., 2020), and thus we predict that grazing likely played a larger role in wildlife-dominated savannas in the past. However, we also find that the episodic grazing associated with migration may have relatively small per-capita impacts on grass biomass. This suggests that, while grazing likely played a larger role in wildlife-dominated savannas in the past, landscape-level effects were probably not as intensive per-capita as they are locally in, for example, grazing lawns. This prediction may even extend to savanna rangelands, if indeed domesticates have lower per-biomass metabolic demands than the wild grazers they have replaced.

Past herbivore communities may also have had different impacts on trees, both indirectly via fire-grass interactions and directly via browsing effects. Firstly, larger grazer control of grass biomass in the past may have reduced fire frequency and intensity (Bakker et al., 2016; Hempson et al., 2019; Malhi et al., 2016) below today's levels, such that fire did not control tree demography (Holdo, Sinclair, et al., 2009; Roques et al., 2001) to the same extent that it does in many savannas today (Pellegrini et al., 2021). Secondly, declines in relative grazer diversity over the last million years may also correspond to an increase in browsing pressure, resulting from the release of forage constraints and top-down predator control on medium-sized mixed feeders (e.g. impala; although note that these are less certain than corresponding trends in grazer diversity and abundance). The sum of these processes may be that both fire and browsing controls on the savanna tree layer are more intense today compared to the past. However, migratory grazer impacts on trees add a wrinkle to predicting past herbivore impacts on trees (see Figure 5a). Tree responses to herbivore exclusion are not well studied in the Serengeti (but see Morrison et al., 2018), but evidence from agricultural systems suggests that grazers can opportunistically eat and/or trample tree seedlings (e.g. Ludvíková et al., 2014; Tjelele et al., 2015), imposing grazer constraints on trees not captured in our synthesis here. Further work should directly evaluate the impacts of grazing – especially migratory grazing – on the tree component of savannas, to better constrain how a grazer-rich history might have shaped the evolution and ecology of African savannas.

In the future, we speculate that small-bodied mixed feeders may continue to play a major role in African savannas, as they do today, but that their effects will depend on other global change impacts in savannas. On their own, high mixed-feeder densities should translate into stronger top-down control on both tree and grass layers in savanna – a prediction inconsistent with current vegetation trends. Woody encroachment is widespread in both agricultural and wildlife savannas (Stevens et al., 2017), ubiquitous (Buitenwerf et al., 2011) albeit especially severe where grazing is intense (Brown & Archer, 1999; Case & Staver, 2017; O'Connor, 1995; Roques et al., 2001). Early evidence also suggests that grass production may be increasing in response to global change (Borer et al., 2020; Reich et al., 2018). However, these trends can be easily reconciled with increases in herbivore pressure. Widespread woody encroachment has been attributed in part to local changes in herbivory and fire (Case & Staver, 2017; Roques et al., 2001), but global drivers are also at play – most notably including increasing atmospheric $CO_2$ (Bond & Midgley, 2012). Savanna grasses, too, may be subject to $CO_2$ fertilization (Norby & Zak, 2011; Reich et al., 2018). In both cases, increasing $pCO_2$ allows both trees and grasses to increase their water use efficiency, increasing productivity but also increasing leaf C:N and eroding forage quality. Faster plant growth and decreasing forage quality may thus allow plants to escape top-down control from both fire and herbivory (Borer et al., 2020), even if mixed feeders remain relatively abundant (see Figure 5b). As such, despite persistent impacts of small-bodied mixed feeders on savanna vegetation, the days of herbivore-controlled savannas may be numbered.

Ideally, we would like quantitative and not just qualitative, speculative constraints on when that is likely to happen (or whether it has happened already). To achieve this, we need to shift our focus from repeatedly testing whether herbivores impact vegetation – after all, they clearly do (see Figure 1; Jia et al., 2018) – to disentangling the magnitude of their effects relative to other determinants of vegetation structure and what causes them to vary. In particular, environmental constraints on herbivore impacts are still unknown, in large part because herbivore exclusion experiments have focused so much on systems where herbivore effects are most intense. This hobbles our predictive capacity but offers a clear avenue for further research to clarify the potential future of herbivore impacts in savanna ecosystems. We suggest that a top priority should be the establishment of herbivore exclusion experiments in arid (<350 mm MAR) and mesic savannas (>900 mm MAR), outside the narrow environmental range where herbivory is most intense. Experiments should also always report basic soil nutrition and texture information. We also suggest that herbivore experiments should more closely consider the mechanisms of herbivore impacts, with experiments designed to evaluate whether and why herbivore impacts so substantially outstrip direct herbivore consumption.

This synthesis also suggests fruitful avenues for integration between physiological and ecosystem approaches to herbivore–vegetation interactions in savanna systems. We found that estimates of grass consumption were highly sensitive to assumptions about herbivore metabolism, but we have by necessity employed an approximation that combines observations of wildlife metabolic scaling (Lovegrove, 2000) with agricultural estimates of consumption by grazers (Dong et al., 2006). Consumption may also differ in wild herbivores and across domesticates in different agricultural contexts, which suggests a clear need for further work to refine estimates of herbivore-driven ecosystem fluxes. Meanwhile, comparable evaluations for tree impacts were impossible, because tree productivity is not well understood. We encourage explicit comparisons of herbivore impact versus consumption and productivity of trees and shrubs, aimed at quantifying the ecosystem impacts of browsing for savanna trees.

## 6 | CONCLUSIONS

In this review, we synthesize vegetation responses to herbivore exclusion across African savannas, demonstrating that herbivory consistently decreased standing vegetation and that the magnitude of herbivore impact scaled directly with herbivore abundance: grass responses increased with grazing herbivore abundance, whereas tree responses increased with browsing herbivore abundance. Migratory grazers and mixed feeders together determined grass responses, whereas mixed feeders were more abundant than browsers and thus mostly responsible for tree responses. Moreover, herbivore impacts from direct observations were much larger than current modelled estimates of consumption using classic scaling relationships for metabolic demand. Here, we estimate that herbivores decreased grass abundance by 57.0% and tree abundance by 30.6% (see Figure 1)—substantially larger than site estimates of 25% of grass productivity consumed (tree productivity less understood, which prevents the equivalent calculation for browsing). This suggests either (a) that the basal metabolic rates of savanna herbivores are substantially higher than global scaling relationships suggest (Lovegrove, 2000), which instead yield estimates of consumption ~55% of biomass consumed (see Figure 2), and/or (b) that herbivores impact net ecosystem productivity not only via consumption but also via direct effects on net primary productivity. Both possibilities demand further research.

The direct relationship between herbivore abundance and herbivore impact allows us to predict how herbivores potentially impacted savannas in the past and how their role is changing into the future (see Figure 5). Grazer and megaherbivore diversity and abundance have declined through time (see Figures 3 and 4), likely resulting in decreases in wild grazer impacts on the grass layer; changes in browser and mixed feeder abundances are less clear and so too are changing tree-layer dynamics (see Figure 5). Today, small-bodied mixed feeders dominate wildlife herbivore communities, except in a few systems with extant grazer migrations (Staver & Hempson, 2020), resulting in intensive impacts from mixed feeders on both tree and grass savanna components. We expect mixed feeder dominance to persist into the future but expect that the relative magnitude of herbivore impacts on savanna vegetation will depend on changing constraints from other limiting processes—including climate, fire and changing atmospheric $CO_2$ (see Figure 5). Disentangling how herbivore impacts vary should be a priority for future research, with respect both to environmental context, including variation in rainfall, soil and resulting forage nutrition, and to variation in herbivore traits, including dietary strategy, migration and metabolism.

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## AUTHORS' CONTRIBUTIONS

A.C.S. wrote the manuscript, with contributions from J.O.A. and G.P.H. on factors influencing herbivore population dynamics and A.T.K., J.T.F. and J.O.A. on temporal trends in herbivore population sizes; A.C.S. compiled herbivore exclosure data and G.P.H. estimated herbivore population densities for Figures 1 and 2 and Figures S1–S3, J.T.F., A.T.K. and J.O.A. synthesized data for Figure 3, J.T.F. and A.T.K. synthesized data for Figure 4, and J.O.A. and A.C.S. workshopped Figure 4. A.C.S. analysed data and produced Figure S4. All authors discussed ideas and provided manuscript feedback.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data synthesised for herbivore impact analyses can be freely accessed via Dryad: https://doi.org/10.5061/dryad.3n5tb2rhk (Staver et al., 2021).

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## SUPPORTING INFORMATION

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

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