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RESEARCH ARTICLE

Large herbivores are linked to higher herbaceous plant diversity and functional redundancy across spatial scales

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Abstract

1. Large herbivores can strongly influence plant communities. However, these effects are highly variable, potentially depending on the herbivore regime, that is, herbivore diversity and density. However, the role of the herbivore regime has been challenging to evaluate across spatial scales due to widespread defaunation and a lack of data on herbivore communities and their densities.
2. Here, we investigated the effects of large herbivores along a gradient of trophic complexity (low to high herbivore diversity) and herbivory intensity (estimated from herbivore biomass and visitation frequency) on plant taxonomic and functional diversity at different scales (plot [$n=250$], site [$n=50$] and landscape [$n=10$]) in 10 reserves in the savanna biome in South Africa.
3. We found higher total plant species richness, driven by higher herbaceous (but not woody) plant species richness, in areas with higher herbivory intensity across multiple scales. While herbivores had no significant relationship with plant functional richness, we observed higher functional redundancy at all scales in areas more frequently visited by herbivores. Overall, herbivore–vegetation relationships were largely consistent across scales, and the strongest effects emerged at the largest scale.

4. Our results show a positive relationship between large herbivores and both herbaceous plant species richness and plant functional redundancy, the latter suggesting higher vegetation resilience (the capacity of ecosystems to quickly recover from disturbances as different species compensate for the loss or decline of others). These effects are largely consistent across scales, indicating that the impact of herbivore regimes on plant communities is predominantly scale-independent and that large herbivores drive vegetation dynamics at both local and large scales. However, the stronger effects observed at the landscape scale imply that herbivore impacts manifest most prominently at larger scales. Altogether, our results suggest that restoring large herbivore populations can be expected to promote herbaceous plant diversity and ecosystem resilience.

KEYWORDS

animal impacts, biodiversity, herbivore–plant interaction, megafauna, megaherbivores, restoration, rewilding, trophic complexity

1 | INTRODUCTION

Large herbivores can strongly impact ecosystems and shape plant community composition (Pringle et al., 2023; Søndergaard, Fløjgaard, et al., 2025), yet the magnitude and direction of herbivore impacts can be highly variable (Malhi et al., 2022; Trepel et al., 2024). An explanation for this variability may be that herbivore impacts depend on the specific herbivore regime (Atkinson et al., 2024; Bakker et al., 2016), and the spatial scale at which vegetation responses are quantified. However, most studies have measured herbivore impacts using local-scale exclusion experiments or other binary presence–absence contrasts (Barbero-Palacios et al., 2024; Trepel et al., 2024), leaving the specific role of the herbivore regime and its dependence on spatial scale in moderating herbivore impacts comparatively poorly understood.

The herbivore regime consists of trophic complexity (i.e. herbivore composition) and herbivory intensity (i.e. herbivore density). For example, vegetation responses are expected to change with herbivore body size, where stronger reductions in plant biomass are related to having the full spectrum of herbivore size classes present (Coverdale et al., 2024). Megaherbivores, defined as species with an adult body mass >1000 kg (Owen-Smith, 1988), are thought to exert particularly strong ecological effects. For example, elephants can reduce woody plant cover by toppling or debarking trees in ways that smaller herbivores cannot replicate (Faith et al., 2020). Similarly, white rhinos, unlike many other wild herbivores, can maintain grazing lawns and thereby influence fire regimes (Waldram et al., 2008). Herbivore density is also a key predictor of herbivore effects, as exemplified by lower burned area and shorter vegetation structure in areas with higher grazer densities (Karp et al., 2021, 2024; van der Plas et al., 2016). Moreover, the effects of herbivores are likely to vary across spatial scales. At the plot scale, for example, the effect of large herbivores on plant diversity appears overall neutral (Trepel et al., 2024). Yet, their heterogeneous space use may produce a mosaic of local suppressions and releases, which, when considered at larger spatial scales, scale up to more heterogeneous vegetation structure and higher diversity across landscapes.

The effects of herbivory can vary substantially among plant life forms. For example, forbs can sometimes be subordinate to grasses and may therefore benefit from the disturbance caused by large grazers (Søndergaard, Ejrnæs, et al., 2025). Conversely, graminoids may be better adapted to grazing pressure and thus ultimately benefit from herbivory (Archibald et al., 2019). Graminoids frequently compete with woody plants (Holdo & Nippert, 2023), which are often more tolerant of disturbance and may gain an advantage if herbivores suppress one or a few hyperdominant grass or woody species. In contrast, woody plants may initially resist herbivory but show slower regrowth and reduced competitiveness with grasses once affected, which can result in negative responses to herbivore impacts. Most studies on herbivore effects on plant diversity, however, have focused on herbaceous vegetation (but see e.g. Joseph et al., 2015; Reikowski et al., 2022; Wigley et al., 2014) and often do not distinguish between grasses and forbs (Coverdale et al., 2024; Manier & Hobbs, 2007) or focus exclusively on one group (van Coller & Siebert, 2020; van der Plas et al., 2016), making it difficult to compare herbivore effects across life forms.

By influencing the composition and structure of plant communities, large herbivores are further thought to impact ecosystem resilience (Forbes et al., 2019), defined as the capacity of an ecosystem to (quickly) regain or maintain functioning after environmental stressors and shocks (Carpenter et al., 2001; Ives & Carpenter, 2007). Resilience is thought to be highest in functionally diverse communities which can maintain functioning under various conditions (Canadell et al., 2007; Schäfer et al., 2019). However, this may not always be true (Lipoma et al., 2024) because a larger functional distance between species could come with a lower overlap in functional space, reducing their ability to compensate for each other's loss (Lipoma et al., 2024). To explicitly account for the functional overlap in a community, functional redundancy has been proposed as an alternative way to relate plant community composition to resilience (Biggs et al., 2020; Naeem, 1998; Rosenfeld, 2002; Walker, 1992). However, how large herbivores influence functional diversity and redundancy remains largely unknown.

Here, we aim to test how the herbivore regime affects plant taxonomic and functional diversity across spatial scales (plot, site and reserve scale) in 10 savanna reserves in and around the Waterberg Biosphere Reserve in South Africa. We focus on this area because the region is home to fenced reserves spanning broad gradients of herbivore diversity and density. Importantly, the herbivore community composition (i.e. which species are present at which densities) in a reserve depends on introduction choices made by landowners (rather than on vegetation characteristics such as productivity) and is therefore comparable to a natural experiment (Diamond & Case, 1986). Although this approach is less ideal than a true experimental setup (which is, unfortunately, nearly impossible as it would require large landscape-scale exclosures in a full-factorial design that encompasses gradients of herbivore composition and density), it may enable us to move beyond inference from presence–absence contrasts at small exclosures and to understand the role of the herbivore regime at scales relevant to management and restoration decisions (e.g. in trophic rewilding (Svenning et al., 2016)). Specifically, we aim to evaluate the following questions:

1. How do large herbivores affect plant species richness?
2. Do plant life forms (i.e. graminoids, forbs and woody plants) respond differently to large herbivore impacts?
3. How do large herbivores affect plant functional diversity and redundancy?
4. How do herbivore effects differ across scales?

2 | METHODS

2.1 | Study area

Our study area was the Waterberg region in Limpopo Province, South Africa. Here, we worked in 10 reserves with large herbivore (≥45 kg adult body mass (Martin, 2005; Moleón et al., 2020)) communities ranging from very low to very high diversity and biomass (herbivore species richness ranged from 1 to 19 and biomass ranged from 0.1 to 240 kg/ha, Table S2). Reserves with the most intact herbivore communities included for example the megaherbivores African savanna elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*) and giraffe (*Giraffa giraffa*). Nine privately owned reserves (Lapalala Wilderness, Kaingo Game Reserve, Dabchick Wildlife Reserve, Ant's Farm, Jembisa, Syringa Sands and Quella, Summerplace, Swebeswebe and Willowisp) and Marakele National Park (government-owned) were surveyed. In Lapalala Wilderness, our sites were placed on the control sites of the Lapalala Elephant Landscape Experiment (LELE) project (Popp & Kalwij, 2023). All reserves are located in the savanna biome, mostly within Central Sandy Bushveld and Waterberg Mountain Bushveld vegetation types (Mucina et al., 2006) and span a gradient from 467 to 712 mm mean annual precipitation (MAP) and 17.4–20.7°C mean annual temperature (MAT; climate data represents the average between 1981 and 2010) (Karger et al., 2017), see Table S2 for more details. There is high within-reserve variation in precipitation due to topography (Marilize Greyling, pers. observation) which may not be sufficiently captured by the global MAP product used here (Karger et al., 2017). The bedrock is mainly composed of nutrient-poor, medium-coarse grained sandstone (Council for Geoscience, 2020). Importantly, all included reserves are fully fenced and the herbivore community composition and density depend on the respective landowner's decision of which species to introduce and in what quantities.

2.2 | Field survey

We established five sites in each reserve, with each consisting of five 2 m × 2 m vegetation plots (total plot $n = 250$) (Figure 1). For each site, the first plot was randomly selected and the remaining four plots were added along a straight line in 50 m distance intervals so that the five plots were lined up on a 200 m transect (composed of four 50 m × 2 m sub-transects). The transect orientation was random. All sites were established on level areas >500 m from the nearest permanent water body (to avoid piosphere effects), at least 100 m from roads and had not been burned in the preceding 2 years. We also avoided areas that were previously used for agriculture. All reserves were used for cattle grazing before the properties were converted to wildlife reserves (≥4 years since conversion). Permission for fieldwork was obtained from the respective landowners, from South African National Parks (SANParks; Research Agreement: SSS1345) and from the Department of Economic Development, Environment and Tourism Limpopo Province (LEDET; permit number: 01798).

To measure plant community composition, we recorded species identities and their percentage cover at each plot and surveyed all woody species with stems in the 50 m × 2 m sub-transects between the plots. In addition, to calculate functional diversity metrics for the plant communities, we assessed plant growth form (e.g. creeping graminoid, multi-stemmed tree; see Table S1 for the full list of categories and their definitions) for each species to get an indication of the broad life history strategy of the plants and we measured plant height as an indicator of competitive performance (e.g. in the competition for light; Westoby, 1998; Westoby et al., 2002), hairiness (hairs on leaves, stems, both or none) as an indicator for invertebrate herbivory defence and heat balance (Moles et al., 2020), plant bulk density (i.e. a rough estimate of the ratio between plant biomass and the volume it occupies) as indicators of biomass accumulation, flammability and palatability (Solofondranohatra et al., 2020; Wigley et al., 2020), and leaf size category (small, medium, large, thin linear, thick linear) as an indicator of the plant's strategy to deal with light limitation (Givnish, 1987) and herbivory (Moles & Westoby, 2000). Leaf

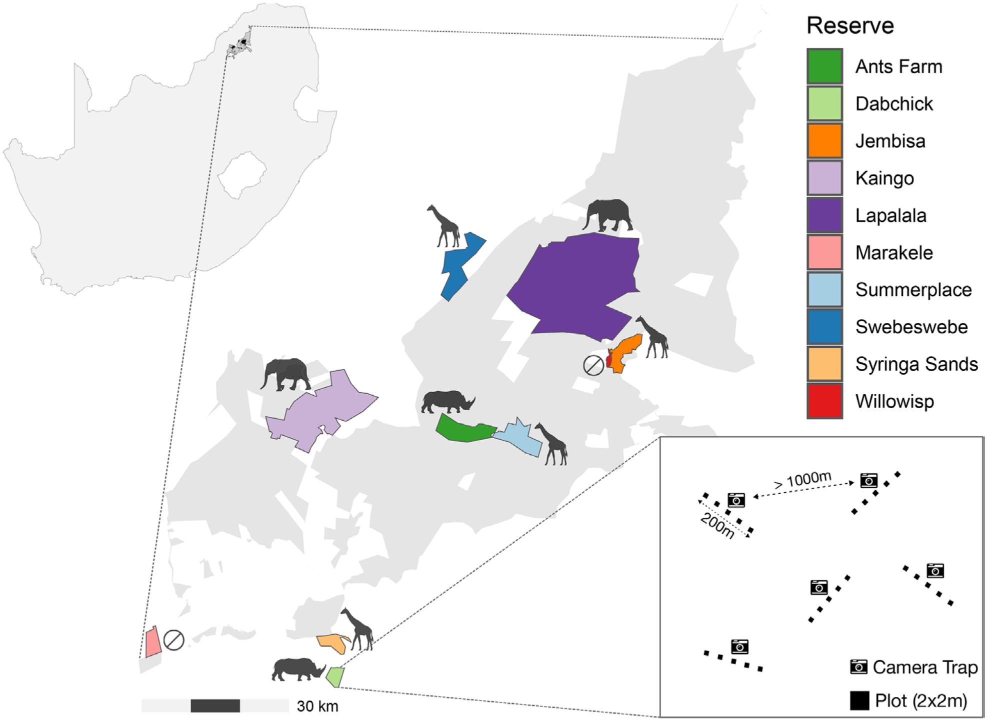

FIGURE 1 Map and distribution of the study sites. The species pictograms next to the reserve shapes represent the heaviest herbivore species in the respective reserve. The crossed circle indicates sites without large herbivores. Note that the Marakele shape (bottom left) differs from the official shape of Marakele National Park as we only worked in a fenced-out part of the park. See Table S2 for details on herbivore densities, species richness and area for each reserve. The grey background polygon represents the Waterberg Biosphere Reserve. The inset map in the bottom right provides a schematic overview of the study design. Each reserve includes five sites, each containing five plots. The plots were connected by 50 m × 2 m transects, where only woody vegetation was sampled. A camera trap was installed at the central plot of each site.

size relates to the full leaf and not to single leaflets. These traits were selected as they indicate important ecological functions and under consideration of the time it takes to measure them in the field in order to increase our sample size as much as possible. Each trait was measured on three individuals per species (if available) on each plot and then averaged to obtain one trait value for each species per plot (see Table S1 for details on how these traits were measured). A total of 287 (66%) out of 435 species on our plots were found on more than one plot, resulting in trait measurements on ≥6 individuals, while 220 species (50%) were found on more than two plots, with traits measured on ≥9 individuals.

Finally, to determine the intensity of herbivore impact, a motion-triggered wildlife camera trap (Alpha Cam Dual Lens No Glow, Alpha Cam, USA) was directed toward the central plot of each site and set to take three consecutive images after a trigger with a minimum interval of 5 min between each trigger (Figure 1). The cameras were in place from February/March 2024 until July 2024 (survey period coincides with the end of the wet season to mid-dry season).

2.3 | Herbivore regime predictors

We calculated the total large herbivore density (henceforth 'herbivore biomass') per hectare for each reserve based on herbivore population estimates (provided by reserve managers). Biomass was based on species with ≥45 kg average body mass (*n* = 23 species) and body mass estimates were extracted from Phylacine (Faurby et al., 2018) and HerbiTraits (Lundgren et al., 2021). Herbivore species richness represents the number of large herbivore species present in a reserve according to the reserve managers.

To estimate herbivore visitation frequency (henceforth 'herbivore visitation'), as an indicator of local herbivory intensity, we calculated the average number of herbivore detections per day from the camera trap images. First, we used the EcoAssist program (Van Lunteren, 2023) which is based on the MegaDetector deep learning algorithm (Beery et al., 2019; Leorna & Brinkman, 2022) to remove empty images (160,593 out of 182,412). MegaDetector has an accuracy of ~90% when used with a confidence threshold of 0.5 (Vélez et al., 2023). We therefore set the confidence threshold to 0.2 to avoid discarding false negatives. We then processed the remaining 21,819 images in the digiKam program, manually assigned species labels to them and read the metadata of the files using the 'exifr' package (version 0.3.2) (Dunnington & Harvey, 2016) in R. We excluded the remaining empty images (*n* = 6010) and recordings of humans, birds, baboons and vervet monkeys (*n* = 2760). Finally, we grouped the remaining sightings (*n* = 13,217 images) according to their temporal separation. As the programmed minimum time between trigger events (5 min) and number of pictures in a blast (three) did not always work (i.e. sometimes a camera took more than three pictures in a row), we considered observations less than 10 s apart as one trigger event ($n = 4393$ unique trigger events). Finally, we summarized the number of trigger events per trap day (average ± standard deviation of 116 ± 20 trap days). We assumed that the herbivore visitation recorded at the central plot is representative of all plots in the transect, as all plots were roughly within ~100 m from the camera. We used both herbivore biomass and visitation as complementary predictors of herbivory intensity: biomass reflects the potential herbivore pressure exerted by the herbivore community, while the visitation rate captures realized local activity at camera-trap sites.

2.4 | Plant community responses

We summarized the number and abundance of all encountered plant species per plot (i.e. alpha diversity), transect (henceforth 'site') and reserve (i.e. gamma diversity). We also summarized species richness for graminoids, forbs and woody plants separately at all scales. We then calculated plant functional richness and redundancy at the three spatial scales (plot (2 m × 2 m), site (2 m × 200 m), and reserve) based on plant growth form, maximum height, leaf size category, hairiness and bulk density (see Figures S1–S5 for their distribution in the most common families in our dataset and Figure S6 for the distribution of species within families) with the R package 'mFD' (version 1.0.7; Magneville et al., 2022). This required one trait value for each species, so we took the most common category for the categorical traits (all but height) and maximum measured height for each species across all scales. To group species into functional entities (unique combinations of trait categories (Magneville et al., 2022)), we split maximum height measurements further in $k = 10$ height classes with equal counts, whereas k was identified using sturges rule ($1 + \log_2(n)$) (Scott, 2009)). We also tested manually specified height classes (<10, 10–30, 30–50, 50–75, 75–100, 100–200, >200 cm) and found the effect directions to be consistent with the automated grouping.

Plant functional richness is based on the volume that a species assemblage (i.e. plot, site, reserve) occupies in multidimensional trait space. Since we were dealing with ordinal and categorical data, the functional space was calculated using the principal components of a principal coordinate analysis based on the gower distances between species pairs (Laliberté & Legendre, 2010; Magneville et al., 2022; Villéger et al., 2008). As we calculated the volume in four-dimensional space, species assemblages must include at least five species (Magneville et al., 2022). Four plots (<2% of our data) had fewer than five species; hence, functional richness could not be calculated for these. To avoid discarding information, we assigned 90% the minimum observed functional richness to these plots, assuming they occupy less volume in trait space due to their low taxonomic diversity. Functional redundancy is calculated as the number of functional entities (a functional entity represents a unique combination of plant growth form, leaf size class, maximum height category, hairiness and bulk density class) divided by the number of species and therefore represents the average number of species per functional group (see Figure S7 for hypothetical plots with high and low plant functional richness and redundancy).

2.5 | Statistical analysis

Unless explicitly stated otherwise, all data preparation and analysis were done in R version 4.5.0 (R Core Team, 2025). We fitted generalized mixed effects models (GLMMs) using the R package 'glmmTMB' (version 1.1.9) (Brooks et al., 2017) to examine the relationship between our response variables (related to plant taxonomic and functional diversity) and herbivore species richness, herbivore biomass and herbivore visitation. Because sample sizes were relatively small, particularly at the reserve scale ($n = 10$), and because we aimed to compare the effects of herbivory across spatial scales, we fitted single-predictor models for each response. This approach ensured comparability of the same bivariate relationships across scales while avoiding overfitting. Importantly, herbivore predictors were quantified at the larger scale only. Our response variables, by contrast, are scale-specific (e.g. alpha vs. gamma diversity). Thus, our models specifically ask how variation in large-scale herbivory regime influences plant communities at multiple spatial scales.

To account for our nested study design, models for plot-scale responses were fitted with a random effect for site nested in reserve (1|reserve/site) and models at the site scale were fitted using reserve as a random effect (1|reserve). Models with taxonomic diversity as the response variable (i.e. count data) were fitted using a Poisson distribution, while the remaining models were fitted using a Gamma distribution (see Figure S8 for the distributions of our response variables). All predictor variables were scaled and centred prior to modelling (see Figures S9–S11 for correlations between variables). As testing multiple hypotheses for the same response may increase false positives (Type I error), we applied a Bonferroni correction to the p-values to minimize the likelihood of false positives (Holm, 1979). As correcting for multiple testing inflates false negatives (Type II error) and the Bonferroni correction has been criticized for reducing statistical power to reject an incorrect null hypothesis (Nakagawa, 2004), we consider the reported results to be conservative.

2.6 | Robustness tests

To test whether our conclusions hold when considering all herbivore-related variables together, we also fitted multivariate models (response ~ herbivore biomass + herbivore visitation + herbivore species richness + random effect) for the scales with sufficient sample sizes (plot, site). Additionally, to assess whether accounting for alternative explanations would alter our conclusions, we fitted GLMMs with our three herbivore regime-related predictors and either mean annual precipitation (Karger et al., 2017), mean annual temperature (Karger et al., 2017) or elevation (Jarvis et al., 2008) as an additional predictor (response ~ herbivore biomass + herbivore visitation + herbivore species richness + abiotic predictor + random effect).

3 | RESULTS

3.1 | Impact of large herbivores on plant taxonomic diversity

We found that plant species richness at the reserve scale was significantly positively associated with herbivore visitation and biomass (Figure 2; Table S3). This association was driven by positive relationships of graminoid and forb richness with both herbivore visitation and biomass at the reserve scale (Figure 2; Table S3). Additionally, forb richness and herbivore visitation were positively correlated at the plot scale. In contrast, woody species richness decreased with herbivore species richness at the site scale. These effect directions remained consistent across scales (Figure 2; Table S3).

3.2 | Impact of large herbivores on plant functional diversity

Plant functional redundancy increased significantly with herbivore visitation at all scales (Figure 3; Table S3). In contrast, we found

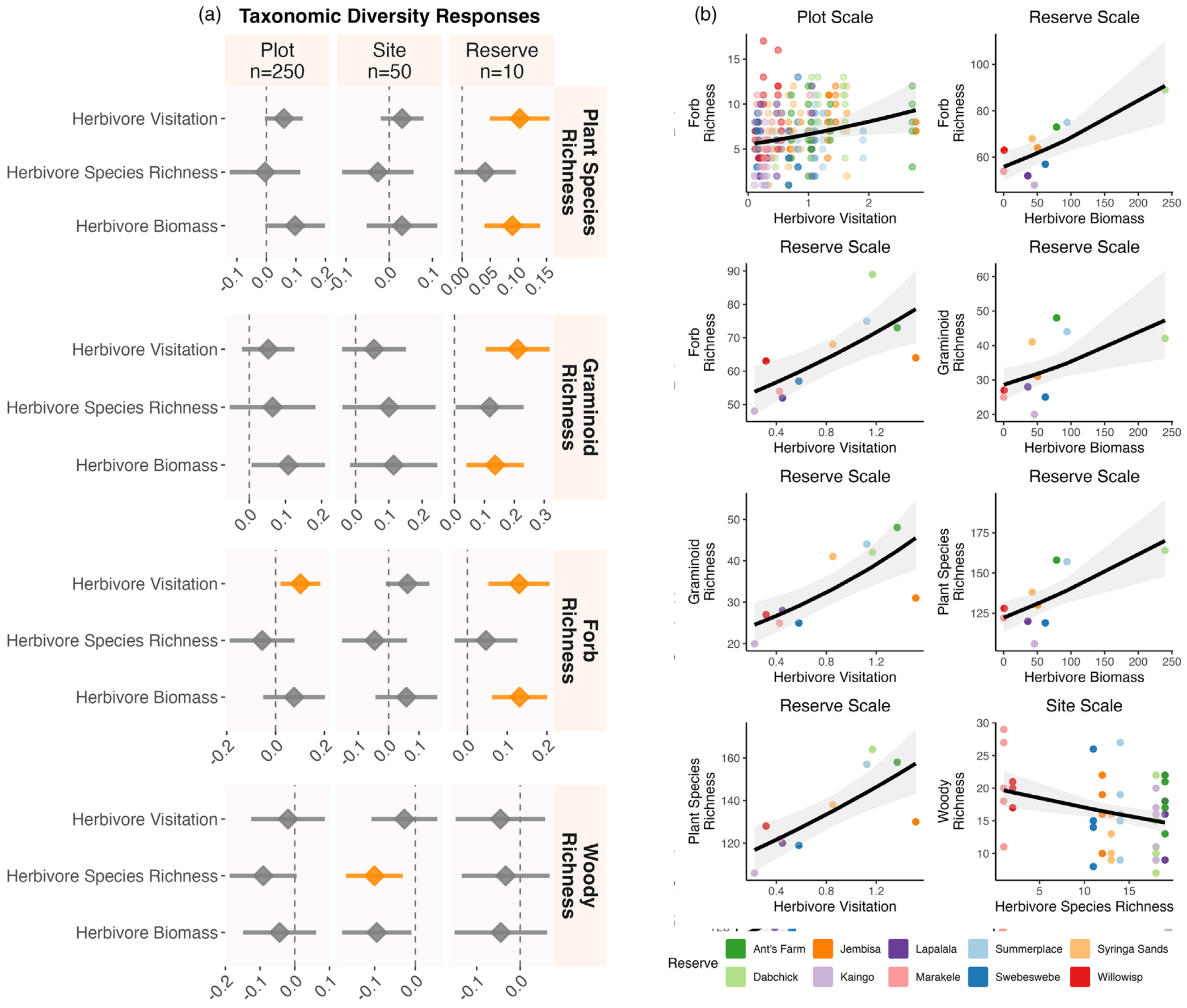

FIGURE 2 Relationships between plant taxonomic diversity and herbivore regime. (a) Panels showing model effect sizes for how the herbivore regime is linked to total, graminoid, forb and woody species richness at the plot, site and reserve scales. The error bars represent the 95% confidence interval and the colour indicates whether the variable has a significant effect (after Bonferroni correction); grey = non-significant, orange = significant. (b) Significant (after Bonferroni correction) bivariate relationships between plant taxonomic diversity and herbivore variables, showing both the data (points) and model predictions (lines). The grey ribbons represent the 95% confidence interval. Herbivore biomass is given in kg/ha and herbivore visitation represents the number of independent detections per day.

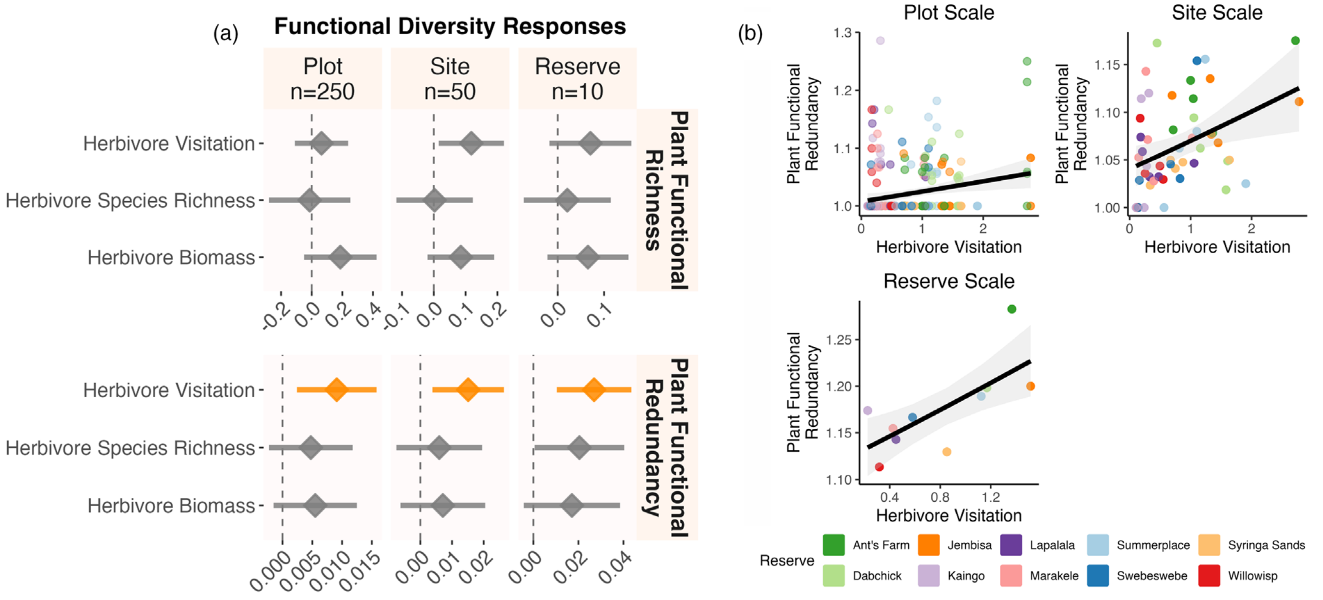

FIGURE 3 Relationships between plant functional diversity and herbivore regime. (a) Panels showing model effect sizes for how the herbivore regime is linked to plant functional richness and functional redundancy at the plot, site and reserve scales. The error bars represent the 95% confidence interval and the colour indicates whether the variable has a significant effect (after Bonferroni correction); grey = non-significant, orange = significant. (b) Significant (after Bonferroni correction) bivariate relationships between plant functional redundancy and herbivore variables, showing both the data (points) and model predictions (lines). The grey ribbons represent the 95% confidence interval. Herbivore visitation represents the number of independent detections per day.

no significant relationship between herbivore-related variables and plant functional richness (Figure 3; Table S3). Similar to plant taxonomic diversity, the effect direction of herbivore-related variables on plant functional diversity remained consistent across scales (Figure 3; Table S3).

3.3 | Robustness analyses

At the plot and site scale, our sample size was sufficient to test alternative modelling approaches which largely confirmed our conclusions. To assess whether our conclusions remain valid when accounting for alternative drivers of plant communities, we fitted GLMMs including all herbivore-related predictors along with rainfall, temperature or elevation. These models mostly corroborated our main conclusions yet revealed a negative relationship between herbivore species richness and forb richness (Figures S12–S15). This relationship was driven by the two reserves without large herbivores. Once those were excluded, the negative relationship between herbivore species richness and forb richness lost significance whereas the positive link of forb richness to herbivore biomass and visitation remained stable (Figure S16).

4 | DISCUSSION

Our analysis shows that total plant species richness, driven by forb and graminoid richness, increased with herbivory intensity (proxied by herbivore visitation and herbivore biomass) across scales in an African savanna. Moreover, plant functional redundancy increased with herbivore visitation. These results suggest an important role of large herbivores in promoting diverse and resilient plant communities.

4.1 | Impact of large herbivores on plant taxonomic diversity

We observed higher herbaceous plant diversity with greater herbivore visitation and biomass, which aligns with previous findings in African savannas and elsewhere (Mata et al., 2025). For instance, Burkepile et al. (2017) reported declines in graminoid and forb diversity following herbivore exclusion, particularly in productive areas, and van Coller and Siebert (2020) found higher forb richness in the presence of large herbivores. Conversely, Coverdale et al. (2024) observed the highest herbaceous plant diversity when both megaherbivores and mesoherbivores were excluded. Unlike most exclosure experiments, where herbivores are either present or absent, our analysis spanned a gradient of herbivore regimes, including herbivore composition, biomass and visitation. Moreover, variations in herbivore visitation rates to the plots, environmental conditions (although, for example, mean annual rainfall is broadly comparable) or biogeographic histories between our study site in the Waterberg and Coverdale et al.'s (2024) study area in Kenya (UHURU experiment) may further explain the differing effect directions. These contrasting findings also highlight the need for future studies across broad environmental, biogeographic and herbivore-related gradients to identify general patterns in herbivore impacts on plant communities.

Surprisingly, we did not find a positive relationship between herbivore species richness and plant diversity. This is consistent with Voysey et al. (2024) who found no strong differences in areas with cattle versus more complex, wild large herbivore communities, suggesting that herbivory intensity (e.g. herbivore visitation and biomass), is a more important driver of herbaceous plant communities than herbivore species richness. Nevertheless, herbivore community composition (e.g. body size or muzzle width) is likely an important moderator of herbivore impacts (Lundgren et al., 2024; Trepel et al., 2024), potentially modulating the effect of herbivory intensity. While total herbivore biomass at the reserve level can serve as a proxy for local herbivory intensity, our herbivore visitation variable indicates actual site usage during the monitoring period. Together, this suggests that herbivores could increase herbaceous plant species richness, but that it can be essential to quantify the actual, local herbivory visitation to detect herbivore effects and properly assess herbivory impacts on plant communities.

A potential mechanism behind the positive relationship between large herbivores and herbaceous plant species richness is disturbance from large herbivore activity (e.g. feeding, trampling), which suppresses dominant plant species and reduces competition for light, water and nutrients, thereby allowing greater species coexistence and enabling a wider range of competitive, stress- and disturbance-tolerant life strategies to be successful (Eskelinen et al., 2022; Koerner et al., 2018). These results could have also been influenced by increased immigration rates due to enhanced dispersal via large herbivores, which is expected to elevate plant diversity (Baltzinger et al., 2019; Fricke et al., 2022; González-Varo et al., 2024). However, we also note that our study areas are fenced reserves with little to no large herbivore movement between, restricting large herbivore-related dispersal to the reserve scale (i.e. between sites and plots).

In addition to the positive effects on herbaceous plant species richness, we also observed a negative association of both herbivore species richness and herbivore biomass (though the latter was not significant after p value correction) with woody species richness at the site scale, consistent with previous findings from large-scale and long-term exclosure experiments in Kenya (Coverdale et al., 2024) and South Africa (Scogings et al., 2012). The negative relationship between woody plant diversity and herbivory may be because of the relatively slow life history of woody plants which makes them potentially more susceptible to repeated disturbance. Due to their ability to remove large quantities of biomass and uproot mature trees, elephants are thought to be particularly effective in suppressing woody vegetation (Faith et al., 2020; Moe et al., 2009; Owen-Smith, 1988). Smaller herbivores can affect woody plants at earlier life stages (e.g. preventing seedlings and saplings from growing, a phenomenon called ‘browse trap’) and thereby prevent woody plant establishment (Staver & Bond, 2014), which is consistent with the negative relationship between woody plants and large herbivores found here.

Notably, we found the direction of presumed herbivory effects to be remarkably consistent across scales, although the trend often reached significance only at the reserve scale. This may be because the impact is more likely to fully manifest at larger scales (e.g. variations in the disturbance regime result in higher gamma diversity). In addition, aggregating data at the reserve level is likely to reduce random noise and make relationships more visible. The strong and significant relationships at the reserve level are unlikely to be spurious as we corrected for multiple testing and achieving significance with a small sample size is generally less likely than with large samples (Lantz, 2013; Tukey, 1991). We therefore suggest that the stronger large herbivore effects at larger scales are because their impact does, at least in part, vary with scale and tends to be most beneficial for biodiversity at larger scales. This would also be in line with theory: that is, at the small scale (i.e. plot or site), herbivory intensity and thus impact may be relatively uniform (i.e. a site is either impacted or not), leading to more similar plant communities among plots within a site. In contrast, the heterogeneous space use of herbivores across a reserve exposes different sites to varying herbivory intensities, resulting in a more diverse plant community (i.e. higher gamma diversity).

4.2 | Impact of large herbivores on plant functional diversity

Importantly, we found a consistently positive relationship between herbivore visitation and plant functional redundancy. This may be because areas more frequently visited by herbivores experience greater disturbance, which may promote the coexistence of functionally similar groups. Or, in other words, as resilience refers to an ecosystem's capacity to recover from disturbance (Van Meerbeek et al., 2021), a frequently disturbed ecosystem may host more resilient communities. Such communities would have a higher number of species per functional group, as observed in this study. Theory predicts that functionally redundant species communities can buffer changes following disturbances, such as species losses, while maintaining ecosystem functioning (Walker, 1992). This is supported by a recent meta-analysis which found a positive relationship between functional redundancy and ecosystem resilience (Biggs et al., 2020).

Despite finding clear signals in functional redundancy and species richness, we did not detect a significant relationship between large herbivores and plant functional richness. The absence of an effect on plant functional richness may be attributed to herbivores promoting grazing-tolerant functional types while simultaneously suppressing grazing-intolerant functional groups (Archibald et al., 2019; Atkinson et al., 2024) whereas the size of the actual functional space stays relatively similar. Within this grazing-tolerant species pool, however, disturbances provided by herbivores may enable more species to avoid competitive exclusion, thus increasing species richness and—by allowing more species with similar ecological roles to coexist—increasing plant functional redundancy.

This also suggests that the greatest plant taxonomic and functional diversity may be reached in ecosystems that have areas with both high and low herbivore pressure, raising interesting questions about the role of predators in creating patches of low herbivore density (Lundgren et al., 2022) and the effects of seasonal changes in herbivore presence (Geremia et al., 2025).

4.3 | Limitations

There are some limitations associated with our design that should be considered when interpreting the results. First, testing multiple relationships inevitably carries a risk of false positives. However, to avoid testing some of the relationships here would have hindered our ability to address our research questions. We therefore aimed to make our analyses as robust and conservative as possible to minimize the likelihood of spurious results. Second, although we standardized various factors across reserves and sites (e.g. land use history, vegetation types, distance to water, distance to roads, slope), unmeasured differences between reserves remain and our dataset is inherently correlational. Nevertheless, herbivore communities and densities in these reserves are not determined by plant communities but rather by landowner preferences, making them comparable to a natural experiment and thus allowing some inference about causal relationships. However, we also acknowledge that we cannot fully rule out alternative explanations for the patterns found in our data. The most robust way to investigate herbivore effects on plant communities would be the establishment of large and replicated exclosure treatments along gradients of herbivore regimes and environmental factors, potentially complemented by herbivore habitat selection data (e.g. long-term camera trapping or GPS-collars). Unfortunately establishing such an experiment is highly resource-intensive and practically impossible in terms of time and funding. In the meantime, we consider our approach a step toward understanding how herbivore regimes shape plant communities and how scale influences the manifestation and detection of herbivore effects.

5 | CONCLUSIONS

Taken together, our results indicate that shifts in herbivore regimes are associated with substantial changes in savanna vegetation communities, including increases in total plant species richness (our first question)—driven by increases in herbaceous plant species richness (our second question)—and potential increases in resilience, as indicated by increased plant functional redundancy (our third question). Moreover, the importance of the herbivore visitation variable underscores the importance of estimating actual herbivory intensity at local scales (e.g. when interpreting results from exclosure experiments). While the relationships between herbivore regimes and plant communities were largely consistent across scales—suggesting the potential to scale up from local measurements to broader effects—most of these effects were only significant at the landscape scale, indicating that herbivore impacts are strongest at larger scales (our fourth question). Based on these results, we propose that the restoration of large herbivores could be a promising way of promoting diverse and resilient ecosystems (Svenning et al., 2024).

AUTHOR CONTRIBUTIONS

Jonas Trepel and Robert Buitenwerf conceptualized the study, with contributions from Elizabeth le Roux, Jens-Christian Svenning, Joe Atkinson, Erick J. Lundgren and Andrew J. Abraham. Jonas Trepel developed the methodology, conducted the formal analyses, prepared the original draft of the manuscript and designed the visualizations. Jonas Trepel, Anika Oosthuizen and Caroline Makofane collected the data with help from Marilize Greyling, Michelle Greve, Londiwe Mokoena, Lukas Lindenthal, Margerie Aucamp, Steven Khosa, Elizabeth le Roux and Robert Buitenwerf. Robert Buitenwerf supervised the work, with co-supervision by Elizabeth le Roux and Jens-Christian Svenning. Funding was acquired by Jens-Christian Svenning, Robert Buitenwerf and Elizabeth le Roux. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code used for the analysis are available at: https://github.com/JonasTrepel/Waterberg2024. An archived version of the repository is available at Zenodo: https://doi.org/10.5281/zenodo.17466232 (Trepel, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Collected traits and their definition.

Table S2: Reserve metadata.

Table S3: Estimates and statistics from the univariate GLMMs used in the main analysis.

Figure S1: Distribution of plant height in families represented with 10 or more species.

Figure S2: Distribution of bulk density in families represented with 10 or more species.

Figure S3: Distribution of leaf size classes in families represented with 10 or more species.

Figure S4: Distribution of hairiness in families represented with 10 or more species.

Figure S5: Distribution of growth forms in families represented with 10 or more species.

Figure S6: Distribution of plant species in families.

Figure S7: Conceptual overview of hypothetical plots with high and low functional diversity and redundancy.

Figure S8: Distributions of response variables.

Figure S9: Relationships between predictor variables.
Figure S10: Correlations between response variables.
Figure S11: Correlations between different herbivore related metrics.
Figure S12: Estimates and trends from GLMMs with all three herbivore predictors (but no alternative abiotic hypothesis).
Figure S13: Estimates and trends from GLMMs with all three herbivore predictors and mean annual precipitation (MAP).
Figure S14: Estimates and trends from GLMMs with all three herbivore predictors and mean annual temperature (MAT).
Figure S15: Estimates and trends from GLMMs with all three herbivore predictors and elevation.
Figure S16: Model predictions and raw data for the relationship between forb richness and herbivore regime.

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